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# Comprendre les interactions biotiques-abiotiques pour accompagner la transition agroécologique des territoires: application au cas des interactions eau-végétation

Fabrice Vinatier

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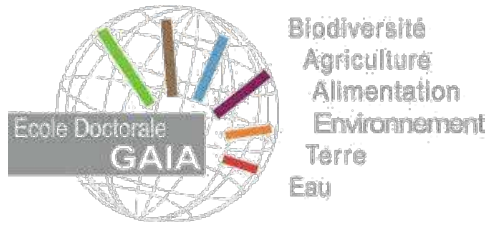
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Mémoire déposé en vue de l'obtention de l'Habilitation à Diriger des Recherches

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# Comprendre les interactions biotiques-abiotiques pour accompagner la transition agroécologique des territoires :

*application au cas des interactions eau-végétation*

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**Fabrice VINATIER**

Soutenu le : 6 juillet 2022

Devant le jury composé de :

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**LISAH**

*" Je déclare avoir respecté, dans la conception et la rédaction de ce mémoire d'HDR, les valeurs et principes d'intégrité scientifique destinés à garantir le caractère honnête et scientifiquement rigoureux de tout travail de recherche, visés à l'article L.211-2 du Code de la recherche et énoncés par la Charte nationale de déontologie des métiers de la recherche et la Charte d'intégrité scientifique de l'Université de Montpellier. Je m'engage à les promouvoir dans le cadre de mes activités futures d'encadrement de recherche."*

## **Avant-propos**

Ce mémoire, structuré en quatre parties selon les préconisations de l'école doctorale GAIA, (i) décrira mon résumé de carrière, (ii) présentera de manière synthétique mes travaux de recherches depuis mon doctorat, (iii) mettra en perspectives mes activités futures, et (iv) se terminera sur une sélection de neuf articles personnels référencés dans la présentation des travaux.

Je remercie tous ceux qui, de près ou de loin, ont participé à l'accomplissement de ce manuscrit, et en particulier Gabrielle Rudi, ma première doctorante.

Un grand merci à mes premiers relecteurs, Françoise Lescourret, Jean-Stéphane Bailly, Philippe Lagacherie et Jérôme Molénat, qui m'ont aidé à rendre ce manuscrit le plus lisible et structuré possible. Ce sont plus que des simples relecteurs car ils m'ont accompagné et guidé avec bienveillance dans ma première partie de carrière, je les remercie donc doublement.

Un grand merci aux étudiants qui m'ont appuyé dans mon activité aussi bien scientifique que pédagogique. Je suis persuadé que cette nouvelle génération de scientifiques consolidera les bases d'une transition durable des écosystèmes face aux changements globaux.

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# 1 Résumé de carrière

## 1.1 Identité

Fabrice Vinatier  
Ingénieur-Docteur

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## 1.2 Formations diplômantes

2007– 2010	<b>AgroParisTech.</b> <i>Thèse de doctorat soutenue le 18 novembre 2010</i> Spécialité Sciences agronomiques
2003– 2006	<b>INA Paris-Grignon.</b> <i>Diplôme d'Ingénieur Agronome</i> Spécialité en PPE (Protection des Plantes et Environnement)
2000– 2002	<b>Lycée Chateaubriant (Rennes).</b> <i>Classes préparatoires aux Grandes Ecoles</i> Spécialité en BCPST (Biologie-Chimie-Physique-Sciences de la Terre)

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### 1.3 Activité de recherche

2020–...	<b>UMR LISAH, INRAE, Montpellier.</b> <i>Animateur d'équipe</i> Ecohydrologie des agrosystèmes
2012–...	<b>UMR LISAH, INRAE, Montpellier.</b> <i>Chargé de recherches</i> Modélisation de l'organisation paysagère des agro-écosystèmes pour l'optimisation éco-environnementale
2011	<b>UMR Agronomie, INRA, Grignon.</b> <i>Post-doctorat</i> Modélisation du réseau tritrophique Colza-Méligèthe-Parasitoïde à l'échelle paysagère
2007–2010	<b>UPR 26, CIRAD, Martinique.</b> <i>Doctorat</i> Dynamique spatiale du charançon du bananier en interaction avec le système de culture et l'organisation paysagère
2006	<b>SRPV, Alsace.</b> <i>Vacation</i> Etude de la dynamique d'émergence de la pyrale du maïs
2005	<b>Université de Melbourne, Australie.</b> <i>Stage</i> Etude de la dynamique populationnelle de l'ormeau
2004	<b>UMR Bio3P, INRA, Rennes.</b> <i>Stage</i> Etude de la dynamique d'infestation du blé par <i>Sitobion avenae</i>

### 1.4 Autres expériences

2007	<b>DuPont Solutions SAS, Département de R&amp;D, Paris.</b> <i>Ingénieur homologation</i>
2006	<b>DuPont Solutions SAS, Département de Communication, Paris.</b> <i>Chef de projet Marketing</i>
2004–2005	<b>GNIS, Paris.</b> <i>Assistant communication</i>
2003	<b>Ferme d'élevage cunicole, Deux-Sèvres.</b> <i>Ouvrier agricole</i>

### 1.5 Langues

Français	<b>langue maternelle</b>
Anglais	<b>lu, parlé, écrit</b>
Allemand	<b>niveau moyen</b>
Espagnol	<b>débutant</b>
Breton	<b>bilingue</b>

## 1.6 Contrats de recherche

Date	Titre court	Appel d'offre	Rôle	Principaux partenaires	Durée (en mois)
2012–2015	<b>LACCAVE</b>	INRA- métaprogramme ACCAF	Resp. tâche	EGVF INNOVA- TION	36
2013–2018	<b>ALMIRA</b>	ANR	Resp. tâche	BRGM INAT	36
2013–2015	<b>FIP</b>	INRA-ONEMA	Partenaire	ONEMA	36
2014–2015	<b>HYDROECO</b>	INRA-Pari scienti- fique	Coordinateur	GEAU AMAP	24
2017–2018	<b>AgriChannels</b>	Agropolis Fonda- tion	Coordinateur	GEAU AMAP	19
2017–2021	<b>TRADEVI</b>	France Agrimer – CNIV	Partenaire	SYSTEM IFV	36
2019	<b>EcoFlow</b>	Agropolis Fonda- tion	Coordinateur	GEAU	7
2022–2024	<b>RIPP-Viti</b>	OFB	Partenaire	ABSYS ECOSYS INNOVATION	36
2021–2023	<b>Waterseed</b>	INRAE- métaprogramme BIOSEFAIR	Coordinateur	GEAU ABSYS CI- TERES	24
2021–2024	<b>MOMAC</b>	Agropolis Fonda- tion	Coordinateur	PSH ABSYS LEPSE	36
2021–2024	<b>Seedbank</b>	Agropolis Fonda- tion	Coordinateur	GEAU ABSYS	24

## 1.7 Responsabilités

Date	Type de responsabilité
2020–...	<b>Animateur d'équipe</b>
2020–...	<b>Membre du conseil de direction du LISAH</b>
2015–2020	<b>Membre élu du conseil d'unité du LISAH</b>
2015–2020	<b>Membre de la commission exposé du LISAH</b>

## 1.8 Organisation de colloques

Date	Événement	nb. participants	Rôle
2013	<b>Workshop NetLogo-R</b>	10	Organisateur
2019	<b>MISS-ABMS</b>	30	Comité organisation
2020	<b>PAYOTE</b>	60	Comité organisation
2020	<b>EGU</b>	20	Organisation session
2021	<b>PAYOTE</b>	60	Comité organisation
2021	<b>EGU</b>	20	Organisation session

## 1.9 Jury de thèses

Date	Doctorant	Ecole Doctorale	Rôle
2013	<b>Mariline Maalouly</b>	ED-A2S	Examinateur
2015	<b>Emile Faye</b>	ED227-MNHN-SU	Examinateur
2019	<b>Gabrielle Rudi</b>	ED-GAIA	Encadrant
2021	<b>Antoine Casquin</b>	ED-EGAA	Examinateur

## 1.10 Relecture d'articles scientifiques

Date	Revue
2011	<b>Journal of Insect Conservation</b>
2011	<b>Journal of Insect Science</b>
2012	<b>Biosystems Engineering</b>
2013	<b>Ecological Modelling</b>
2014	<b>Ecological Modelling</b>
2014	<b>Land Use Policy</b>
2016	<b>Earth Surface Processes and Landforms</b>
2017	<b>Biological control</b>
2017	<b>Science of the Total Environment</b>
2018	<b>Journal of Hydraulic Research</b>
2019	<b>Applied Geography</b>
2021	<b>European Journal of Soil Science</b>
2021	<b>River Research and Applications</b>

### 1.11 Encadrement de post-doctorat

Date	Nom	Titre	Durée (en mois)	Co-encadrants
2019	<b>Gabrielle Rudi</b>	Experimental assessment of 2D flow velocity fields induced by plant biodiversity	5	J.S. Bailly

### 1.12 Comités de pilotages de thèse

Date	Nom	Ecole Doctorale	Laboratoire
2013	<b>Anicet Diassou</b>	ED SEVAB	GECO
2014	<b>Nicolas Salliou</b>	ED A2S	PSH
2016-2018	<b>Blanche Collard</b>	ED A2S	PSH-GECO
2018-2019-2020	<b>David Muru</b>	ED SVS	BPI
2018	<b>Nirina Ratsimba</b>	ED SEVAB	DYNAFOR
2019	<b>Patrizia Zamberletti</b>	ED A2S	BioSP
2020-2021	<b>Esther Diouf</b>	ED 2DS	CBGP-AIDA
2020-2021	<b>Mariem Dhouib</b>	ED GAIA	LISAH

### 1.13 Bilan scientifique

Métrique	Valeur
H-index	<b>14.00</b>
Nombre Citations depuis 2009	<b>676</b>
Article le plus cité	<b>105</b>
IF moyen	<b>4.40</b>
IF maximum	<b>8.90</b>
IF minimum	<b>1.70</b>

Revue	IF 2020	2009	2010	2011	2012	2013	2016	2017	2018	2020	2021	TOTAL
ISPRS Journal of Photogrammetry and Remote Sensing	9								1			1
Methods in Ecology and Evolution	8			1								1
Soil Biology and Biochemistry	8				1							1
Advances in Ecological Research	7					1					1	2
WIREs Water	6										1	1
Agriculture, Ecosystems and Environment	6				1							1
Land Use Policy	6										1	1
European Journal of Soil Science	5										1	1
Remote Sensing	5								1		1	2
Pest Management Science	5			1								1
Frontiers in Environmental Science	5						1					1
Agricultural Water Management	4							1				1
Applied Geography	4								1			1
Landscape Ecology	4				1	1			1			3
Basic and Applied Ecology	3			1			1					2
Vadose Zone Journal	3								1			1
PloS ONE	3			1					1			2
Ecological Modelling	3	1						1				2
Animal Behaviour	3		1									1
Ecohydrology	3							1		1		2
Ecohydrology and Hydrobiology	3									1		1
Journal of Applied Entomology	3					1						1
River Research and Applications	2								1			1
Entomologia Experimentalis et Applicata	2					1						1
Bulletin of Entomological Research	2				1				1			2
TOTAL	-	1	1	4	4	4	2	3	8	2	5	34

## 1.14 Enseignement

Date	Ecole	Ecole Doctorale	Engagement	Durée
2014–...	<b>AgroParisTech</b>	UE Geoprospective, Paysage et Eau	Responsable UE	26h
2013–2015	<b>AgroParisTech</b>	Projet scientifique	Conception et MEP	10h
2014–2015	<b>SupAgro</b>	Ecologie du paysage	Intervention	2h
2018–2019	<b>SupAgro</b>	UE Démarche expérimentale	Conception et MEP	15h
2015–...	<b>AgroParisTech</b>	Pratique des SIG avec R	Responsable UE	18h

## 1.15 Encadrement de stagiaires

Date	Nom	Niveau	Titre du stage	Formation	Co-encadrant(e)(s)	Publications
2009	<b>Anaïs Chailleux</b>	M2	Etude de la dynamique spatiale du charançon du bananier, <i>Cosmopolites sordidus</i> (Germar) par marquage RFID	ENITA Bordeaux		
2009	<b>Anne Vidie</b>	M1	Epidemiologie spatiale de <i>Cosmopolites sordidus</i> dans les jachères, approche par télémétrie RFID	AgroCampus Ouest		
2010	<b>Kemy Cordemy</b>	BTSA	Etude du comportement du charançon du bananier, <i>Cosmopolites sordidus</i> (Germar) par marquage RFID		Philippe Tixier	
2012	<b>Matthieu Bourmaud</b>	M1	Analyse diachronique des paysages sur le bassin versant de la Peyne	ESA Angers		
2013	<b>Benoit Bellot</b>	M1	Flore de fossés à l'échelle d'un bassin versant : analyse des conditions physiques de présence-absence	AgroParisTech	Jean-Stéphane Bailly	
2013	<b>Khawla Benitou</b>	M2	Végétation de fond de canal et rugosité : test d'un nouveau protocole expérimental	IAV	Jean-Stéphane Bailly	
2013	<b>Marie-Noëlle Morismau</b>	M2	Flore des fossés en région viticole méditerranéenne : Etude des facteurs de distribution spatio-temporelle	ESA Angers		
2013	<b>Marina Chauvet</b>	M2	Structure du parcelle agricole et services écosystémiques paysagers : Simulation de géométries de parcelles adaptées aux paysages de collines	Université de Tours		1 ACL
2014	<b>Alexandre Basini</b>	M2	Diversité, caractéristiques structurales et physiques de la flore des fossés agricoles en région Languedoc-Roussillon	SupAgro		
2014	<b>David Combe-male</b>	M2	Suivi de l'évolution de la structure d'espèces végétales en très haute résolution spatiale dans un réseau de fossés agricoles : Comparaison des approches LiDAR et stéréophotogrammétriques	SupAgro	Jean-Stéphane Bailly	
2014	<b>Dénes Kiraly</b>	M2	Développement d'un protocole de mesure d'un lâcher d'eau en canal contrôlé par vidéo infra-rouge	SupAgro	Jean-Stéphane Bailly	
2015	<b>Ana Gonzalez Arnaiz</b>	M2	Reconstitution and analysis of diachronic land use series : application in Bourdic's watershed, France	Université Polytechnique de Madrid		1 ACL
2015	<b>Alberto Bolletin</b>	M2	Using Structure from Motion photogrammetry and Terrestrial Laser Scanning to estimate blockage factor of vegetation in open channels	Université de Pa-doue	Jean-Stéphane Bailly	
2015	<b>François-Xavier Weber</b>	M2	Analyse diachronique d'un paysage viticole languedocien	ESGT		
2015	<b>Maxime Jourde</b>	M2	Utilisation de la photogrammétrie pour caractériser la structure 3D de la végétation des fossés agricoles	SupAgro		
2016	<b>Alice François</b>	M1	Etude de la biodiversité végétale dans un fossé agricole en région méditerranéenne	Faculté de Montpellier		
2018	<b>Sebastien Claus</b>	M2	Implementing a biological regulation model into Maelia	Wageningen UR	Olivier Therond	
2018	<b>Sylvain Edouard</b>	M1	Hétérogénéité intra-parcellaire et échantillonnage de couples cep dépérissant/cep sain dans différents contextes viticoles	SupAgro	Guillaume Cou-louma	
2019	<b>Bernat Lavaquiol</b>	M1	Study of vineyard decline in mediterranean region	Université de Lleida	Guillaume Cou-louma	
2020	<b>Alec Sicard</b>	M1	Modèle de croissance des peuplements végétaux	SupAgro		
2020	<b>Loic Lehnhoff</b>	M2	Identification d'espèces végétales d'intérêt écohydrologique dans les paysages agricoles	AgroCampus Ouest	Nicolas Parisey	
2021	<b>Martin Faucher</b>	M2	Validation d'un modèle de croissance des peuplements végétaux non cultivés en milieu viticole méditerranéen	Université de Rennes 1		

## 1.16 Publications scientifiques

01. Fovet, O., Belemtougri, A., Boithias, L., Braud, I., Charlier, J.-B., Cottet, M., Daudin, K., Dramais, G., Ducharne, A., Folton, N., Grippa, M., Hector, B., Kuppel, S., Le Coz, J., Legal, L., Martin, P., Moatar, F., Molénat, J., Probst, A., ... [Vinatier, F.](#), Detry, T. (2021). Intermittent rivers and ephemeral streams : Perspectives for critical zone science and research on socio-ecosystems. *WIREs Water*, e1523. <https://doi.org/10.1002/wat2.1523>
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03. Hérivaux, C., [Vinatier, F.](#), Sabir, M., Guillot, F., & Rinaudo, J. D. (2021). Combining narrative scenarios , local knowledge and land-use change modelling for integrating soil erosion in a global perspective. *Land Use Policy*, 105. <https://doi.org/10.1016/j.landusepol.2021.105406>
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## 2 Mémoire des travaux scientifiques

### 2.1 Introduction

Le monde est inévitablement **spatial** (TILMAN et KAREIVA, 1997). Les organismes vivants, quel que soit leur règne (végétal, animal voire humain) investissent l'espace et l'espace impacte leur coexistence à différentes échelles (MCGILL, 2010). De nombreuses théories, de la théorie de la biogéographie insulaire (MACARTHUR et WILSON, 1963) à la théorie neutre (HUBBELL, 2001) en passant par la théorie des métapopulations (LEVINS, 1969), éprouvées par des années de résultats expérimentaux (ALONSO, ETIENNE et MCKANE, 2006) viennent appuyer l'importance des processus spatiaux dans le fonctionnement des écosystèmes. Les organismes vivants, en se dispersant via un moteur physique (via un flux d'eau comme l'hydrochorie dans NILSSON et al. (2010), comportemental (via la recherche de nourriture (GOULSON, 1999)) ou complètement aléatoire (comme la marche aléatoire (CODLING, PLANK et BENHAMOU, 2008)), vont augmenter leur chance (ou malchance) d'entrer en interaction avec les autres et leur milieu, participant à l'équilibre des populations et la résilience des écosystèmes. Les fluides, gazeux ou liquides, circulent également dans l'espace selon des lois physiques. Ils sont généralement considérés comme une variable continue, caractérisée par une certaine densité et une vélocité qui varient dans le temps et l'espace. Dans le cas de l'eau, la pertinence des lois physiques qui régissent les écoulements a été largement démontrée par l'observation, comme les équations de Navier-Stokes qui régissent l'écoulement de surface dans les cours d'eau (STOKES, 1850), l'équation de Richards qui régit les écoulements en milieu non

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saturé (RICHARDS, 1931), etc.. Dans certaines conditions de régime hydraulique, ces équations dont la résolution analytique s'avère très complexe, voire impossible, peuvent être simplifiées (équation de Manning-Strickler ou équation de l'onde diffusante)(MOUSSA et BOCQUILLON, 1996; MOUSSA, VOLTZ et ANDRIEUX, 2000)).

Le monde est incroyablement **dynamique**. Chaque élément qui le compose, biotique ou abiotique, aura une dynamique propre de destruction, d'augmentation ou de transformation, plus ou moins cyclique, et sur des échelles de temps très variables. On peut citer les exemples des dynamiques d'accroissement et extinction des populations végétales et animales (JOHNSON et al., 2005), de transformation des molécules dans les cycles du carbone (SIPPEL et al., 2018) ou de l'azote (GALLOWAY et al., 2008), de variation des pluies (OGUNTUNDE, ABIODUN et LISCHIED, 2011). Étudier les propriétés de la dynamique d'un élément, en termes de cyclicité, de période de retour à plusieurs échelles de temps est un élément déterminant pour expliquer le fonctionnement des écosystèmes.

Temps et espace sont étroitement liés. KRAUSE et al. (2015) a introduit la notion de **fenêtre critique**, littéralement *windows of opportunities*, pour caractériser la fenêtre de temps et d'espace où les interactions entre les conditions **biologiques** et **environnementales** sont les plus favorables, dans le cas d'interactions biotiques-abiotiques. On peut citer pour illustrer ce concept l'exemple des conditions de températures et d'humidité du sol qui sont optimales pendant quelques jours et coïncident avec la levée de dormance des graines au printemps, cette fenêtre critique pouvant être très réduite dans les milieux arides (D'ODORICO et al., 2010). Bien que l'expression *windows of opportunities* soit peu présent dans la littérature en écologie, nous pourrions l'employer pour désigner la fenêtre de temps et d'espace où deux organismes vivants et mobiles entrent en interaction, comme par exemple le parasitoïde et son hôte (ROST, VÁRKONYI et HANSKI, 2001) ou une proie et son prédateur (HUFFAKER, 1958). Il peut également s'appliquer à expliquer certaines dynamiques épidémiques cycliques reliant le stade nourricier d'un bioagresseur à l'optimum de développement de sa ressource, comme le campagnol (BERTHIER et al., 2014), la limace (CHOI et al., 2006) ou les criquets (ANTOANETA ROUSSI, 2020), entres autres.

En élargissant la définition de la fenêtre critique à **toutes interactions entre deux composantes d'un système qui entraîne une diminution, augmentation ou transformation de l'un et/ou l'autre**

**des composantes**, on peut également ajouter d'autres exemples d'interactions biotiques-abiotiques, ou l'eau et sa circulation dans un milieu peut impacter la faune et la flore qui s'y trouve. Par exemple, la mise en eau d'un fossé entraînera un arrachage de la végétation qui s'y trouve et la dispersion d'une partie des insectes se déplaçant dans le fossé. Ce concept de fenêtre critique sera régulièrement évoqué dans le mémoire, car j'estime qu'il s'agit d'un élément déterminant à prendre en compte pour mieux comprendre la réactivité des écosystèmes et pourquoi ils présentent parfois des points de bascule vers des systèmes modifiés, sans possibilité de retour à leurs états antérieurs, avec des changements brutaux de fonctionnement (KRAUSE et al., 2015).

**Climat et saisonnalité** vont modifier les interactions biotiques-abiotiques, en réduisant ou augmentant les fenêtres critiques d'interactions entre les multiples composants des systèmes. On peut supposer que ces interactions s'expriment différemment en fonction des biomes, et que les conditions de résilience des macro-écosystèmes seront également différentes en fonction des climats régionaux (tempéré, tropical ou méditerranéen). Par exemple, les variations saisonnières importantes des températures en climat tempéré ou méditerranéen vont contribuer à la synchronisation des cycles des espèces poïkilothermes (i.e. température dépendantes) avec leurs plantes-hôtes, et donc les fenêtres critiques seront d'autant plus réduites pour ces organismes. Cet effet sera exacerbé en milieu méditerranéen, où la concentration annuelle des précipitations réduit la période de développement de la végétation. À l'inverse, en climat tropical, la relative homogénéité des températures et des précipitations contribuera à la désynchronisation des cycles et à l'augmentation de la durée des fenêtres critiques. Par conséquent, la **résilience** des écosystèmes qu'on peut supposer dépendante de la fréquence des fenêtres critiques, s'exprimera différemment suivant les biomes.

Outre ces phénomènes naturels considérés comme des variables de forçage dans le système, **l'homme**, par son action sur le milieu, a aussi la possibilité de jouer sur cette fenêtre critique pour contrôler ces interactions. Ces interactions biotiques-abiotiques étant à l'origine de nombreux services et dysservices écosystémiques (COSTANZA et al., 1997), il y a un réel enjeu à mieux les comprendre pour les contrôler afin de réduire l'impact néfaste de l'homme sur son environnement (ROCKSTRÖM et al., 2009). Parmi les milieux terrestres susceptibles d'être influencés par l'homme,



les **surfaces agricoles** (prairies et terres cultivées), qui couvrent 40% de la surface terrestre (FOLEY et al., 2011), sont un cas d'étude pertinent car elles représentent un entrelacement de milieux semi-naturels et anthropisés à différentes échelles spatiales. Leur gestion agronomique nécessite une vision intégrée et holistique de toutes les composantes du système agricole dans sa dimension sociale, économique et écologique (LOUIS et al., 2009).

**L'agroécologie**, dans son acception restreinte, est une discipline visant à manipuler des processus écologiques pour résoudre des problèmes agronomiques (ALTIERI, 1995). Elle tire partie des services rendus par la biodiversité ordinaire et s'appuie justement sur cette fenêtre critique, en augmentant par exemple la durée et la surface d'interaction entre un bioagresseur et son auxiliaire dans le cas de régulations biologiques ou en réduisant la durée et la surface d'interaction entre un bioagresseur et sa plante-hôte dans le cas d'infestations des cultures (MÉDIÈNE et al., 2011). Par exemple, il a été montré qu'une modification des dates de plantation permettait une désynchronisation des cycles entre ravageur et plante-hôte (MÉDIÈNE et al., 2011). L'utilisation d'une plante piège peut, en attirant les bioagresseurs hors de la zone culture pendant un temps suffisant, réduire la fenêtre critique entre le ravageur et la culture (COOK, KHAN et PICKETT, 2007). Selon la théorie de la hiérarchie, tout phénomène est situé dans une certaine gamme d'espace et de temps (O'NEILL et al., 1987) et l'efficacité des mesures agroécologiques sera conditionnée par l'échelle spatiale et temporelle des processus en jeu.

Le **paysage** devient l'échelle de travail privilégiée pour appliquer la transition agroécologique des systèmes agricoles. En effet, le paysage forme un système écologique dont la composition en éléments surfaciques et linéaires et leurs arrangements spatiaux contrôlent la présence d'espèces, mais aussi leurs déplacements et leurs interactions. L'agriculteur, via ses pratiques d'assolement, contribue à l'évolution de la composition du paysage (évolution saisonnière des éléments du paysage) (BAUDRY et al., 2003). Il contribue également à l'évolution de la structure du paysage en mettant en place des infrastructures agroécologiques (talus, haies, etc.) (FORMAN et BAUDRY, 1984). Cette mosaïque organisée d'éléments cultivés, surfaciques et linéaires, naturels et semi-naturels est le support de flux biotiques et abiotiques dont l'abondance en un lieu et un instant donné est un indicateur de services écosystémiques (par exemple, la co-occurrence de nombreuses espèces végétales

avec de grandes populations d'insectes pollinisateurs est un bon indicateur du service de pollinisation). La fragmentation et la perte d'habitats favorables ont tendance à réduire la fenêtre critique entre organismes tandis que la connectivité des habitats par des trames vertes ou bleues, et l'augmentation des zones d'interfaces ont un effet inverse. Dans la suite du mémoire, le paysage considéré pourra varier en étendue, en résolution et en nombre de strates en fonction de l'échelle des processus spatiaux considérés. Par exemple, un paysage traversé par un insecte marcheur sera beaucoup plus petit que pour un insecte volant.

La composante **biotique** en interaction avec les activités humaines a été longuement étudiée à l'échelle des paysages, en mêlant sciences agronomiques, écologiques et sociales, regroupée sous la dénomination d'écologie du paysage (FORMAN et BAUDRY, 1984). A contrario, la composante **abiotique** circulant dans les paysages (eau, air, nutriments et sédiments) a été plutôt traitée par d'autres disciplines biophysiques (hydrologie, climatologie ou mécanique des fluides par exemple) (SCHRÖDER, 2006). Or je considère que l'une et l'autre, même si elles présentent des dynamiques spécifiques, sont indissociables et doivent être appréhendées selon un **cadre commun**. Dans la suite du mémoire, la composante abiotique traitée portera essentiellement sur l'**eau** comme vecteur et ressource pour le matériel végétal.

Mon thème de recherche porte ainsi sur l'étude des **interactions biotiques-abiotiques dans les paysages agricoles**. Je présenterai ici le cheminement scientifique méthodologique et conceptuel m'ayant amené à traiter d'abord des interactions biotiques puis des interactions biotiques-abiotiques dans les paysages.

D'un point de vue méthodologique, j'ai poursuivi mes recherches selon un **continuum mêlant observation, expérimentation et simulation**, en appliquant des avancées scientifiques issues d'autres disciplines, suivant une fertilisation pluridisciplinaire (WU et HOBBS, 2002). La partie observation-expérimentation de mon projet s'appuie sur des méthodes innovantes de suivi des phénomènes spatio-temporels et la partie simulation s'appuie sur une modélisation à base mécaniste spatialement explicite. Face à des phénomènes qui s'expriment dans l'espace et dans le temps, et selon une démarche itérative, j'utilise les statistiques spatiales pour caractériser les motifs spatiaux observés sur le terrain. Si ces motifs ont une certaine structure, les statistiques inférentielles permettront de

les relier aux facteurs environnementaux et/ou intrinsèques à l'espèce étudiée. Les résultats des analyses statistiques spatiales et inférentielles serviront à la validation et/ou la calibration de modèles mécanistes. Enfin, la simulation par des modèles mécanistes, spatialement explicites, permettra d'analyser et de sélectionner les processus sous-tendant les motifs spatiaux par confrontation des jeux de données d'observation et de simulation. Les modèles ainsi construits sur des hypothèses écologiques seront utilisés comme écosystèmes virtuels pour tester l'impact du réarrangement des paysages sur les interactions biotiques-abiotiques. Je ferai régulièrement le bilan de l'utilisation de ce continuum observation-expérimentation-simulation à chaque étape du mémoire (Figure 2.1).

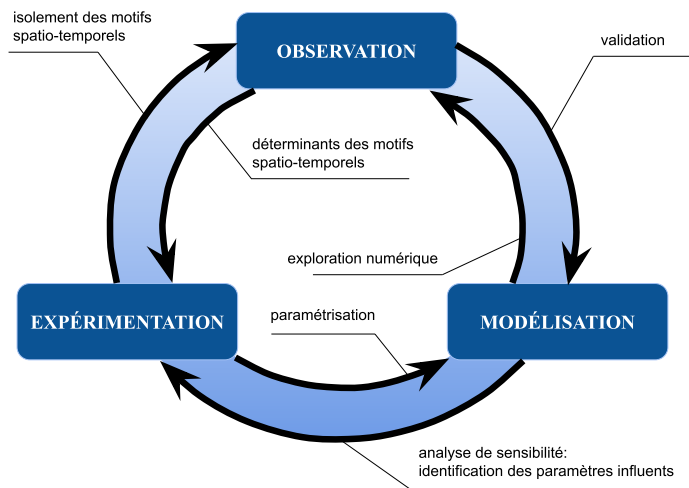


FIGURE 2.1 – Présentation du continuum observation-expérimentation-simulation

D'un point de vue conceptuel, je m'appuie sur une **vision multi-strate du paysage** partagée par le réseau Payote (INRAE), où nous faisons l'hypothèse que la matrice paysagère est le support physique d'un ensemble de flux biotiques et abiotiques, contraint par la géomorphologie, la couverture pédologique et les activités humaines (Figure 2.2).

Concrètement, pour un paysage donné, je définis **six strates en interactions**, avec, du plus pérenne au plus variable, la géomorphologie du paysage définie par un modèle numérique de terrain, la couverture pédologique et en particulier ses propriétés hydriques et agronomiques, la matrice paysagère constituée d'éléments surfaciques (parcelles agricoles) ou linéaires (fossés, bordures, routes), les activités humaines qui vont affecter la matrice paysagère et les flux qui y circulent par des actes socio-techniques, les flux abio-

tiques (eau principalement) et les flux biotiques (espèces animales et végétales constituant la biodiversité associée des cultures). J'ai volontairement écarté le climat, pourtant considéré comme une variable de contrainte du système, car je n'ai retenu que les strates ayant une hétérogénéité spatiale avérée à l'échelle du paysage (même si les champs de précipitations ou les températures peuvent varier sur de petites étendues). Je considère donc que c'est en jouant sur ces hétérogénéités et en prenant en compte de manière équilibrée les flux biotiques et abiotiques en interaction que l'on pourra accompagner la transition agroécologique des territoires.

Le thème présenté dans ce mémoire est l'aboutissement d'un parcours atypique, fruit de révélations successives. Passionné **d'entomologie** et bercé par les écrits de Jean-Henri Fabre (FABRE, 1989; FABRE, 1996, rééditions), j'étais décidé de travailler sur les lépidoptères selon une approche naturaliste et systématique. Le pragmatisme aidant, j'ai embrassé une carrière d'ingénieur agronome, spécialisé en protection des plantes et environnement, afin de pouvoir répartir les insectes entre les "bons" et les "mauvais". S'agissant des mauvais insectes, ou bioagresseurs des cultures, j'ai poursuivi en tant qu'ingénieur homologation chez Dupont Solutions, puis en thèse au CIRAD Martinique sur l'écologie spatiale du charançon du bananier. S'agissant des bons insectes, ou auxiliaires des cultures, j'ai réalisé un post-doctorat dans l'UMR Agronomie sur les interactions tri-trophiques melligèthe-parasoïde-colza. Enfin, j'ai rejoint l'UMR LISAH en 2011 pour travailler initialement sur la représentation numérique des paysages agricoles pour l'optimisation des services écosystémiques. J'y ai développé un programme de recherche portant sur les interactions entre l'eau et la végétation, et j'anime actuellement l'équipe écohydrologie des agrosystèmes.

Le plan du mémoire, en trois parties pour le bilan, suivra ma vision du paysage en traitant en premier lieu de la matrice paysagère, puis des flux biotiques dans les paysages (interactions insectes et plante-hôte), et enfin des flux biotiques-abiotiques (interactions eau-végétation). Les activités humaines seront présentes dans toutes les parties en tant que levier du système. La partie perspective sera scindée en deux parties, l'une consacrée au diagnostic et la compréhension des patrons de distribution des espèces en fonction de la contrainte hydrique, et l'autre à l'évolution et à la modulation de ces patrons en fonction du changement global et via la modification des pratiques et la réorganisation des paysages

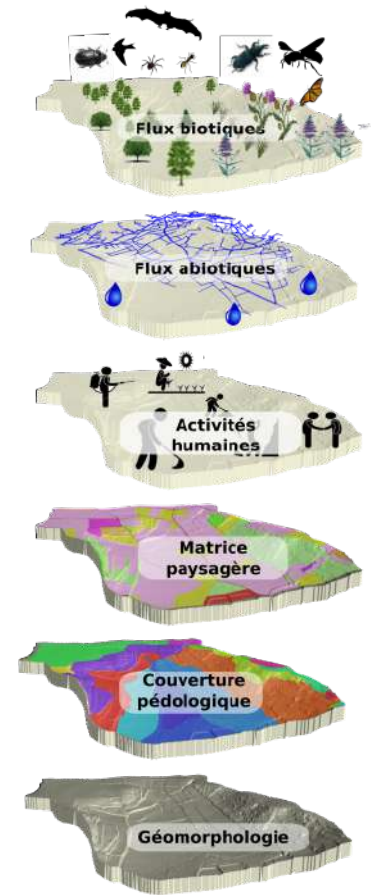


FIGURE 2.2 – Représentation des différentes strates du paysage ainsi que les interactions étudiées dans mon projet de recherche.

agricoles. Je montrerai en quoi mes travaux passés et mon expérience de la simulation des systèmes complexes alimenteront ces deux parties de perspective.

## 2.2 Simulation de la matrice paysagère

Comme présenté ci-dessus, la matrice paysagère est le **support physique** qui va contraindre les flux biotiques et abiotiques qui y circulent (POGGI et al., 2018)<sup>o</sup>. La matrice paysagère est constituée d'éléments surfaciques, i.e. parcelles, taches urbaines, mares, etc. et d'éléments linéaires, i.e. limites de parcelles, fossés, routes, rivières, etc.. Ce support présente une hétérogénéité de **configuration** (i.e. complexité d'arrangement spatial et de forme de ces éléments) et de **composition** (i.e. diversité des éléments présents) à des degrés divers (Figure 2.3). Cette hétérogénéité a des conséquences sur les services écosystémiques que les paysages fournissent (FAHRIG et al., 2011).

**L'intensification des activités humaines** aura tendance à réduire la naturalité du milieu (FERRARINI et TOMASELLI, 2010), avec pour conséquence une réduction de la complexité et donc de la durabilité des systèmes. En effet, un paysage avec une plus grande diversité fournira plus d'habitats aux espèces pour se nourrir, se reproduire et se réfugier (TSCHARNTKE et al., 2012). Un habitat avec une configuration complexe aura une plus grande densité d'interfaces, pouvant être bénéfiques (corridors écologiques) ou néfastes (effet barrière des routes) aux déplacements des organismes vivants (TSCHARNTKE et al., 2007). Cette densification des interfaces rencontre également des limites liées aux contraintes socio-économiques des agriculteurs, qui doivent circuler facilement dans toutes les parcelles de leur exploitation agricole (MEKKI et al., 2018).

La composition et la configuration d'un paysage ont une histoire qui est le fruit de transformations cycliques, graduelles et/ou brutales liées à l'intervention humaine, aux règles sociales et contraintes par le milieu (topographie, pédologie, environnement climatique) (POGGI et al., 2018). Afin de simuler finement l'hétérogénéité des paysages, il est nécessaire de comprendre et qualifier les **déterminants de ces transformations**.

En me posant la question *de la mesure et de la simulation des déterminants des transformations des paysages*, je situe les travaux qui

o: Toutes les références en bleu correspondent aux publications personnelles

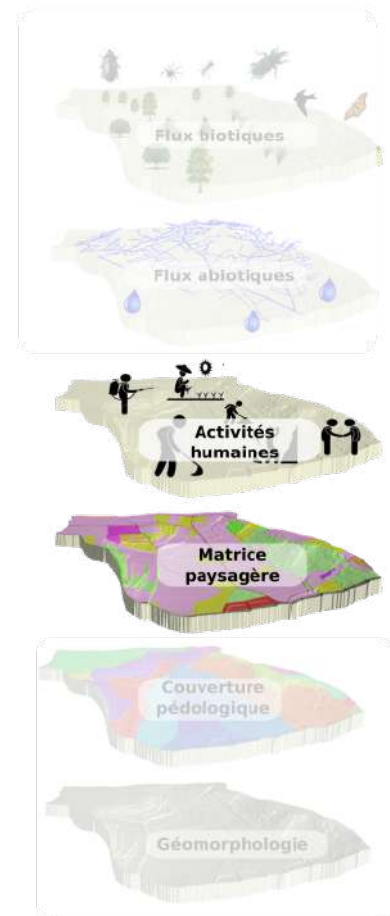


FIGURE 2.3 – Mise en relief de la matrice paysagère dans ma vision du paysage.

seront présentés ci-dessous dans une démarche de **géoprospective** (HOUE, VERBURG et LOVELAND, 2010), prônant l'intérêt de l'analyse à une échelle fine des déterminants du changement des paysages, via des analyses rétrospectives de séries diachroniques d'occupation du sol. Ces déterminants sont ensuite intégrés dans des modèles d'occupation du sol (Land Use Change Cover : LUCC) qui seront utilisés pour tester des scénarios prospectifs en faisant l'hypothèse que certains déterminants du changement des paysages seront conservés dans le futur (Figure 2.4).

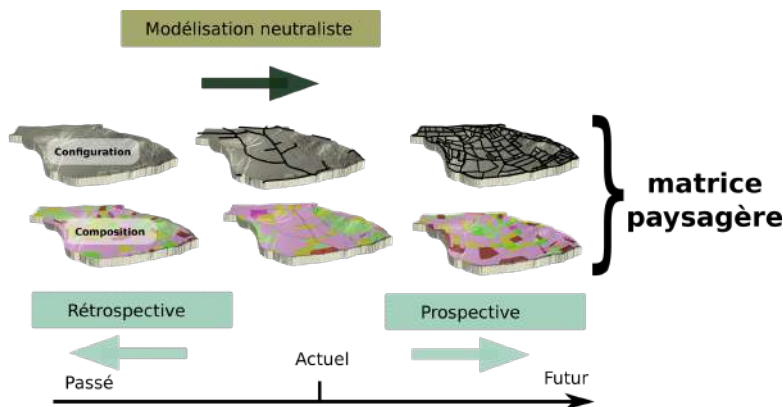


FIGURE 2.4 – Illustration des travaux sur la matrice paysagère.

Ma contribution à la géoprospective est principalement d'ordre méthodologique, en proposant (i) une chaîne de traitement des images aériennes anciennes pour l'analyse rétrospective (ii) un modèle de simulation neutraliste de la configuration d'un paysage aménagé, et (iii) un modèle de simulation LUCC de la composition des paysages méditerranéen.

### 2.2.1 Analyses diachroniques et détection de changements

Analyser et quantifier l'évolution des paysages nécessite d'utiliser des séries **diachroniques** à une résolution spatiale et temporelle en cohérence avec les processus à identifier. Dans notre cas, il s'agit d'étudier l'évolution des paysages aménagés méditerranéens dont l'artificialisation est en constante augmentation du fait de l'exode rural et la croissance démographique. Ce sont des milieux très complexes formant une mosaïque de surfaces agricoles et de zones urbaines et semi-naturelles entremêlés (POGGI et al., 2021). L'évolution de cette mosaïque a des effets sur le fonctionnement écologique des paysages : la déprise agricole participe à l'augmentation des milieux semi-naturels et donc à la naturalité des paysages, à l'inverse l'expansion urbaine, en créant des milieux totalement

Cette partie a bénéficié de collaborations internes au LISAH (Denis Feurer, IRD, Anne Biarnès, IRD, Guillaume Coulouma, INRAE) et nationales (Réseau Payote via la rédaction d'articles de synthèse communes et l'encadrement d'un master 2 (Ana Gonzalez Arnaiz, Espagne))

anthropisés, contribue à la disparition d'habitats favorables à la biodiversité et à la fragmentation des paysages.

Mes travaux ont mis en évidence les facteurs géomorphologiques et socio-économiques expliquant les changements non-cycliques d'utilisation des terres, tels que le changement de conduite du vignoble, l'artificialisation et la déprise agricole en Méditerranée (VINATIER et ARNAIZ, 2018) (Figure 2.5). L'analyse diachronique a nécessité une résolution spatiale sub-métrique pour distinguer les différents modes de conduite de la vigne et une résolution bisannuelle pour rendre compte des dynamiques d'arrachage et de replantation.

La constitution de séries diachroniques a été facilitée par une nouvelle méthode de construction de séries diachroniques à partir d'images aériennes issues des archives de l'IGN. Cette méthode dénommée **TimeSIFT** (FEURER et al., 2018), applique l'algorithme SIFT (scale Invariant Feature Transformation) à des images d'époques différentes pour obtenir des séries diachroniques d'images orthorectifiées et de modèles numériques de surface recalées au pixel, avec une précision inégalée permettant d'identifier des changements très fins (changement de conduite des cultures, artificialisation des sols, croissance du couvert végétal, modification d'infrastructures).

### 2.2.2 Simulation de la configuration des paysages

La **configuration** spatiale des paysages, comme la forme et l'arrangement des différents éléments qui le constituent, est complexe à simuler. Il existe de nombreux modèles de simulation basés sur la reconstitution des propriétés géométriques des éléments polygonaux et linéaires du paysage (parcelles, routes, etc), recensés dans POGGI et al., 2018. Ils se basent généralement sur des approches par tessellation de l'espace et sont considérés comme des modèles neutralistes, i.e. qu'ils représentent des motifs spatiaux caractéristiques en l'absence de processus susceptibles d'affecter ces motifs (GARDNER et WALTERS, 2006). Généralement bien adaptés aux petits parcellaires agricoles, ces modèles neutralistes ne permettent pas la simulation de la configuration de plus grands territoires cultivés avec une hiérarchie de réseaux (routes, chemins, bordures d'îlots et de parcelles).

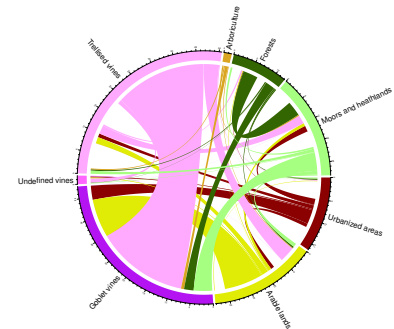


FIGURE 2.5 – Changements d'utilisation des terres en méditerranée entre 1960 et 2015 : mise en évidence du changement d'utilisation des terres (rose et jaune), de l'extension urbaine (en bordeaux) de la déprise agricole (en vert clair et foncé), à partir de VINATIER et ARNAIZ, 2018.

Cette partie a bénéficié de collaborations nationales (Réseau Payote) et l'encadrement d'un master 2 (Marina Chauvet, France)

En lien avec le réseau Payote, je me suis inspiré des travaux réalisés sur des petits paysages agricoles (ANGEVIN et al., 2008 ; LE BER et al., 2009) pour proposer un modèle neutraliste, basé sur la superposition hiérarchique de différents réseaux anthropiques (autoroutes, routes, chemins, bordures de parcelles) (Figure 2.6).

La déformation de ces réseaux a été simulée en inversant l'algorithme de Douglas-Peucker (VINATIER et CHAUVET, 2017), cette inversion permet, pour la première fois dans les modèles neutralistes, de paramétrer le degré de déformation des différents réseaux anthropiques dans les paysages. Le modèle a été calibré à partir d'un réseau réel de parcelles digitalisées sur le bassin versant de la Peyne. Il apporte plus de réalisme aux simulations neutralistes de grands territoires aménagés et répond à une exigence de la communauté (HOLLAND et al., 2007) d'introduire des géométries irrégulières pour diminuer les biais liés à la simulation de services écosystémiques s'appuyant sur des paysages virtuels.

Replacé dans le contexte de l'écologie du paysage et de la géoprospective, le modèle proposé aide à simuler, ex-nihilo, le réseau complet d'un territoire aménagé et permet d'identifier les zones susceptibles de jouer le rôle de corridors écologiques (bordures d'îlots et de parcelles pour lesquels sont installés préférentiellement des haies, fossés ou autre infrastructure agroécologique) et les zones de barrière physique aux déplacements (réseaux routiers). Complétant les modèles de simulation neutralistes existants, récapitulés dans (HOLLAND et al., 2007), il nécessite encore d'être amélioré pour tenir compte des changements de densité parcellaire observés en contexte collinaire, i.e. une plus forte densité de parcelles sur les zones de relief que celles de plaine.

### 2.2.3 Simulation de la composition des paysages

Une fois la configuration des paysages simulée, il s'agit de définir sa **composition**, i.e. le type d'occupation du sol à l'intérieur de chaque polygone. Les modèles de simulation de la composition du paysage, de type LUCC (MAS et al., 2014), ont pour objectif de traduire les phénomènes cycliques ou tendanciels en cartes dynamiques. Les phénomènes cycliques sont régis par les règles d'assolement des cultures et ceux non-cycliques sur la dynamique d'expansion ou de contraction des milieux anthropisés (surfaces urbaines), naturels (forêts) ou semi-naturels (garrigues). Il existe une diversité de



FIGURE 2.6 – Présentation du modèle neutraliste de simulation de la configuration du paysage, illustrant la superposition de plusieurs réseaux à l'échelle d'un territoire, à partir de VINATIER et CHAUVET, 2017.

Cette partie a bénéficié de collaborations internes au laboratoire : Frédéric Jacob (IRD), Anne Biarnès (IRD), nationales : Cécile Herivaux (BRGM) et internationales : Mohamed Sabir (INAT) et Insaf Mekki (INRGREF)



modèles de LUCC, de l'échelle du paysage agricole (LANGHAMMER et al., 2019) à celle du grand territoire (HOUEY, VERBURG et LOVELAND, 2010).

Ma contribution porte sur la traduction de scénarios narratifs en cartes pour simuler l'impact de l'érosion sur le bassin versant du Tleta, au Maroc (Figure 2.7). Quatre scénarios contrastés de la dynamique d'occupation du sol ont été proposés, (i) le scénario "Business as usual" où les tendances passées sont extrapolées dans le futur sans rupture, (ii) le scénario "Urbanisation" où la priorité est donnée à l'expansion urbaine au détriment des zones agricoles, (iii) le scénario "Vert" prônant une agriculture intensive et innovante, et (iv) le scénario mixte mêlant agriculture de proximité et expansion urbaine contrôlée. L'utilisation des cartes spatialisées à un grain fin a permis de faciliter l'appropriation des scénarios narratifs par les parties prenantes (HÉRIVAUX et al., 2021). La principale difficulté a été de combiner une approche

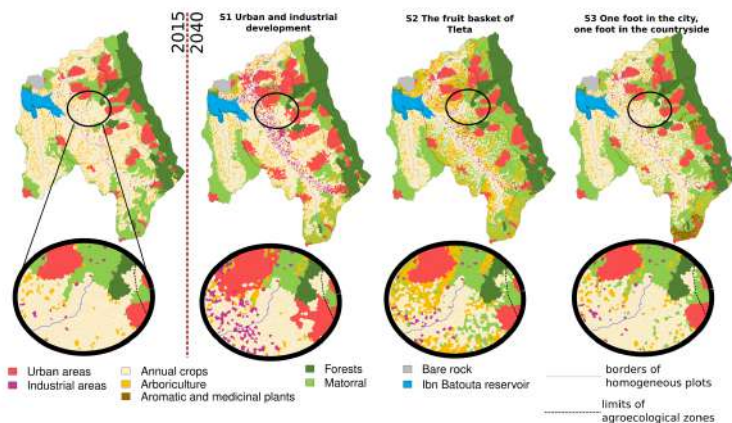


FIGURE 2.7 – Illustration des scénarios narratifs spatialisés à l'échelle d'un bassin versant Marocain, issus d'une modélisation LUCC, à partir de HÉRIVAUX et al., 2021.

mécaniste pour simuler des processus dynamiques (étalement urbain, succession de cultures) avec une approche scénario ou devaient être respectées les proportions finales d'occupation du sol proposées dans les scénarios narratifs. En effet, l'approche mécaniste suppose une méconnaissance, a priori, des proportions finales qui émergent des simulations car ces proportions sont conditionnées par les paramètres locaux du modèle. Pour pallier cette difficulté, les paramètres des processus dynamiques ont été réévalués de manière itérative pour converger vers les proportions finales des scénarios narratifs.

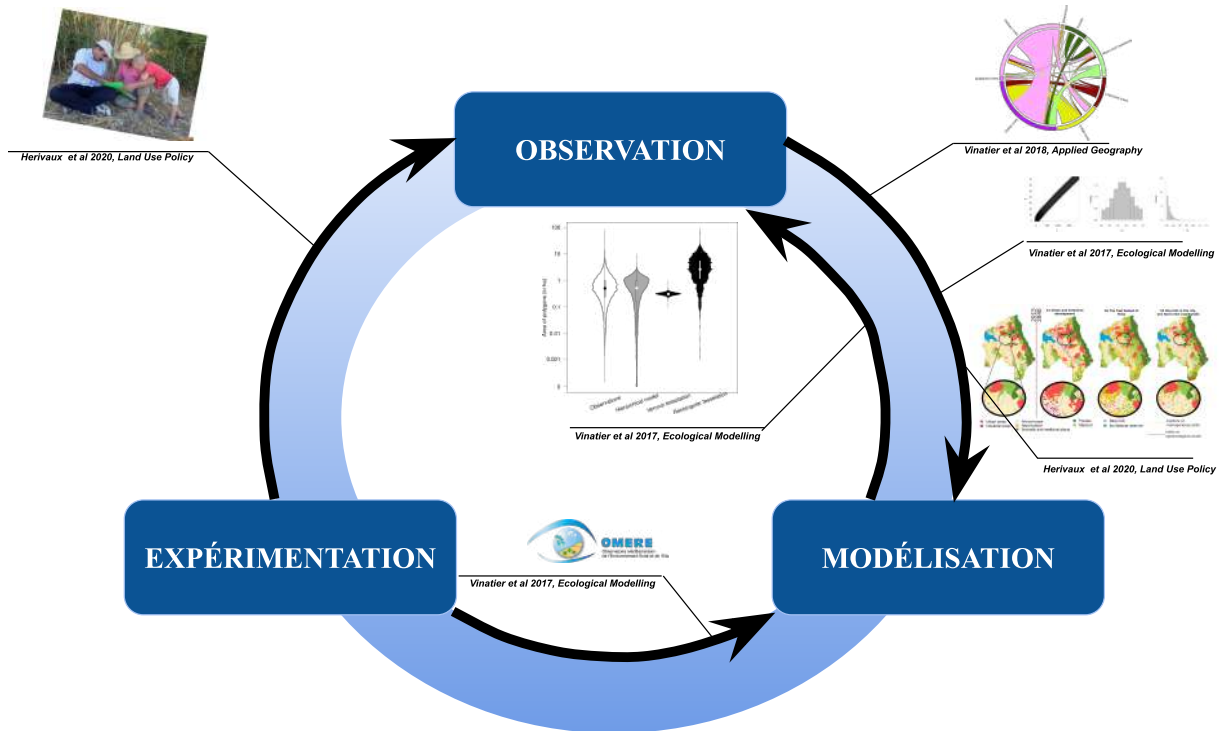


FIGURE 2.8 – Continuum observation-simulation-modélisation appliqué à la simulation de la strate paysagère.

## Synthèse

Mes travaux ont mis en avant l'importance de la simulation numérique de la matrice paysagère pour mieux comprendre les déterminants de son évolution sur le long terme et aussi appliquer des scénarios de perspectives sur des supports réalistes, en choisissant de représenter explicitement de grands territoires à une résolution très fine (Figure 2.8).

Les méthodes et approches que j'ai développées pour des processus tendanciels sur des surfaces viticoles sont difficilement applicables à des parcellaires plus dynamiques avec des rotations culturales par exemple, pour lesquels il existe déjà de nombreux modèles opérationnels (Landsfacts, APIland, etc). Ma contribution se situe plutôt en amont, en définissant la répartition des grandes classes d'occupation du sol au Niveau 2 du Corine Land Cover (incluant les terres arables, les cultures pérennes, etc), la succession des différentes cultures annuelles dans les terres arables se ferait dans un second temps, sur une plage temporelle plus étroite.

Les travaux présentés dans cette partie n'ont suivi que partiellement le continuum observation-expérimentation-simulation, l'expérimentation à l'échelle paysagère de scénarios prospectifs étant difficile à envisager, à part si on inclut les enquêtes chez les agriculteurs comme une expérimentation. La place de l'observation dans ce continuum est à redéfinir, en particulier dans la classification des séries diachroniques servant aux analyses rétrospectives : même si

une grande partie des distinctions entre occupations du sol peut être effectuée par analyse visuelle des ortho-images récentes, en particulier au deuxième niveau du Corine Land Cover, les distinctions plus subtiles nécessitent des jeux de données d'observation terrain conséquent sur le long terme. De ce point de vue, les observatoires long terme (OMERE ou Zones Ateliers) sont particulièrement pertinents pour la collecte de ces jeux de données et doivent être pérennisés.

Le thème de la simulation de la matrice paysagère a été largement débattu au niveau national et international. Les échanges fructueux avec les membres du réseau Payote ont permis une avancée significative de mes connaissances dans ce domaine. Lors de nos premières discussions autour de ce thème, se posait la question stratégique de simuler ex-nihilo des paysages avec des contraintes géométriques données ou de piocher dans des banques de paysages réels ceux qui recueillaient les jeux de contraintes géométriques d'intérêt. Nous avons privilégié l'approche de simulation ex-nihilo à l'époque, les banques de paysages réels étant limitées, mais cette question doit être reposée au vu des avancées en télédétection (RPG, CESBIO, etc.).

J'estime à présent qu'il existe un nombre suffisant d'outils pour simuler (ou télécharger) des paysages complexes et dynamiques. A mon sens, le front de science se situe à présent à l'interface entre les modèles de paysage et les modèles biophysiques ou économiques, domaine pour lequel je n'envisage pas de développer une activité de recherche.

Ces travaux s'inscrivant essentiellement sur des temps longs et appliqués à des processus tendanciels, le concept de fenêtre critique n'a pas été évoqué explicitement, même si les changements d'occupation du sol (assolements, déprise agricole, expansion urbaine) ou les changements de pratiques (mode de conduite de la vigne), sont autant d'éléments susceptibles de redéfinir les fenêtres critiques d'interactions entre les organismes et leurs habitats.

## 2.3 Flux biotiques dans la matrice paysagère

Les **flux biotiques** circulant dans la matrice paysagère dépendent fortement du comportement des individus pour la recherche de nourriture, la ponte ou la protection contre les prédateurs (VINATIER et al., 2011a) (Figure 2.9). Dans certains cas, le cycle de vie des organismes nécessite plusieurs habitats de nature différente pour être achevé (complémentation), et la survie des organismes nécessite plusieurs habitats de même nature (supplémentation) (TSCHARNTKE, RAND et BIANCHI, 2005). Les propriétés des habitats varient également dans le temps et en fonction des pratiques agricoles, créant des pulses de ressources pour les organismes. Par exemple, le semis ou la destruction d'une culture provoque une apparition ou une disparition plus ou moins brutale d'une ressource dans le paysage, avec des effets de débordement des ravageurs ou auxiliaires entre les milieux interstitiels et la culture (TSCHARNTKE, RAND et BIANCHI, 2005). Pour une culture donnée, la période favorable aux bioagresseurs est dépendante de l'attractivité de la plante cultivée, cette attractivité pouvant être maximale en période de floraison pour certains insectes (Cook et al., 2002).

Les travaux présentés dans cette partie ont été principalement réalisés au cours de la première partie de ma carrière (doctorat et post-doctorat). Tous contribuent à la **transition agroécologique** des milieux agricoles. En me posant la question suivante : *comment jouer sur l'hétérogénéité des ressources pour contrôler la population d'un bioagresseur ?*, je manipule des processus écologiques pour résoudre un problème agronomique, selon la définition stricte de l'agroécologie (ALTIERI, 1995). Les processus écologiques étudiés sont principalement les interactions spatiales et temporelles entre les organismes et leurs habitats, que j'utiliserai comme levier de limitation des niveaux de populations des insectes bioagresseurs des cultures afin de réduire les pertes de rendement. Moduler cette dispersion via un ré-arrangement spatial et temporel des habitats permet de réduire la fenêtre critique d'interaction maximale entre le ravageur et la plante cultivée.

Ces travaux sont présentés selon un niveau de complexité croissant : des relations bi-trophiques (ravageur-plante-hôte) aux relations tritrophiques (ravageur-auxiliaire-plante-hôte). Le paysage considéré est dépendant des stratégies de déplacement des organismes considérés, i.e. petits paysages pour insectes marcheurs et grands



FIGURE 2.9 – Mise en relief de la strate biotique dans ma vision du paysage.

territoires pour insectes volants. Les milieux considérés varient du climat tropical au climat tempéré, avec des conséquences directes sur la synchronisation saisonnière des populations étudiées, et donc sur les fenêtres critiques d'interactions entre les organismes.

### 2.3.1 Interaction hôte-ravageur en milieu tropical

La **dispersion** des organismes est un processus fondamental impactant les flux écologiques dans les paysages (SCHICK et al., 2008). Dans le cas d'une interaction entre une plante hôte (en l'occurrence une plante cultivée) et son ravageur, la dispersion va conditionner la diffusion de ce ravageur dans les parcelles agricoles et donc la fenêtre critique propice à la cause de dégâts et de perte de rendement. En contexte tropical, les oscillations de populations sont moins marquées par les variations saisonnières qu'en milieu tempéré (GODFRAY et HASSELL, 1987), de même que les cycles de développement des plantes hôtes (TIXIER, MALEZIEUX et DOREL, 2004). Par conséquent, la fenêtre critique où le pic d'attractivité des plantes coïncide avec le pic de ravageur est continue au cours de l'année et à l'origine d'un cumul important des dégâts.

De par leur physiologie, phénologie et comportement, les organismes appréhendent leur environnement à des échelles spatiales différentes (TSCHARNTKE, RAND et BIANCHI, 2005). Dans le cas des bioagresseurs des cultures ayant une mobilité limitée, comme les insectes marcheurs, l'hétérogénéité de paysage qu'ils rencontrent s'exprime sur une étendue réduite, en l'occurrence la parcelle agricole et son environnement immédiat. Les principaux leviers de gestion se situent donc à cette échelle, en jouant sur les schémas de plantation des cultures ou la gestion des espaces interstitiels (entre les rangs de culture ou à la bordure des parcelles).

J'ai élaboré un modèle spatialement explicite, nommé COSMOS, simulant l'ensemble des interactions d'un ravageur du bananier avec sa plante-hôte. Ce modèle a permis d'identifier de nouvelles hypothèses écologiques et a été utilisé pour étudier l'impact de nouvelles solutions agroécologiques permettant la régulation des populations de ce ravageur (Figure 2.10).

A court terme, la diffusion d'un bioagresseur dans un paysage, i.e. son épidémiologie, sera régie par ses capacités de dispersion. En utilisant le modèle COSMOS, j'ai proposé une nouvelle hypothèse

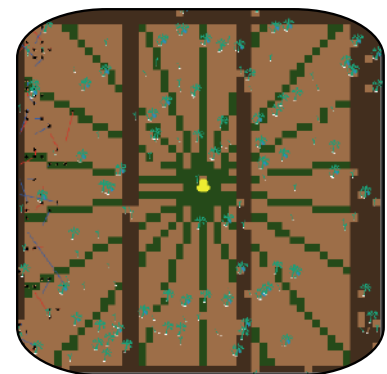


FIGURE 2.10 – Illustration d'une parcelle de bananiers (vert clair) avec une gestion différenciée des résidus de culture (vert foncé) faisant converger les charançons (points noirs) vers un piège à phéromone (en jaune). Le modèle nommé COSMOS est codé en NetLogo, à partir de VINATIER et al., 2009.

d'habitat-dépendance de la **perception du mouvement** pour ce type d'insecte. En m'appuyant sur une démarche itérative mêlant observations de terrain (DUYCK et al., 2012), expérimentation via des méthode de suivi par télémétrie (VINATIER et al., 2010) et modèle à base de processus (VINATIER et al., 2011b), j'ai démontré que la distance de déplacement du charançon était dépendante de son milieu de départ, i.e. les charançons situés sur du sol nu (matrice hostile) se déplaçaient plus activement que ceux situés au pied des bananiers ou de leurs résidus (matrice favorable).

Pour ce faire, j'ai utilisé une méthode de marquage originale utilisant des micro-capteurs RFID (Radio-Frequency Identification) pour suivre individuellement chaque insecte en limitant les perturbations liées à sa recapture (Figure 2.11). Cette méthode est particulièrement adaptée pour suivre des insectes cryptiques ayant des capacités de dispersion modérées (VINATIER et al., 2010). Le support physique du déplacement du charançon était constitué de différents habitats plus ou moins favorables (pieds de bananiers, résidus de culture, sol nu, plantes de couverture). Les trajectoires de déplacement mesurées par radiotélémétrie ont permis de calibrer un modèle de déplacement individu-centré et de sélection de l'habitat, dont l'algorithme se base sur un modèle probabiliste intégrant la distance et la qualité de l'habitat de départ et d'arrivée.



FIGURE 2.11 – Photo d'un charançon déplaçant sa puce RFID fixée aux élytres à l'aide d'un fil tressé, à partir de VINATIER et al., 2010.

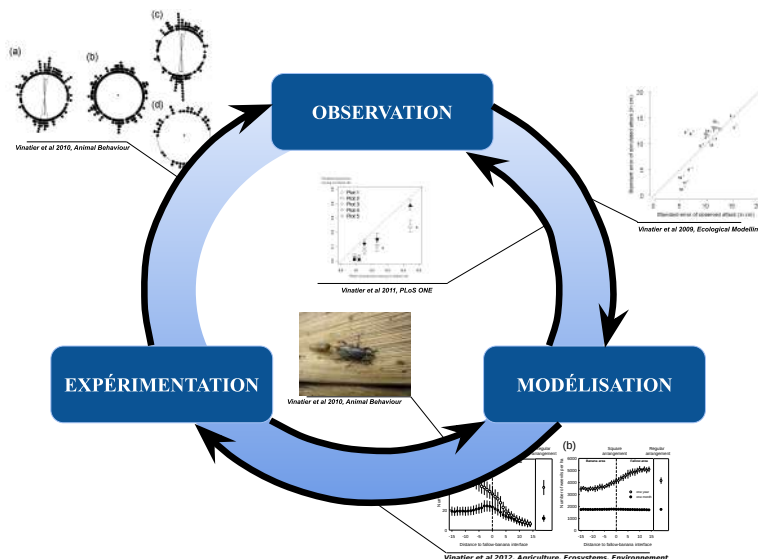


FIGURE 2.12 – Continuum observation-expérimentation-simulation appliqué aux travaux sur le charançon du bananier.

Cette dépendance à l'habitat de départ a pu être quantifiée en s'appuyant sur la démarche du **Pattern-Oriented Modelling** (GRIMM et al., 2005), i.e. en sélectionnant le processus le plus à même de reproduire le ou les motifs spatiaux observés sur le terrain, en

comparaison à d'autres hypothèses alternatives.

En reprenant le précepte de la fenêtre critique appliquée à l'interaction charançon-banancier, cette dernière sera rallongée pour des pieds de bananier hébergeant des charançons, ces derniers ayant tendance à réduire leurs déplacements dans un habitat favorable, et réduite pour des pieds de bananiers isolés et encore vierges de charançons (Figure 2.13).

A plus long terme interviennent les **processus démographiques** dans la diffusion d'un ravageur dans un paysage. Toujours sur le charançon du bananier, j'ai testé différentes stratégies de contrôle du ravageur en jouant sur l'hétérogénéité spatiale des ressources (VINATIER et al., 2012; VINATIER et al., 2009). Ces stratégies s'appuient toutes sur une modification de la dynamique spatiale de l'insecte, via le réarrangement des schémas de plantation des bananeraies ou la gestion des résidus de culture et l'organisation spatiale de pièges à phéromones. Le test des stratégies a été réalisé par exploration numérique d'un modèle individu-centré, spatialement explicite, construit et validé pour le charançon du bananier (VINATIER et al., 2009). Le modèle a montré que la vitesse de colonisation d'une parcelle dépend fortement du type de plantation. En lien avec l'hypothèse de débordement entre zones cultivées et milieu interstitiel (TSCHARNTKE, RAND et BIANCHI, 2005), le modèle a révélé l'importance de la zone de transition entre le sol nu et la plantation pour l'optimisation du piégeage, et la manipulation des résidus de culture aux abords des pièges permettant d'augmenter significativement l'efficacité de ces derniers (Figure 2.14).

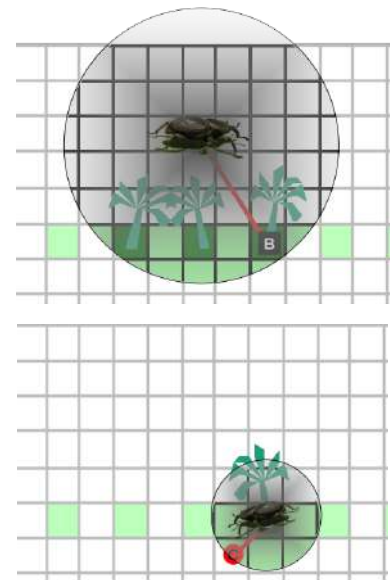


FIGURE 2.13 – Illustration de la variation du rayon de perception en fonction de l'habitat de départ, à partir de VINATIER et al., 2010.

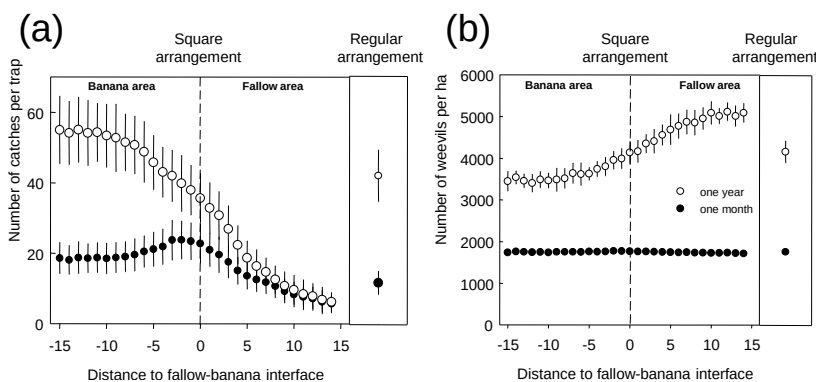


FIGURE 2.14 – Impact des arrangements paysagers sur l'efficacité du piégeage de masse, à partir de VINATIER et al., 2012.

### 2.3.2 Interaction hôte-ravageur-auxiliaire en milieu tempéré

Les interactions entre les ravageurs et les auxiliaires sont déterminées par la complexité du paysage (THIES et TSCHARNTKE, 1999), la

**régulation biologique** des bioagresseurs étant favorisée dans les paysages plus complexes. Le système méligèthe-colza-parasitoïde en est un excellent cas d'étude. Dans le paysage, les prairies et les parcelles de colza servent de ressources pour le complexe méligèthe-parasitoïde (complémentation), alors que les sols des forêts et des zones cultivées ayant eu un précédent colza, servent de lieu d'hivernage pour les méligèthes et les parasitoïdes, respectivement (supplémentation). Contrairement au cas d'étude précédent, les interactions agissant en milieu tempéré, la forte variabilité saisonnière va synchroniser l'apparition et la disparition de ces insectes poïkilothermes au cours de l'année. Par conséquent la fenêtre critique d'interaction où coïncident floraison de la culture, pontes des méligèthes et leur parasitage est très étroite et doit être maximisée pour assurer le meilleur contrôle biologique. Les principaux leviers du système sont les schémas de rotation des cultures, agissant sur la composition de la mosaïque paysagère, et certaines pratiques agricoles, telles que le labour qui a un impact sur la dynamique d'émergence des parasitoïdes et les plantes pièges sur l'attractivité des cultures.

Suivant l'hypothèse que la régulation biologique des méligèthes du colza sera influencée par les leviers énoncés ci-dessus, j'ai construit un modèle spatialement explicite de type Coupled Map Lattice intégrant les paramètres de vie des espèces et le développement du colza (Figure 2.15). J'ai intégré dans le modèle une fonction de dispersion inspirée de mes travaux précédents sur le charançon du bananier pour rendre compte de la différence d'attractivité des milieux suivant le stade des insectes et la distance à parcourir. Les paramètres du modèle ont été définis via la littérature existante sur chaque espèce (ou son plus proche taxon). En considérant une analyse de sensibilité et un jeu de données d'observations de terrain, j'ai réduit l'espace d'incertitude des paramètres du modèle afin qu'il reflète au mieux les tendances du système étudié (VINATIER, GOSME et VALANTIN-MORISON, 2013).

L'analyse de sensibilité a été conduite en faisant varier simultanément les paramètres de deux familles de paramètres, ceux des paramètres biologiques des espèces (démographique et dispersion) et ceux de la complexité des paysages. Dans le deuxième cas, les différents niveaux de complexité étaient tirés d'une banque de paysages de complexité croissante (Figure 2.16). L'intérêt de cette analyse à double niveau a été de comparer l'influence des paramètres des espèces au regard de certaines propriétés du paysage,



FIGURE 2.15 – Illustration du modèle tri-trophique Mosaic-Pest, à partir de VINATIER, GOSME et VALANTIN-MORISON, 2013; VINATIER, GOSME et VALANTIN-MORISON, 2012.



en utilisant des matrices de co-inertie. On a pu montrer que les paramètres de dispersion des espèces étaient sensibles aux proportions de forêts et de prairies dans les paysages, tandis que les paramètres démographiques étaient sensibles à la proportion de zones de cultures de colza (VINATIER, GOSME et VALANTIN-MORISON, 2013).

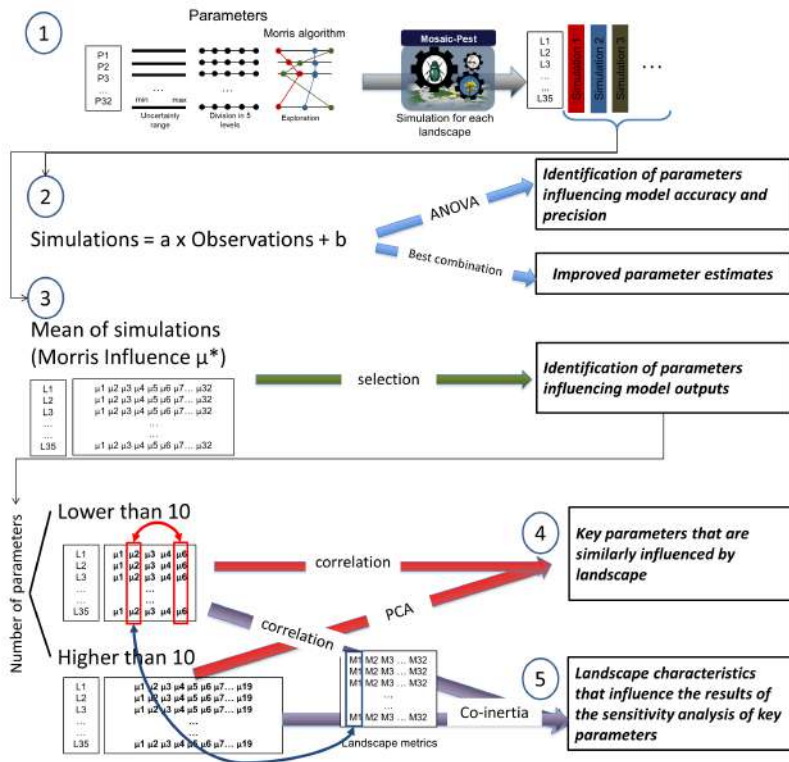


FIGURE 2.16 – Démarche d’analyse d’un modèle spatialisé complexe, à partir de VINATIER, GOSME et VALANTIN-MORISON, 2013.

Le modèle a été utilisé comme laboratoire virtuel sur une diversité de paysages réels pour tester certaines pratiques culturales, comme l’utilisation de plantes pièges, la rotation culturale et le labour (VINATIER, GOSME et VALANTIN-MORISON, 2012). En organisant l’exploration numérique du modèle selon un plan d’expérience à deux niveaux : diversité des paysages et paramètres démographiques/écologiques, le modèle a montré l’effet équivalent de la configuration du paysage et des pratiques dans la régulation des méligèthes. Il a confirmé que le taux de parasitisme augmentait avec la proportion en prairie dans les paysages.

Un résultat original issu de cette étude vient confirmer l’importance de la fenêtre critique dans les interactions hôte-ravageur-auxiliaire : augmenter la durée de la séquence de rotation entraîne une réduction du contrôle biologique (Figure 2.17). En effet, la fragmentation plus importante des parcelles de colza issue des longs schémas

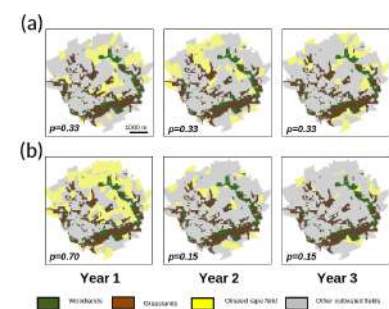


FIGURE 2.17 – Illustration de deux schémas de rotation marquant une fragmentation plus importante des parcelles de colza lorsque les rotations sont synchronisées dans le temps, à partir de VINATIER, GOSME et VALANTIN-MORISON, 2012.

de rotation empêche la bonne circulation des parasitoïdes dans le paysage, ces derniers ayant des capacités de dispersion plus limitées que les méligèthes.

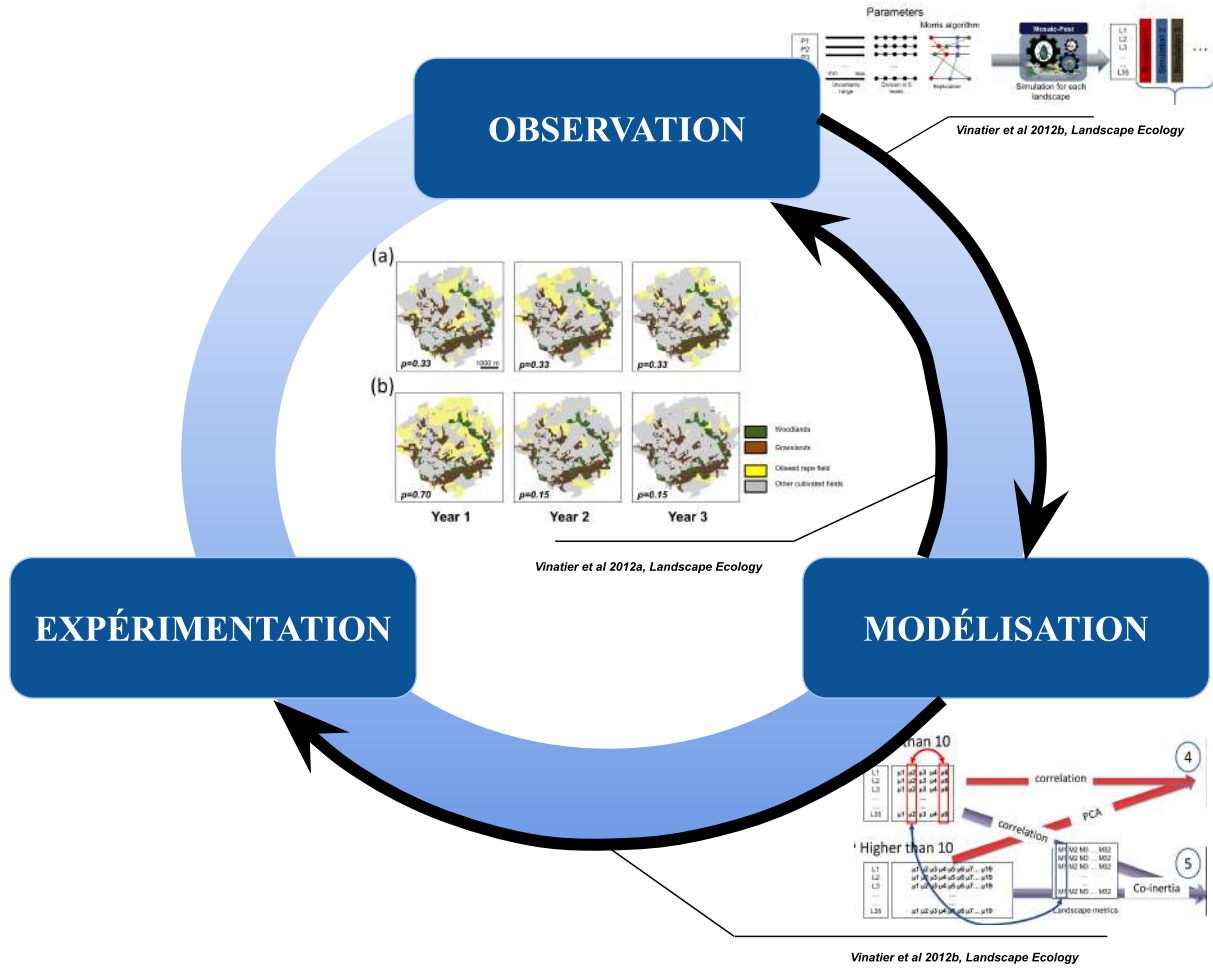


FIGURE 2.18 – Continuum observation-expérimentation-simulation appliqué aux travaux sur le méligèthe du colza.

## Synthèse

Je me suis permis une certaine liberté en considérant une parcelle agricole comme un paysage complexe selon le point de vue du charançon du bananier. Cette distorsion de l'échelle "classique" du paysage agricole pour une étendue beaucoup plus réduite est à juger au regard de la variabilité des autres processus s'exerçant à cette échelle (environnement, activités humaines, etc).

Les travaux présentés dans cette partie participent à la transition agroécologique en axant sur les interactions spatiales entre les organismes dans des milieux complexes. Même si la ré-introduction de biodiversité associée ou planifiée n'a pas été abordée explicitement dans ces travaux, l'idée était de ré-arranger les ressources dans l'espace, qu'elles soient semi-naturelles ou cultivées, pour (i) réduire les interactions entre un bioagresseur et sa plante hôte, et (ii) maximiser la régulation biologique d'un bioagresseur. L'originalité du travail repose sur l'utilisation du modèle comme un laboratoire virtuel pour explorer différents arrangements paysagers, en se basant sur des hypothèses écologiques connues, liées à la concentration des ressources et aux effets de complémentation et de supplémentation des habitats. Le principal apport cognitif de cette partie est l'introduction d'habitat-dépendance dans la perception qu'ont les insectes marcheurs de leur milieu. Cette hypothèse d'habitat-dépendance mériterait d'être testée dans d'autres cas d'étude.

Plusieurs formalismes de modélisation ont été sélectionnés en fonction des besoins. Pour le charançon du bananier, insecte marcheur, le formalisme type individu-centré est particulièrement adapté pour des organismes dont les niveaux de populations sont faibles dans les zones simulées (< 1 million d'individus), avec des interactions individuelles importantes (comportements d'agrégation) et une désynchronisation des cycles de vie, entraînant un mélange de stades de développement à chaque pas de temps de simulation. Pour le méligèthe, insecte volant, les niveaux de populations à l'échelle des zones parcourues sont trop élevés pour être traitées avec un formalisme individu-centré, et la synchronisation des cycles ainsi que la faible part des comportements individuels autorisent un formalisme de type coupled-map lattice, où se sont des cohortes d'individus qui sont suivies au cours du temps, chaque case de la grille représentant un niveau de population. Enfin, la segmentation de l'espace en raster plutôt qu'en vecteur était motivée par une volonté de rendre compte des effets de bords dans les éléments surfaciques.

Cette partie a donné lieu à deux modèles de simulation (COSMOS et MOSAIC-PEST) programmés dans une plateforme de simulation multi-agent NetLogo, ayant une interface graphique intuitive. Les modèles deviennent des objets frontières (REILLY, DILLON et GUIKEMA, 2021) permettant la communication entre différents membres d'une communauté scientifique sur des questions interdisciplinaires. Je tire de cette expérience de modélisation une meilleure appréhension des difficultés liées à la paramétrisation et validation des modèles spatio-temporels complexes. Trouver a priori le bon niveau de parcimonie d'un modèle, assez complexe pour faire apparaître des comportements émergents et suffisamment simple pour être interprétable a été difficile. Le formalisme de type individu-centré permet une plus grande plasticité des modèles aux données de calage et de validation au prix d'une plus grande complexité. J'estime, à posteriori, avoir

dépassé la medawar zone telle que GRIMM et al., 2005 l'exprime en créant des modèles plus réalistes que nécessaires pour répondre à la question de recherche qui m'animait. J'y vois par contre un avantage car les modèles ainsi construits ont été réutilisés dans d'autres projets, étant donné leur réalisme.

J'ai mesuré l'importance du continuum observation-expérimentation-simulation ainsi que l'utilisation de méthodes innovantes de suivi pour lever des verrous de connaissances sur des processus spatio-temporels fins, tels que la dispersion d'un insecte marcheur cryptique. J'ai découvert l'intérêt des nouvelles technologies (RFID) pour faciliter le suivi des espèces, et le Pattern-Oriented Modelling (GRIMM et al., 2005) pour comprendre leur comportement. Ces méthodes innovantes peuvent être un bon substitut aux observations naturalistes et patientes de FABRE, 1989; FABRE, 1996, rééditions.

J'ai adoré traiter, avec empathie, du comportement des insectes dans les paysages. J'aspire à ce que cette expérience en écologie comportementale, réduite dans la suite de mon projet de recherche portant sur des objets inanimés (végétation et eau), soit re-mobilisée par la suite via une ré-intégration des insectes dans ma vision multi-strate du paysage.

## 2.4 Flux biotiques-abiotiques dans la matrice paysagère

L'eau contrôle la dynamique des écosystèmes terrestres, comme ressource pour le biote et vecteur de dispersion biotique (Figure 2.19). Le biote, en retour, module de nombreux processus hydrologiques, comme l'évapotranspiration, le ruissellement, la nature des écoulements et la recharge des nappes par infiltration et percolation (D'ODORICO et al., 2010). Cette interaction duale entre eau et végétation est particulièrement prégnante dans les milieux méditerranéens où l'eau est un facteur limitant (PORPORATO et RODRIGUEZ-ITURBE, 2002).

Reprenant ma vision multi-strate du paysage encore orientée par des processus écologiques (cf parties précédentes), j'ai proposé un cadre conceptuel pour **coupler des modèles de flux biotiques et abiotiques**, en classant les multiples objets du paysage en éléments mobiles (matière, populations), circulant dans des éléments du paysage immobiles (parcelles, linéaires, unités de sol, etc.) selon des processus paysagers (ruissellement de l'eau, dispersion des organismes, etc.). On retrouve dans les éléments immobiles les éléments du paysage qui sont susceptibles de varier en composition et en configuration selon une mosaïque changeante, en écho aux travaux exposés dans la Partie 2.2. Les activités humaines influencent à la fois les éléments mobiles et immobiles et sont susceptibles d'être modulées, ce qui les différencie des conditions extérieures (saisonnalité, changement climatique, invasions biologiques, etc.) (VINATIER et al., 2016). Ce cadre offre l'avantage de placer phénomènes écologiques et hydrologiques à un même niveau avec une dynamique intrinsèque. Dans ce cas, nous n'avons pas un phénomène biotique avec une variation préétablie qui contraint un phénomène abiotique, mais bien deux phénomènes en interaction contraints par les conditions extérieures et les activités humaines.

Je me suis principalement intéressé aux éléments du paysage que sont les fossés agricoles intermittents, objets de travail emblématiques du LISAH et cas d'étude des interactions biotiques-abiotiques intéressants car hotspot de biodiversité et lieux de rencontre entre les milieux terrestres et aquatiques. Initialement creusés pour drainer les eaux de pluie, les fossés sont régulièrement soumis à des pratiques d'entretien pour restaurer leurs capacités hydrauliques (LEVAVASSEUR et al., 2014). Vu, selon notre cadre

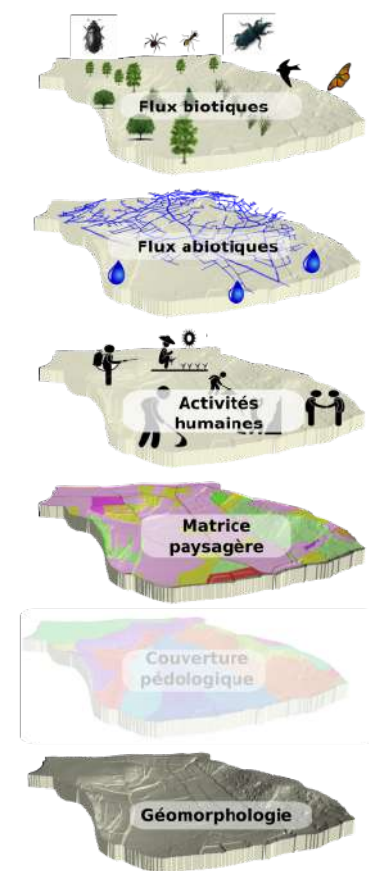


FIGURE 2.19 – Mise en relief des strates biotique et abiotique dans ma vision du paysage.

conceptuel, comme des éléments immobiles du paysage, les fossés vont interagir avec la végétation et l'eau, éléments mobiles du paysage. Ces interactions sont cycliques et continues, via des phénomènes de croissance et d'évapotranspiration liés à la saisonnalité, et les cycles sont parfois rompus par des phénomènes climatiques extrêmes ou des pratiques d'entretien. Le concept de fenêtre critique s'applique également aux interactions biotiques-abiotiques dans les fossés : les saisons automnales et hivernales vont correspondre à des pulsations de flux d'eau au gré des épisodes pluvieux, en phase avec la production de graines des végétaux (VINATIER et al., 2016). Les saisons printanières et estivales correspondent à un pic d'activité biologique (croissance des végétaux, déplacement des organismes) nécessitant un remplissage maximal des réserves en eau du sol.

Reprenant les concepts de **l'écohydrologie**, science transdisciplinaire fondée sur l'existence d'**interactions duales eau-biote** (McCLAIN, 2016), j'ai décliné aux fossés l'hypothèse formulée par ZALEWSKI, JANAUER et JOLÁNKAI, 1997 selon laquelle intensité et durée des écoulements sont affectées par les caractéristiques biologiques des corridors fluviaux, ces dernières étant modifiées en retour par le régime hydrologique.

La question posée dans ce cadre est : *Comment jouer sur les interactions eau-végétation pour assurer une préservation de la ressource en eau et un maintien de la biodiversité ?* Je fais l'hypothèse que l'homme, via les pratiques d'entretien des couverts végétaux spontanés et via des aménagements modifiant le circuit de l'eau dans les paysages cultivés, aura une influence déterminante dans la modulation du fonctionnement écohydrologique des agrosystèmes.

Je présente ici mes travaux en écohydrologie selon trois thèmes, les deux premiers illustrant les boucles de rétroaction eau-végétation proposées par ZALEWSKI, JANAUER et JOLÁNKAI, 1997 en traitant (i) de l'impact de la végétation sur les écoulements, (ii) de l'impact de l'eau sur la dispersion des graines, et (iii) de l'intégration des boucles de rétroaction eau-végétation dans un modèle de dynamique de croissance des couverts végétaux.

Les deux premiers thèmes, ayant l'eau libre comme principal moteur de fonctionnement, vont porter sur des événements rapides (ordre de la minute ou seconde) alors que le second thème portant sur la croissance végétale traitera d'échelles de temps plus longues (mois ou années). Il s'agit donc de coupler des processus agissant

à des échelles de temps différentes afin d'expliciter les fenêtres critiques entre eau et végétation susceptibles d'être modulées par les pratiques agricoles.

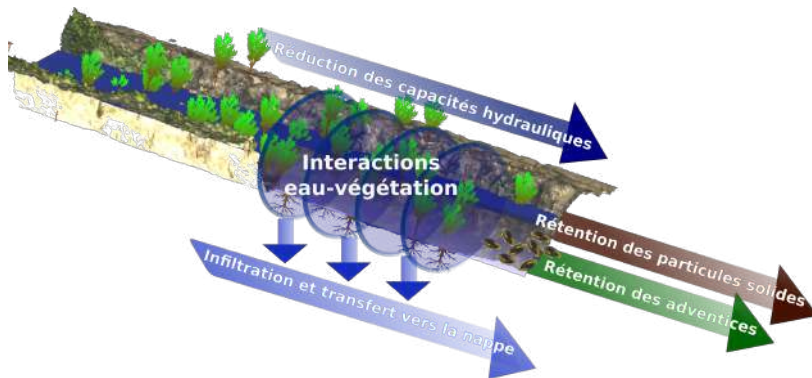


FIGURE 2.20 – Illustration des interactions entre la végétation et l'eau dans les linéaires agricoles avec un écoulement canalisé.

#### 2.4.1 Impact de la végétation sur les flux d'eau

La végétation va exercer une force de **friction** sur les écoulements, comme démontré par de nombreuses études réalisées en conditions contrôlées (JÄRVELÄ, 2005 ; LUHAR et NEPF, 2013 ; NEPF, 2012 ; VARGAS-LUNA, CROSATO et UIJTTEWAAL, 2015). Cet effet de friction est formalisé en hydraulique par des lois de type Manning-Strickler régissant les capacités de charge des écoulements en régime stationnaire. La loi de Manning-Strickler relie débit et propriétés de porosité du couvert végétal aux flux d'eau (NEPF, 2012). Il est supposé que cette propriété du couvert est liée à la surface (ou au volume) de végétation en contact avec la colonne d'eau, et on définit le facteur de blocage comme le rapport entre la surface de végétation projetée sur la section d'un canal (GREEN, 2005). Les expérimentations déjà réalisées en canal pour mesurer cet effet de friction se sont basées sur des substituts très simplifiés (cylindres plastiques) du couvert végétal, et sont peu représentatifs de l'architecture complexe des couverts spontanés trouvés dans les fossés agricoles.

Ma contribution à ce domaine a été d'estimer de manière non invasive un indicateur de l'effet de friction d'un couvert spontané sur les flux d'eau (VINATIER et al., 2016). Quatre espèces végétales ont été sélectionnées selon une diversité d'architecture et de rigidité, puis plantées au fond d'un canal hydraulique selon différentes densités. La structure de la végétation a été estimée par un lidar terrestre pour la convertir en un facteur de blocage des écoulements. L'effet de friction a été estimé par la méthode de Manning en mesurant

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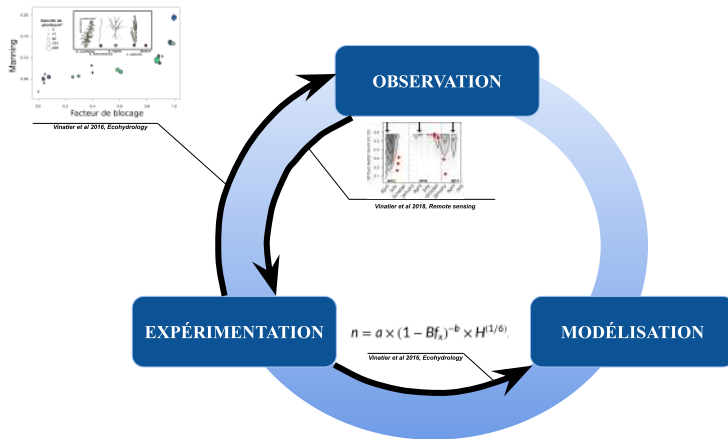


FIGURE 2.21 – Continuum observation-expérimentation-simulation appliqué aux impacts eau-végétation

la perte de charge de la ligne d'eau le long du canal. Les résultats ont montré que la coefficient de Manning varie d'un facteur 10 au maximum au cours de l'expérimentation, indiquant que la capacité hydraulique, i.e. le volume maximal d'eau susceptible d'être transporté lorsque le canal est en pleine charge, était parfois 10 fois plus important dans un canal non végétalisé. D'autre part, l'architecture de la plante joue sur la friction, avec une capacité hydraulique beaucoup plus faible pour les espèces sclérophylles et ramifiées que pour les espèces herbacées (Figure 2.22). Cet effet de

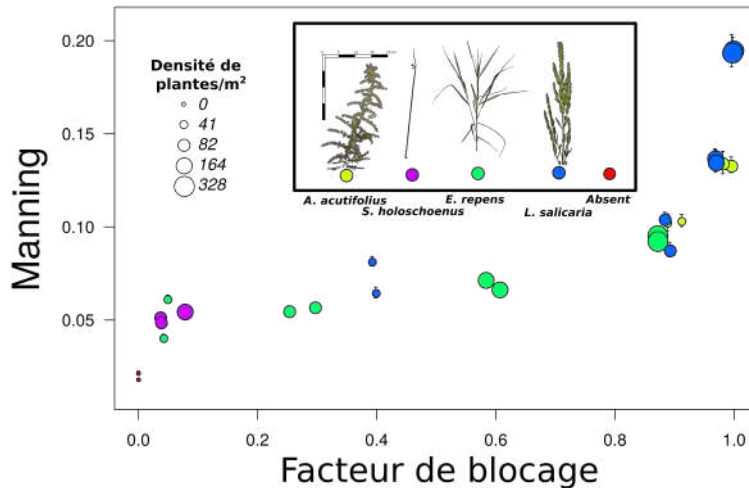


FIGURE 2.22 – Evolution du coefficient de friction (Manning) en fonction d'une propriété fonctionnelle des couverts (facteur de blocage), à partir de VINATIER et al., 2016.

friction a été déterminé par une formule empirique liant le facteur de blocage des plantes ( $Bf$ ) et la hauteur d'eau ( $H$ ) au coefficient de Manning ( $n$ ) :

$$n = a \times (1 - Bf)^{-b} \times H^{1/6} \quad (2.1)$$



avec  $a$  et  $b$  des constantes du modèle.

L'effet de friction exercé par le couvert végétal est relié à la dynamique du couvert végétal au cours du temps (DOLLINGER et al., 2018), elle-même influencée par la saisonnalité et les pratiques d'entretien. Sur la base d'un dispositif expérimental long-terme de suivi du couvert d'un fossé agricole soumis à différentes pratiques d'entretien des fossés (brûlis, désherbage chimique, fauche, curage)(Figure 2.23), nous avons proposé une méthode de suivi non destructif et répétable capable d'estimer les hauteurs et densités de végétation au cours du temps. Cette méthode s'appuie sur un suivi par photogrammétrie pour estimer un modèle 3D fin caractéristique de la végétation, son analyse permettant de mesurer la dynamique du facteur de blocage au cours du temps. En juxtaposant cette dynamique avec les mises en eau des fossés suite aux épisodes pluvieux, on identifie la fenêtre critique correspondant au maximum de biomasse végétale et au maximum d'écoulement, où les fossés ne remplissent plus leur rôle de drainage des eaux de pluie (VINATIER et al., 2018) (Figure 2.24).



FIGURE 2.23 – Illustration des pratiques d'entretien des fossés agricoles, avec, de gauche à droite et de haut en bas, le curage, le désherbage chimique, le brûlis et la fauche (crédits photo, Jeanne Dollinger et Fabrice Vinatier)

#### 2.4.2 Impact des flux d'eau sur le déplacement et l'établissement de la végétation

Les flux d'eau contribuent à structurer les **patrons de distributions** des espèces végétales dans les paysages (SILVERTOWN, ARAYA et GOWING, 2015), soit en maintenant une hétérogénéité spatiale de l'humidité du sol, soit en favorisant la dispersion des graines par **hydrochorie**. Beaucoup étudié dans les milieux naturels (NILSSON et al., 2010), l'impact des flux d'eau sur les patrons de biodiversité végétale est encore méconnu dans les milieux agricoles, alors qu'ils renferment des infrastructures agroécologiques (fossés, haies, talus, terrasse) modifiant les flux d'eau et susceptibles d'être transformés par l'homme.

La dispersion des graines dans les paysages a des causes abiotiques, biotiques et agronomiques (BENVENUTI, 2007). Les causes agronomiques de la dispersion des graines, via le transport de matériel végétal ou la fixation sur les engins agricoles ont été beaucoup étudiées (BENVENUTI, 2007 ; PETIT et al., 2013). L'**hydrochorie** par contre, c'est-à-dire la dispersion des graines par l'eau, a fait l'objet de peu d'études dans les milieux agricoles, alors que les réseaux hydrographiques sont susceptibles de déplacer les espèces sur de

Cette partie a bénéficié de collaborations internes au laboratoire : Jean-Stéphane Bailly (AgroParisTech), nationales : Gilles Belaud (G-EAU). La thèse de Gabrielle Rudi a été déterminante.

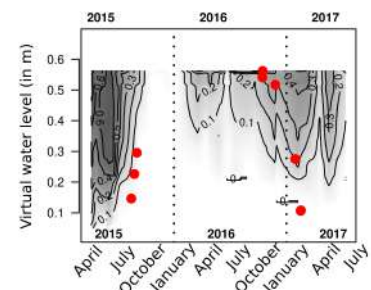


FIGURE 2.24 – Illustration des fenêtres critiques entre les mises en eau des fossés (points rouges) et le niveau de porosité de la végétation aux écoulements (dégradés de gris), à partir de VINATIER et ARNAIZ, 2018.

longues distances au gré des événements pluvieux (BOEDELTE et al., 2004). Notre contribution à cette thématique repose sur la mise en évidence et la caractérisation des déterminants de l'hydrochorie du sorgho d'Alep (Figure 2.25), espèce nuisible pour les cultures (RUDI et al., 2018).

La caractérisation des déterminants de l'hydrochorie a été réalisée en conditions semi-contrôlées sur une section de canal d'irrigation pour lequel l'arrivée d'eau et son débit étaient maîtrisées (RUDI et al., 2018). Les graines de sorgho ont été marquées via une poudre réfléchissante aux ultra-violets puis relâchées en début de section. En fin d'expérimentation, les graines déplacées ont été comptées via l'analyse d'images prises en pleine nuit avec une lampe UV. Une étude fine des caractéristiques micro-topographiques de la section végétalisée a été effectuée via un relevé photogrammétrique. En ajustant un arbre de régression (CART) sur le nombre de graines retenues par unité de section, nous avons mis en évidence l'importance des caractéristiques morphologiques du canal (largeur, présence d'ouvrages hydrauliques) dans la rétention des graines. L'impact de la végétation du fossé, par contre, était plus complexe, avec un effet de seuil de densité avant d'avoir un effet de rétention marqué.



FIGURE 2.25 – Graine de sorgho d'Alep, à partir de RUDI et al., 2018.

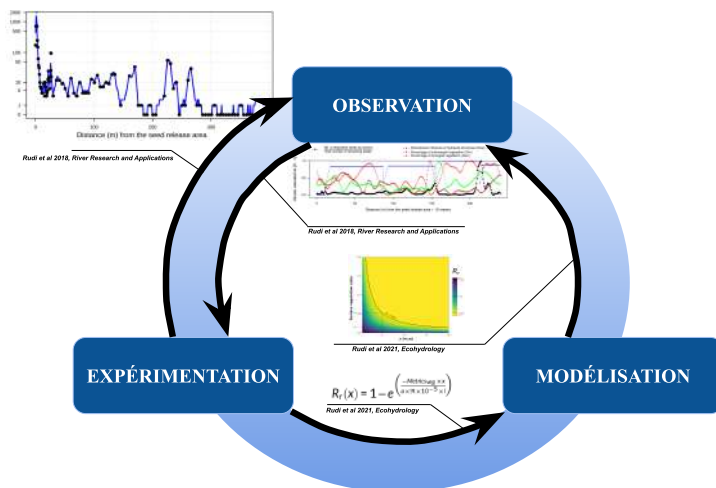


FIGURE 2.26 – Continuum observation-expérimentation-simulation appliqué à l'hydrochorie

Sur la base de ces résultats, et en particulier de l'effet ambivalent de la végétation du fossé sur la rétention des graines, une expérimentation en conditions contrôlées a été réalisée en canal hydraulique pour estimer quelle propriété de végétation permettait d'expliquer **la rétention des graines** (RUDI et al., 2020b), en s'appuyant cette fois sur des graines de *Rumex sp.* (Figure 2.27), autre adventice des cultures. En plaçant de la végétation artificielle présentant des

morphotypes contrastés dans le fond du canal et en faisant varier les débits, nous avons estimé le pourcentage de graines retenues dans l'ouvrage. A l'aide d'une formule semi-empirique, nous avons montré que le taux de rétention variait selon le type de végétation et sa densité, et que la surface de végétation à la surface de l'eau, potentiellement en contact avec les graines flottantes de *Rumex sp.*, était le meilleur prédicteur de la rétention des graines, quel que soit le type de végétation. Le modèle proposé constitue la première étape de modélisation biophysique de la dispersion des graines par hydrochorie dans les paysages agricoles.

La formule semi-empirique proposée reliant la proportion de graines retenues ( $R_r$ ) à la métrique de végétation  $Metrics_{veg}$  en fonction de  $x$  la distance parcourue, et  $\mathcal{R}$  le nombre de Reynolds caractérisant l'écoulement est de la forme :

$$R_r(x) = 1 - e^{-\frac{Metrics_{veg} \times x}{a \times \mathcal{R}}} \quad (2.2)$$

avec  $a$  étant une constante adimensionnelle.

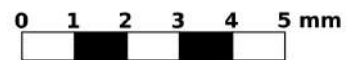
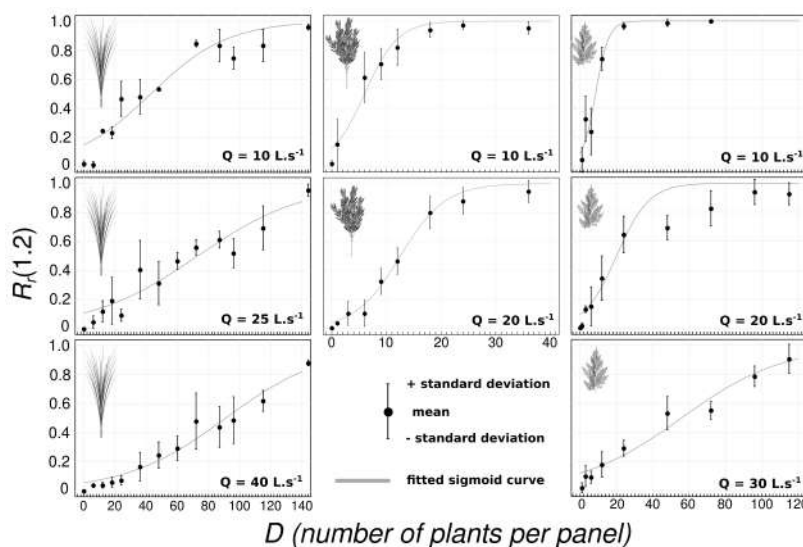


FIGURE 2.27 – Graine de *Rumex sp.*, à partir de RUDI et al., 2020b.

FIGURE 2.28 – Evolution du pourcentage de rétention des graines ( $R_r$ ) en fonction de la densité de plante ( $D$ ), du débit ( $Q$ ) et du type de végétation artificielle (de gauche à droite : Cypereaceae, Buxaceae et Cupressaceae), à partir de RUDI et al., 2020b.

### 2.4.3 Observation de la biodiversité végétale pour l'hydrologie

**La biodiversité végétale des milieux interstitiels** (fossés, bordures de parcelles, etc) est le déterminant biophysique de nombreux services écosystémiques, à la fois écologiques (par exemple en tant que ressources pour les auxiliaires des cultures) et hydrologiques (par exemple en participant à la régulation de la ressource en eau ou en sol) (DOLLINGER et al., 2015; HERZON et HELENIUS, 2008). Si

l'impact de la biodiversité végétale sur les services écosystémiques a été longuement étudié (CLERGUE et al., 2009; RICOU et al., 2014), son impact sur les services liés à la ressource en eau est encore un front de recherche à explorer à l'interface entre deux disciplines : écologie et hydraulique.

L'importance de la richesse spécifique des milieux interstitiels méditerranéens est une force pour rendre des services écosystémiques mais une difficulté pour le chercheur. Il est admis que le nombre d'espèces végétales rencontrées est supérieur dans les milieux méditerranéens, hot-spot de biodiversité, qu'en milieu tempéré (COWLING et al., 1996). On suppose qu'en zone agricole, les milieux interstitiels (bordures de champs mais également inter-rangs des cultures pérennes) abritent une diversité floristique bien supérieure aux parcelles cultivées, même si à notre connaissance, il n'existe pas d'études validant cette supposition. On a dénombré jusqu'à 60 espèces sur 100 mètres de linéaires de fossés (RUDI, 2019) et on estime à plus de 200 le nombre d'espèces trouvées dans les vignobles (FRIED et al., 2019). Par conséquent, étant donnée la diversité des espèces trouvées, il est nécessaire de définir des méthodes d'interpolation des propriétés fonctionnelles d'effets des espèces sur les flux hydriques via des regroupements écologiques d'espèces.

Notre contribution à ce front de recherche repose sur une revue de littérature montrant en quoi le concept de trait fonctionnel peut s'adapter aux propriétés de la végétation en lien avec les transferts d'eau (RUDI et al., 2020a). Il pose la question de comment agréger les traits fonctionnels des espèces à l'échelle du couvert en propriétés fonctionnelles aptes à être intégrées dans des modèles physiques, comme par exemple des modèles de résistance hydraulique ou des modèles de rétention des particules. Il ressort de cette revue de littérature que la plupart des études traitant de biodiversité et de services écosystémiques dans les milieux interstitiels se sont focalisées sur la richesse et la diversité des espèces, mais que peu d'études ont abordé la question de la mesure de la diversité des traits fonctionnels des espèces en lien avec les fonctions hydrologiques.

A ce titre, nous travaillons actuellement au phénotypage de certains traits fonctionnels (facteur de blocage) des espèces méditerranéennes pour pallier ce manque. Le phénotypage repose sur des prises de vue verticales de chaque plante en conditions contrôlées



FIGURE 2.29 – Le fossé à l'interface entre milieux terrestre et aquatique (crédit photo : Olivier Huttel).

pour estimer la surface de végétation soumise à un flux d'eau qui est un bon indicateur du facteur de blocage des plantes. Nous étudions également des méthodes de classification automatique des images pour la détection d'espèces dans l'espace et dans le temps. Pouvoir mieux caractériser les propriétés fonctionnelles des couverts végétaux dans l'espace et dans le temps devrait permettre de moduler la fenêtre critique d'interaction entre l'eau et la végétation pour optimiser certains services écosystémiques.

Selon la **théorie des niches**, chaque espèce possède un ensemble de conditions environnementales nécessaires à sa survie (VANDERMEER, 1972). En intégrant des variables environnementales spécifiques à l'hydrologie de surface comme les surfaces drainées par les réseaux de fossés, nous avons montré que ces dernières pouvaient expliquer l'occurrence des espèces selon leur caractère xérophile ou hygrophile (RUDI, BAILLY et VINATIER, 2018). Dix espèces d'intérêts ont été a priori sélectionnées selon trois critères : niche hydrologique spécifique ou non, espèce commune et facilement reconnaissable, pour être recensées de manière exhaustive le long du réseau d'une longueur totale d'environ 35 km (Figure 2.31).

Le suivi a été rendu possible via la création d'une application smartphone dédiée, enregistrant la trajectoire de déplacement de l'observateur et facilitant la saisie du type d'occurrence (ponctuel ou linéaire) et de l'espèce considérée (Figure 2.30). Au-delà des variables environnementales classiques utilisées pour expliquer la distribution des espèces (ensoleillement, pédologie, altitude, distance aux éléments semi-naturels, agricoles ou urbains du paysage), les surfaces drainées ont été calculées à partir du modèle numérique de terrain du bassin versant. Un modèle de distribution des espèces (Maxent) a été ajusté sur les données d'occurrence pour chacune des dix espèces étudiées, en réduisant l'autocorrélation spatiale des espèces.



FIGURE 2.30 – Illustration de l'application smartphone dédiée à la facilitation des relevés linéaires pour plusieurs espèces végétales d'intérêt.

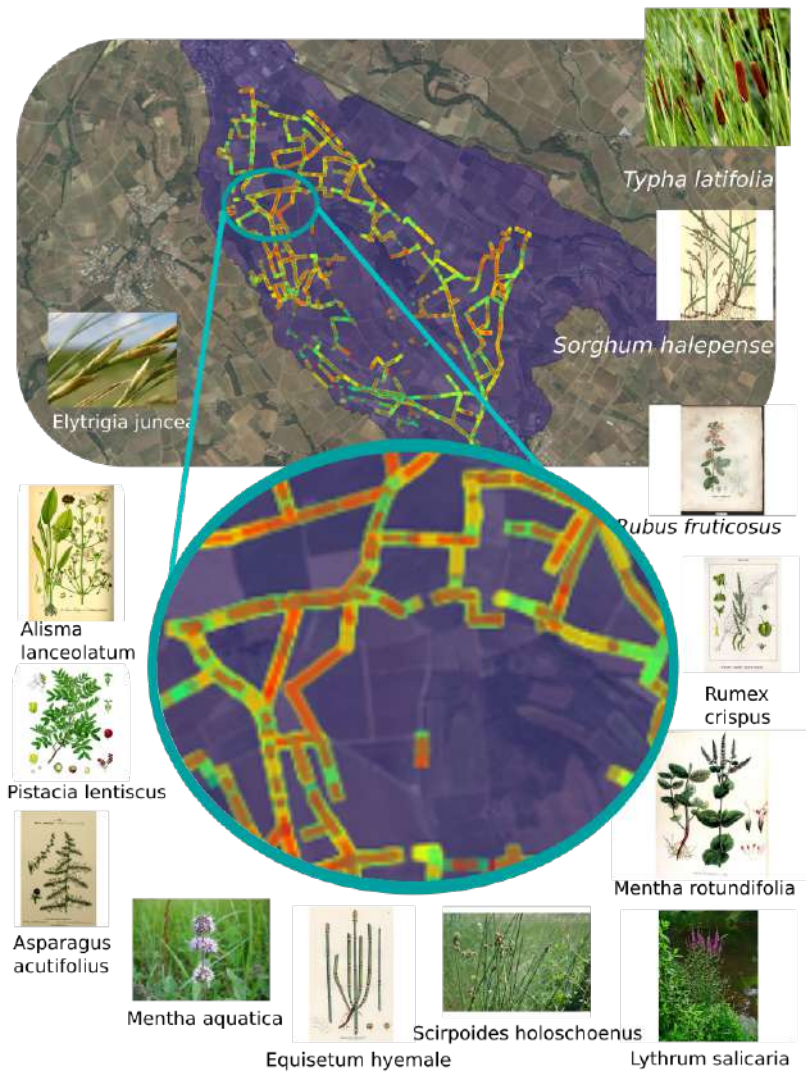


FIGURE 2.31 – Relevé de 10 espèces végétales d'intérêt écohydrologique sur un réseau de 80 km de fossés au fonctionnement intermittent, à partir de RUDI, BAILLY et VINATIER, 2018.

## Synthèse

Compléter les flux biotiques circulant dans les paysages par des flux abiotiques (eau, sédiments, contaminants) nécessite de solliciter un nouveau cortège de disciplines. Le principal challenge pour moi a été d'intégrer les flux biotiques et abiotiques dans les paysages en privilégiant une approche équilibrée entre disciplines écologiques et hydrologiques.

Un deuxième challenge a été de passer d'une approche lagrangienne, individu-centrée, des interactions spatiales à une approche eulérienne adaptée à l'étude des flux abiotiques dans les paysages.

L'imagerie, en particulier l'analyse d'image, que ce soit pour la photogrammétrie, le comptage de graines ou la mesure automatisée du facteur de blocage, a été favorisée dans cette partie pour l'étude des processus spatiaux. A posteriori, bien que cette méthode offre des avantages indéniables pour l'analyse fine et exhaustive de motifs spatiaux, elle nécessite une grande rigueur dans la prise de vue et un temps de post-process des images non négligeable, rendant son automatisation et sa diffusion à l'extérieur de la communauté encore difficile. D'autre part, la nécessité d'utiliser des calculateurs puissants pour les analyses, en particulier de photogrammétrie, et la nécessité du stockage de ces données images lourdes, me questionnent quant à l'empreinte écologique de ces approches.

L'ensemble des études présentées dans cette partie se sont focalisées sur un objet très spécifique du paysage qu'est le fossé agricole, véritable concentrateur de biodiversité et de flux d'eau. Il est temps pour moi de sortir du fossé pour aborder les dynamiques de connectivité entre les éléments interstitiels et les parcelles cultivées.

Mon travail a porté sur l'étude de la biodiversité au service des flux hydrologiques. Au regard de l'intérêt croissant pour la communauté de l'importance de la biodiversité dans toutes ses composantes : patrimoniale et fonctionnelle, et des nouvelles perspectives offertes par le renouvellement quadriennal du projet du laboratoire, je souhaite étudier l'impact de l'hydrologie sur la biodiversité.



## 3 Perspectives de recherche

### 3.1 Introduction

En exposant mes activités de recherche de la sorte, j'ai mis en exergue une volonté de comprendre et simuler le fonctionnement des différentes strates qui composent un paysage, de sa matrice physique jusqu'au flux biotiques et abiotiques qui y circulent, en considérant les activités humaines comme leviers principaux du système. Mes expériences variées en écologie du paysage m'ont permis de décliner le concept de fenêtre critique à de nombreux éléments en interactions, qu'ils soient biotiques, abiotiques et anthropiques. En privilégiant un continuum observation-expérimentation-simulation pour comprendre les mécanismes en jeu incluant plusieurs strates du paysage et en proposant des méthodes innovantes pour le suivi et la compréhension des processus spatiaux, j'ai pu prendre en compte de manière équilibrée les composantes biotiques et abiotiques du paysage ainsi que leurs interactions.

L'eau a pris une place centrale dans mes questionnements. L'évolution de la redistribution de l'eau dans les paysages par les activités humaines et l'intermittence des régimes hydriques accentuée par le changement climatique (FOVET et al., 2021) sont autant de levier et/ou variables de forçages susceptibles d'avoir un impact sur la flore des milieux interstitiels, avec vraisemblablement des conséquences en cascade sur la faune inféodée à ces milieux. S'agissant des activités humaines, la création, la modification et l'entretien des réseaux hydrographiques vont conditionner la biodiversité végétale dans ces milieux, en augmentant leur complexité et en

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favorisant les échanges avec les parcelles agricoles. S'agissant du changement climatique, les événements extrêmes (épisodes pluvieux, vagues de chaleur) (Figure 3.1) d'intensité temporelle et spatiale variables vont redéfinir les fenêtres critiques affectant les interactions biotiques-abiotiques, avec parfois des conséquences durables sur les agrosystèmes. L'évolution graduelle de certaines variables clefs du fonctionnement des agrosystèmes, telle la température, sera à même de modifier également les fenêtres critiques des interactions biotiques-abiotiques.

Cette nouvelle réflexion autour de la place de l'eau dans les paysages implique de redéfinir de nouvelles questions de recherche :

- *L'eau, en modifiant la flore des milieux interstitiels, est-elle en mesure de moduler les services ou dysservices écosystémiques impliquant des organismes animaux inféodés à cette flore ?*
- *Comment surveiller l'impact du changement climatique sur ces interactions entre l'eau, la couverture végétale et les communautés animales inféodées ?*
- *Au niveau de la strate paysagère, comment les échanges d'eau dans les paysages vont conditionner les échanges d'organismes animaux et végétaux entre les milieux productifs et non productifs ?*

Toutes ces questions peuvent être rassemblées en une seule, vibrante : *comment jouer sur la redistribution de l'eau dans les paysages pour moduler la biodiversité végétale ou animale inféodée susceptible de fournir des services écosystémiques ?*

Traiter cette question de recherche nécessite des collaborations, mon cœur de métier reposant sur la détection, le suivi et la modélisation des **processus spatiaux** impliquant l'homme, le végétal et l'animal dans le paysage. Il faut impliquer les écologues du milieu animal pour identifier les espèces susceptibles d'être affectées en cascade par une modification eau-végétation. Il faut également trouver des méthodes de suivi multi-taxonomiques et automatisées de la biodiversité végétale, en lien avec les extrêmes hydroclimatiques. Il faut impliquer des hydrologues pour convenir de la cohérence spatiale et temporelle entre les observables de la biodiversité et ceux de l'hydrologie. Ce travail de cohérence doit être poursuivi en modélisation, si l'on souhaite coupler du multi-taxonomique avec des modèles hydrologiques. Il faut raisonner avec les géo-agronomes les possibilités de re-conception paysagère avec à l'esprit la renaturalisation des milieux interstitiels par l'eau.



**FIGURE 3.1** – Illustration des effets du changement climatique sur un vignoble languedocien : vagues de chaleur, épisodes pluvieux, épisodes de gel

Cette question des flux d'organismes animaux et végétaux a été traitée avec succès dans les milieux naturels traversés par des réseaux de rivières (CID et al., 2021), en mobilisant la théorie, récente, des métacommunautés (CID et al., 2020) et en étudiant comment ces communautés vont réagir aux changements de régime hydrique des réseaux de rivière (BRUNO et al., 2019). Il s'agira dans mes perspectives de recherche de mettre en exergue ces liens structure-fonction entre les strates biotiques et abiotiques des paysages agricoles traversés par des réseaux hydrographiques intermittents (fossés) et constitués de cultures pérennes (vigne), même si ces liens peuvent être moins tenus que pour la strate "rivière" qui forme un écosystème à part entière (WARD et al., 2002) avec une circulation des organismes vivants alimentée essentiellement par le moteur hydrique. En particulier, l'identification de communautés animales directement inféodées aux communautés végétales contraintes par la ressource hydrique dans les paysages agricoles sera un pré-requis à ces perspectives de recherche.

Plusieurs collaborations sont déjà effectives via des nouveaux projets de recherche nationaux dont je suis co-porteur (projet MOMAC 2021-2024) et internationaux via la proposition du site d'étude du LISAH (observatoire OMERE) dans une plateforme eLTER. Mon inclusion dans un projet de consortium INRAE proposé au méta-programme Biosefair sur l'étude de la diversité multi-taxonomique à l'échelle paysagère participera également au déploiement de ce programme de recherches sur plusieurs observatoires de la biodiversité.

Mes perspectives de travail s'articulent selon deux axes, (i) diagnostic et compréhension des patrons de biodiversité en fonction de la contrainte hydrique, (ii) modulation de ces patrons via la modification des pratiques et la réorganisation des paysages agricoles. Ces perspectives seront appliquées aux agrosystèmes méditerranéens à dominante viticole, avec un focus sur les interfaces entre milieux cultivés et milieux interstitiels. Les deux axes seront menés de front, avec des apports méthodologiques et cognitifs d'un axe vers un autre.

## 3.2 Caractérisation des interactions entre biodiversité et contrainte hydrique

### 3.2.1 Interactions à l'échelle pluriannuelle

La contrainte hydrique, très présente en milieu méditerranéen, est susceptible d'affecter les zones de biodiversité végétale dans les milieux interstitiels. La première étape est de caractériser les patrons de distribution de cette biodiversité et leur évolution afin de la relier à de nouveaux services écosystémiques. Selon l'hypothèse de **ségrégation par la niche hydrologique**, littéralement *hydrological niche segregation* (HNS), évoquée par (SILVERTOWN, ARAYA et GOWING, 2015), les communautés végétales peuvent être structurées dans l'espace et dans le temps selon des contraintes hydrologiques ou hydrauliques. En effet, l'eau, en circulant dans les paysages, va contribuer à l'hétérogénéité spatiale de l'humidité du sol, avec pour conséquence un partitionnement de l'espace selon des gradients fins d'humidité du sol et une spécialisation des espèces selon leurs préférences hydrologiques. D'autre part, les précipitations et la dynamique d'écoulement de l'eau vont contribuer directement à la dispersion des espèces par hydrochorie.

Il s'agira donc d'identifier des patrons de distribution spatiaux des espèces végétales en fonction de la contrainte hydrologique, et de mesurer si **ces patrons sont susceptibles d'évoluer sur le long terme** en fonction du changement climatique. Pour se faire, à l'échelle du réseau linéaire, les relevés ayant été effectués sur le réseau du Bourdic en 2013 (RUDI, BAILLY et VINATIER, 2018) seront répétés tous les dix ans environ (2022, 2032, 2042) pour évaluer si la niche réalisée des espèces étudiées évolue sur le long terme en fonction de la toposéquence amont-aval, en lien avec le changement global. Plutôt que d'estimer l'évolution de la diversité de l'ensemble des espèces (diversité gamma et alpha), déjà étudiée sur le long terme pour des bordures de parcelles (ALIGNIER et al., 2018), il s'agit de mettre en évidence des déplacements d'espèces vers des nouvelles niches hydrologiques, liés à l'intermittence des réseaux de fossés, intermittence devant également être surveillée dans le temps avec des capteurs hydrologiques.

Une autre patron de distribution à identifier portera sur **les différences de diversité végétale réalisée entre milieux interstitiels à l'intérieur et aux bordures des zones de culture**. Sur la base des

Cette partie sera basée sur des collaborations internes au laboratoire (Jean-Stéphane Bailly), nationales (Gabrielle Rudi G-EAU/LISAH, Séraphine Grellier CITERES, Léo Garcia et Aurelie Metay ABSYS) et fait l'objet d'une thèse (Martin Faucher 2021-2024)

relevés floristiques déjà effectués dans les fossés (RUDI *et al.*, 2020a), mais non publiés, il s'agira d'élargir le domaine d'application de la ségrégation par la niche hydrologique aux autres éléments de l'agrosystème susceptibles de présenter des hétérogénéités hydrologiques, comme les milieux interstitiels à l'intérieur (inter-rangs) ou en bordure de parcelles (bandes enherbées), et aussi entre les zones de friches et les parcelles présentant des occupations du sol ou des modes de conduites différents : vigne, oliviers, en agriculture biologique ou conventionnelle, irrigué ou non. La difficulté sera de décorrélérer le facteur hydrologique des autres facteurs environnementaux (pédologiques, agronomiques, etc.) susceptibles de perturber la relation eau-végétation (ex pH, CaCO<sub>3</sub>, etc). Pour cela, les relevés seront effectués sur les observatoires du LISAH pour bénéficier de l'ensemble des co-variables mesurées sur les sites.

Ces études se basant sur des relevés floristiques seront complétées par des mesures de **la banque de graine**, variable clef de la succession pluriannuelle des espèces végétales, établissant le lien entre la biodiversité potentielle et réalisée (GARDARIN, DÜRR et COLBACH, 2012). Cette banque a l'avantage de renseigner sur le cumul de dépôt des graines sur le long terme. Insuffisamment connue dans les fossés, elle est susceptible d'être beaucoup plus riche qu'en dehors du réseau. Par conséquent, des études expérimentales seront déployées pour mieux caractériser la distribution spatiale de cette banque de graines en fonction de la redistribution de l'eau à l'échelle locale.

Le potentiel des **données spatiales multi-sources** sera évalué pour estimer l'évolution des milieux semi-naturels (zones ripariennes, inter-rangs de vignes, bordures de parcelles, zones de déprise, etc.) à relier aux changements des régimes hydriques sur le long terme. A partir des données à notre disposition, (i) images aériennes IGN (résolution 20-50 cm, profondeur temporelle : 1950-présent, grain : 2 ans, mesure RGB), (ii) les données d'observation de l'ORE OMERE (résolution parcellaire, profondeur temporelle : depuis 1992, grain : un mois, mesure de la classe de couverture végétale), (iii) les données satellites Sentinel-2 (résolution 10 m, profondeur temporelle : depuis 2015, grain : 5 jours, NDVI), il est possible de recréer une chronique spatialisée de la couverture végétale de ces milieux.

### 3.2.2 Interactions à l'échelle événementielle

Une modification de la flore est susceptible d'affecter les patrons de distribution des **espèces animales inféodées à ces communautés végétales**, que ce soit pour la reproduction, l'alimentation ou la protection, avec des effets directs ou indirects sur les services ou dysservices écosystémiques que ces communautés animales et végétales fournissent en milieu viticole : pollinisation (KRATSCHMER et al., 2019), régulation biologique (WILSON et al., 2017), dégâts sur cultures. Il s'agira de tester si cette hypothèse de ségrégation par la niche hydrologique explique également l'augmentation de biodiversité animale fournisseuse de services écosystémiques, en créant des ressources supplémentaires. Par exemple,

- *Est-ce que l'eau, en favorisant les espèces hygrophiles, va sélectionner des espèces nectarifères susceptibles de favoriser le service de pollinisation par les insectes ?*
- *Est-ce que ces mêmes espèces hygrophiles sont une meilleure ressource pour les insectes auxiliaires ?*
- *Est-ce que les milieux interstitiels situés dans les réseaux hydrographiques abritent une flore arborée ou arbustive plus susceptible d'abriter des mammifères ou oiseaux pouvant jouer le rôle d'auxiliaires ?*

Ce questionnement étant très exploratoire, il s'agira de mener des **campagnes d'observation multi-taxonomiques**, en lien avec les milieux interstitiels et en mesurant leurs conditions hydrologiques, pour repérer de nouveaux patrons de distribution. Cet objectif ambitieux ne pourra être relevé qu'en s'adossant à des observatoires déjà existants qu'il faudra compléter par des mesures de l'une ou l'autre des composantes à étudier conjointement (eau, flore, faune). Se baser sur des observatoires en place permettra de faciliter la connaissance du terrain, les échanges avec les agriculteurs et les relevés de terrain.

Il s'agira également d'imaginer des nouvelles méthodes de suivi à haut-débit de la biodiversité et des conditions environnementales, pour multiplier les sites de mesures et faciliter la déconvolution des effets du milieu et des pratiques du signal hydrologique sur la biodiversité. L'intérêt principal **d'automatiser les relevés de biodiversité**, malgré une possible réduction de la profondeur de classification taxonomique des espèces, sera d'associer ses relevés

Cette partie se basera sur des collaborations nationales (Bertrand Gauffre, Thomas Delattre PSH et Benoit Ricci ABSYS) pour la définition des interactions végétal-animal et l'implémentation de méthodes de suivi de la biodiversité animale.

Les campagnes d'observation ayant vocation à compléter les observables des sites du LISAH, leur mise en place et la pérennisation des moyens humains pour assurer le suivi seront décidées avec les gestionnaires du site OMERE du LISAH (Jérôme Molénat et Guillaume Coulouma) et le pôle technique du laboratoire (Sébastien Troiano, Olivier Huttel, David Fages et Manon Lagacherie), en se basant sur des protocoles déjà existants (REN 500, Sebiopag et Bacchus).

L'utilisation de méthodes innovantes de suivi de la biodiversité se fera en étroite collaboration avec les initiatives déjà existantes (Pierre Bonnet AMAP, Alexis Joly LIRMM, Nicolas Parisey IGEPP).

à des observatoires où les compétences (botanistes, entomologistes, ornithologues) sont manquantes. Les taxons étudiés seront sélectionnés en fonction de l'avancée des technologies de reconnaissance des espèces par les sons (oiseaux, ornithoptères), ultra-sons (chauve souris) et images (mammifères et flore) (Figure 3.2).

Les effets du milieu (température, humidité du sol, niveaux d'eau), constituant des données à faible bande passante, pourront être collectés en s'appuyant sur des réseaux de capteurs connectés selon la technologies IoT (Internet of Things), très utilisée en hydrologie (SALAM, 2020) et bioclimatologie (KAMA et al., 2018). La biodiversité se basera sur l'utilisation de capteurs à forte bande passante (imagerie, vidéo, audio), utilisés en zoologie (O'CONNELL, NICHOLS et KARANTH, 2011), appuyée par de l'intelligence artificielle pour faciliter la reconnaissance des espèces. Ces observations seront spatialisées pour étudier des effets du paysage et des interfaces parcelle-milieus interstitiels.

Ces mesures seront également répétées dans le temps afin de mettre en évidence un effet des extrêmes climatiques sur les interactions eau-végétation-biodiversité animale inféodée. Je suppose que ces relevés automatisés pourront préfigurer les **signaux précoces** d'une réduction ou augmentation de la fenêtre critique d'interactions entre flux biotiques et abiotiques. Comme exemple de signaux précoces, on peut évoquer les dates de floraisons des espèces en fonction des arrivées des pollinisateurs, la dynamique de fermeture de la canopée et le déplacement des insectes marcheurs, etc..



FIGURE 3.2 – Exemples de capteurs pouvant être utilisés simultanément dans une parcelle et sa bordure avec, de haut en bas et de gauche à droite, un piège photo, un enregistreur sonore et une centrale de mesure des conditions édaphiques.

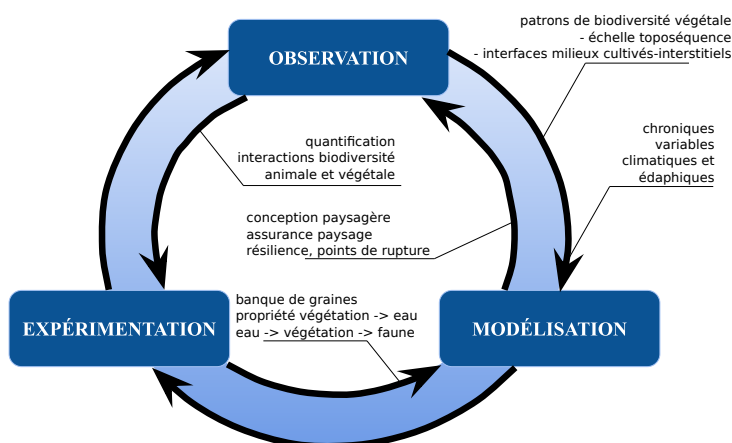


FIGURE 3.3 – Application du continuum observation-expérimentation-simulation aux perspectives du travail.

Des expérimentations ciblées, spécifiques d'un échange particulier

entre milieux, seront mises en place sur des parcelles expérimentales attenantes aux observatoires. Parmi les thèmes privilégiés figure la dispersion des graines par hydrochorie entre les parcelles et les milieux interstitiels qui permettra de compléter les apports cognitifs précédents (RUDI et al., 2020a). D'autres expérimentations pourront être mises en place en fonction des résultats des observations multi-taxonomiques, comme les transferts d'arthropodes, d'oiseaux ou de chauve-souris vers des parcelles vers les bordures ou inversement, en fonction de la qualité écologique des bordures.

### 3.3 Simulation des interactions entre biodiversité et contrainte hydrique

#### 3.3.1 Modélisation des processus-clefs du système

Une partie des observables identifiés dans la section précédente serviront à alimenter des modèles de simulation spatialement distribués simulant les flux biotiques et abiotiques dans les paysages, comme l'occurrence des espèces animales et végétales dans les fossés et les parcelles et les variables édaphiques associées (température du sol, humidité, rayonnement). Plusieurs formalismes pourront être mobilisés en fonction des données disponibles et des échelles de temps considérées (court terme ou long terme).

Les impacts du changement climatique, traduits par une multiplication des événements climatiques extrêmes, seront considérés comme des variables de forçage dans le modèle et s'appuieront sur les chroniques longues acquises par le laboratoire.

Les pratiques agricoles (labour, désherbage ou enherbement) et d'entretien des fossés (brûlis, fauche, désherbage chimique, curage) seront intégrées dans le modèle en fonction de leur impact direct sur le couvert herbacé (disparition, modulation de composition, transformation).

Concernant **les formalismes d'interactions long terme**, les interactions entre biodiversité végétale et contrainte hydrique à l'échelle pluri-annuelle seront simulées via un modèle plurispécifique sensible aux variations de la contrainte hydrique, qui reprend les formalismes de (BRADFORD, 2002 ; CELETTE, RIPOCHE et GARY, 2010 ; DURU et al., 2010). Une première difficulté sera de le paramétrer

Cette partie nécessitera des collaborations nationales pour simuler la croissance d'un couvert végétal spontané (Aurélien Metay et Léo Garcia ABSYS) et les transferts de faune entre habitats (Benoit Delattre PSH, Nicolas Parisey IGEPP).

Pour la partie abiotique seront nécessaires des collaborations sur la modélisation hydrologique (Jérôme Molénat) et hydraulique (Roger Moussa LISAH, Vincent Guinot HydroSciences).

Enfin seront sollicités les membres de l'équipe OpenFLUID du LISAH pour travailler au couplage de modèles à des résolutions spatiales et temporelles variables (Jean-Christophe Fabre et David Crevoisier LISAH).

pour chaque espèce via nos connaissances sur les milieux interstitiels méditerranéens et via des bases de données (KATTGE et al., 2020). Sa paramétrisation reposera sur des regroupements écologiques d'espèces (BLAUM et al., 2011) en privilégiant une approche par traits fonctionnels. Une deuxième difficulté sera de coupler ce modèle de biodiversité à un modèle de redistribution des eaux, pluri-événementiel, capable de simuler des événements extrêmes et leurs conséquences à long terme sur les conditions environnementales des espèces végétales (humidité du sol, transferts d'eau dans les bordures enherbées, etc.). Les patrons de distribution des espèces végétales observés seront comparés aux patrons simulés en privilégiant la démarche de Pattern-Oriented Modelling.

Concernant **les formalismes d'interactions à court terme**, les interactions entre la végétation et l'eau à l'échelle événementielle seront simulées en transformant les sorties du modèle plurispécifique en **propriétés fonctionnelles** vis-à-vis de la ressource en eau : réduction des capacités hydrauliques par la végétation (VINATIER, BAILLY et BELAUD, 2017), pourcentage de rétention des graines hydrochores (RUDI, 2019), sur la base des travaux de fin de thèse de RUDI, 2019. Le modèle agrégera les connaissances acquises sur ces phénomènes spécifiques. Pour la partie hydraulique, il s'agira d'adapter le modèle de l'onde diffusante à simuler des écoulements en milieu poreux. Les expérimentations ciblées sur les transferts de graine à mettre en place ou déjà acquis (RUDI, 2019) serviront à la validation ou la calibration des modèles.

Les flux et stocks de biodiversité végétale et animale inféodée pourront être simulés via des modèles de métapopulation parcimonieux (POGGI et al., 2021) représentant les transferts d'un milieu à un autre. Les fonctions de transfert seront ré-estimées à partir des modèles simulant les flux spatiaux à l'échelle événementielle dégradés. Toujours selon la démarche de Pattern-Oriented Modelling, les patrons de distribution simulés par le modèle serviront également à tester des hypothèses de comportement et d'activité de la faune qui expliquent aux mieux les patrons observés par les campagnes de mesure multi-taxonomique. Les expérimentations ciblées serviront à calibrer certains processus du modèle. Les niveaux de biodiversité dans chaque milieu seront traduites en **propriétés fonctionnelles** vis-à-vis de la régulation biologique des cultures, de la pollinisation des milieux et des refuges pour les organismes, en sélectionnant certaines espèces pourvoyeuses de services écosystémiques.



### 3.3.2 Conception de paysages résilients par exploration numérique

L'**exploration numérique** du ou des modèles développés se fera en jouant sur des variables de forçage liées au changement climatique et des leviers liés au ré-arrangement spatial et temporel des occupations et usages des sols, découlant d'analyses de prospective. Les modèles seront composés de modules simulant les différentes strates en interaction du paysage : occupation du sol, activités humaines et flux biotiques et abiotiques. L'exploration numérique consistera à simuler sur différentes matrices paysagères figurant des agrosystèmes avec une gestion plus ou moins extensive des milieux interstitiels, divers scénarios climatiques incluant une multiplication des événements pluvieux extrêmes, une hausse des températures et une augmentation des assecs des réseaux hydrologiques liés à l'aridification (Figure 3.4).

Les différentes matrices paysagères seront établies en tenant compte des champs de contraintes liées aux règles de décision des parties prenantes, aménageurs ou agriculteurs. Par exemple, la gestion extensive des milieux sera privilégiée dans des zones de faible accessibilité, difficilement mécanisables. Ces champs de contrainte réduiront l'espace des possibles en terme de diversité de matrices paysagères, mais offriront l'avantage d'une meilleure adéquation avec les comportements des parties prenantes et faciliteront leur adoption. Des scénarios de rupture seront également envisagés tout en gardant un caractère plausible.

On peut schématiser le devenir des agro-écosystèmes à long terme selon trois évolutions possibles, soit **une rupture, ou point de bascule**, vers des agrosystèmes dégradés avec une réduction de leur multifonctionnalité, soit **un maintien de leurs fonctions écosystémiques** via une meilleure résilience, soit **une amélioration d'un agrosystème dégradé** vers un agrosystème plus productif et durable. Dans le premier cas, le changement global est trop important pour permettre un maintien des fonctionnalités de l'écosystème. On peut donner l'exemple de l'aridification des écosystèmes, l'augmentation de l'intermittence des cours d'eau ou la fragmentation du paysage. Dans les deux cas suivants, l'idée est de poursuivre la transition agroécologique voire l'utilisation d'ingénierie écologique pour augmenter les fenêtres critiques bénéfiques fournissant des services (interactions plantes-pollinisateurs

Cette partie bénéficiera de collaborations internes au laboratoire (Jean-Stéphane Bailly, David Crevoisier) pour l'exploration numérique de modèle et la conception de paysages.



FIGURE 3.4 – Illustration de la zone riparienne comme ressource particulièrement sensible aux flux hydriques dans les paysages

ou hôtes-parasitoïdes, humidité du sol et croissance végétale) et réduire les fenêtres critiques fournissant des dysservices (interactions bioagresseur-culture, écoulements-végétation). Au niveau du paysage, cela passe par une augmentation de la biodiversité végétale et des interconnexions entre les milieux, ou le développement d'aménagements ad-hoc pour maximiser une ou plusieurs fonctions écosystémiques.

Concernant le changement climatique, l'idée étant d'évaluer à partir des modèles simulant **les formalismes d'interactions long terme** la résilience ou les points de bascule des agro-écosystèmes lorsque l'on modifie les régimes hydrologiques. En première hypothèse, la multiplication des événements extrêmes et les changements graduels de température vont contribuer à sélectionner des espèces végétales plus aptes à survivre dans ce milieu changeant. On peut supposer qu'une modification des propriétés fonctionnelles d'une communauté végétale aura des conséquences sur la communauté animale inféodée et les services écosystémiques associés (Figure 3.5). Par exemple, un basculement vers une communauté majoritairement herbacée, réduira la ressource nectarifère pour les auxiliaires, ou un basculement vers des communautés RGR+ (forte croissance en biomasse) offrira de meilleurs refuges pour les arthropodes.

Concernant l'effet des pratiques, l'idée étant d'évaluer à partir des modèles simulant **les formalismes d'interactions court terme** comment une modification des pratiques peut influencer en cascade la végétation et sa faune inféodée à l'échelle du paysage.

L'analyse des résultats de simulation portera sur les tendances des agrosystèmes à évoluer selon les trois tendances possibles exprimées ci-dessus, à savoir le point de bascule vers des agrosystèmes dégradés, le maintien des agrosystèmes via une meilleure résilience, voire l'amélioration d'un agrosystème dégradé vers plus de productivité et de durabilité.

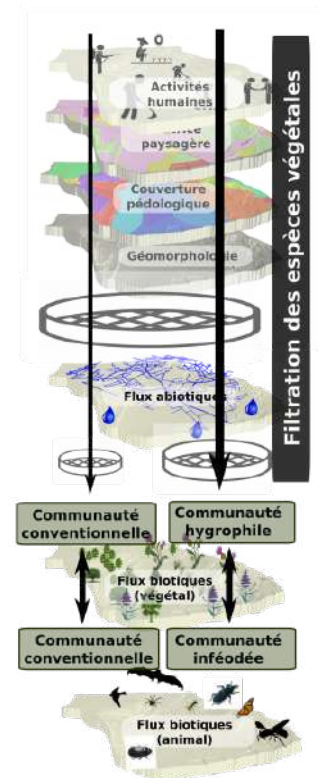


FIGURE 3.5 – Conceptualisation des interactions eau-végétation-animal : parmi les filtres abiotiques susceptibles de sélectionner les communautés végétales, l'eau, en filtrant les espèces hygrophiles, peut favoriser une communauté animale spécifique qui y est inféodée

## Synthèse

Les méthodes de suivi, automatisées ou non, devront être faciles à mettre en place pour pouvoir impliquer les parties-prenantes dans les suivis (agriculteurs, gestionnaires de bassins, conservatoires des espaces naturels) afin de démultiplier l'effort d'échantillonnage. En se basant sur des initiatives récentes telle l'application écobordure (ALIGNIER et al., 2018), l'utilisation de réalité augmentée pour l'appropriation des services écosystémiques (GOSME, 2021), l'objectif est de sensibiliser les agriculteurs à la mesure de la richesse en biodiversité de leurs bordures de parcelles, pour qu'ils justifient la haute valeur environnementale (HVE) de leurs bordures plantées (GUILLAUME, 2021).

J'espère pouvoir apporter des éléments de réponse à l'hypothèse de l'assurance paysage, reprise par (TSCHARNTKE et al., 2012) : la complexité du paysage assure une stabilité spatiale et temporelle, i.e. une plus grande résilience des processus écologiques du paysage dans un environnement changeant. Un paysage plus résilient comprend une diversité d'espèces avec des redondances fonctionnelles, i.e. assurant un maintien des fonctions écosystémiques même si certaines espèces disparaissent. Cette diversité d'espèces est également assurée par des échanges nombreux et réguliers entre les milieux productifs et non productifs. En reprenant la vision multi-strate du paysage il s'agit de mieux définir la part de l'abiotique dans cette hypothèse. Nous l'avions évoqué également (POGGI et al., 2021) en nous interrogeant sur la place des transferts d'eau dans la résilience des processus écologiques. La question que je souhaite aborder est de définir comment les échanges d'eau entre les éléments du paysage vont conditionner les échanges d'espèces.

## 3.4 Conclusion

Définir une colonne vertébrale à l'organisme polymorphe constituant ma carrière de recherche fut un exercice extrêmement stimulant. Avec le recul, je confirme un intérêt pour l'étude des processus spatiaux, quels qu'ils soient, en considérant une combinaison d'approches (observation, expérimentation, simulation) et des méthodes de suivi innovantes, adaptées aux organismes étudiés. Colmater les vides de connaissance expliquant les patrons de distributions spatiaux engendrés par des animaux, végétaux, voire humains a été ma principale source d'inspiration scientifique.

Mon intérêt pour la transdisciplinarité, et en particulier la fertilisation croisée entre disciplines : écologie-agronomie et écologie-hydrologie, m'a permis d'établir des collaborations nouvelles pour poser des ponts entre certaines disciplines parfois cloisonnées. *En croisant les sciences, on participe à la consolidation des bases scientifiques de la transition agroécologique.*

Les perspectives de développement de recherches proposées, amenées à évoluer, serviront de base de travail pour développer un programme de recherche à long terme, déjà engagé avec des partenariats nationaux, et en voie de déploiement à l'international. Pleinement inscrit dans le champs de l'écohydrologie, j'aspire à intégrer et développer la communauté scientifique gravitant

autour des relations duales eau-végétation, en intégrant les écologues spécialistes des organismes animaux.

Le programme proposé s'appuiera sur l'encadrement de doctorants, futurs chercheurs, pour lesquels je partagerai mes expériences méthodologiques et conceptuelles. Je les intégrerai dans mes réseaux scientifiques afin qu'ils s'épanouissent dans leur thèse.

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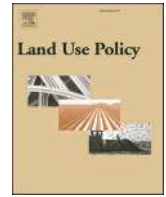
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**TIRÉS À PART**

## Simulation de la matrice paysagère

- Hérivaux, C., [Vinatier, F.](#), Sabir, M., Guillot, F., & Rinaudo, J. D. (2021). Combining narrative scenarios , local knowledge and land-use change modelling for integrating soil erosion in a global perspective. *Land Use Policy*, 105. url<https://doi.org/10.1016/j.landusepol.2021.105406>
- [Vinatier, F.](#), & González Arnaiz, A. (2018). Using high-resolution multitemporal imagery to highlight severe land management changes in Mediterranean vineyards. *Applied Geography*, 90, 115–122. <https://doi.org/10.1016/j.apgeog.2017.12.003>
- [Vinatier, F.](#), & Chauvet, M. (2017). A neutral model for the simulation of linear networks in territories. *Ecological Modelling*, 363. <https://doi.org/10.1016/j.ecolmodel.2017.08.022>



# Combining narrative scenarios, local knowledge and land-use change modelling for integrating soil erosion in a global perspective

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## ARTICLE INFO

### Keywords:

Narrative scenarios  
LUCC modelling  
Participation  
Land system  
Soil erosion  
Morocco

## ABSTRACT

Mediterranean soil resources are heavily affected by water erosion. There is a need for anticipating the potential impact of land-use change at the catchment scale, considering a range of contrasted possible changes, in order to prepare a relevant adaptation strategy. While participatory scenario approaches are useful for unveiling the diversity of possible futures, their outputs generally take the form of narratives that may be difficult to relate to biophysical models used for simulating soil and water processes. We addressed this challenge by developing a methodology combining narrative scenarios and land-use change modelling at the catchment scale, interacting with local stakeholders who were involved throughout the research, in line with current Land System research. First, we built contrasted scenarios, each with a narrative story and quantitative assumptions for key variables. Then we drew up rules for translating narrative scenarios into spatially explicit maps based on expert groups and local knowledge, simulating the evolution of land use over time. Third, we evaluated and validated the final scenarios by conducting two workshops with scientists and local stakeholders. Finally, we assessed the impact of these scenarios on agricultural production and erosion control. This approach was implemented in the Tleta basin (Morocco), a 180 km<sup>2</sup> rural watershed, 10 km from Tangiers and heavily affected by water erosion. As a result, we propose three contrasted spatially explicit land-use change scenarios by 2040. Our work highlights the interest of combining narrative storylines and land-use modelling when developing spatially explicit scenarios at the catchment scale, incorporating the local knowledge of stakeholders. The combination of Land System and ecosystem frameworks contributes to integrating the soil erosion issue in a more global perspective, and lays the foundation for building sustainable strategies for Mediterranean catchments affected by soil erosion.

## 1. Introduction

Soil degradation, and in particular soil loss due to water erosion, is a major threat to the future of the Mediterranean basin (Lagacherie et al., 2018; Raclot et al., 2018). Soil losses lead to lower soil fertility that can affect agricultural production (Panagos et al., 2018), and reduce water-supply capacity due to siltation in reservoirs (Ben Slimane et al., 2016; Kondolf and Farahani, 2018). This phenomenon is expected to increase in the future due to climate change (Lagacherie et al., 2018) and land-use changes (Van Rompaey et al., 2007; Borrelli et al., 2013). Several recent studies on the combined effects of climate and land-use changes on water erosion have shown that land use has a predominant effect (Parioissien et al., 2015; Simonneaux et al., 2015; Luetzenburg

et al., 2020), although uncertainties attached to its evolution are clearly recognized. Anticipating future land-use changes is therefore particularly important for mitigating and/or reducing their potential negative effects on water erosion.

An approach commonly used in erosion-process modelling is to simulate purely technical land-use change scenarios. These can involve a minor change in the value of one variable of the land-use change model (Van Rompaey et al., 2007), or extreme scenarios involving several variables simultaneously, but which have the disadvantage of being rather implausible (Ashagre et al., 2018). This type of approach formulates clear-cut land-use change hypotheses, which are simple to quantify and spatialize, and easy to use as input for biophysical models. A second approach consists of predicting a land-use scenario based on

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trends in land-use change observed in the past (Maeda et al., 2010; Ferreira et al., 2016; Zare et al., 2017). This predictive approach is based on the assumption of a continuation of past trends, without envisaging potential economic, political or social breakdowns. Conversely, participatory scenario approaches allow exploring different futures for a territory by considering a wide range of driving factors that influence land-use change, and by formulating assumptions related to their possible evolution. Although the driving factors to be considered are case dependent, they usually cover economic, regulatory, social and technical dimensions, including those driving changes in farming systems and practices (e.g., agricultural policy, agricultural commodity markets, technological change, environmental regulation, water resources availability), and factors determining the form of urban development, such as population growth, economic development and income.

An increasing number of studies relies on the development of contrasted narrative scenarios, to facilitate the exploration of potential land-use changes and their impact by experts and stakeholders together (Rinaudo et al., 2013; Oteros-Rozas et al., 2015; Vacquie et al., 2015; Houet et al., 2017). However, a direct use of such scenarios can be difficult when trying to transform them into spatial and dynamic representations over time (Shackley and Deanwood, 2003; Kok et al., 2007; Alcamo, 2008), or as maps of land-use change that can be used as input for biophysical models. Translating these narrative scenarios into spatially explicit maps requires a numerical description of the rates of change in land use and, above all, of the constraints of their plausible locations at fine scales (Mallampalli et al., 2016). There are several methods for achieving this numerical description, including fuzzy set theory (Kok et al., 2014), pairwise comparison (Abildtrup et al., 2006; McDaniels et al., 2012) and role-playing games (Castella et al., 2005; Lamarque et al., 2013). Yet, the translation of narrative scenarios into quantified hypotheses that can be used in land-use and -cover change (LUCC) modelling remains a challenge, particularly at catchment scale where local processes—such as urbanization or agricultural management—interact with global drivers (Booth et al., 2016). Our paper addresses this challenge by developing an empirical approach based on input from expert groups and local knowledge. This provides the flexibility and specificity necessary for translating narratives with a large set of drivers, into quantitative-input models that vary in space and in time (Vacquie et al., 2015; Booth et al., 2016).

There are several LUCC models for a fine description of the processes involved. These range from multi-agent systems describing social behaviour, such as LUDAS (Le et al., 2008), MP-MAS (Schreinemachers and Berger, 2011), or cellular automata for urban growth (Guan et al., 2011), to Markovian-type probabilistic models for describing heavy trends (Paegelow and Camacho, 2008; Ruiz-Benito et al., 2010), including Clue-S (Verburg and Veldkamp, 2001), Dinamica (Maeda et al., 2011), SPA-LUCC (Schirpke et al., 2012) and Land Change Modeler (Aguéjdad and Houet, 2008). Improving LUCC predictions can be done by adding spatial constraints related to geomorphological or anthropic factors, such as distance maps to fixed landscape elements, or crop aggregation criteria (Castellazzi et al., 2007; Houet et al., 2010). When simulating land use, Brown et al. (2005) described the constant tension between the desire for accurate prediction and the accuracy of the process. In the case of a prescriptive approach, the goal is to obtain the closest map to the narrative scenarios; in the second case, the explanatory approach, the main goal is to explain the underlying mechanisms of change and, if so, the maps showing a path-dependency according to the process included and its parameterization. These LUCC models are used with varying degrees of stakeholder involvement. Historically, LUCC models were built in isolation, with stakeholders being involved primarily as end-users (Kok et al., 2007). Gradually, however, stakeholder involvement increased, especially with the “Storyline and Simulation approach” defined by Alcamo (2008), constructing participatory scenarios that were translated into quantitative LUCC input (Houet et al., 2017). Today, Land System research articulates around three pillars: scenarios, land-use change modelling, and

participation (Castella et al., 2007; Kok et al., 2007; Rounsevell et al., 2012; Houet and Gourmelon, 2014; Houet et al., 2016), with a high degree of involvement by local actors throughout the process. To our knowledge, this integrated approach of the Land System combining narrative scenarios, LUCC models and stakeholder participation has not yet been used for analysing soil-erosion problems.

Our paper bridges this gap, describing a methodology that combines narrative scenarios and LUCC at the catchment scale, in interaction with local stakeholders who are involved throughout the research, for developing land-use scenarios that will serve as input for estimating future soil erosion. We illustrate its potential use (1) as a concrete support for discussion with local stakeholders, and (2) as input data for ecosystem service assessment at the catchment scale. This approach is applied to a rural catchment in northern Morocco facing major soil losses. It enriches the corpus of Land System studies, validating the relevance of our approach in a regional, socio-economic and environmental context that is complementary to those of existing studies.

## 2. Study area

In Morocco, water erosion affects more than ten million hectares, with a particularly high rate of erosion in the catchment areas of the Western Rif where average soil loss is 35 t/ha/year (REEM, 2015). (Croitoru and Sarraf, 2017) estimated the Moroccan crop-yield loss due to water erosion at 1.1 billion dirhams (100.8 million euros) by 2040. In addition, the loss of storage capacity through silting up of reservoirs is currently 75 million m<sup>3</sup> per year, leading to a commensurate decrease in regulated volume for users (Croitoru and Sarraf, 2017). The total cumulative loss is estimated at 1.75 billion m<sup>3</sup>, or 10% of the total initial storage capacity behind Morocco’s dams (Chentouf, 2016).

The Ibn Batouta dam, supplying drinking water to the city of Tangiers, illustrates this silting phenomenon. Built in 1977, its storage capacity has dropped from 43.6 to 29.1 Mm<sup>3</sup> between 1978 and 2013, a loss of 33%, due to the progressive deposition of soil by water erosion processes. Its catchment area, the Tleta (180 km<sup>2</sup>), is essentially rural with farms oriented towards polyculture and livestock farming (Fig. 1a). Due to scarce water resources, irrigation is almost non-existent in this basin, which is mainly oriented towards rain-fed production of cereals, sorghum and vegetables, mainly for self-consumption and livestock. A significant proportion of the basin (20%) is covered by matorral (Mediterranean bush vegetation). Though soil- and water processes in the Tleta have been extensively studied since the 1970s, investigating the influence of changes in agricultural land use and practices on erosion processes (Hammouda, 2010; El Bazi, 2014; Kouatli, 2015; Sahraoui, 2015), there has been almost no work to understand and analyse changes in human activities and resulting land-use changes. Located 10 km from Tangiers, this basin shows accelerated changes in land use, driven mainly by rapid urban growth. Recently, it saw strong industrial, commercial and residential development on both sides of the national road traversing it, the development of new roads serving remote rural settlements, and the construction of a new industrial city in its northern part (Fig. 1b). Several new olive orchards and the arrival of agricultural investors from outside the basin further modified the agricultural landscape mosaic of this territory (Sabir et al., 2019).

## 3. Methodology

Consistent with Land System research (Kok et al., 2007; Rounsevell et al., 2012), our approach was structured around three closely linked key methodological components (Fig. 2): scenario development, land-use change modelling, and active stakeholders’ participation in all phases.

The first step consisted in building scenarios, each consisting of a narrative story and quantitative variables. The second step was to simulate land use in time and space. The third step evaluated and validated the final land use (LU) scenarios by conducting workshops, first

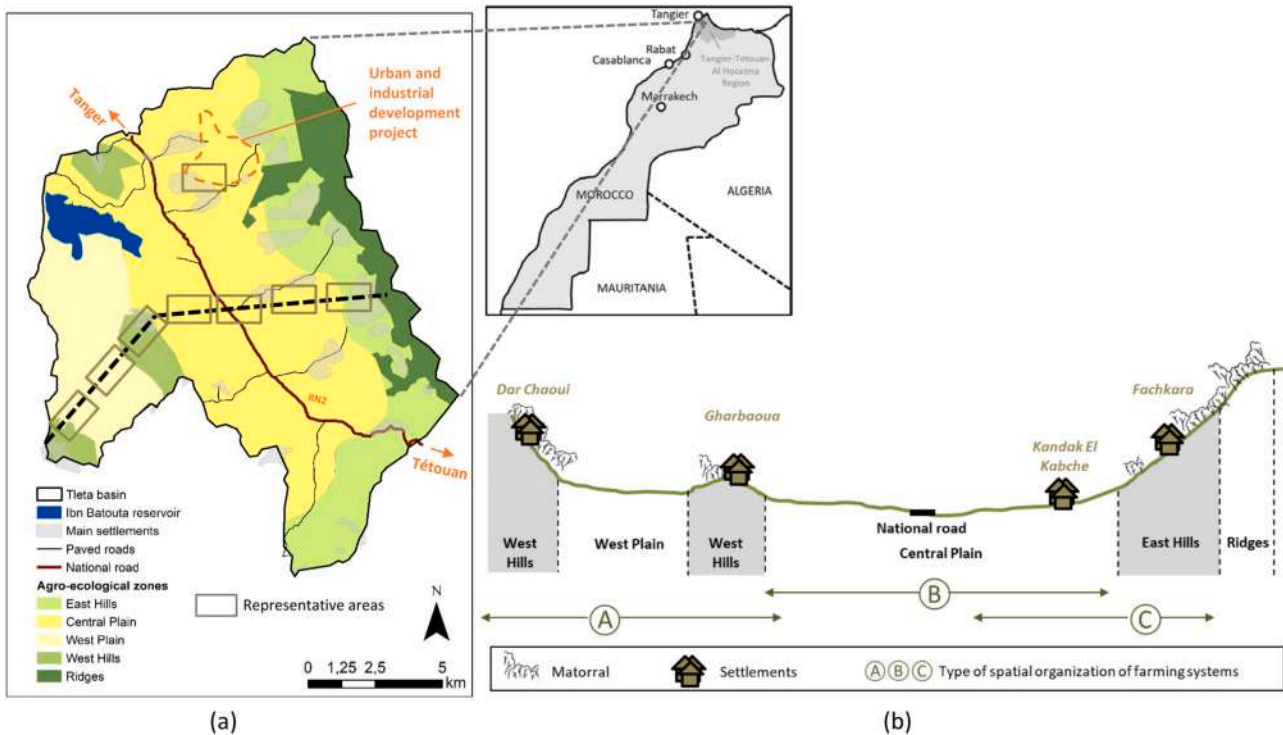


Fig. 1. The Tleta basin: (a) Agro-ecological zones, transects and representative areas studied; (b) Simplified cross-section of transects studied. Adapted from Sabir et al. (2019).

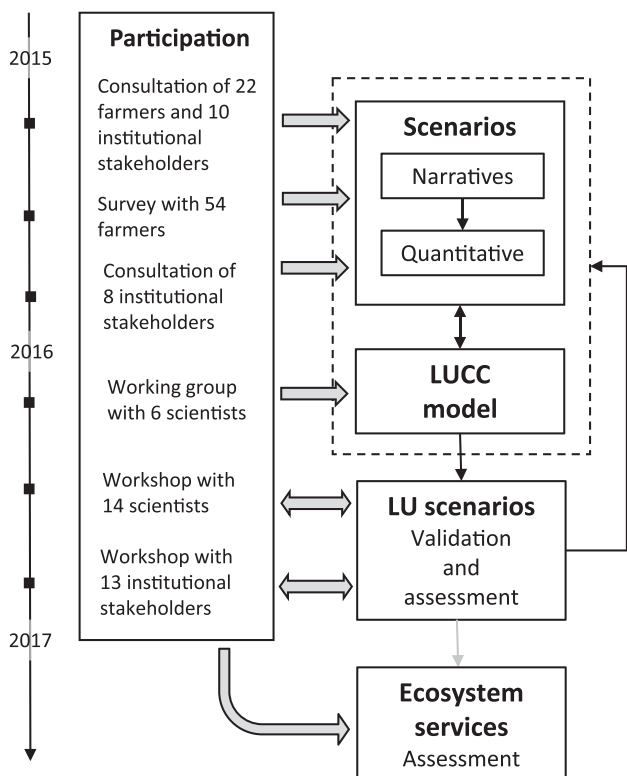


Fig. 2. Overview of our approach to building and assessing land-use (LU) scenarios.

with a group of scientists and then, after reworking the LU scenarios, with a group of institutional actors. The workshops improved the plausibility of the assumptions of the narrative scenarios, and of the

assumptions used for the land-use change model. Each step called upon local knowledge and/or scientific expertise, mobilized through surveys, interviews, and working-group meetings. Finally, following Ellis et al. (2019), we show how LU scenarios can be used for analysing spatially the resulting ecosystem services, through assessing agricultural production and the erosion-control service associated with each LU scenario.

### 3.1. Scenarios: development of narratives

Construction of the narrative scenarios took place in two phases, following Godet's (1994) scenario method: analysis of the system (past and present situation) and elaboration of narratives.

#### 3.1.1. System analysis (past and present situation)

This step consisted in an, as complete as possible, global and explanatory description of the current system and of its past temporal dynamics, and in identifying all the factors influencing land-use change. The objective was to develop a conceptual representation of the local socio-ecological system, where policies, economic actors and natural components interact. This systemic approach helped understanding the system dynamics, allowing the formulation of assumptions concerning its future evolution. Sabir et al. (2019) described in detail the tools used for this step. Similar to Castella et al. (2007), our approach combined the use of a regional/basin scale and a local scale. First, the analysis was carried out at the scale of the Tleta basin, based on field observations of the landscape, and on vegetation maps for the period 1977–2007 (Hammouda, 2010; El Bazi, 2014), census data, and consultation of 10 institutional stakeholders and 22 farmers in the basin (Fig. 2). This resulted in identifying five main agro-ecological zones in the basin, from west to east: Western hills, Western plain, Central plain, Eastern hills and Ridges—the latter being entirely occupied by State forest for which land use is considered to be stable over time—as well as their land use and past trends. This identification was, however, limited in the understanding of underlying finer mechanisms of land-use change.

In a second step, a refined analysis was carried out at the scale of eight local representative areas (rectangles of 1.5 by 1 km) in four agro-ecological zones, where land use is likely to change over time (Fig. 1a). These representative areas are distributed along two transects in the northern part of the basin, which is more affected by the economic development of the Tangiers area. We carried out a detailed analysis of the historical evolution of land use in these eight representative areas, based on digitizing of the plots and the observation of satellite images over the period 2003–2015. This analysis identified and quantified the main changes in land use over this period (cultivation of matorral areas, establishment of arboriculture, construction of buildings), serving as a basis for in-depth surveys with 56 farmers working plots in the representative areas, and providing quantified data on past land-use changes. This finer analysis provided quantitative data on farming systems in 2015, their spatial organization and their historic evolution, in relation to the observed land-use changes. This highlighted contrasting land-use dynamics between the agro-ecological zones of the basin, demographic dynamics, and the different forms of spatial organization of the basin’s farming systems.

### 3.1.2. Elaboration of narratives

Nine main factors of change were identified from the previous stage (Sabir et al., 2019), five on the global/national scale (national agricultural policy and the Green Morocco plan; influx of external capital invested in the land; economic development of Tangiers; political choices of the State in terms of land-use planning; climate change) and four on the basin scale (availability of water resources for irrigation; technical innovations; rural-development choices; land-use planning choices). Several evolution hypotheses were formulated for each of these factors, based on additional interviews with eight key institutional stakeholders in the basin, involved in land-use planning, agriculture, forestry, water and soil management (Table 1.A.) and consultation of planning documents (Royaume du Maroc, 2006; Omrane, 2010; Fahs-Anjra, 2015). We then combined these hypotheses, in order to write contrasted narratives describing possible future land-use scenarios for the Tleta basin (Table 1.C.).

### 3.2. Scenarios: quantifying land-use change hypotheses

The narratives were broken down into quantified assumptions for simulation by the land-use change model. These hypotheses were based on the consultation of local stakeholders and scientific experts, on the analysis of data from surveys conducted in 2015 among 56 farmers in the basin (Sabir et al., 2019), on census data (HCP, 2007) and on key planning documents. This part of the work was carried out in two steps (Fig. 3). First, we formulated hypotheses on the evolution of human activities (urban projects, demography, agricultural production

systems) consistent with each narrative scenario. This was done by answering two questions: What changes? and How much? In a second step, each change in human activities was linked to the types of land use concerned, using the Corine Land Cover nomenclature expanded to a supplementary level of detail for specific land use, such as including aromatic and medicinal crops, for which assumptions were also formulated according to three questions: What changes? Where? How much?

- Assumptions related to urban projects were mainly based on planning documents (Royaume du Maroc, 2006, 2011; Omrane, 2010; Fahs-Anjra, 2015), considering different construction phases of the new town and the industrial areas. Concerning diffuse (unplanned) urbanization, we assumed a continuation of trends observed over 2003–2015 in representative areas on either side of the national road (Sabir et al., 2019). These data helped estimating, for each scenario, the areas for construction of the new town and industrial zones, as well as their location.
- The quantified demographic assumptions were based on different growth rates per settlement over the period 1994–2004 (local census data). Population growth rates differ between scenarios according to each agro-ecological zone.
- The hypotheses related to evolving farming systems were based on data from surveys conducted in 2015 among 56 farmers in the basin (Sabir et al., 2019). First, our hypotheses for evolution of the urban and industrial areas were used for evaluating the available agricultural area in each agro-ecological zone. Then, the number of farms was assessed as a function of the population. To simplify, we considered only three types of spatial farm organization (Fig. 1b): Type A for those located both on the Eastern hills and in the Central plain with a 50%/50% distribution of their agricultural area; Type B for those entirely located in the Central plain; and Type C for those located both on the Western hills and in the Western plain with a 10%/90% distribution of their agricultural area. The number of farms was considered proportional to the population of settlements (Eastern hills settlements for Type A, Central plain settlements for Type B, and Western hills settlements for Type C). Finally, we selected, for each agro-ecological zone and each scenario, a ‘typical’ farming system observed in 2015 that would become the ‘average’ farming system of the agro-ecological zone in 2040. The distribution of crops within each agro-ecological zone is thus based on the crop rotation of these ‘typical’ farming systems.

The results of this scenario quantification step were the proportions of the different land-use types in 2040, for each agro-ecological zone that served to calibrate the LUCC model.

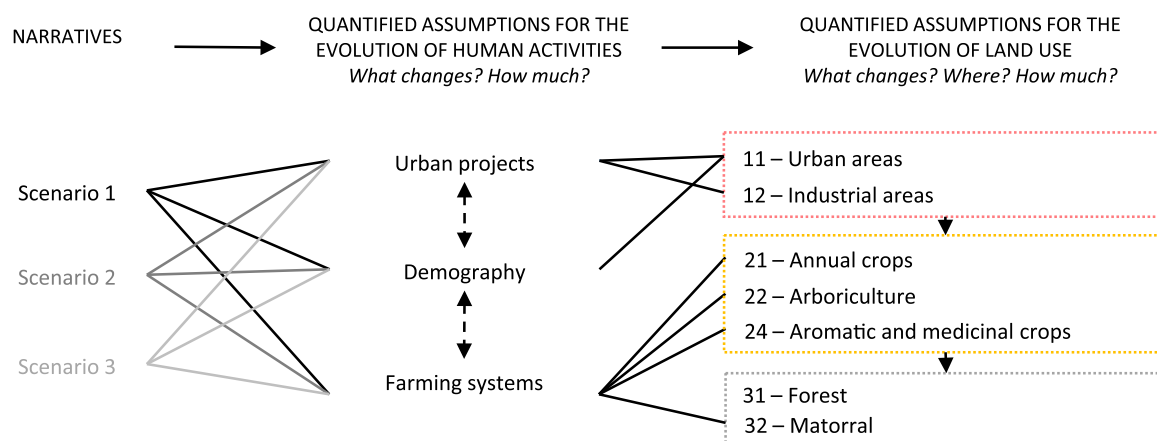


Fig. 3. Approach for translating narrative scenarios into quantified and spatially explicit hypotheses.

### 3.3. Land-use change modelling

The approach chosen for simulating land-use changes was defined in an ad-hoc manner, according to the constraints of spatio-temporal scales and the characteristics of the land uses to be simulated. As the maps had to be produced over spatial and temporal scales of 180 km<sup>2</sup> and 25 years, respectively, only the major evolutionary trends were simulated, without considering annual crop rotation. We also had to simulate diffusive processes, such as urban sprawl. Consequently, for running the simulations we preferred a Markov-type formalism combined with a cellular automaton [Markov-CA model (Guan et al., 2011)] rather than a multi-agent system, the latter being more case-specific and less user-friendly.

Considering the tension emphasized by Brown et al. (2005) and presented above, our method is at an intermediate stage between a prescriptive approach reflecting narratives, and an explanatory approach considering annual dynamics of urban expansion and land change. Consideration of the prescriptive approach in LUCC helped stakeholders to project themselves into possible futures; the explanatory approach helped simulating specific processes, such as urban sprawl constrained by geomorphological factors, creating the possibility of modifying system behaviour. By fitting the LUCC model parameters to land demand, we constrained the path-dependency of the model.

Spatialization criteria for land cover were constrained by geomorphological and pedological criteria, and by the distance to hydrographic networks. Each constraint map was based on expert knowledge in pedology, agronomy, hydrology, economics, forestry, and land-use change modelling, being a linear combination of several spatial criteria. For example, the location of olive groves was constrained by clayey soil and steep slopes, the constraint map being 1 for clayey areas on steep slopes (no olive trees) and 0 for everything else (olive crop possible). Note that for the same land use, the constraint maps can be expressed differently depending on the narrative scenarios. Constraint maps are presented in Appendix B.

The grain of the model is the agricultural plot, a polygon of varying shape delimiting a homogeneous agronomic unit defined by a planted crop managed in a specific manner by farmers. The mean area of agricultural plots was defined from representative areas of the agro-ecological zones (Fig. 1a). Basin segmentation used a simple Dirichlet (Voronoi) tessellation, considering different mean values of plot area in each agro-ecological zone (Holland et al., 2007), as digitization of the whole basin was not possible. The matorral and forest areas were also divided in multiple polygons, to anticipate their future modification according to the narrative scenarios. All distance maps were defined according to plot centroids. As the average plot size remained constant over the period 2003–2015, we decided to keep the same segmentation during the model simulations.

The proposed model, based on plot scale and annual time steps, is a function of two sequential processes. First, we defined a Markovian land-use transition process according to a transition matrix that controls temporal changes between land-uses; and then we defined a diffusion process of urban areas according to a cellular automaton governed by local neighbourhood rules between plots. Contrary to the study by Guan et al. (2011), for which only the cellular automaton was constrained, both processes were modified by specific constraint maps.

For each plot, the (first order) Markovian process consists in defining a land-use class according to a probability that is assumed only to depend on the previous class. All transition probabilities of land-use classes from one year to the next were estimated from the transitions over the period 2015–2040. Due to a lack of data on such land use, small-scale aggregation of land use other than urban areas was not considered in the model.

To realize the cellular automata, all distances between plots were estimated at the start of simulation. Then, for each year, the evolution of urban spots was defined as follows: For each urbanized plot, all adjacent plots were collected within a certain radius for which the constraint map

is 1; then, a certain proportion of the collected plots was changed into urbanized plots at the next time step.

Thus, for each scenario and, if possible, each agro-ecological zone, a transition matrix was defined between all land uses, generating a set of constraint maps for establishing each land use (including urban areas), and setting the radius and proportion of the cell automaton. All parameters were calibrated *a posteriori* to obtain, at the end of the simulation, the final land-use proportions defined in the quantitative scenario descriptions. The model was built with R (R Core Team, 2018) using specific libraries for spatial data, such as raster, maptools, rgdal, rgeos, or gdistance.

### 3.4. Participation

Construction of the narrative scenarios (3.1), and their breakdown into quantified and spatially explicit hypotheses (3.2), relied on local knowledge through interviews with farmers and institutional stakeholders (Fig. 2), as well as on scientific expertise acquired during several joint missions in the basin and the creation of a multidisciplinary working group for construction of the scenarios.

The resulting scenarios were submitted to debate and evaluated in two participatory workshops (Appendix A). The first, at Rabat in May 2016, brought together 14 scientists specialized in the Western Rif and/or erosion management of rain-fed agrosystems of Morocco. The second workshop, held in Tangiers in November 2016, included 13 key institutional stakeholders of the basin (Table 1.A.). The workshops were held over one day in three main sessions. After a short introduction, the first session presented the Tleta basin in 2015 and its past dynamics. The second session presented the LU scenarios. After each LU scenario presentation, the participants were invited to assess its expected impact on the agricultural economy, the state of the environment and the social dimension, by completing a questionnaire and then sharing their assessment during a round table discussion. A synthesis session closed the workshop, summarizing the main conclusions. Each participant was then invited to choose which scenario he or she would prefer—if he or she had to support one—and which one seemed most likely, and to evaluate the approach and tools used (narratives, land-use maps, quantitative data).

A description of the basin in 2015 and of the scenarios had been sent to the participants one week before each workshop, as synthetic accounts of two pages each for the scientific experts, and as fictitious press articles for the institutional stakeholders. We used four A0 posters for presentations during the workshop, including the main hypotheses of basin evolution, the land-use map, photos of typical landscapes, and a few quantified key variables (population, number of farms, etc.).

The workshops helped verifying the relevance and improving the plausibility of our assumptions for the narratives, and further adjusted the quantitative data and the land-use change model. Concerning the method, the first workshop showed that it was difficult for some participants to project themselves into the future solely on the basis of posters. To improve this point, fictitious press articles were used for the second workshop.

The first workshop also helped improving the plausibility of the LU scenarios for the second workshop: the time horizon was shifted from 2030 to 2040; detailed historical statistical data for all settlements in the basin were analysed for defining past trends; a detailed analysis of the spatial distribution of farming systems in the different agro-ecological zones improved the understanding of their past evolution; and it improved the description of the assumptions common to all three scenarios. These changes led to improvements in the narrative scenarios and maps produced for the second workshop. The second workshop was used for validating the plausibility and consistency of the founding assumptions of the scenarios, and for improving a few land-use change assumptions. The latter concerned the hypotheses of both settlement expansion by agro-ecological zone, and of the conversion of crops back to matorral, which were integrated into the latest simulations.

### 3.5. Using land-use scenarios for assessing future erosion control and agricultural production

Land-use scenarios are meant to evaluate changes in terms of potential soil erosion, but also in terms of future agricultural production. Here, we simply test the direct use of land-use scenarios for estimating their potential effects on two types of services: erosion control and agricultural production.

#### 3.5.1. Erosion control

We used a simplified approach for capturing the potential effect of land-use change on soil erosion. For this, we used the Cover-Management factor (C-factor) that reflects the influence of land use and management on the risk of soil erosion within the Universal Soil Loss Equation (USLE).<sup>1</sup> The C-factor accounts for how land cover, crop types and crop management cause soil loss to vary from those losses occurring in bare fallow areas.

On the Tleta, we estimated C-factor values for six main land-use types based on Wischmeier and Smith (1978): aromatic and medicinal plants (0.003), forests (0.11), matorral (0.18), arboriculture (0.28), annual crops (0.38), urban areas (0), considering that practices for a type of land use are constant over time. As a first estimate, the analysis of variations in C-factor values due to changes in land use provides an indication of the potential evolution of the level of erosion control service at the catchment level for each scenario  $x$ :

$$I_{Er}^x = - \sum_i C_i \times (S_i^x - S_i^{Ref})$$

with  $C_i$  the value of the C-factor for land-use type  $i$ ,  $S_i^x$  the area occupied by land-use type  $i$  in 2040 in scenario  $x$ , and  $S_i^{Ref}$  the area occupied by land-use type  $i$  in 2015.

#### 3.5.2. Agricultural production

We estimated the value of agricultural production with a market price approach at basin scale for the 2015 and 2040 land-use scenarios, prices and yields remaining equal. All agricultural production was valued at selling prices, whether sold or self-consumed. The annual agricultural production was estimated as a function of the area  $S$  by agricultural land-use type (LU maps), the proportion  $\alpha_{ij}$  of each crop  $j$  in the area of the main types of agricultural land-use type  $i$  (survey results and local agricultural statistics), the yields  $r_j$  (farm survey data and local agricultural statistics), and selling prices  $p_j$  (FAOSTAT data: average producer prices over the period 2007–2016). Comparison of the value of agricultural production of 2040 land use with land use of the reference year (2015) provided a rough estimate of changes in the level of service for each scenario  $x$  at the catchment scale:

$$I_{Ag}^x = \sum_i (S_i^x - S_i^{Ref}) \sum_j \alpha_{ij} r_j p_j$$

## 4. Results

### 4.1. Three contrasted land-use scenarios

We constructed three contrasted LU scenarios for the Tleta basin until 2040. The assumptions for the evolution of driving factors are detailed in Appendix C (Table 1.C).

<sup>1</sup> The C-factor is one of the five factors that are used to estimate the risk of soil erosion within the USLE (Wischmeier and Smith, 1978). We used it for estimating the effect (positive or negative) of land use changes on the erosion process, not for estimating resulting soil loss that would require the use of a soil erosion model.

#### 4.1.1. Scenario 1 “Urban and industrial development”

The first scenario assumes that, due to the proximity of Tangiers, the Tleta basin continues its economic and industrial development. The Central plain is urbanizing very rapidly around the new town and the national road. The agricultural area decreases, and remaining farms use simplified crop rotation. In the Eastern hills, the decrease in settlement population continues, small farms remain, and the clearing of matorral plots is necessary to compensate in part for the loss of urbanized plots on the plain. The western part of the basin remains isolated and little affected by urbanization.

#### 4.1.2. Scenario 2 “The fruit basket of Tleta”

The second scenario assumes that industrial development of the basin has not been as successful as expected. In this context, the State supports many agricultural development projects targeting rain-fed arboriculture (olive-, fig- and walnut trees) and the related value chain. In the Central plain, larger farms are gradually created, specializing in arboriculture. On the Eastern hills, small farms strongly oriented towards arboriculture are maintained. The western part of the basin remains isolated and little impacted by agricultural development projects.

#### 4.1.3. Scenario 3 “One foot in the city, one foot in the countryside”

The third scenario assumes that gradual development of the new town benefits the surrounding settlements; many inhabitants of the rural areas have found work in or around it. The income generated is reinvested in the development of small-scale agricultural activities. Cooperatives are set up to launch the production of local products, such as honey, goat cheese, prickly pears and aromatic plants. The farms located on the Eastern hills are the key players in this development. In the Central plain, the farms remain on a more traditional model. The western part of the basin stays isolated and little affected by these changes.

Fig. 4 shows the 2040 land-use maps corresponding to these different scenarios, after using the rules for translating narrative scenarios into spatially explicit maps by agro-ecological zones (Table 2.C). The annual maps are presented in Appendix D.

Fig. 5 highlights differentiated land-use changes by agro-ecological zone. For example, there are relatively few differences between the scenarios for the Western plain, whereas land-use is more contrasted between scenarios for the Central plain and the Eastern hills. In particular, we observe a doubling of urban areas in the Central plain for S1, a strong increase in arboriculture in the Central plain for S2, and the development of aromatic and medicinal plants in the Eastern hills for S3.

Fig. 4 shows a salt-and-pepper effect affecting land use, due to assumptions of the model that do not consider possible aggregation at this scale. Some hypotheses of the model, such as space segmentation by tessellation, or absence of spatial aggregation of some land uses, could be improved by digitizing and classifying the entire basin using aerial images, and making spatial analyses of the land-use patterns. Adding more constraint to the model should limit the risk of equifinality for the calibration procedure of the explanatory model part.

### 4.2. Evaluation by institutional stakeholders

The three LU scenarios were presented and discussed during the second workshop for institutional stakeholders with different views and interests.

First, the participants commented on which LU scenario was considered most likely, and which they would choose if they were to support one (Fig. 6). The discussions between stakeholders provided opportunities for exchanging viewpoints and expressing fears regarding the proposed scenarios. This helped assessing the degree of plausibility of the LU scenarios: S1 and S3 were considered by far the most plausible, compared to S2 (Fig. 6a). They also discussed the LU scenarios in terms of desirability, in particular with regard to three impact criteria: on the

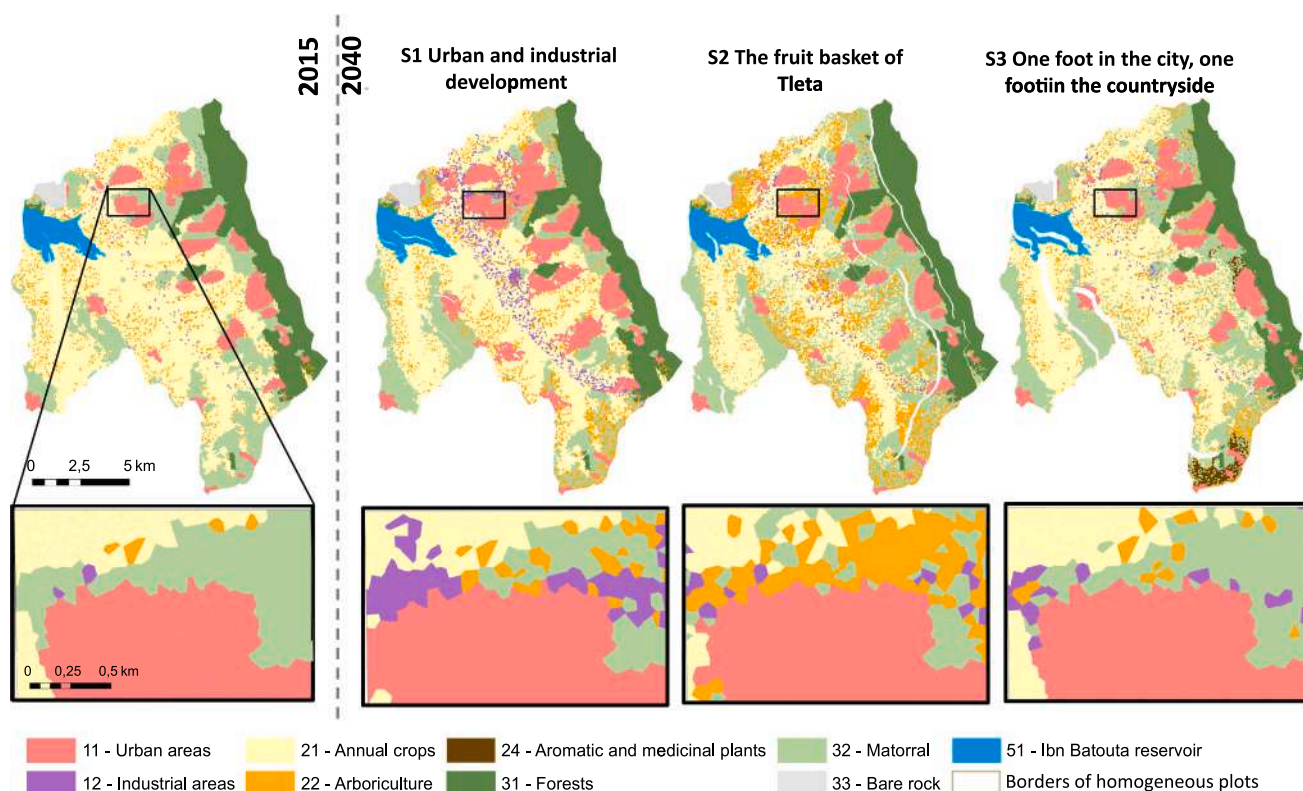


Fig. 4. Land-use maps in 2015 and 2040 by scenario: basin scale and zoom on a representative area.

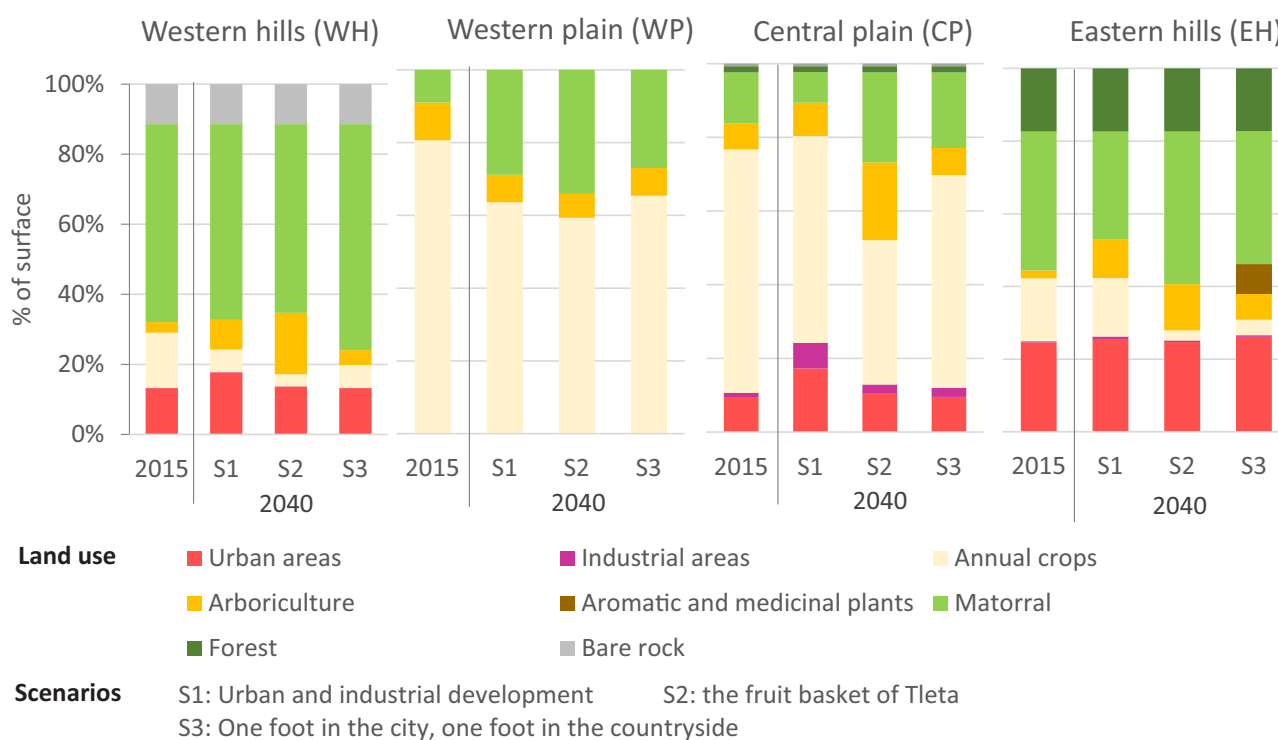


Fig. 5. Land use in 2015 and for the three 2040 land-use scenarios by agro-ecological zone.

agricultural economy, on the state of the environment, and on the social dimension. Although perception of the impacts differed depending on the actors, scenario S3 was the preferred one for most actors, and also the one considered—on average—to have the most positive effects on the agricultural economy, the social dimension and the state of the

environment (Fig. 6b). On the contrary, for S1 the participants anticipated mostly negative effects on the agricultural economy and the state of the environment.

Second, a process evaluation after the workshops showed that most (82%) participants considered the workshops as useful for their daily

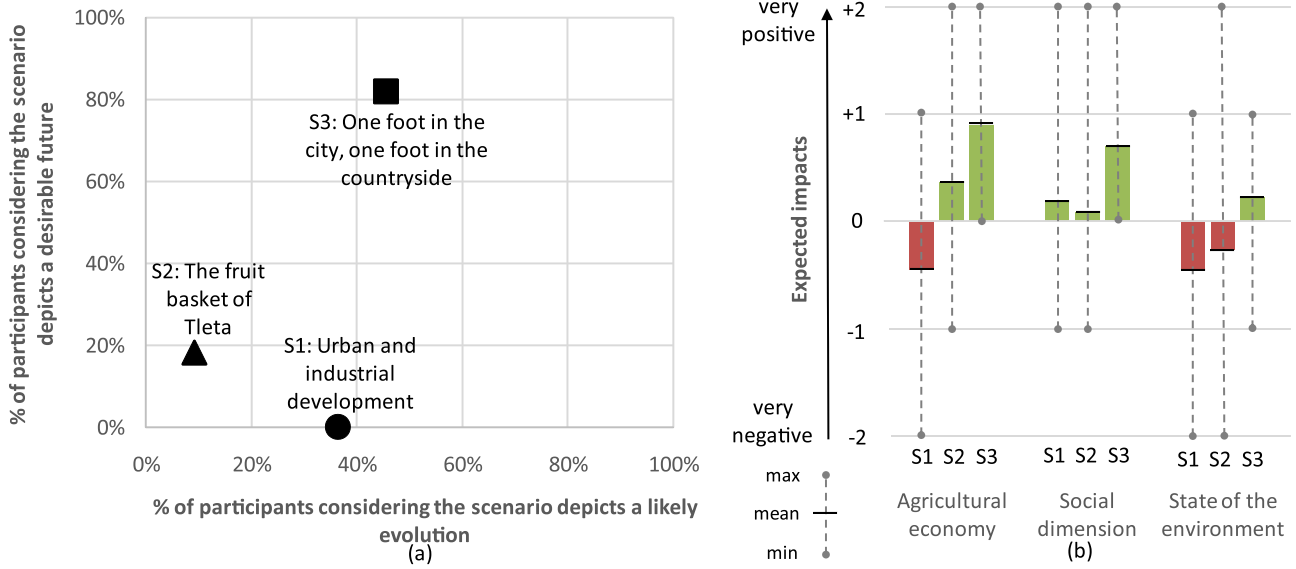


Fig. 6. Evaluation of land-use scenarios by institutional stakeholders (N = 11): (a) desirability and plausibility; (b) expected economic, social and environmental impacts (rating ranging from -2 = very negative to +2 = very positive).

work. Overall, they found the tools proposed during the workshops useful for exploring possible agriculture and landscape futures on the Tleta, especially the narratives (73% of the participants) and the land-

use maps (73%). The salt-and-pepper effect of some land uses on the maps was not discussed. The quantitative data—though essential to the research team for the transition from scenarios to maps—were

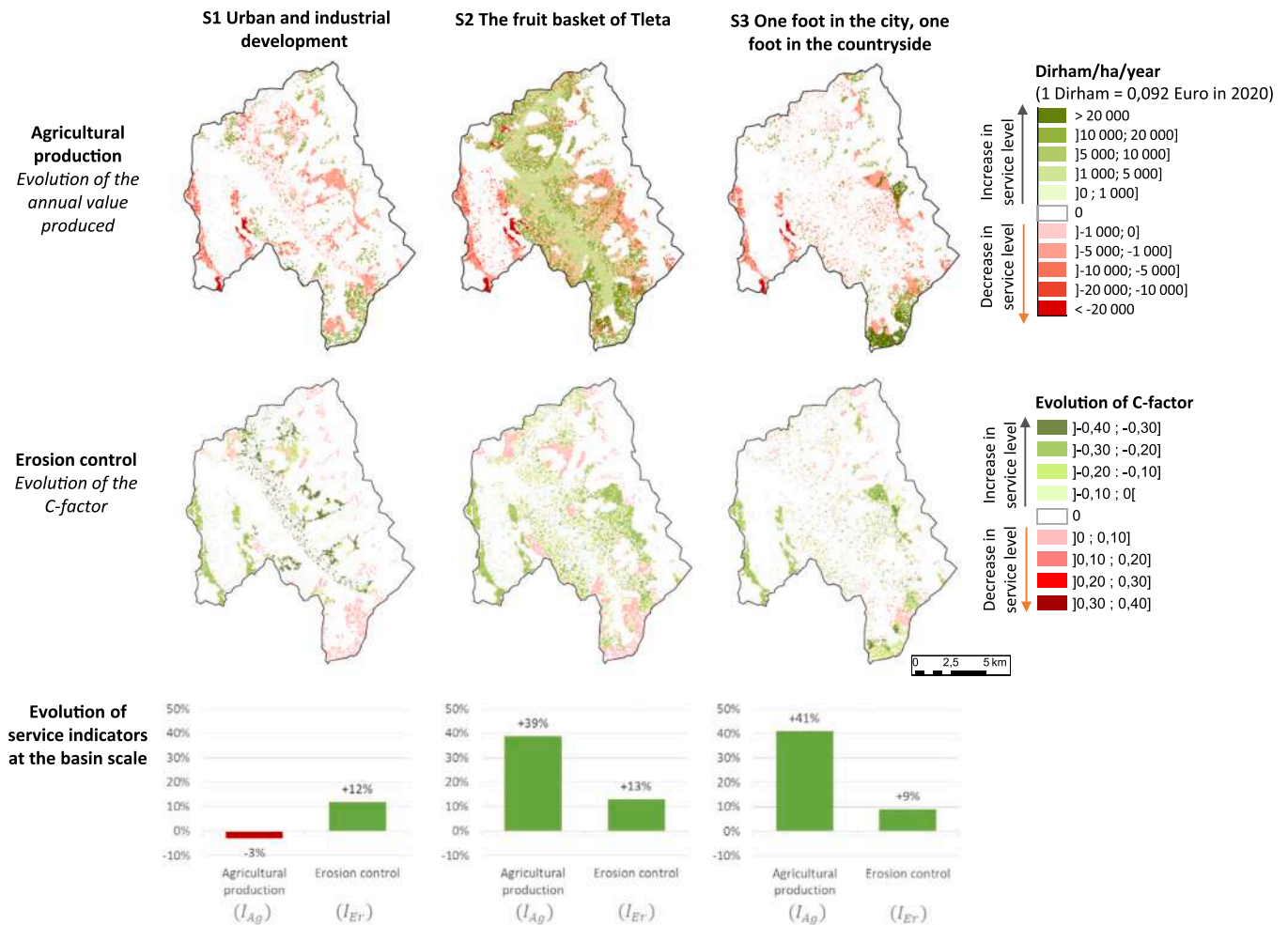


Fig. 7. Change in agricultural production and erosion control services from 2015 to 2024 for the three LU scenarios.

considered relatively less useful (36%). As a result, our approach created a win-win situation: for the research team that was interested in deriving scenarios and learn more about the Tleta basin, but also for the participants who got to know other stakeholders, exchanged knowledge, and took new information back home. The stakeholders also expressed a strong demand for the description of the scenarios to be accompanied by a complete evaluation of their social, economic and environmental impacts, in order to better position themselves on their desirability. This points at the fact that land-use change scenarios, though designed to simulate future water erosion processes, will also have contrasted effects on economic, social and environmental conditions.

#### 4.3. Expected impact on agricultural production and erosion control

The use of LU scenarios provided rough estimates of their impact on erosion control and on agricultural production. At the basin scale, the three LU scenarios may lead to a 9–13% improvement in the erosion-control service, with different spatial changes between scenarios (Fig. 7). The impact on agricultural production, however, is stronger: at the basin scale, scenarios S2 and S3 lead to a strong increase in the value of agricultural production (+39% and +41%, respectively), while S1 leads to a decrease (−3%). Spatially, however, the effects of S2 and S3 are quite different, with a diffuse increase in value in the Central plain for S2, and a much more localized increase in certain sectors of the Eastern hills for S3. The salt-and-pepper effect observed did not affect the calculated impact at basin scale.

This first estimate of scenario impact shows that S2 and S3 both improve the level of erosion-control service and the value of agricultural production. These two scenarios lead respectively to an increase in the share of arboriculture and of aromatic and medicinal plants in the agricultural area: these two crop types increase the value of agricultural production produced per hectare and have lower C-factor values compared to annual crops. The spatially explicit results, however, show distinct evolution patterns according to agro-ecological zone. While S2 favours a diffuse improvement of services in the Central plain, S3 leads to an improvement in more localized sectors of the Eastern hills. In other words, the results highlight trade-offs not between services, but between agro-ecological zones.

However, these initial estimates remain rough, and can be improved in a number of ways. First, our estimate of the effect of land-use changes on erosion only relies on the evolution of the C-factor, which does not consider the real complexity of the processes. Moreover, the effect of land sealing due to urbanization is badly captured with this factor, which ignores downstream erosion processes due to the fact that land sealing can amplify urban runoff.

## 5. Discussion and conclusions

Through a Land System approach, based on a combination of narrative scenarios, land-use change modelling, and the consultation and participation of local stakeholders, we built three contrasted and spatially explicit 2040 LU scenarios at the Tleta catchment scale, and then analysed the preferences of institutional stakeholders for these possible futures. The addition of an ecosystem services framework illustrates how LU scenarios can be used for assessing the consequences for agricultural production and erosion control. To our knowledge, this is the first study that uses such an integrated approach of the Land System combining narrative scenarios, LUCC models and stakeholder participation for analysing soil-erosion problems.

There are several perspectives for the operational use of this work. The first step will be to present the results of the evaluation of the impacts of the scenarios on the levels of services to the institutional actors, who expressed this need during the second workshop. This will not only allow an assessment of the socio-cultural preferences for the different levels of services (Martin-Lopez et al., 2012), but also ensure the continued involvement of stakeholders by improving their

understanding of the impacts of the different scenarios.

The second step will then be to involve these same actors in the implementation of the Moroccan Sustainable Development Strategy 2030 (Royaume du Maroc, 2017) at their catchment scale. Following Houet et al. (2017), engaging stakeholders with various opinions contributes to a common vision of the possible futures for their catchment. This common understanding is likely to provide sound future foundations for defining a shared strategy to control erosion and optimize the life span of dams and reservoirs, while improving agricultural production, alleviating poverty and mitigating climate change. This work will consist in mobilizing the entire framework presented in this article with a normative objective, thus contributing to the sustainability-science agenda. This normative approach, advocated by Rounsevell et al. (2012) and Nielsen et al. (2019), will provide a better link between Land System research and the sustainability agenda, contributing to the Sustainable Development Goals of the UN's 2030 Agenda (Biermann et al., 2017).

In a third step, representative farmers from different agro-ecological zones should then be involved in construction of the strategy, to anticipate possible constraints and oppositions. This will lead to a better understanding of the potential trade-offs between agro-ecological zones (who would be winners/who would be losers?) that might cause social, economic and environmental inequalities.

From a methodological perspective, we anticipate three ways of validation and further development of our approach. First, due to the scarcity of data in the basin, we focused our in-depth analyses (plot scale, farm survey) on eight representative areas distributed along transects of the main agro-ecological zones of the basin, creating an as precise as possible picture approaching the work carried out in other well-studied areas, such as in Houet and Hubert-Moy (2006) or Vacque et al. (2015). This methodological choice, although having a strong potential for implementation in data-scarce basins, should further gain from comparing our results with LU maps incorporating a larger number of representative zones.

Second, our methodology for constructing LU maps can be refined, as our maps are constrained by different drivers, some being similar to the “suitability maps” of Houet and Hubert-Moy (2006). However, our “suitability maps” suffered from a lower discretization level than those in Houet and Hubert-Moy (2006) due to a lack of data. It will be interesting to test the added value of using the Fuzzy set theory developed by Kok et al. (2014) to render the suitability maps more realistic, by letting the stakeholders express how different drivers constrained each land use, using terms such as “low”, “medium” or “high” for example.

Third, assessing the impact of LU scenarios on services, which remains limited in this paper, will be extended. It has since been reinforced by SWAT modelling (Choukri et al., 2020). They used LU scenarios as a basis for the biophysical modelling of changes in soil movement and water flow at the catchment scale, in combination with climate scenarios, to anticipate future water availability and sediment load in the reservoir. A more complete analysis of the diverse impacts of contrasting land-use scenarios on the levels of services should highlight possible trade-offs between services (Nelson et al., 2009). These different levels of services can be assessed from a perspective of value pluralism, using biophysical, economic and socio-cultural indicators (Jacobs et al., 2017).

Overall, two main lessons can be drawn from our work. First, the use of a Land System approach helps integrating the soil-erosion problem into a more global perspective on land-use planning and economic and rural development. Through its systemic approach, Land System research considers a whole range of drivers influencing changes in land use and, ultimately, erosion processes. The strong involvement of farmers and institutional stakeholders in the identification of drivers and the analysis of scenarios, provides a broader perspective on soil erosion by exploring and analysing different possible futures. Although we developed LU scenarios for use as input to biophysical models for simulating future soil losses, our results show that such scenarios can



also be used for initiating participatory processes with various stakeholder groups, and for encouraging reflection on alternative futures (Griewald et al., 2017). We show that the coupling of narratives and LUCC modelling produces future LU maps that make sense to stakeholders. Indeed, the map, a technical object whose creation is beyond them, is clearly perceived as the representation of a narrative scenario that they have helped building and that they have appropriated. The combination of narrative scenarios and LU maps constitutes a concrete support for discussion, deemed truly relevant by the scientific experts and institutional stakeholders to explore possible future agricultural and landscape changes in the basin. We recommend their combined (and not separate) use in Land System research when debating scenarios with the actors.

Second, the coupling of Land System research and the Ecosystem Services framework places the issue of erosion in the more general perspective of Nature's Contribution to People (NCP) (Ellis et al., 2019) and the United Nations Sustainable Development Goals (Biermann et al., 2017). Services provided by agro-ecosystems are not limited to erosion control. Mediterranean rain-fed agro-ecosystems provide various other services such as agricultural production, biodiversity conservation, soil carbon sequestration, water conservation, preservation of employment and local knowhow, downstream water delivery, or mitigation of rural exodus (MA, 2005; Almagro et al., 2016). Contrasting land-use scenarios can have quite different impact on the levels of services provided to society. Institutional actors also have expressed a strong need for better understanding of this diversity of impacts on the agricultural economy, the social component and the state of the environment, in order to be able to judge the desirability of the scenarios. By assessing agricultural production and the erosion control service associated with each LU scenario, our approach illustrates how a diversity of impacts can be assessed and represented spatially, and how Land System science and the NCP framework can be combined, as recommended by Ellis et al. (2019). Our research thus contributes to a better integration of the erosion issue from a global sustainability perspective.

Finally, our approach has a strong potential for implementation in the Mediterranean context, where ongoing demographic, agricultural and economic changes are very rapid and can strongly affect erosion processes at the catchment scale, with a resulting loss of soil fertility and silting-up of reservoirs. Engaging stakeholders in the exploration of possible futures and their potential impact is an essential step for building sustainable trajectories in these watersheds.

#### CRediT authorship contribution statement

**Cécile Hérivaux:** Conceptualization, Methodology, Formal analysis, Investigation, Supervision, Writing - original draft, Writing - review & editing. **Fabrice Vinatier:** Methodology, Software, Formal analysis, Writing - original draft, Writing - review & editing. **Mohamed Sabir:** Conceptualization, Investigation, Resources. **Fanny Guillot:** Investigation. **Jean-Daniel Rinaudo:** Conceptualization, Methodology, Investigation, Writing - review & editing.

#### Acknowledgements

This work was carried out within the framework of the MISTRALS/SICMED Lebna project (INRA and IRD grants, contract 303015/00) and the French National Research Agency (ANR) TRANSMED ALMIRA project (contract ANR-12-TMED-0003). The authors also thank the PAYOTE scientific network (INRAE) for fruitful discussions that contributed to the Land Use change modelling part of the paper, and the two anonymous reviewers for their constructive comments on the first version of the paper. The authors warmly thank all farmers, institutional stakeholders and scientific experts who participated in the interviews, surveys and workshops. H.M. Kluijver edited the final English version of the manuscript.

#### Appendix A. Supporting information

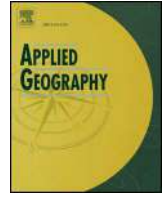
Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.landusepol.2021.105406](https://doi.org/10.1016/j.landusepol.2021.105406).

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## Using high-resolution multitemporal imagery to highlight severe land management changes in Mediterranean vineyards

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### A B S T R A C T

Mediterranean vineyards are subjected to drastic changes due to socio-economic, physical and environmental drivers. Whereas global trends affecting the evolution of Mediterranean land cover are well-known, their descriptions at a fine spatial scale, i.e., a plot level of several decametres, and over long time periods are still underexplored. This lack of exploration persists despite the increase in multitemporal imagery at fine resolutions. As scale and stakeholders are often correlated, we hypothesize that monitoring land cover at fine spatial and temporal scale would help understanding the local drivers shaping landscapes. To that end, we exploited a database of aerial pictures to obtain classified and vectorized land uses at the field level during the past five decades of a large watershed. The land uses were analyzed to detect changes at the field level considering the evolution of vineyard management. Changes in land management were synthesized in transition matrices expressing gains, losses and swaps for each land use category and illustrated using chord and Sankey diagrams. The results showed both a change in land management through a severe transformation of vineyards areas, from goblet to trellised vineyards, during the 1980s and a progressive evolution of land uses from vineyards to urban areas, arboriculture areas and arable lands. This transformation resulted from the local policies on vineyard replanting and the arrival of mechanization.

### 1. Introduction

Landscape organization, in terms of land uses and management, is the result of centuries-old interaction between man and the environment (Agnoletti et al., 2011; Lieskovský et al., 2014). By definition, the land use encompasses the intentional role of people to adapt the natural land cover to their benefit (Verheye, 2004) whereas land management defines the way in which a given land use is administered by people (Foley et al., 2005). Among the variety of landscapes on Earth, vineyards are excellent case studies, as they represent a strong cultural legacy and support a crucial socioeconomic sector in European countries (Salome et al., 2014). Historical maps of vineyards were widely studied because they have faced several crises (Lieskovský et al. 2013, 2015, 2017; Pazúr, Lieskovský, Feranec, & Otáhel, 2014; Incze & Novák, 2016). In Europe, the phylloxera aphid caused a total collapse of vineyard production in 1860s, until the grafting onto American vines finally succeeded. In France, the introduction of the Common Market in 1970, which allowed the Italians and Spanish to invest in the French interior market, caused a decrease in the growing of table grapes (Galet, 2008) in conjunction with a decrease in pesticides used in agriculture. In 1990, the arrival of vines “du nouveau monde” from the United

States, Australia and Chile influenced vine production (Touzard & Laporte, 1998). As the global drivers affecting evolution of vineyards are well known, their monitoring at landscape scale to understand their driving forces is an essential step still under investigation (Houet, Verburg, & Loveland, 2010).

The driving forces shaping landscapes are both socio-economical and physical. Landscape consolidation is driven by political forces because it helps making large fields more suitable for industrial agriculture (Lieskovský et al., 2014). Landscape composition in land uses is also affected by social forces and particularly the land abandonment (Incze & Novák, 2016). Physical forces driven also landscape architecture and composition in land uses. For instance, geomorphological variables driven land use changes such as slope that affects field accessibility with machinery (Sluiter & Jong, 2006; Lieskovský, Lieskovský, & Piscová, 2017). Altitude gradient can also affect the loss of natural areas in favour of agriculture expansion (Tovar, Seijmonsbergen, & Duivenvoorden, 2013). The pedological factors are also important to understand land settlement on fertile soils for example (Lieskovský et al., 2014, 2015). As explained below, land management is also affected by socio-economical and physical forces.

Historical evolution of vineyards in regards to other land uses have

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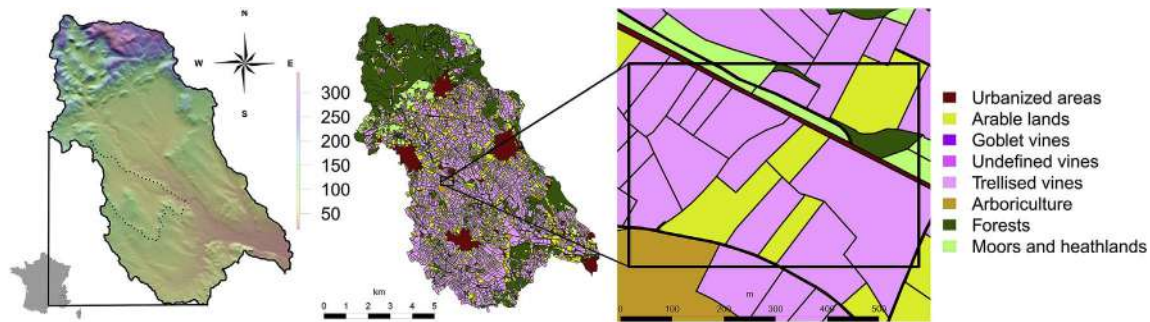


Fig. 1. Localization of watersheds in the zone. Borders of the Peyne watershed and Bourdic subwatershed are symbolized by plain and dotted lines on the altitude map, respectively. Land use categories are also represented with white crosses indicating the locations of towns.

been largely analyzed in Europe, but a change in land management of the vineyards is still lacking. Tracking subtle changes in land management is sometimes more difficult than for land uses because it necessitates a resolution of the historical maps higher or equal to the metre to distinguish between vineyard types (Delenne et al., 2008). In the same way, changes in land management acted at a smaller scale than for changes in land uses. For example, weeding practices in vineyards were mainly governed by local government areas (Biarnes, Bailly, & Boissieux, 2009). As scales and stakeholders are often correlated (Hein, van Koppen, de Groot, & van Ierland, 2006), monitoring the evolution of vineyard management help us explain the role of local stakeholders in a given area. There is now a large number of available images (Wulder, Masek, Cohen, Loveland, & Woodcock, 2012) to create diachronic maps but they have not always a sufficient resolution to detect changes in land management at field scale whereas the field scale is the main unit on which most decisions on the land management operate in agricultural landscapes (Thenail et al., 2009).

A large amount of research has been conducted on the study of land cover in various fields from LANDSAT images: urban expansion (Chen, Zhao, Li, & Yin, 2006; Qin, Jianwen, & Yun, 2006; Yuan, Sawaya, Loeffelholz, & Bauer, 2005), urbanization of agricultural zones (Liu, Liu, Zhuang, Zhang, & Deng, 2003; Stefanov, Ramsey, & Christensen, 2001; Yang & Lo, 2002), forest disturbance (Gibbs et al., 2010; Huang et al., 2010; Mertens & Lambin, 2000; Tovar et al., 2013), desertification monitoring (Dawelbait & Morari, 2012; Symeonakis, Calvo-Cases, & Arnau-Rosalen, 2007) and several ecological applications (Cohen & Goward, 2004). However, image classification for determining land cover categories is limited by satellite resolution (higher than 30 m) for these series, and changes in land use or land management operation at the field scale cannot be evaluated by LANDSAT images.

The texture of the field entity could provide information about the type of land use (Trias-Sanz, 2006) and even the land management of vineyards (Delenne et al., 2008; Wassenaar, Robbez-Masson, Andrieux, & Baret, 2002). Furthermore, spatial segmentation is driven by the raster dataset, which is composed of regular squared cells from one to several decametres, and is different from the irregular shapes that form the field entities, the latter being studied using object-based image analysis (OBIA).

By extracting valuable information from various satellite images at different spatial resolutions, from 50 cm to several metres, OBIA is well suited for performing land change studies at the field scale (Benz, Hofmann, Willhauck, Lingenfelder, & Heynen, 2004; Blaschke, 2010). A large number of studies has been devoted to ecological applications (Xie, Roberts, & Johnson, 2008; Yu et al., 2006 for example) or urban features (for a review, see Blaschke (2010)), but only few OBIA studies have been conducted at the field level (Karakizi & Karantzalos, 2015; Qiu, Wu, & Miao, 2014; Zhou & Troy, 2008), and never during long time periods.

The difficulty in studying land use changes at the field scale for large spatial and temporal extents is mainly driven by dataset resolution. The availability of remotely sensed data over long time periods

(Wulder et al., 2012) and the constant improvements of photogrammetric and digitalization tools for such spatial database analyses make these studies possible (Grekousis, Mountrakis, & Kavouras, 2016). Arnaud et al. (2015) realized historical geomorphic analysis over 80 years in France thanks to the release of aerial photographs from the Institut Geographique National (IGN), for instance.

The study reported land use changes at the field scale over a time period of 50 years using aerial images of Mediterranean vineyards. We hypothesize that a high-resolution database could provide information about changes in land management of vineyards, providing that the time period encompasses the wine crises periods with sufficient temporal resolution. We aim to determine changes in land use categories at the field level using both field number and field area.

## 2. Materials and methods

### 2.1. Composition and configuration of the dataset at the field scale

The study area corresponds to the Peyne watershed, which covers approximately 76 km<sup>2</sup> and is located in Languedoc-Roussillon in southern France (43° 35'N, 3° 19'E). The smaller enclosed watershed is called the Bourdic subwatershed and covers 7 km<sup>2</sup>. Both the Peyne and Bourdic watersheds were used for further analyses depending on the temporal richness of the dataset. The area of the Peyne watershed is mostly covered by perennial crops (mainly vineyards), and five towns are present in the zone (Fig. 1). The climate is submediterranean sub-humid with a long dry season, an average annual temperature of 14 °C, an annual rainfall varying between 400 and 1400 mm and an altitude varying between 0 and 350 m.

In 2012, the IGN released a large, open-access database of aerial black-and-white photographs from 1937 until the present. We selected a sample of images from the IGN database covering the Peyne watershed from 1962 to 2003 with a time interval between 4 and 5 years. We completed the series by taking orthophotos from 2005 to 2012 processed by the IGN from colour photographs (see Table 1 for more details on the imagery database). The time period was chosen in accordance with the major changes in vineyard composition. Because the goals of our study focused on change detection at the field scale, the diachronic dataset used for retro-observation needs to be processed at a fine resolution to distinguish field unit limits and their land use or land cover. The aerial photographs were orthorectified using structure-from-motion approach (Midgley & Tonkin, 2017) and corrected from vignetting effects (Lebourgeois et al., 2008) to get orthophotos defined at pixel resolution of less than 1 m. The satellite images were also sampled at the same resolution.

The raster database was then transformed into polygons with a minimal area of approximately 200 m<sup>2</sup> using manual digitizing and classification procedures to separate field entities and their associated land use categories using QGIS software (QGIS Development Team, 2016) and GRASS (GRASS Development Team, 2016).

Land uses of each homogeneous polygon were classified according

**Table 1**  
Characteristics of the imagery database.

Acquisition date	Bands	Resolution	Database
08/12/1962	Single grey band	0,3	Sample of 167 images
21/06/1971	Single grey band	0,3	Sample of 52 images
02/06/1974	Single grey band	0,6	Sample of 17 images
08/07/1978	Single grey band	0,3	Sample of 78 images
16/06/1981	Single grey band	0,6	Sample of 21 images
01/05/1986	Single grey band	0,6	Sample of 57 images
25/06/1990	Single grey band	0,7	Sample of 20 images
14/07/1992	Single infrared band	0,4	Sample of 49 images
22/05/1996	Single grey band	0,6	Sample of 34 images
05/06/2001	Multiple colour bands (Red, Green, Blue)	0,7	Sample of 34 images
07/12/2003	Single grey band	0,3	Sample of 60 images
20/05/2005	False colour (multiple colour bands but band 1 in grey)	0,5	1 orthorectified image
06/05/2009	Multiple colour bands (Red, Green, Blue)	0,5	1 orthorectified image
16/06/2012-17/07/2012	Multiple colour bands (Red, Green, Blue)	0,2	1 orthorectified image

to the Corine Land Cover nomenclature (Burkhard et al., 2012) expanded to the fourth level of detail for vineyards to distinguish goblet vines from trellised vines, with a special case noted for undefined vines when the difference in land management was difficult to detect. We considered this fourth level of detail only for different vineyard patterns because we wanted to distinguish the change in land management for this particular land use that reflected a change in land management practices related to both environmental and sociocultural factors. The distinction between goblet and trellised vineyards was based on the presence of a clear row orientation in the pictures (Fig. 2). According to Delenne et al. (2008), two main patterns can be observed on high-resolution orthophotos: (i) a grid pattern describing vine stock plantation on a square grid with approximately 1,5 m x 1,5 m spacing, corresponding to goblet vines, and (ii) a line pattern where vineyards are trained using horizontal wires spaced by 2,5 m, corresponding to trellised vines. In the latter case, the vine stocks belonging to the same wire are spaced by 1 m.

The distinction between vineyards and arboriculture was based on row widths measuring approximately 2 m and 5 m, respectively (Biarnes et al., 2009; Bonachela, Orgaz, Villalobos, & Fereres, 1999). Fig. 2 illustrates the eight land uses chosen: urbanized areas, arable lands, goblet vines, undefined vines, trellised vines, arboriculture, forests, and moors and heathlands.

All land categories were checked for consistency across years according to the previous time steps to correct transitions that were unlikely to have occurred, such as urbanized areas transitioning to other land uses or successions of different perennial crops (arboriculture, vines, and forests) for the same plot in the limited time period. Once land categories had stabilized, we derived from the raster database a vector database that included all field entities for each time period. All raster-vector conversion, spatial and transition analyses were conducted using R software with the raster, sp, maptools, rgdal, and spatstat packages (R Core Team, 2017).

## 2.2. Analysis of the transition between land use categories at the field scale

The objective was to analyse how the preceding land use is linked to the current one in order to highlight the severe change in land management during the period. For this purpose, we adapted improved methods used for larger scales (Cuba, 2015; Gu, Gu, Eils, Schlesner, & Brors, 2014; Pontius Jr. et al., 2004) to the field scale. The frequencies of each specific land use area were determined for each time period by summing each land use area and dividing this sum by the total area of the zone, i.e., the Peyne watershed. Transition matrices were calculated for each time period of the study, taking the field as the elementary unit. For each transition rate between time  $n$  and  $n-1$ , we calculated the land use of the fields at time  $n$  and the land use of their associated overlapping fields at time  $n-1$ . Transition matrices were derived from

the years 1962 and 2012 for the whole study area corresponding to the Peyne watershed. Values derived from transition matrices expressing gains, losses and swaps for each land use category were calculated using the method described by Pontius Jr. et al. (2004) but applied at the field level instead of the pixel level. Transitions between land use categories were illustrated using a chord diagram (Gu et al., 2014). Transition matrices were also calculated for each time period for the study area corresponding to the Bourdic subwatershed. They were represented using a simplified version of Sankey diagrams (Cuba, 2015).

## 3. Results

### 3.1. Evolution of landscape architecture at field scale

The number of field entities in the entire area started at 15000 in 1962 but decreased to 8400 in 2012. The median area of field entities increased from 2600 m<sup>2</sup> in 1962–4500 m<sup>2</sup> in 2012. The highest evolution of field numbers was found during the period of 1970–1990 (data not shown). When considering cultivated areas, other land areas, goblet vines and arboriculture exhibited a median area that was approximately half the size of the median area of trellised, transition vines fields (5500 m<sup>2</sup>).

### 3.2. Analysis of transitions between land use categories

Table 2 shows the values of changes and persistence for each land use category for the Peyne watershed between 1962 and 2012 in terms of surface area. The total change in surface area represented 77% of the study area, whereas only 23% of the landscape has undergone no change in land use. The swap, expressing the change in location of a given land use category, was the most important for arable lands and moors and heathland; however, the quantity of these land uses remained the same. Fig. 3 shows a chord diagram of the transitions between land uses categories in terms of surface area. Fig. 4 shows in more detail the evolution of these surface areas across categories for the Bourdic subwatershed. Fig. 4 shows that arable land was a categorical variable throughout the series, experiencing ups and downs at each time.

### 3.3. Evolution of vineyard management at field scale

The goblet vines category experienced the largest loss to the benefit of trellised vines, arable lands, urbanized areas and moors and heathland. According to the data in the loss column (Table 2), the category showing the largest gross loss from 1962 to 2012 was goblet vines, which lost 51% of landscape area. In contrast, trellised vines and arable lands gained 35% and 15% of total surface area, respectively.

In Fig. 4, vineyards planted as goblets presented a declining trend

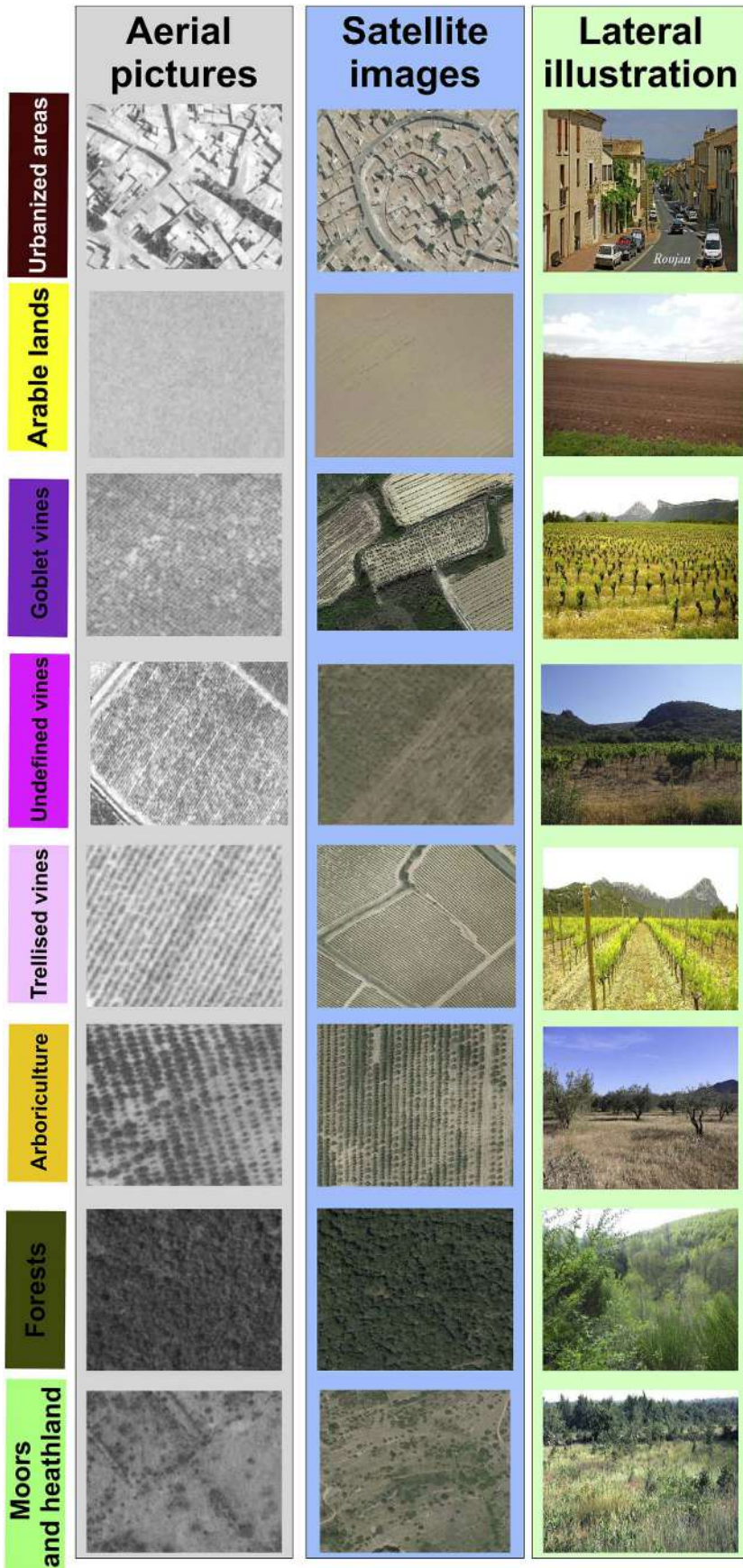
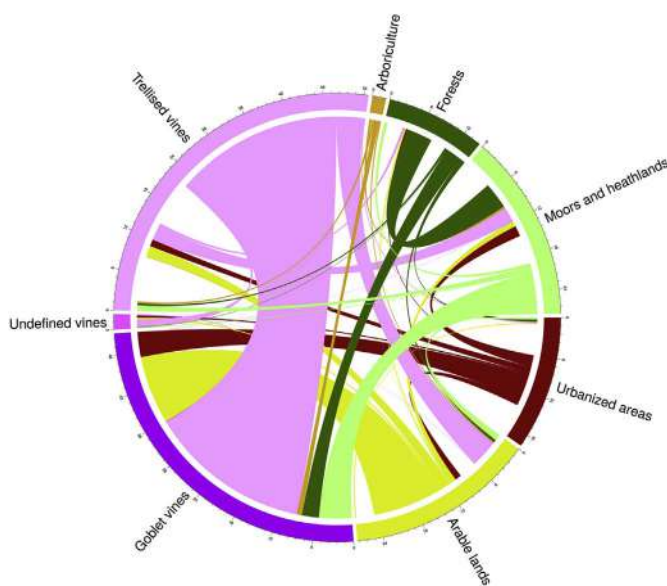


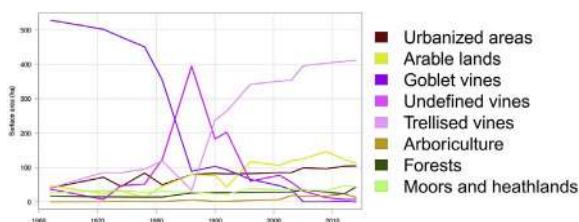
Fig. 2. Illustration of the land use categories classified in the database.

**Table 2**  
Values of changes and persistence for each land use category in terms of surface area between year 1962 and year 2012 for the Peyne watershed.

Land use (in % of total area)	Gain	Loss	Persistence	Total change	Swap	Absolute value of net change
Urbanized areas	8	1	5	10	2	7
Arable lands	15	7	3	22	14	8
Goblet vines	0	51	0	51	0	51
Undefined vines	0	2	0	2	0	2
Trellised vines	35	5	7	40	9	31
Arboriculture	2	0	0	2	0	2
Forests	8	1	3	10	3	7
Moors and heathland	8	10	5	18	17	1
Total	77	77	23	77	23	54



**Fig. 3.** Visualization of land use transitions in terms of surface area between the years 1962 and 2012 for the Peyne watershed using a chord diagram. Small numbers correspond to the percentages of each land use in relation to the whole study area.



**Fig. 4.** Temporal dynamics of cumulative areas for each land use category for the Bourdic subwatershed during the period of 1962–2012.

over years, with a total decrease of 100% in field numbers from the start to the end of the series. On the other hand, trellised vines had a continuous growth trend from the beginning to the end, with the only exception in 1986, when a decrease of 77% over the previous year occurred, which coincided with the highest value of the undefined vines category.

Regarding field number, the adaptation of the Sankey diagram (Fig. 5) illustrates the temporal dynamics of transitions between land uses during the whole period for the Bourdic subwatershed. The most important transitions occurred during the period of 1980–1990, with a severe diminution in the number of fields of goblet vineyards to transition vineyards and then to trellised vineyards. In the same period, a constant proportion of vineyards were transformed into other arable lands. We also observed transitions from trellised vines to undefined

vines.

#### 4. Discussion

##### 4.1. Transitions between land use categories at the field scale are explained by regional history

The transition between land use categories over time, as determined using Sankey and chord diagrams, revealed the history of the zone during the past century, driven by a profound transformation of vineyards and an expansion of urbanized areas, with the introduction of new land uses, such as arboriculture and annual crops (Galet, 2008; Sluiter & Jong, 2006).

Land reparcelling from 1970 to 1990 strongly influenced the evolution of the landscape, resulting in a decrease of the number of land plots as a result of grouping those that belonged to the same owners. Touzard and Laporte (1998) reported a reduction of farm numbers from 61% during this period, and one-third of the farmers earned their principal income from vine production. This plot grouping that is linked to the arrival of mechanization has enabled farmers to work faster and to gather their properties in order to have larger plots. The evolution of the plots is logical and in line with the land use evolution, as observed in other countries (Aslan, Gundogdu, Yaslioglu, Kirmikil, & Arici, 2007). Arboriculture and perennial crops require larger plots than annual crops for mechanization purposes. The large plots planted in perennial crops are transformed in built-up areas at the periphery of cities, this change in land use contributing to urban sprawl.

The decrease in vineyards in our study area confirms the overall trend in the region and the consequences of the crisis in the tradition of wine-growing country. In the early 1980s, the Languedoc vineyards experienced a deep crisis that involved table wine mass production, which was related to exogenous factors (Touzard & Laporte, 1998); declining demand for table wines in France; increased competition; and integration into the international market, but Languedoc vineyards also experienced the development of a regional economy that caused a reduction in the economic and demographic weight of viticulture.

Clear growth was observed over time in urbanized areas, which increased by more than 300%. Urbanized areas have continued to expand, especially since the 1980s. This urban growth is partly explained by “contagion”: urbanization occurs around the city centre, on the plots adjacent to homes or close to the major highways, to minimize the costs of networks such as water, electricity, and sanitation (Cheylan, 2001).

The development of fallow areas reflects the lack of agricultural opportunities in many territories (Cheylan, 2001). In addition, moors and heathland gained 8% of the landscape area at the expense of goblet vines. This fact could be explained by two phenomena: (i) Some plots near urbanized areas are grown with durum wheat before being sold as building land. The ultimate goal of wastelands near urbanized areas is turning these wastelands into urban spaces. Many farmers and growers anticipate or wait for this future classification (Cheylan, 2001) and therefore participate in the suburbanization phenomenon; (ii) Some wine plots are ideal for the production of wines but are not appropriate for the development of other activities (especially those presenting certain types of soil) (Sluiter & Jong, 2006). Only aromatic and medicinal plants or extensive farming (sheep and goats) can replace viticulture in some of these areas. Moreover, the Mediterranean climate usually requires the use of irrigation in the summer (Arnal, 2015).

The increase in the arboriculture category may have occurred by taking the place occupied by grubbed-up vines. The forest category has a global growth trend presenting 1.5 times more surface area in 2012 than in 1962. This phenomenon may be due to the fact that some wastelands are grubbed up because of their inability to replace the vine with other crops. Therefore, these fallow zones return to the natural environment (Arnal, 2015). They are sometimes maintained in order to preserve the agricultural use of the land and may be reforested.



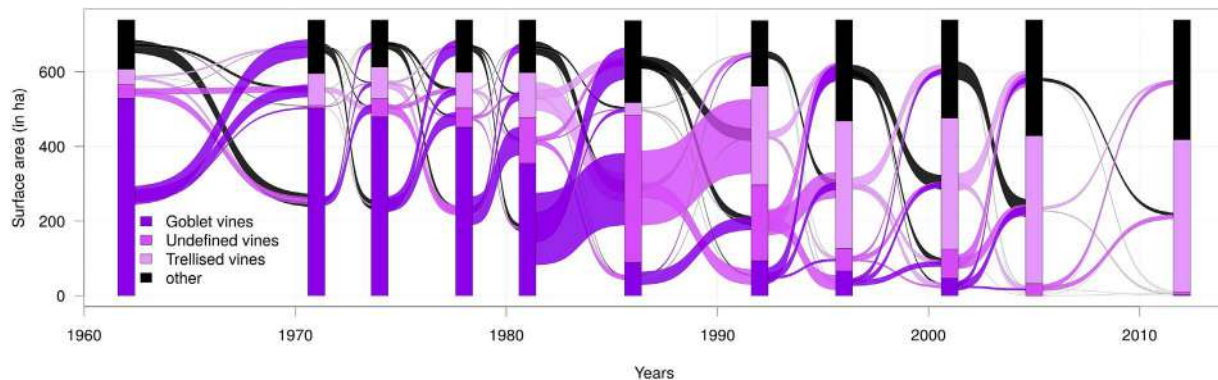


Fig. 5. Adaptation of a Sankey diagram for the representation of transition dynamics between vineyard management categories at the field scale for the Bourdic subwatershed during the period of 1962–2012.

#### 4.2. Evolution of vineyard management is explained by local stakeholders

One of the most significant results of the transition matrix is the evolution of vineyard management that occurred during the 1980s (transition from goblet vines to trellised vines). This transition coincided with the arrival of mechanization in viticulture in the Hérault region (Galet, 2008). This major transformation in the sector began in the 1970s by the modification of land management through the evolution of vineyard planting (Touzard & Laporte, 1998). Agricultural machines need space between vines and it is easier to treat them if they are aligned (Biarnes et al., 2009). The category of undefined vines could correspond to the passage from goblet vines to trellised vines. This change could be done in three different ways: grubbing up and replanting vines in rows of each plot, eliminating one vine on two, or by pruning the vines differently. These three types of training systems, which are characteristic of the transition from goblet vines to trellised vines, are highlighted in the Sankey diagram.

As explained by Touzard and Laporte (1998), the change in land management took time to be adopted by farmers because they were confronted with two strategic orientations that are contradictory. On one hand, the land consolidation and the mechanization helped gain productivity. On the other hand, farmers have to ameliorate vine quality through both a modification of line spacing between ranks and a harvest date in optimal conditions, with a consequential increase in their activity. The labour input induced by these changes was maximal in the 1980s when the number of undefined vines (i.e., vineyards in transition) reached a peak and decreased progressively until 1995, when all vineyards were replanted and when the land consolidation was finished.

#### 4.3. Use of high-spatial-resolution remote sensing data for classification

Aerial photograph processing using SFM tools provided the same accuracy (1 m) as did other mosaic tools applied on similar photographs, such as Erdas<sup>®</sup> described by Sluiter and Jong (2006). The interest in using SFM tools on historical database content helped in the assessment of other variables such as the DTM at each date of the study period to estimate DTM evolution, as was performed for other landscape elements (Midgley & Tonkin, 2017).

Automatic tools are available for vineyard detection and the characterization of OBIA methods, but with a classification error of more than 20% due to size of the plot, width between ranks and age of the vine plot were used (Delenne et al., 2008). Furthermore, the distinction between trellised and goblet vineyards was rarely achieved with this method (Delenne et al., 2008). Consequently, manual classification combined with a high temporal range helped determine the land management of the zone for fields with an area smaller than 1.2 ha rather than using the automatic tool used by Delenne et al. (2008).

Regarding the high diversity of land covers in LANDSAT studies,

only the second level of the Corine Land Cover nomenclature was used due to the resolution of the LANDSAT images: cultural fields, forests, grassland, and artificial areas (Dawelbait & Morari, 2012; Liu et al., 2003; Marraccini et al., 2015; Symeonakis et al., 2007; Tovar et al., 2013; Yang & Lo, 2002; Yuan et al., 2005). Consequently, the distinction between agricultural crops occurring at the 3rd level of the Corine Land Cover could not be reached using LANDSAT series, making the use of high-resolution aerial images indispensable for analysing change in land management for some land uses.

## 5. Conclusion

The methodology presented in this paper is devoted to the analysis of high resolution dataset in time and space, with a particular attention to the transformation of vineyards management due to local policies. It necessitates a dataset with a spatial resolution sufficient to detect subtle differences between land managements of a given land use. It is best suited to perennial crops rather than annual ones because it is primarily devoted to the study of global trends rather than cyclic variations in the history of the database. The last point is justified by the limited availabilities of high resolution images over long time periods. Future researches should be oriented toward a better comprehension of the physical and environmental factors driving the changes in land management.

## Acknowledgements

The authors thank Matthieu Bourmaud, Florent Levavasseur, Marina Chauvet, François-Xavier Weber, and Maxime Jourde for their help in manual digitalization of land use categories. This research was supported by the French National Research Agency (ANR) through the ALMIRA project (ANR-12-TMED-0003). This work was also supported by the metaprogramme Adaptation of Agriculture and Forests to Climate Change (AAFCC) of the French National Institute for Agricultural Research (INRA) through the LACCAGE project. The authors thank also the INRA Payote research group for helpful advice on landscape analyses, and Frederic Jacob for his helpful advice on the paper.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.apgeog.2017.12.003>.

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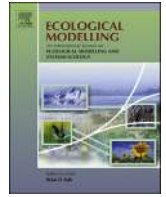
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# Ecological Modelling

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## A neutral model for the simulation of linear networks in territories



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### ARTICLE INFO

#### Article history:

Received 14 April 2017

Received in revised form 4 August 2017

Accepted 22 August 2017

#### Keywords:

Landscape  
 Periurban  
 Douglas–Peucker  
 Tessellation  
 Networks

### ABSTRACT

A landscape matrix is the support of biotic and abiotic flows, and in that sense, requires increased interest from ecological modellers. This matrix is partly composed of linear elements, such as roads and field borders, that delimit land uses and are the result of socio-economic drivers. The geometrical properties of these elements could affect flows of water bodies, fauna, and flora. A large amount of research on landscape matrix simulation has been conducted using neutral models, but the efforts have been limited to 1 km<sup>2</sup> and have been principally devoted to field borders. However, simulating largest territories in neutral models requires consideration of supplementary elements, such as road networks. Furthermore, the sinuosities of the linear elements in territories have rarely been considered *per se*. We proposed a hierarchical model based on successive imbrication of deformed networks, with the deformation being realized on the basis of a reverse Douglas–Peucker algorithm. We first isolated the hierarchical levels of the landscape and analyzed their relative deformations. Then we constructed the hierarchical model and we tested it on a real territory in the Mediterranean zone. Its structural realism was tested against other common neutral models using the pattern-oriented modelling approach. The hierarchical model was the only neutral model able to represent simultaneously the variabilities of three patterns having implications in ecological processes: polyline lengths, sinuosities and polygon areas. Possible improvements of the model to address non-stationary processes and its potential for implementing geopropective scenarios are discussed.

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### 1. Introduction

A landscape is formed by the spatial arrangement of polygons delimited by interconnections (Turner, 1989). The interconnections are composed of linear elements, such as roads, ditches, hedgerows, lines of trees and field borders (van der Zanden et al., 2013). Several ecological processes that occur in landscapes are driven by those interconnections, especially biotic and abiotic flows (Vinatier et al., 2016). On the one hand, biotic flows can be blocked, such as the dispersal of crawling insects by steep ditches (Vinatier et al., 2010) or flying insects by scrub hedges (Purse et al., 2003). On the other hand, interconnections can act as ecological corridors for species that take advantage of the potential refugia of vegetation (Bertuzzo et al., 2007) or road networks facilities (Forman, 2003). Abiotic flows can be either blocked or accelerated by landscape interconnections, such as water flows by banks (Griffin et al., 2005) or ditches (Levvasseur et al., 2014). In addition to the properties

of the interconnections, their organization in space has a strong influence on the flow. For example, the connectivities of linear elements greatly affected the migration fronts of fauna (Bertuzzo et al., 2007; Kramer-Schadt et al., 2004) or the sinuosities of successive elements affected water flow transport (Raska and Emmer, 2014). It is also of primary importance to understand the drivers affecting landscape interconnections for simulation purposes.

The drivers shaping territory structures are generally socio-economic and geomorphological. A large part of the literature has focused on the study of territory changes (Houet et al., 2010). For this purpose, researchers gathered diachronic maps of a given area to study the driving forces that shaped the land cover changes. These forces were latter incorporated into dynamic models for prediction purposes related to environmental issues. It is also possible to explore multiple change scenarios and their impacts on ecosystem services (Houet et al., 2010). It appears that driving forces affect the territory structure at a larger scale than previously encountered in landscape ecology (Houet et al., 2010). Consequently, models that consider both socio-economic forces and ecological processes necessitate to be addressed at a large scale and at fine spatial resolution.

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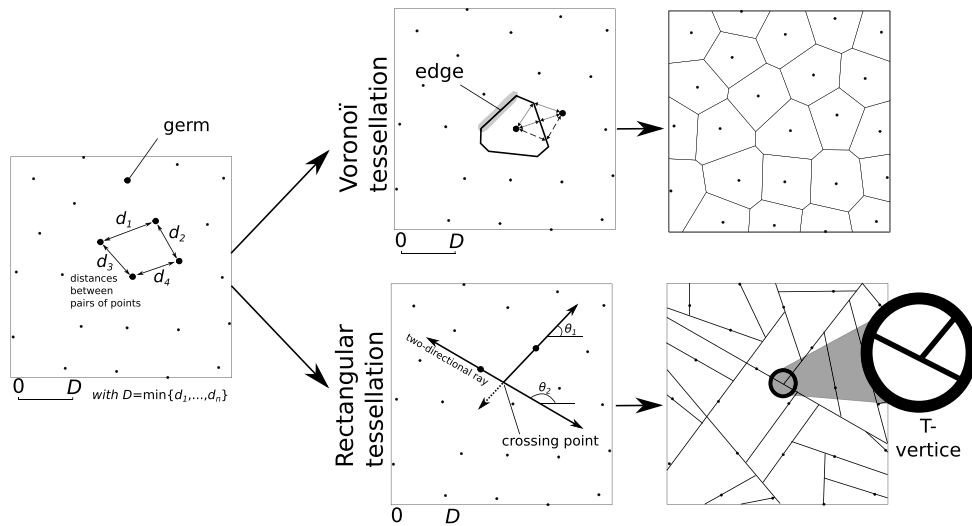


Fig. 1. Illustration of two vector-based approaches for the simulation of territory structures.

In the last decade, the simulation of territory structures has been widely studied in landscape ecology and agronomy (Adamczyk et al., 2007; Etherington, 2012; Gaucherel, 2008; Holland et al., 2007; Le Ber et al., 2009; van Strien et al., 2016). Models are generally considered as neutral, i.e. they model no explicit process giving rise to the landscape pattern (Le Ber et al., 2009). The neutral models rapidly shifted from a raster approach for which space was divided in a grid with homogeneous cells (Hargrove et al., 2002) to a vector approach for which space was divided in lines or polygons with varying shapes (Gaucherel, 2008; Le Ber et al., 2009). The vector approach appeared to be more suitable when considering the diversity of field borders. The extent of the considered area is generally restricted to a 1 km<sup>2</sup> window to simulate field polygons because the vector-based approaches are mainly devoted to effects of field mosaic on an ecological process, such as gene flow across agricultural landscapes (Le Ber et al., 2009). But the spatial rank of the linear elements in territories is not considered in the neutral models raised below, despite its primary importance to link ecological processes to drivers of territory changes.

When upscaling simulation models to a larger extent, i.e. several km<sup>2</sup>, we need to include supplementary hierarchical levels such as road networks (Forman, 2003). They have ecological effects on the landscape they penetrate, affecting both biotic and abiotic components of terrestrial and aquatic ecosystems (Coffin, 2007). Roads differed from lower hierarchical levels with respect to their connectivities, their sinuosity levels, and their hierarchy (motorways, national roads, or local roads, for example, in France). To the best of our knowledge, there has been no attempt to simulate road networks because they are considered more static than field borders. Although rarely performed, the simulation of the different road networks at a large extent appears to be necessary in neutral landscape models. It is also necessary to take into account both the spatial hierarchy between the different networks shaping the landscapes and their relative sinuosities.

We propose a new approach to simulate territory structures called the hierarchical model. It provides a baseline for researchers studying spatial processes at a large extent. The main novelty of the paper is the attempt to finely parameterize the real sinuosities of territory networks at different scales.

We first expose the principles of vector-based approaches for the generation of neutral modelling, and then the principle of the deformation algorithm. Then, we define the hierarchical model and their calibration. We finally tested the hierarchical model against other vector-based approaches on a real territory covering 25 km<sup>2</sup>

in the Mediterranean zone using the pattern-oriented modelling (POM) approach.

## 2. Material and methods

### 2.1. Presentation of vector-based approaches

The vector-based approaches are based on tessellation methods (Le Ber et al., 2009). The basic principle is to cover a surface area by polygons without gaps and overlaps. To this end, a set of points, called germs, is generated from which polygons are built. There are two different ways of creating the polygons, following Le Ber et al. (2009) and illustrated by Fig. 1. First, the Voronoi tessellation consisted in polygons for which every point of their edges is at equal distance from two germs. Secondly, the rectangular tessellation consisted in creating edges by crossing two-directional rays starting from a set of points, forming T-vertices at the intersection between edges (Fig. 1).

We defined the distance threshold  $D$  that governs the positions of the germs for both Voronoi and rectangular tessellations. We defined a supplementary parameter,  $\theta$ , for the orientation angle of rays only for rectangular tessellation. By controlling  $D$  and  $\theta$ , we could approximate the shapes of fields in agricultural landscapes (Le Ber et al., 2009; Gaucherel, 2008). For example, reducing  $D$  decreases the size of the fields, or having the same  $\theta$  for all rays produces long and regular rectangles.

However, there is no possibility to constrain geometrical properties of the polygons' edges other than by the germs' positions and rays' orientations following the approaches described above. It is important to develop an algorithm that could simulate the deformation of linear elements with a set of parameters independent from  $D$  and  $\theta$  to recapture roads or even large field borders' deformations.

### 2.2. Presentation of the Douglas–Peucker algorithm and its reversed form

Here are some definitions to understand the principles of this section. An endpoint is a node that connects more than two segments, and a polyline is a continuous line composed of a series of segments joining two endpoints. The points that connect exactly two segment situated at the middle of the polyline are called intermediate points (Fig. 2).

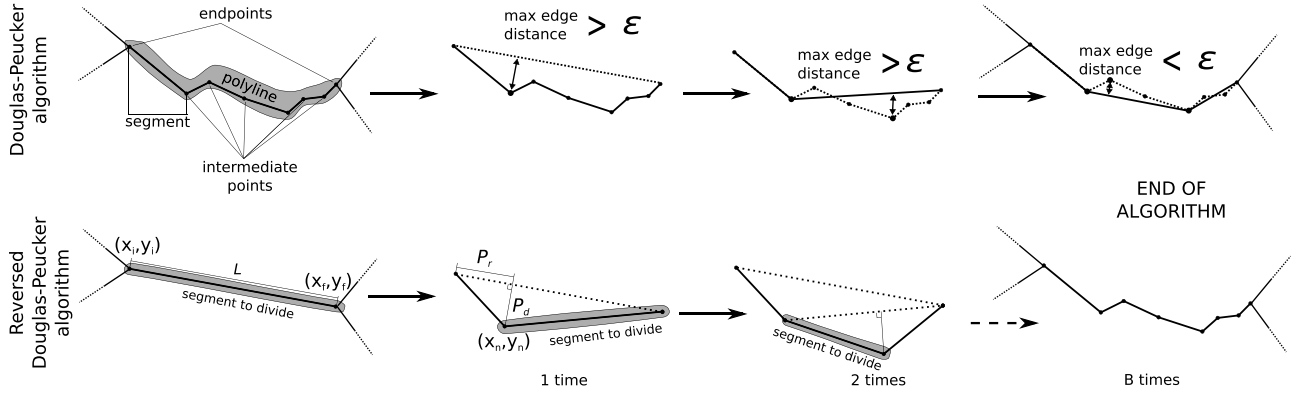


Fig. 2. Illustration of the Douglas–Peucker algorithm and its reversed form.

We developed an algorithm to deform artificially the edges that formed the polygon, on the basis of Douglas and Peucker (1973) algorithm. They proposed an algorithm to reduce the number of segments necessary to represent a digitized polyline. The algorithm consisted in defining the segment linking the endpoints of a polyline and calculating the distance of each intermediate point of the polyline to this segment (Fig. 2). If the point is closer than a given distance  $\epsilon$ , it is removed from the polyline. The algorithm is recursively called until there are no intermediate points closer than  $\epsilon$ .

Our approach reversed the Douglas–Peucker algorithm to artificially deform a given segment, as illustrated in Fig. 2. The basic principle of the reverse Douglas–Peucker (RDP) algorithm is to create an intermediate point between two endpoints of a simple segment in order to get two segments, then a new intermediate point is created between the endpoints of the largest resulting segment, and so on.

At each time, the position  $(x_n, y_n)$  of the intermediate point is determined by a couple of parameters,  $P_r$  and  $P_d$ . With basic trigonometry, we can deduce the new coordinates of the point  $\{x_n, y_n\}$  from the coordinates of the endpoints of the segment  $\{x_i, y_i\}$  and  $\{x_f, y_f\}$  and the two variables,  $P_d$  and  $P_r$ , according to Eqs. (1) and (2):

$$x_n = \cos \left( \arctan \left( \frac{y_f - y_i}{x_f - x_i} \right) + \arccos \left( \frac{P_r}{\sqrt{P_r^2 + P_d^2}} \right) \right) \sqrt{P_r^2 + P_d^2} + x_i \quad (1)$$

$$y_n = \sin \left( \arctan \left( \frac{y_f - y_i}{x_f - x_i} \right) + \arccos \left( \frac{P_r}{\sqrt{P_r^2 + P_d^2}} \right) \right) \sqrt{P_r^2 + P_d^2} + y_i \quad (2)$$

We considered an additional parameter  $B$  which is the number of times an intermediate point is created, i.e. the number of breaks minus one of the resulting polyline (Fig. 2). Consequently, there are  $B$  couples of  $\{P_r, P_d\}$  values for each polyline. Each parameter  $B$ ,  $P_d$  and  $P_r$  has a different influence on polyline deformation, as shown in Fig. 3:

### 2.3. Description of the hierarchical model

#### 2.3.1. Classification of the digitized territory in groups of polylines

In this section, we explained how the polylines constituting a manually digitized territory are split in hierarchical groups of same length. First, we broke the linear elements of a digitized territory at each endpoint to form a polyline. Then the polylines are joined together according to a threshold angle of  $\pi/10$ . Finally we computed the total length and the number of segments of each group of joined polylines.

The groups of polylines are classified according to their length to represent the hierarchical levels of the territory. The number of

hierarchical levels is chosen empirically according to the complexity of the territory from  $max_D$ , the mean distance between towns of the territory, to  $min_D$ , the mean distance between centroids of all polygons of the territory.

#### 2.3.2. Calibration of the reverse Douglas–Peucker algorithm on the groups of polylines

In this section, we estimated the distributions of the four parameters  $L$ ,  $B$ ,  $P_d$  and  $P_r$  across hierarchical levels and the potential links between them. The parameters  $L$  and  $B$  were calculated directly from the groups of polylines,  $L$  being the total length of the group and  $B$  the number of segments composing the group of polyline. Then  $P_r$  and  $P_d$  are estimated by applying the Douglas–Peucker algorithm on each group and gathering, for each call of the algorithm, the couples  $\{P_r, P_d\}$ .

We tested the correlations between variables  $(L, B, P_d$  and  $P_r)$  using the Pearson product-moment correlation test with a threshold fixed at 0.6 to distinguish strong correlations from noise (Graham, 2003). The test was conducted on both the whole dataset and also on each hierarchical level. The distributions of each variable across hierarchical levels were also tested for similarities using Kolmogorov–Smirnov tests.

When two variables were correlated, a regressive model was fit to represent the correlation. Variations of the predicted variable that were not explained by the model were simulated using a normal law fitted on the model residuals. In the absence of a correlation between variables, known laws were fitted to the distributions, and the validity of the fitting procedure was tested using a Kolmogorov–Smirnov test.

#### 2.3.3. Simulation of hierarchical networks

Each set of germs of the network is simulated according to a random simple sequential inhibition process (rSSI) with parameter  $D$ . The principle of the rSSI is to add points one-by-one in a window. If the new point lies closer than  $D$  from an existing point, it is rejected and another random point is generated until the window is completely covered. The value of  $D$  is chosen according to the geometric series  $\{max_D, \dots, min_D\}$ , beginning with  $max_D$  for the highest hierarchical level and finishing with  $min_D$  for the lowest hierarchical level.

Set of germs are linked to form segments according to two laws: for the first hierarchical level, we privileged a radial orientation of segments by linking each germ to its  $k$ -nearest neighbours, and we chose a rectangular tessellation for the other hierarchical levels. The angle direction  $\theta$  in the latter cases is selected according to a uniform law between 0 and  $\pi$ .

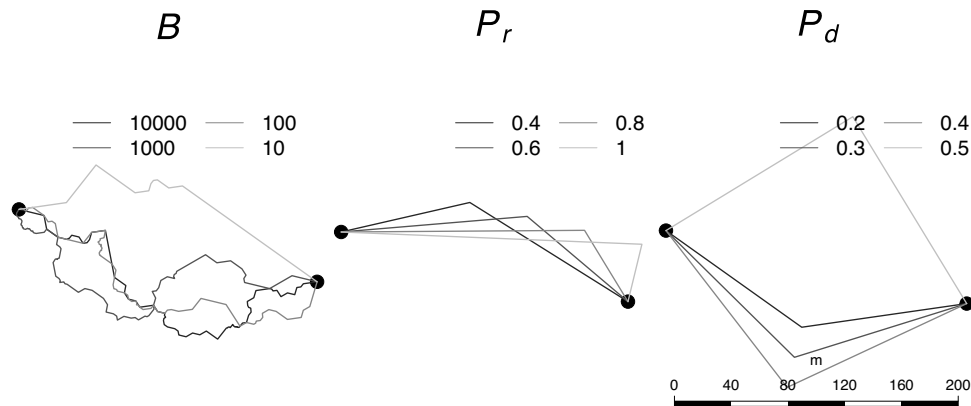


Fig. 3. From left to right, illustration of the influence of increasing  $B$ ,  $P_r$  and  $P_d$  on polyline deformation.

## 2.4. Application to a real dataset

### 2.4.1. Presentation of the study area

The study area corresponds to Peyne watershed which covers approximately 76 km<sup>2</sup> in Languedoc–Roussillon in southern France (43° 35'N, 3° 19'E). The climate is submediterranean sub-humid with a long dry season, an average annual temperature of 14 °C, an annual rainfall varying between 400 and 1400 mm and an altitude ranging between 0 and 200 m.

The area of the Peyne watershed is mostly covered by perennial crops, mainly vineyards, and five towns are contained within the zone (Fig. 4). The structure of the territory was manually digitized on the basis of an orthophoto at 20 cm resolution taken in 2012 (<http://www.siglr.org/>), with a minimal area of approximately 200 m<sup>2</sup> and at a scale of 1:1000 using Qgis software (QGIS Development Team, 2016). Field entities were separated on the basis of homogeneity of shape, texture and tone. Adjacent field entities separated by linear elements were considered as distinct, as, for example, two fields of cropland separated by a ditch. Towns were considered as unique homogeneous polygons, i.e. streets and districts were not digitized considering their too fine resolution. Other land uses were classified using visual interpretation in six classes according to the Corine Land Cover: discontinuous urban area, orchards, other arable lands, road and rail networks, semi-natural habitats and vineyard (Fig. 4).

### 2.4.2. Calibration of the model

The study area is composed of almost 6300 polygons, with a mean distance between polygons of 60 m. The five towns constituting the zone are 4 km apart. The breaking procedure produced a total of 8500 polylines. After applying the RDP, we only found a correlation between  $B$  and  $L$  over the whole dataset ( $r > 0.6$ , Pearson tests). For this case, we considered a linear combination of a power model of the form  $B = a * L^b$  on the data using non-least squares regression and a normal law on the distribution of the residuals (Eq. (3)):

$$B \sim a \times L^b + \mathcal{N}(\mu, \sigma^2) \quad (3)$$

The distributions of  $P_r$  were similar across distance groups ( $P$ -value  $> 0.05$ , Kolmogorov–Smirnov tests), and we found the same results for the  $P_d$  distributions ( $P$ -value  $> 0.05$ , Kolmogorov–Smirnov tests). Normal and exponential laws were fitted to the whole distributions of  $P_r$  and  $P_d$ , respectively.

### 2.4.3. Comparison of the hierarchical model with other neutral approaches using Pattern-Oriented modelling

Grimm et al. (2005) proposed the POM approach to design, test and analyze the general principles underlying the internal organi-

zation of a system. To realize the POM approach, we defined a set of patterns observed at different scales to contrast alternative models. The models are compared using a rigorous statistic on the basis of the observed patterns to eliminate models that fail to reproduce the whole set of patterns. Following the POM approach, a model that is able to reproduce multiple patterns is more likely to be structurally realistic than the others.

To implement the POM approach in our case study, we considered two alternative models from the work done by Le Ber et al. (2009):

**Voronoi tessellation:** The neutral model is based on a Voronoi tessellation of germs corresponding to the real positions of polygon centroids.

**Rectangular tessellation:** The neutral model is based on a rectangular tessellation of the same germs' positions as in Voronoi tessellation. The angle direction  $\theta$  is selected according to a uniform law between 0 and  $\pi$ .

The hierarchical model and the two alternative models were transformed into groups of polylines using the procedure explained in Section 2.3.1. Then, we selected three observed patterns to implement the POM approach, considering their influence on ecological processes:

- The distribution of the lengths of the polylines.
- The distribution of the mean turning angles of the polylines. A turning angle is formed by the difference in the directed and absolute angles of two consecutive segments forming the polyline.
- The distribution of polygon areas. The neutral model is transformed in polygons, and the area of each polygon is computed.

The observed patterns are then compared between neutral models using the Kolmogorov–Smirnov tests. The models for which at least one pattern is significantly different from the observations is eliminated from the pool of structurally realistic models.

## 2.5. Statistical and simulation methods

All statistical analyses and the simulation model were performed with the R software (R Core Team, 2017) using packages “spatstat” (for the simulation of point patterns) and “rgrass7” (for accessing the v.clean function of grass software (GRASS Development Team, 2016)).

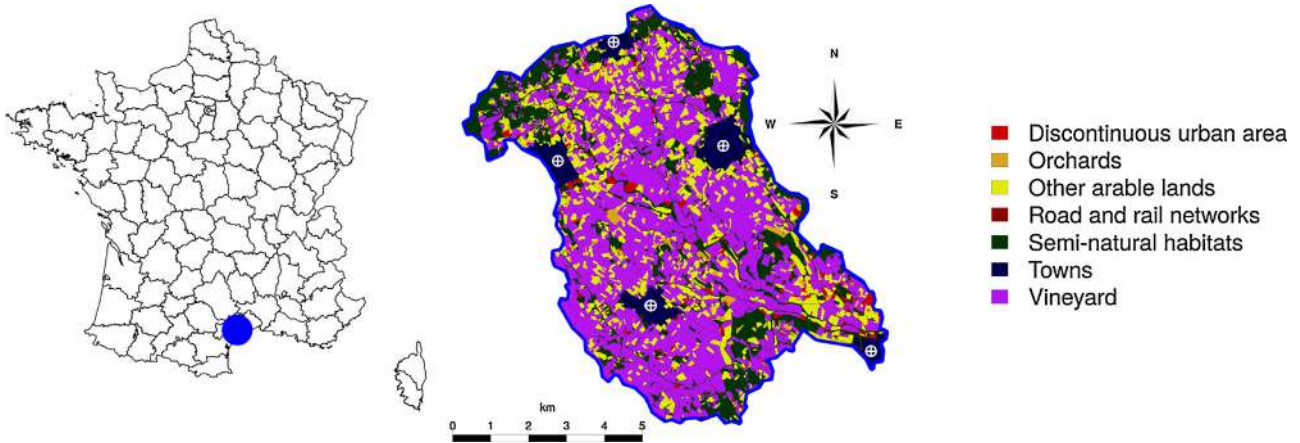


Fig. 4. Illustration of land use categories classified according to the Corine Land Cover. Centers of towns are represented by white crosses.

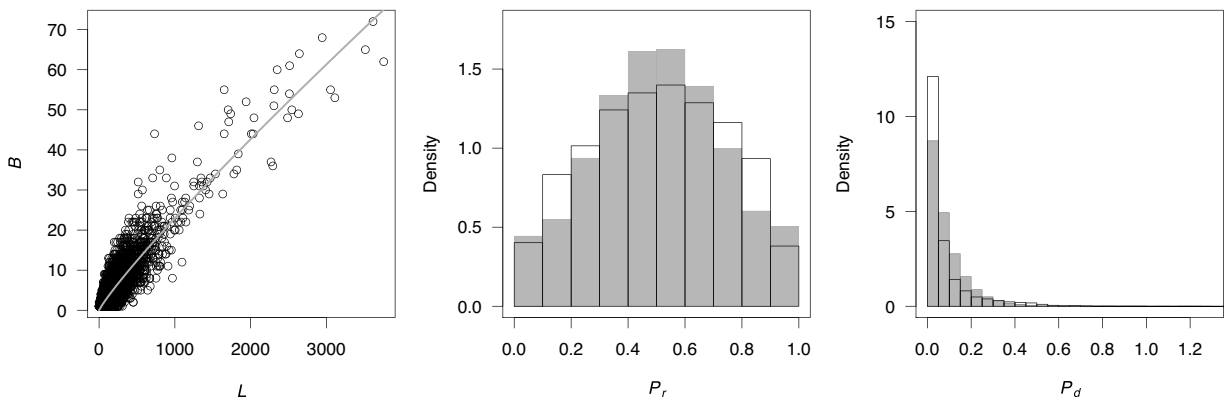


Fig. 5. At left, the relation between  $B$  and  $L$  is represented by white points for the observation and grey line for the fitted power model. The two histograms on the right represent the distribution of  $P_r$  and  $P_d$ , respectively for the observations (white bars) and the simulation (grey bars).

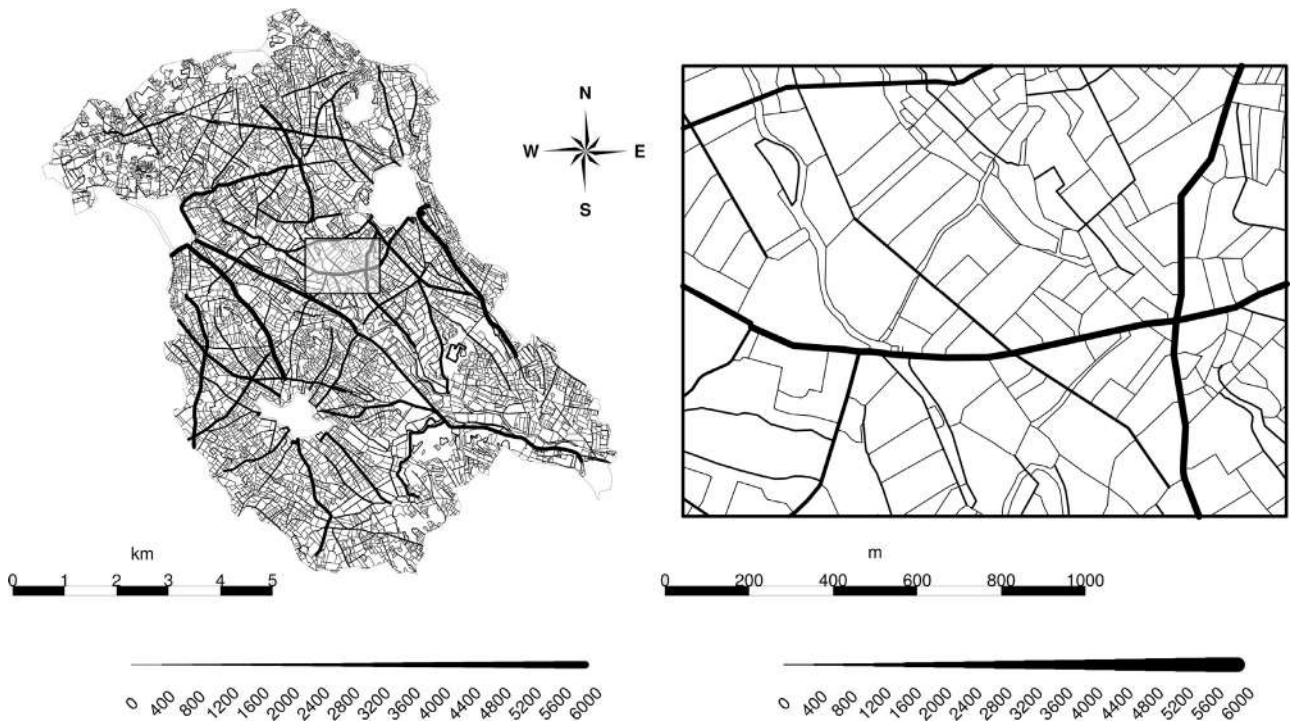
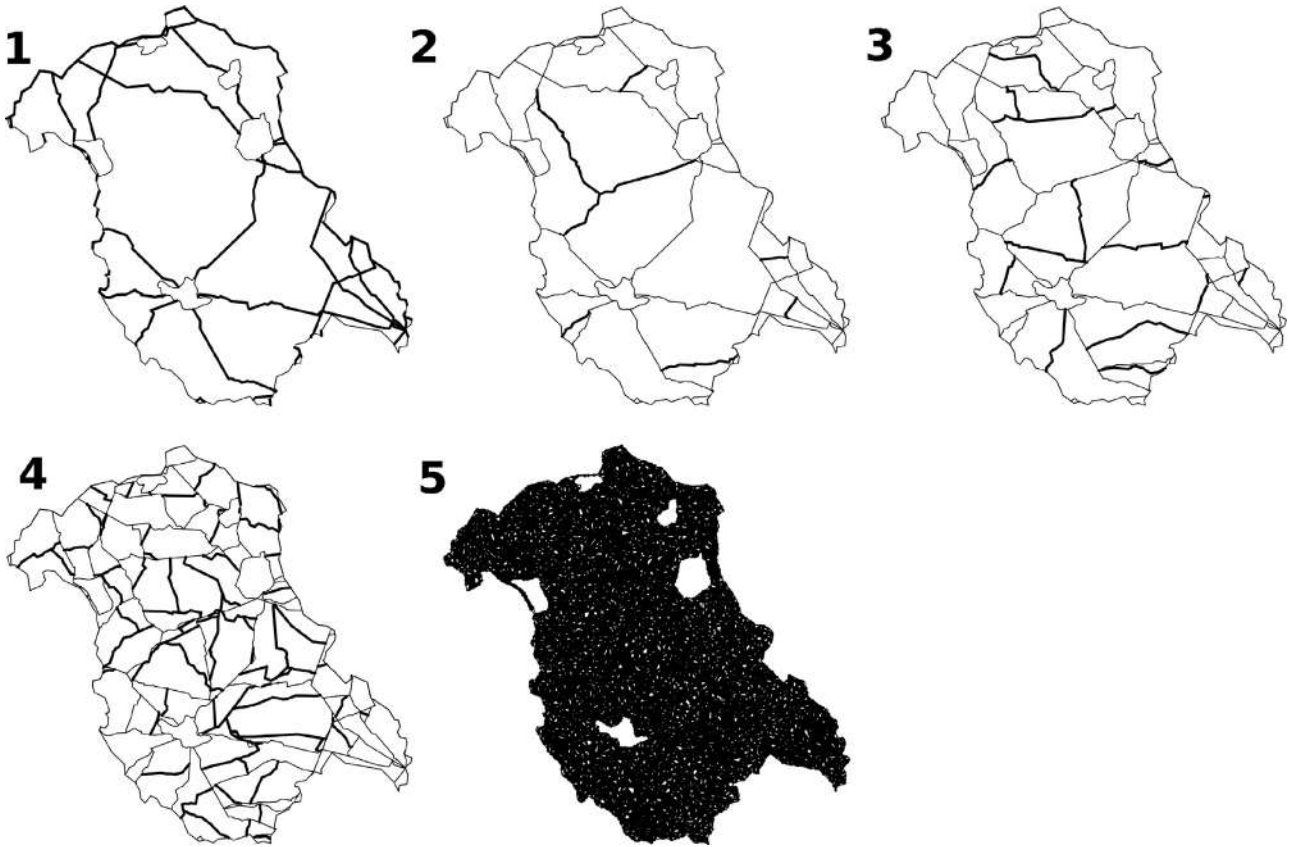
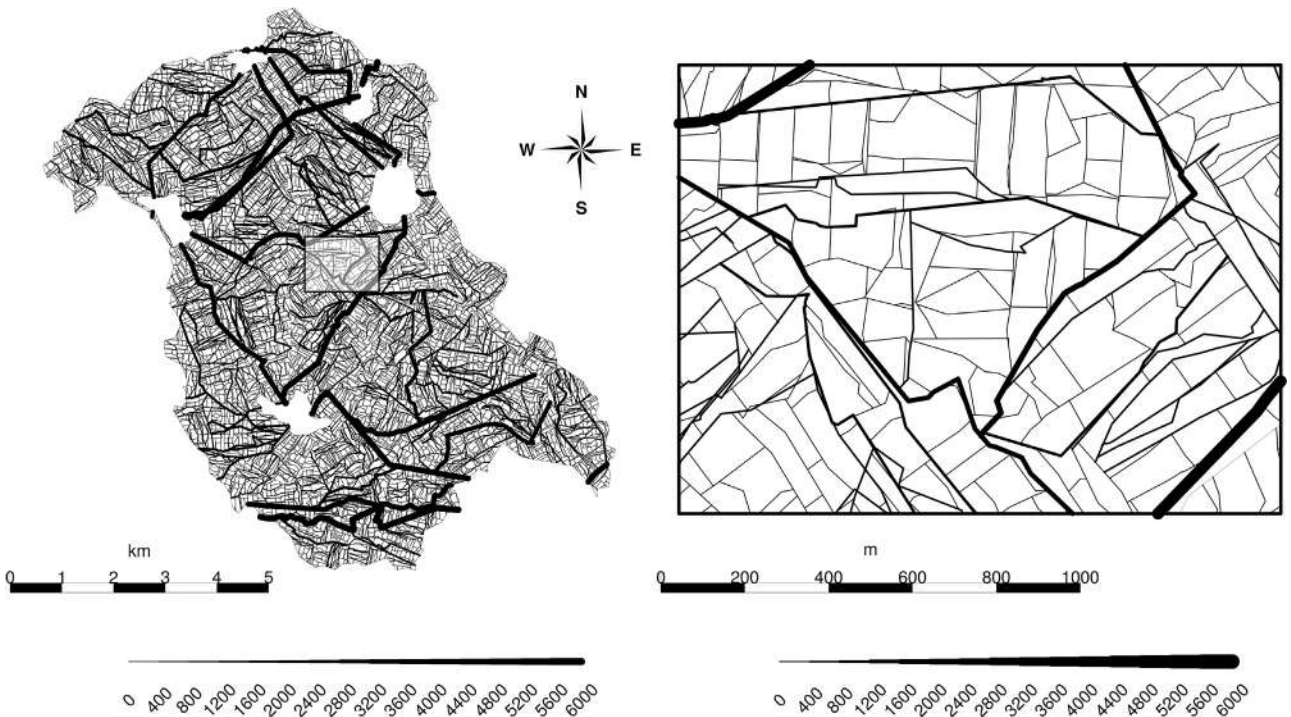


Fig. 6. Illustration of the **observed** polylines for the Mediterranean territory with line thickness proportional to their hierarchical level in the network. The framed box on the right corresponds to a zoomed view in the middle of the zone to distinguish the lowest hierarchical levels.

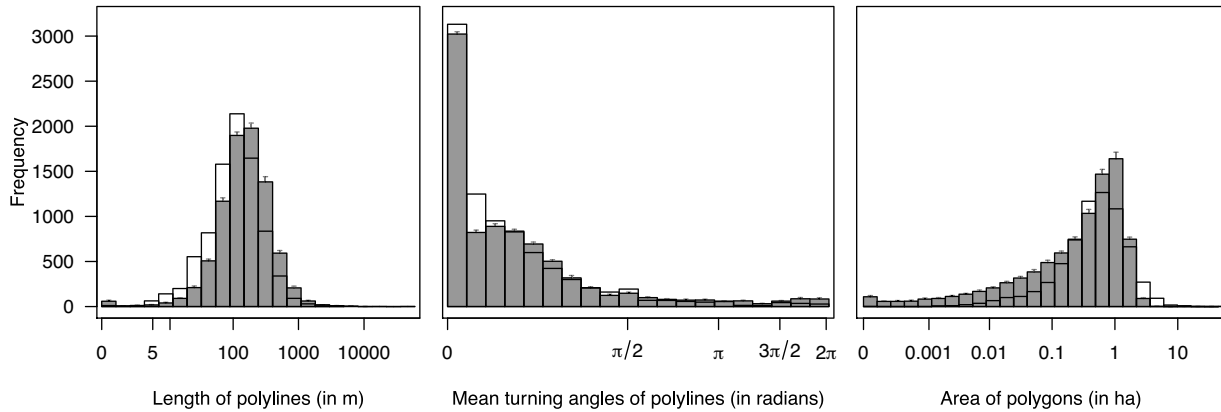




**Fig. 7.** Illustration of the successive networks simulated by the model according to the five hierarchical levels. The thick lines corresponded to the new network, and the thin lines correspond to the preceding hierarchical level.



**Fig. 8.** Illustration of the **simulated** polylines using the hierarchical model with line thickness proportional to the hierarchical level in the network. The framed box on the right corresponds to a zoomed in view of the middle of the zone to distinguish the lowest hierarchical levels.



**Fig. 9.** Barplots of the three observed patterns obtained from (i) the real territory (white rectangles) and (ii) the hierarchical model (grey rectangles). Error bars correspond to the standard deviation of the barplots against 100 simulations of the hierarchical model. Please note that the x-axis is presented in logarithmic scale.

### 3. Results and discussion

We estimated on the basis of  $max_D = 4$  km and  $min_D = 60$  m five hierarchical levels for the study area. Fig. 6 presents the groups of polylines on the study area. We observed a relation between the hierarchical levels of the polylines, with the highest and lowest hierarchical levels corresponding to the main roads linking towns of the territory and field borders, respectively. We also observed that polylines with highest hierarchical level were split into a radial plane, whereas the lowest levels represented more T-vertices.

The non-least squares model fitted from Eq. (3) gave a 73% accuracy with coefficients  $a = 0.05$  and  $b = 0.89$ . The values of the residuals were normally distributed ( $P$ -value = 0.67, Shapiro–Wilk test) with  $\mu = 0.08$  and  $\sigma = 2.25$ . Only 0.1% of the total points were outside the envelope of the model constructed using Eq. (3) (Fig. 5). The coefficients of the normal law fitted on  $P_r$  were  $\mu = 0.51$  and  $\sigma = 0.24$ . The exponential law fitted on  $P_l$  had a coefficient  $\lambda = 19.5$ . The fitted distributions were similar to the observed distribution for all hierarchical levels ( $P$ -value > 0.05, Kolmogorov–Smirnov tests).

It is interesting to note that, in our study case, the shapes of the polyline deformations did not vary across hierarchical levels. Consequently, the polyline construction procedure helped to identify territories exhibiting invariance in scale (Holling, 1992). Applying the procedure to other territories should help researchers to understand the factors shaping territory structures. For example, the procedure could help distinguish between natural and anthropic linear elements, supposing that the invariance in scale is expressed differently.

The networks were simulated successively according to the hierarchical levels (Fig. 7). The first hierarchical level, representing inter-town roads, reproduced the radial organisation of the network. The three following levels represented secondary roads that linked the first hierarchical network. The highest density levels of polylines was defined for the lowest network level representing the field borders.

We could suppose that the hierarchical levels highlighted by the polyline construction procedure are linked to the temporal inertia of the structures, i.e. polylines with the highest level or highest lengths corresponded to major roads and polylines with the smallest levels or smallest lengths corresponded to intra-field borders. Considering this temporal inertia represents a further move toward neutral models that simulate dynamics of field regrouping or fragmentation (Hu et al., 2011).

Fig. 8 shows the territory simulated using the hierarchical model whose groups of polylines were isolated according to Section 2.3.1. Roads were depicted by the hierarchical model as elements with the largest lengths in the territory. With a lowest sinuosity level in com-

parison with field borders, roads have large impacts on both biotic and abiotic components of the ecosystem (Coffin, 2007). Road networks interact with stream or ditches networks when the drainage swales along roads is connected to the stream or ditch networks (Coffin, 2007). By dividing the territory in fragmented patches, road networks, by their linearities and their densities, contributed to negative effects on ecosystem structures and flows (Forman, 2003). Finally, roads can have adverse effect by favouring the long-range dispersal of invasive plants (Christen and Matlack, 2006). The hierarchical model, by separating the roads from the other networks, helped simulating the effect of road density in the territories.

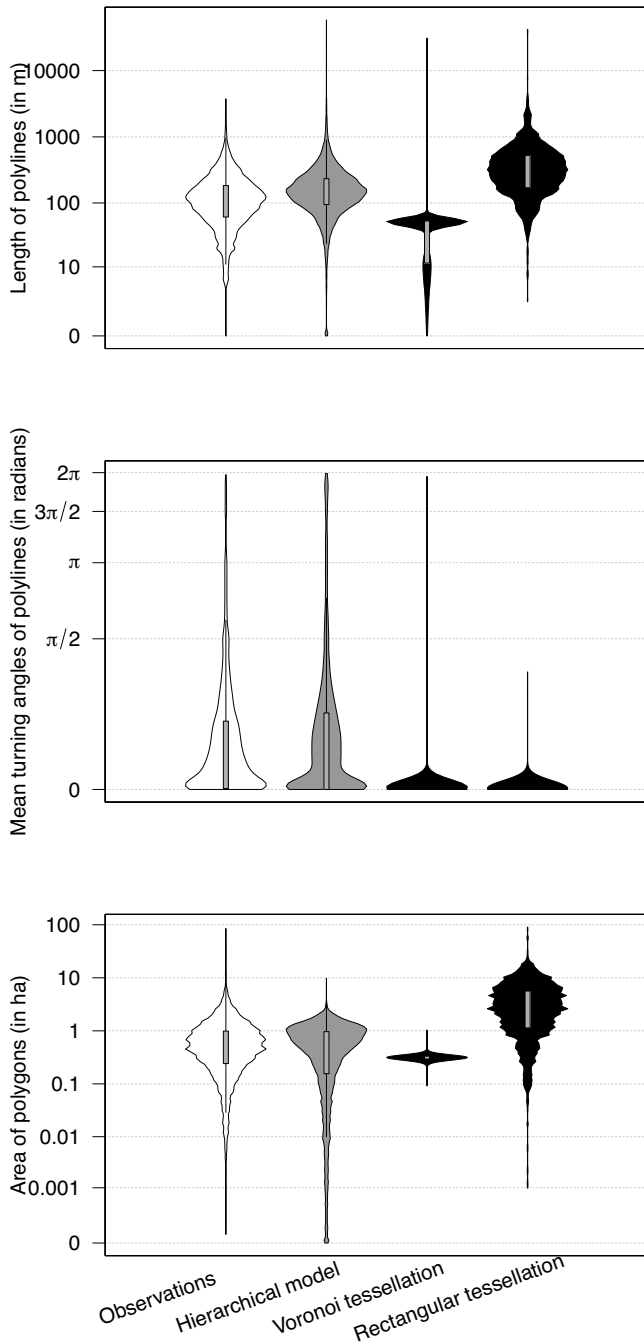
By construction, the hierarchical model divides space into independent zones at various scales. It is possible, for each zone, to change the parameters that governs the tessellation process, such as  $D$  and  $\theta$ . For example, as hedgerows created a protected area downwind, it is possible with the hierarchical model to simulate territories with borders oriented according to the prevailing wind. The resulting landscape could be considered in process-based models on flying insects, the latter being affected by wind velocities (Ricci et al., 2011). More generally, the hierarchical model could simulate finely landscapes that exhibited heterogeneities in field densities and orientation (Evans and Winterhalder, 2000).

Fig. 9 compares the observations and simulations using the POM procedure. As distributions of observations were zero-inflated, they are  $\log(x+1)$  transformed before plotting. The distribution of observations against 100 simulations produced by the hierarchical model were non-significantly different ( $P$ -value > 0.05, Kolmogorov–Smirnov tests) for the three observed patterns, despite a weak positive and negative shift of the mean length of polylines and the area of the polygons for the hierarchical model, respectively.

When comparing the hierarchical model to the two alternative models (Fig. 10), we observed that Voronoi tessellation failed to describe the three observed patterns ( $P$ -value =  $1e-5$ , 0.02, 0.001, Kolmogorov–Smirnov tests). The rectangular tessellation failed to describe the last two observed patterns but was able to represent the first pattern ( $P$ -value = 0.06, 0.01, 0.01, Kolmogorov–Smirnov tests).

The sinuosities of the linear elements represented by the model exhibited both convexities and small variations that were not reached by the Voronoi or rectangular tessellations (Le Ber et al., 2009). These sinuosities should affect the process-based models simulating biotic or abiotic flows at interfaces between fields (Griffin et al., 2005; Viaud et al., 2008).

The shape of generated landscapes may biased movement of organisms (Holland et al., 2007). In fact, the linear elements of the territories contained sometimes hedgerows that acted as corridor



**Fig. 10.** From top to bottom, distributions of the three observed patterns against the observations (in white), the hierarchical model (in grey) and the two alternative neutral models (in black). Distributions are represented by a violin plot which is a combination of a box plot and a kernel density plot. The points at the middle of each violin plot represented the median of the distribution. Please note that the y-axis is presented in logarithmic scale.

for animals dispersal (Forman and Baudry, 1984). By representing with accuracy the deformation of the field borders, and consequently the hedgerows contained in these borders, the hierarchical model is the best suited for the study of process-based model on organism's dispersal in landscapes.

Some linear elements of territories contained also ditches that are primarily designed for waterlogging control and erosion prevention (Dollinger et al., 2015). By draining water flows through the landscape, ditches constituted a physical driver for hydrochorous plant species (Favre-Bac et al., 2016; Soomers et al., 2010).

Consequently, properties of water flows, such as velocity and turbidity could be affected by geometry of the linear elements that constrained the flow, and especially their sinuosities (Rhoads and Kenworthy, 1995). In other words, an increase in sinuosity favoured the establishment of aquatic plants in ditch sections by creating dead-water zones (Bornette et al., 1998). As the hierarchical model proposed in this paper best explained the real sinuosities observed for real landscapes, it is the best suited for the simulation of process-based models linking biotic and abiotic flows.

The hierarchical model best explained the mean area of polygons' territory, the Voronoi and rectangular tessellations being below and above the observed data, respectively. This parameter is important for explaining ecological processes, such as weed species richness, as illustrated by Gaba et al. (2010). They demonstrated empirically that weed richness and diversity increased significantly as field size decreased, probably because small fields contained more edges that can shelter weed species.

#### 4. Conclusions

The hierarchical model presented in this paper went beyond the traditional vector-based approaches used in landscape simulation. Compared to other neutral modelling approaches (Le Ber et al., 2009; Gaucherel, 2008), the model proposed in this paper considered the multiscale characteristics of territory structures. By taking in to account for the first time intrinsic deformations of the linear elements, the hierarchical model should be better adapted to process-based models simulating biotic and abiotic flows in landscapes. The hierarchical model is also a good candidate to understand the effects of roads on the dynamics of ecosystem function (Coffin, 2007).

Finally, the hierarchical model is a good tool to explore the ecological impacts of socio-economic scenarios implying land cover change (Houet et al., 2010). Indeed, considering a territory with both an agricultural area divided in fields, and a unique semi-natural area corresponding to a forest, the model could be calibrated on the agricultural area and extrapolated to the semi-natural area. The model could be applied to the ecological impacts of deforestation in the Brazilian Amazon, for example (Mertens et al., 2002).

#### Acknowledgments

Authors thank Matthieu Bourmaud, Florent Levavasseur, François-Xavier Weber, and Maxime Jourde for their help with the manual digitization of the study area. This research was supported by the French National Research Agency (ANR) through the ALMIRA project (ANR-12-TMED-0003). This work was supported by the metaprogramme Adaptation of Agriculture and Forests to Climate Change (AAFCC) of the French National Institute for Agricultural Research (INRA) through the LACCAVE project. The authors also thank the INRA Payote research group for helpful advice on landscape analyses.

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## Flux biotiques dans la matrice paysagère

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# Explaining host–parasitoid interactions at the landscape scale: a new approach for calibration and sensitivity analysis of complex spatio-temporal models

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Received: 4 April 2012 / Accepted: 3 November 2012 / Published online: 16 November 2012  
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**Abstract** Linking spatial pattern and process is a difficult task in landscape ecology because spatial patterns of populations result from complex factors such as individual traits, the spatio-temporal variation of the habitat, and the relationships between the target species and other species. Mechanistic models provide tools to bridge this gap but they are seldom used to study the influence of landscape patterns on

biological processes. In this paper, we develop a methodological approach based on sensitivity and multivariate analyses to investigate the relationship between the biological parameters of species and landscape characteristics. As a case study, we used a tritrophic system that includes a host plant (oilseed rape, *Brassica napus* L.), a pest of the host plant (the pollen beetle, *Meligethes aeneus* F.), and the main parasitoid of the pest (*Tersilochus heterocerus*). This tritrophic system was recently represented by a model (Mosaic-Pest) that is spatially explicit at the landscape scale and that includes 32 biological parameters. In the current study, model simulations were compared with observed data from 35 landscapes differing in configuration. Sensitivity analysis using the Morris method identified those biological parameters that were highly sensitive to landscape configuration. Then, multivariate analyses revealed how a parameter's influence on model output could be affected by landscape composition. Comparison of simulated and observed data helped us decrease the uncertainty surrounding the estimated values of the literature-derived parameters describing beetle dispersal and stage transition of the parasitoid at emergence. The advantages of using multivariate sensitivity analyses to disentangle the links between patterns and processes in landscape-scale spatially explicit models are discussed.

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**Electronic supplementary material** The online version of this article (doi:10.1007/s10980-012-9822-4) contains supplementary material, which is available to authorized users.

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**Keywords** Tritrophic model · Sensitivity analyses · Inverse modeling · Co-inertia · Morris method

## Introduction

Spatially-explicit simulation models are powerful tools for understanding the links between patterns and processes (Grimm et al. 2005; McIntire and Fajardo 2009). Because spatial models explicitly consider the processes responsible for the observed patterns, i.e. spatio-temporal variation of the population of a given species itself (Tscharntke and Brandl 2004), or in interaction with other species (Bianchi and Schellhorn 2009) they can be used as virtual laboratories (Charnell 2008) to test the effects of a given set of processes on a spatial pattern. Thus, the effects of habitat heterogeneity (Frair et al. 2005), demographic parameters and dispersal (Wiegand et al. 2004), or gene flow (Viaud et al. 2008) on population patterns have been successfully studied using spatially-explicit simulation models. However, simulation models require often many parameters to represent the complexity of the simulated system that is necessary to respond to the biological question.

To better predict the real trends of the system, spatially-explicit simulation models need to be parameterized on the basis of one of several observed datasets. Optimizing the match between observed and simulated system responses is done via inverse modelling (Kramer-Schadt et al. 2007), i.e. searching the model parameterizations that fit the observed data best. Optimization tools suitable for use with spatially-explicit simulation models are scarce because model complexity generally makes conventional statistical techniques (e.g., sum of squares, maximum likelihood) unusable for parameter estimation. Bayesian tools such as approximate Bayesian computation are alternatives but require a large number of simulations to be efficient, which makes the study of spatially-explicit simulation models computationally expensive (Csilléry et al. 2010; Hartig et al. 2011). Inverse modelling techniques have been used with success to calibrate a large range of spatially-explicit simulation models, generally in association with a global sensitivity analysis (Kramer-Schadt et al. 2004; Wiegand et al. 2004; Beaudouin et al. 2008; Martinez et al. 2011).

The modelling of the processes underlying spatial patterns is greatly affected by parameter estimation because of non-linear dependencies, threshold effects, and/or negative feedbacks. Consequently, it is crucial to use accurate parameter estimates in order to point

the information which is most lacking for further reducing uncertainty in model predictions (Wiegand et al. 2004). Because not all parameters have the same influence on model output, it can be useful to determine whether uncertainties in particular parameter values lead to large uncertainties in the output, i.e., it is useful to determine which parameter estimates warrant the most attention. This is done with sensitivity analysis, which measures the impact of input factors on a selected output (Saltelli et al. 2000). Several methods are available for sensitivity analysis and can be classified into two categories: local sensitivity analyses (one-at-a-time methods, such as FAST or Sobol' methods), in which the effect of the variation of a single factor is estimated, and global sensitivity analyses (e.g., the Morris method), in which the output of a factor is studied when all the factors are varying (Cariboni et al. 2007). Selection of sensitivity analysis method depends first on the scientific question asked, then on the number of parameters under consideration and on the existence of non-linear effects or interactions between parameter effects. The use of sensitivity analysis to investigate how uncertainties in parameter values affect a model's inferential power is an integral part of modelling (Cariboni et al. 2007).

However, an additional difficulty in studying spatially-explicit simulation models is that the biological processes may respond differently depending on landscape composition and structure. For example, the importance of dispersal may be greater in fragmented than in homogeneous landscapes (Vinatier et al. 2012b). Disentangling the link between ecological processes and landscape composition and structure has been of particular importance in landscape ecology, for example, respect to the question of the relative impact of habitat loss and fragmentation on population dynamics (Wiegand et al. 1999, 2005; Fahrig 2003). As before, sensitivity analyses can provide insight because such analyses provide a convenient framework for understanding the behaviour of complex mechanistic models. However, sensitivity analysis of spatially-explicit simulation models is especially challenging because there is no straightforward method to include landscape characteristics into the analysis.

We present here a new approach for disentangling the complex link between ecological processes and landscape composition and structure. The approach

combines sensitivity and multivariate analyses of a spatially-explicit simulation model. To demonstrate this approach, we use a tritrophic system that includes a pest, its parasitoid, and its host plant and for which a spatio-temporal model has been developed (Vinatier et al. 2012a). The development of the model, called Mosaic-Pest, was motivated by the need to design landscape-scale methods to control an important pest of oilseed rape, the pollen beetle *Meligethes aeneus*, and also to manage an important parasitoid of the beetle, *Tersilochus heterocerus*. Mosaic-Pest considers landscape composition because both the pollen beetle and parasitoid are sensitive to the proportion of semi-natural habitats (i.e., woodlands and grasslands), which are overwintering sites for the pollen beetle and nectar sources for the parasitoid (Rusch et al. 2011). Mosaic-Pest also considers agricultural practices that affect pest densities, such as crop rotation (Rusch et al. 2011), ploughing (Nilsson 2010) and precocity of rape varieties (Cook et al. 2007). The choice of this case study was also motivated by the availability of previously collected data on pollen beetle densities and parasitism rates in farmer fields located at the centre of 35 maps differing in landscape composition and structure (Rusch et al. 2011).

The overall goals of this research were to develop a general method for studying the relationship between parameters and landscape composition and structure with spatially-explicit simulation models and to develop a general method for improving the estimation of parameter values. With respect to our tritrophic study system, the specific objectives were (i) to assess via a global sensitivity analysis the impact of parameter uncertainties on population densities of pollen beetles and parasitism rates, (ii) to narrow the range of confidence intervals for parameters obtained in the literature by using a variance decomposition technique for the comparison of simulated and observed data, and (iii) to determine how the main effects of biological parameters vary with landscape composition via sensitivity and multivariate analyses.

## Methods

### Overview of the model

The Mosaic-Pest model was described in detail by Vinatier et al. (2012a) and in Appendix 1 (Supple-

mentary Material). It simultaneously represents crop planting and development, and host and parasitoid dynamics and their interactions. The model is spatially explicit, i.e., it is based on a  $100 \times 100$  grid of 50-m cells. The model considers four different habitat types (oilseed rape fields, previous oilseed rape fields, woodlands, and grasslands) because of their different influences on insect overwintering, feeding, and egg laying. The model was developed with Netlogo software (Wilensky 1999).

In the Mosaic-Pest model, populations of pollen beetles are divided into five stages: egg, 1st instar larva, 2nd instar larva, pupa, and adult. The adult changes status during its life cycle from dispersing towards overwintering sites, overwintering, dispersing for feeding, dispersing for egg laying, to egg laying and finally to death. Populations of parasitoids are divided into immature and adult stages, and adult parasitoids change status as described for pollen beetles, except for dispersing towards overwintering sites status. At the end of oilseed rape-growing season, the new generation of parasitoids remains as diapausing adults within host cocoons in the soil, whereas new adults of pollen beetles disperse to the overwintering sites, i.e., woodlands. The size of populations of each species varies with time according to transition probabilities depending on their stage, status, and location. Parasitism of pollen beetles is described by a Thompson model (Jourdeuil 1960; Mills and Getz 1996) that represents the functional response of the parasitoid, i.e. the rate at which the hosts are parasitized as a function of hosts and parasitoids densities. Dispersion events of populations occur according to a cell-to-cell redistribution mechanism, depending on both a dispersal kernel and relative attractiveness of habitat elements. Survival probability of adults depends on the power of the distance covered by the population during dispersal.

This model includes 32 parameters describing the demographics and dispersal of the pest and the parasitoid (Table 1). Parameters controlling demographic processes are densities of insects in overwintering sites ( $N_0^{\text{Ma}}$ ), temperature threshold for emergence ( $\theta^{\text{Ma}}$ ), proportion of the population surviving at emergence ( $\pi^{\text{Th,immature,NT}}$  or  $\pi^{\text{Th,immature,ploughing}}$  if ploughing is applied) and at each stage transition ( $\pi^{\text{Ma,adult,egg,larva,or pupa}}$ ), and duration of each stage ( $\delta^{\text{Ma,adult,egg,larva, or pupa}}$ ). Parameters controlling dispersal are the maximum dispersal distance (in meters) travelled by insects before feeding ( $\omega^{\text{Ma,adult}}$ ), the proportion of individuals that



**Table 1** Model parameters, range of values used in the sensitivity analysis, sensitivity indices, and corresponding references

Parameter	Abbreviation	Unit	Uncertainty ranges selected for sensitivity analysis	Importance of parameters regarding the two outputs (sensitivity indexes)	Parasitism rate		Best value for pollen beetle density and parasitism rates	Reference
					Pollen beetle density	Parasitism rate		
<b>Pest demographic parameters</b>								
Density <sub>overwintering</sub>	$N_0^{Ma}$	–	200–1,000	0.1	0.1	200	Rusch et al. (2011)	
Threshold	$\theta^{Ma}$	°C	9–21	2	1.9	15	Nilsson (1988a)	
Emergence	$\pi^{Ma,winter}$	–	0.4–0.8	<b>10.8</b>	2.2	0.7	Cook et al. (2004)	
StageTransition <sub>egg</sub>	$\pi^{Ma,egg}$	–	0.6–1	4.9	3.2	0.9	Cook et al. (2004)	
StageTransition <sub>1st instar larvae</sub>	$\pi^{Ma,11}$	–	0.4–0.8	1.5	2.8	0.8	Cook et al. (2004)	
StageTransition <sub>2nd instar larvae</sub>	$\pi^{Ma,12}$	–	0.4–0.8	0.9	3	0.5	Cook et al. (2004)	
StageTransition <sub>pupa</sub>	$\pi^{Ma,pupa}$	–	0.6–1	0.7	4.5	0.7	Cook et al. (2004)	
StageDuration <sub>egg</sub>	$\delta^{Ma,egg}$	days	6–14	1.9	3.1	8	Cook et al. (2004)	
StageDuration <sub>1st instar larva</sub>	$\delta^{Ma,11}$	days	2–6	3.1	1.1	5	Cook et al. (2004)	
StageDuration <sub>2nd instar larva</sub>	$\delta^{Ma,12}$	days	3–7	2.4	6.4	6	Cook et al. (2004)	
StageDuration <sub>pupa</sub>	$\delta^{Ma,pupa}$	days	6–14	1.7	5.7	10	Cook et al. (2004)	
StageDuration <sub>adult</sub>	$\delta^{Ma,adult}$	days	36–84	3.1	2.5	60	Cook et al. (2004)	
Fecundity	$\phi^{Ma}$	–	3–7	3.9	2.2	5	Nilsson (1988b)	
<b>Dispersal parameters</b>								
FlightDuration <sub>feeding</sub>	$\delta^{Ma,feeding}$	days	6–14	4.9	1	14	Cook et al. (2004)	
FlightDuration <sub>egg-laying</sub>	$\delta^{Ma,egglaying}$	days	0–4	3.3	2.2	2	Cook et al. (2004)	
FlightSurvival	$\tau^{Ma}$	m <sup>-1</sup>	0.996–1	<b>20.4</b>	1	0.999	–	
FlightKernel	$\beta^{Ma}$	m <sup>-1</sup>	1–5	3.4	5.3	1	Taimr et al. (1967)	
FlightWindow <sub>before feeding</sub>	$\omega^{Ma,adult}$	m	100–500	<b>10.1</b>	1	300	Rusch et al. (2011)	
FlightWindow <sub>after feeding</sub>	$\omega^{Ma,feeding}$	m	7,200–16,800	2.3	2.2	9,600	Rusch et al. (2011)	
<b>Parasitoid demographic parameters</b>								
Density <sub>overwintering</sub>	$N_0$	–	500–2,500	0.1	0.7	400	–	
Threshold	$\theta^{Th,immature}$	Day–degrees	360–840	0.3	1	70	Jourdheuil (1960)	
Emergence	$\pi^{Th,immature,NT}$	–	0.1–0.5	0.6	1.3	0.2	Herrström (1964)	
Emergence <sub>ploughing</sub>	$\pi^{Th,immature,ploughing}$	–	0.2–1	0	<b>33.4</b>	0.0	Nilsson (2010)	
StageDuration <sub>immature</sub>	$\delta^{Th,immature}$	days	50–90	0.4	0.5	0.5	Jourdheuil (1960)	
StageDuration <sub>adult</sub>	$\delta^{Th,adult}$	days	24–56	0.3	0.4	50	Jourdheuil (1960)	
AttackRate	$\rho^{Th}$	–	50–250	0.4	0.6	250	–	
<b>Dispersal parameters</b>								
FlightDuration <sub>feeding</sub>	$\delta^{Th,feeding}$	days	2–10	0.2	0.7	8	–	
FlightDuration <sub>egg-laying</sub>	$\delta^{Th,egglaying}$	days	0–4	0.2	0.1	1	–	
FlightSurvival	$\tau^{Th}$	m <sup>-1</sup>	0.996–1	0.1	0.3	0.999	–	

**Table 1** continued

Parameter	Abbreviation	Unit	Uncertainty ranges selected for sensitivity analysis	Importance of parameters regarding the two outputs (sensitivity indexes)		Best value for pollen beetle density and parasitism rates	Reference
				Pollen beetle density	Parasitism rate		
FlightKernel	$\beta^{Th}$	$m^{-1}$	1–5	0.1	0.4	3	–
FlightWindow <sub>before feeding</sub>	$\omega^{Th,adult}$	m	100–500	0.1	0.1	500	Rusch et al. (2011)
FlightWindow <sub>after feeding</sub>	$\omega^{Th,feeding}$	m	1,000–2,000	0.2	0.5	1,750	Rusch et al. (2011)

Values in italics correspond to the most influential parameters; a most influential parameter was one whose value for the Morris  $\mu^*$  was among the three highest for at least one map. Values in bold correspond to the most influential parameters based on the sensitivity index of an ANOVA on  $R^2$  values of the linear regression between observed and simulated data. Parameters lacking a reference were set arbitrarily within a biologically reasonable interval

survive per meter travelled ( $\tau^{Ma}$ ), and the decrease in habitat attractiveness with distance travelled ( $\beta^{Ma,adult}$ ). Values for most of the parameters were obtained from the literature (Table 1), but some parameters were not present in the literature and others were present but with a large uncertainty around the estimated values.

*Observed data used for model initialisation and optimization*

The realism of the Mosaic-Pest model was increased by comparing simulation data with observed data. The observed data set consisted of pollen beetle densities and parasitism rates sampled along a transect in the central field of 35 different landscapes at the end of the flowering period during the years 2008 and 2009 [for more details on sampling and observations, see Appendix 2 (Supplementary Material)].

The observed data were collected in an agricultural territory located in northwestern France (49°25'N, 1°12'E) and consisting of landscapes of arable land, small woodland fragments, hedgerows, and grasslands. We considered 35 non-overlapping maps of 2.5-km radius centred on an oilseed rape field within the region. The maps were generated from aerial photographs (BD ORTHO®, IGN, 2004). Each map contained different proportions of winter oilseed rape, other crops, grassland, and woodland, with landscapes ranging from simple (i.e., <5 % semi-natural habitats) to more complex (i.e., up to 58 % semi-natural habitats). Semi-natural habitats were grasslands, woodlands. Agricultural practices (i.e., crop allocation, rotation sequences, and ploughing) were determined based on intensive field inspection (Rusch et al. 2011) and on the official GIS-based system used by farmers to declare crops and apply for subsidies (Registre Parcellaire Graphique, Reglement communautaire no. 1593/2000). The landscapes were then rasterized using a 50 × 50 m resolution. Examples of the resulting maps are presented in Appendix 3 (Supplementary Material).

The simulations were conducted so that the modelled system was as similar as possible to the real conditions: GIS polygons representing cultivated fields, forests, and pastures were rasterized, and observed crop allocation, rotation sequences, and ploughing were applied to the model. For initialising insect populations, we assigned to every cell of the grid the same number of parasitoids or pollen beetles,

which were at the immature stage for parasitoids and at the adult stage for pollen beetles (the initial densities were considered as a parameter in the sensitivity analysis). Every simulation began on 1 January, and simulations were run for 300 days, from the beginning of the overwintering period to the emergence of new pollen beetle adults.

### Sensitivity analyses and inverse parameter estimation

We propose a five-stage approach for improving the estimation of parameter values, analysing the sensitivity of complex models to biological parameters, and assessing interactions between influence of biological parameters and landscape conditions while keeping the number of simulations reasonably small (Fig. 1). In stage 1, well-established methods for sensitivity analysis of complex models (i.e., the Morris method) are used. In stage 2, results of the sensitivity analysis are analysed to reduce the range of uncertainty surrounding important and poorly estimated biological parameters and thus to make the model more precise, accurate, and unbiased. In stage 3, the most influential parameters are selected on the basis of the Morris method. In stage 4, parameters that are similarly influenced by the landscape are identified. In step 5, landscape characteristics that substantially affect the key parameters' influences are determined. Statistical analyses were conducted with R software (R Development Core Team 2010) using the base, the package "sensitivity" for the construction of the sensitivity plan, the package "Ade4" for multivariate analyses, and the package "RNetlogo" to embed Netlogo into the R environment (Thiele and Grimm 2010).

#### *The Morris method for sensitivity analysis of biological parameters (stage 1)*

For stage 1, we used the Morris screening method (Morris 1991) to identify the parameters that had the most influence on the variability of the two output variables in the observed data set, which were densities of pollen beetles and parasitism rates. The Morris method is suitable for models that have many input parameters and that are computationally expensive (Cariboni et al. 2007). We preferred the Morris method over other parameter search methods, such as the Latin hypercube sampling, because the latter

encounters computational limitations when number of parameters exceeded 10–15 (Hartig et al. 2011). The Morris method identifies influential parameters with a relatively low number of model evaluations.

Following the Morris method, the possible range (defined according to the uncertainty surrounding estimates in the literature) of each of the 32 parameters was divided into five levels with a resolution  $\Delta$  (see Table 1). A starting point was defined by sampling a set of start values within the possible values for all parameters. From this point, a trajectory was defined by increasing (or decreasing) each parameter in turn with a step size of  $\Delta$  and the model was run at each of the  $k + 1$  steps of the trajectory. This procedure was repeated 40 times to explore a significant fraction of the total uncertainty space, thus leading to  $40 \times (32 + 1) = 1,320$  sensitivity runs. Furthermore, each sensitivity run is repeated for the 35 maps, leading to  $1,320 \times 35 = 46,200$  simulations.

The elementary effect ( $EE_i$ ) of a parameter  $\theta_k$  on a trajectory  $j$  was calculated as:

$$EE_{i,j}(\theta_k) = \frac{y_j(\theta_k + e_i \Delta_k) - y_j(\theta_k)}{\Delta_k} \quad (1)$$

with  $e_i = \pm 1$  and  $y_j$  the model output.

The mean ( $\mu^*$ ) and the standard deviation ( $\sigma$ ) of the absolute values of the elementary effects over the trajectories were used as sensitivity measures to ascertain the importance of the factors. A large  $\mu^*$  indicates a large overall influence of the parameter and a large  $\sigma$  implies a dependency of the parameter on the value of the other parameters through non-linear or interaction effects.

#### *Comparison between observed and simulated data (inverse modelling, stage 2)*

For stage 2, we selected among the 1,320 tested parameterizations those that optimized the relationship between observed data and simulated data for the two output variables (pollen beetle densities and parasitism rates) across all landscape maps. This was necessary because no single parameterization yielded a good fit of the model to both output variables. We preferred considering this relationship rather than comparing directly the squared differences between predicted and observed variables because the model is devoted to exploratory analyses, i.e. our objective was

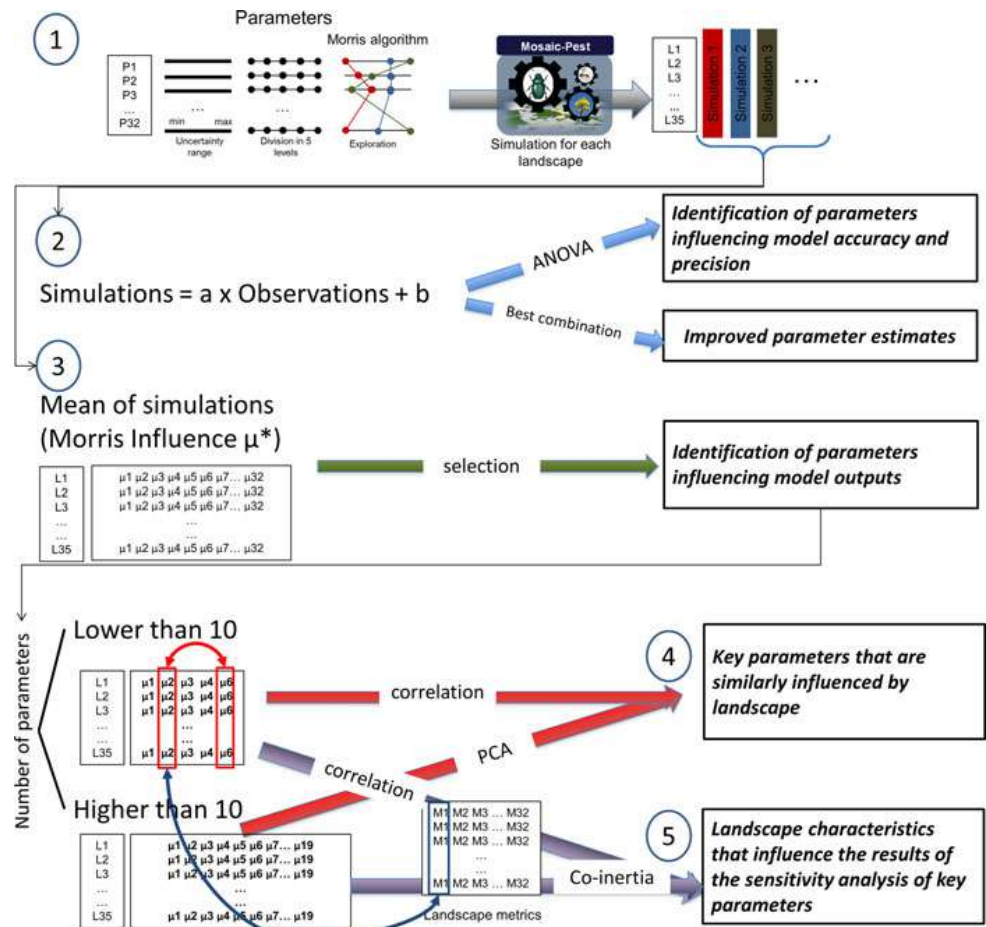
to analyse how the system responds to landscape configuration, rather than prediction analyses, i.e. predicting without error the response variables for a given map. Consequently, bias was not considered a problem and precision was less important than accuracy. For each sensitivity run, which corresponds to a set of 35 simulated map values, we fitted a linear model on simulated versus observed data for pollen beetle and parasitism rate separately. The linear model of the form  $Y = aX + b$  was used to estimate the realism of the Mosaic-Pest model, where  $Y =$  simulation data,  $X =$  observation data. Good accuracy leads to a slope close to 1, good precision leads to a high  $R^2$  and absence of bias is reflected, when the slope is close to one, by the intercept being close to 0.

We first selected the parameterization for which (i) the linear model was significant ( $P < 0.05$ ) for both output variables in the data set, (ii) the slope and the intercept were non-significantly different from 1 and 0, respectively, and (iii) the value of the  $R^2$  was higher

than 0.2. On the basis of this first selection of parameters' combinations, we selected the unique combination of parameters that was both in the tenth highest levels of  $R^2$  for pollen beetles and parasitism rates, respectively. We preferred the linear model to the Spearman's or the root-mean-square deviation statistics because the latter two were less discriminatory for our data set (data not shown).

We conducted a multiple ANOVA analysis on the 1,320 sensitivity runs to test the overall influence of each parameter on this linear model, taking separately the  $R^2$ , intercept, and slope of the linear model as a response variable. Each biological parameter was treated as an input factor with five modalities (the five levels along the range of possible parameter values). The normality of the response variable and residuals was tested using the Shapiro–Wilk test. Following Monod et al. (2006), a sensitivity index of each factorial term (biological parameter) was calculated on the basis of its sum of squares to assess the relative

**Fig. 1** Overview of the five-stage approach used in the study.  $P_i$ ,  $L_i$ ,  $\mu_i$ , and  $M_i$  correspond to the abbreviate of the  $i$ th parameter, landscape, Morris influence, and landscape metric, respectively. *Black boxes* illustrate the objective (in *italics*) of each intermediate stage of the approach. *Thin arrows* illustrate the transition steps of the approach. *Large coloured arrows* illustrate (i) the statistical (ANOVA, PCA and co-inertia for Principal Component and co-inertia analyses, respectively, correlation for multiple correlation using Pearson's coefficient) and (ii) the mechanistic (the Mosaic-Pest logo figures the model functioning) parts of the approach. (Color figure online)



influence of each parameter on the relationship between the observed and simulated data.

#### *Selection of the most influential parameters (stage 3)*

In stage 3 we identified the parameters with the strongest influence on the model outputs. To this end we determined the parameters for which the values of the Morris  $\mu^*$  were among the three highest for at least one map. The ordered sum of the Morris  $\mu^*$  for the different maps showed that for almost all maps only the three highest  $\mu^*$  were the most important, whereas the others were closed to zero. The Morris method enabled us to estimate the mean  $\mu^*$  and the standard deviation  $\delta$  of the elementary effect of each parameter on the model's outputs, i.e., densities of pollen beetles and parasitism rates.

Note that the parameters identified as influential in stages 2 and 3 were not necessarily the same because stage 3 focused on the parameters that influenced value of model output for the highest number of landscapes, whereas stage 2 focused on the parameters that influenced model accuracy and precision when compared against real observations. Because observations were made in landscapes chosen specifically to vary in terms of landscape factors (proportion of different land uses), a large effect of a biological parameter on the agreement between observations and simulations indicated that this parameter plays a key role in the relationship between landscape factors, pests, and parasitoids.

#### *Effect of landscape composition on the influence of biological parameters (stage 4)*

For stage 4, we compared the medians of the values for the Morris  $\mu^*$  for biological parameters in each pair of maps to determine whether the influence of parameters shared the same behaviour across landscape maps. This analysis was based on (i) multiple correlation analysis between parameter influences for a low number of key parameters, or (ii) principal component analysis (PCA) of parameters influences for a high number of key parameters (we highlighted groups of biological parameters depending on the species and the type of parameter, i.e., dispersal or demographic). The box-cox transformation ( $\lambda = 2$ ) was applied to the values of Morris'  $\mu^*$  for normalization, as no a priori exists on the distribution of this variable.

#### *Determining landscape characteristics that influence values of Morris $\mu^*$ parameters (stage 5)*

For stage 5, we used multiple correlation or multivariate analyses to understand the relationships between the values of Morris'  $\mu^*$  for parameters and landscape metrics on the two outputs of the model (densities of pollen beetles and parasitism rates). The choice of multiple correlation methods or multivariate analyses depends on the number of influent parameters. In our case, we considered arbitrarily a threshold of ten parameters. For a parameters' number exceeding this threshold, combination of correlations between variables was too important to be considered in a synthetic table whereas they have been calculated (data not shown) and the use of PCA as a more aggregative techniques was preferred.

Landscape metrics were computed on each of the 35 maps via buffer analyses (Ricci et al. 2009; Rusch et al. 2011) [Appendix 3 (Supplementary Material)]. We considered the proportion of four habitat classes (i.e., woodland, grassland, previous-year oilseed rape fields, and oilseed rape fields) in eight circular zones with radii ranging from 250 to 1750 m around the centre of each map. The matrix of landscape metrics by map (i.e., a data set of 32 *Landscape metrics*  $\times$  35 maps) was named the *Landscape metrics* data set.

For a number of key parameters lower than ten, the correlation between the value of Morris'  $\mu^*$  for a given parameter and a given *Landscape metric* was calculated across landscapes to determine whether the influence of a given parameter on the model output depended on the conditions (in terms of landscape composition) under which it was evaluated and which habitats influenced the model's response to biological parameters and at what scale. For a number of key parameters higher than 10, we used multivariate analyses to describe the relationship between parameters and landscape. The values of Morris'  $\mu^*$  and *Landscape metrics* data sets were first re-projected separately using a principal component analysis (PCA) to define aggregated variables that represented groups of biological parameters and descriptors of landscape complexity. Subsequently, a co-inertia analysis was applied on the two PCAs. The co-inertia analysis is a multivariate method that identifies trends or co-relationships in multiple data sets that contain the same samples. The significance of co-inertia analyses was tested using the Monte-Carlo random

permutation test. The ways in which groups of parameters (demographic or dispersal parameters for each species separately) and landscape composition descriptors (buffer radii and habitat types) were related to co-inertia axes were described.

## Results

### Sensitivity analysis using Morris method and selection of the most influential parameters (stage 1 and stage 3)

Of the 32 parameters of the Mosaic-Pest model that were tested, six and 19 parameters were identified as influential (i.e., they had Morris  $\mu^*$  values that were among the three highest for at least one map) for pollen beetle densities and parasitism rates, respectively (Table 1). The six parameters for pollen beetle density were the pest dispersal parameters  $\omega^{\text{Ma,adult}}$ ,  $\tau^{\text{Ma}}$ , and  $\beta^{\text{Ma}}$  and the pest demographic parameters  $\pi^{\text{Ma,winter}}$ ,  $\delta^{\text{Ma,adult}}$ , and  $N_0^{\text{Ma}}$ . The 19 parameters for parasitism rates included both pest and parasitoid dispersal and demographic parameters. Some parameters did not influence pollen beetle density or parasitism rate because their uncertainty level (estimated from the literature) was small and/or their influence in the model (as characterised by the Morris method) was negligible (e.g.,  $\delta^{\text{Ma}}$  and  $\pi^{\text{Ma}}$  of pollen beetles eggs, larvae, and pupae).

Figure 2 shows the relative importance of the values of Morris'  $\mu^*$  and  $\delta$  for each parameter. The large size of box plots indicates that Morris  $\mu^*$  was highly variable across map patterns, highlighting that landscape composition of maps greatly affected parameter influence (Fig. 2a). Spread of the  $\delta$  values across landscape maps was low for  $\pi^{\text{Ma,winter}}$  and  $N_0^{\text{Ma}}$  parameters and high for dispersal parameters and  $\delta^{\text{Ma,adult}}$  (Fig. 2b), indicating that the interactions between other parameters and  $\pi^{\text{Ma,winter}}$  or  $N_0^{\text{Ma}}$  was low regardless of the landscape composition while the importance of the interaction between the influence of dispersal parameters of  $\delta^{\text{Ma,adult}}$  and the other parameters depended on the landscape context. The boxplot medians of  $\delta$  parameters among biological parameters mirrored the temporal sequence of events in the model, i.e.,  $\delta$  values progressively increased for parameters controlling events during the overwintering period, dispersal events, and then adult death.

Because the Morris  $\delta$  indicates non-linear and interaction effects, this is not surprising: the value of  $\delta$  increased with the cumulative number of events.

### Inverse modelling (stage 2)

When a linear model was fitted to the relationship between observed data and each run of the sensitivity analysis plan,  $R^2$  values ranged from 0.15 to 0.43 for pollen beetle densities and from 0.01 to 0.25 for parasitism rates. The ANOVA models accounted for more than 80 % of the variability of each response variable. Three parameters for pollen beetle density and one parameter for parasitism rate had sensitivity indices  $>10$  % (Monod et al. 2006) (Table 1). Figure 3a shows how parameter levels of  $\tau^{\text{Ma}}$  and  $\omega^{\text{Ma,adult}}$  affected  $R^2$ , intercept, and slope values of the linear regression model, with an optimum of  $0.999 \text{ m}^{-1}$  for  $\tau^{\text{Ma}}$  and 300 m for  $\omega^{\text{Ma,adult}}$ . The optimum for the parameter  $\pi^{\text{Th,immature,ploughing}}$  was 0.2, i.e., the presence of ploughing destroyed 80 % of the pupae (Fig. 3b). The parameter  $\pi^{\text{Ma,winter}}$  was not presented in Fig. 3a because its influence on the relationship between observation and simulation was not clearly emphasized by the graph. Some parameters, such as  $N_0^{\text{Ma}}$ ,  $\delta^{\text{Ma,adult}}$ , and  $\beta^{\text{Ma}}$ , greatly affected pollen beetle densities as determined by the Morris method (Fig. 2) but had little effect on the agreement between the simulated and observed pollen beetle data sets [sensitivity indices below 5 % (Monod et al. 2006)], indicating that these parameters were independent of landscape, i.e., they had a high influence on the absolute value of pollen beetle density but a weak influence on the variation in these densities across maps.

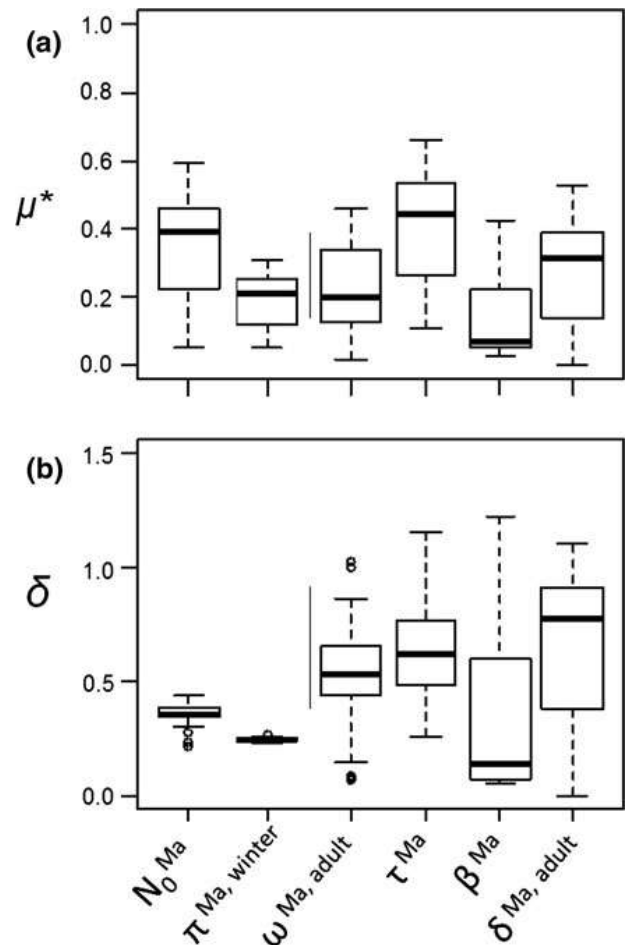
A total of 23 parameterizations were selected on the basis of a significance of the linear model, the non-significance of slope and intercept in comparison to 1 and 0, respectively, and a  $R^2$  value higher than 0.2. Table 1 and Fig. 4 show parameterizations that most improved the prediction of observations by Mosaic-Pest on the basis of the  $R^2$  of the linear regression between observed and simulated data for pollen beetle density ( $n = 35$ ,  $Y = 1.05 X + 2.4$ ,  $R^2 = 0.44$ ,  $P < 0.001$ ) and for parasitism rate ( $n = 35$ ,  $Y = 0.8 X + 2.2$ ,  $R^2 = 0.25$ ,  $P = 0.03$ ). The root mean squared error of standard deviation was 90 and 15 for pollen beetle density and parasitism rates, respectively.

Effect of landscape composition on the influence of biological parameters and identification of the landscape characteristics involved (stage 4 and stage 5)

For pollen beetle density, the value of Morris'  $\mu^*$  for demographic parameters was highly correlated across maps ( $r > 0.8$ ,  $P < 0.05$  in all cases). The influence of dispersal parameters such as  $\tau^{\text{Ma}}$  and  $\beta^{\text{Ma}}$  were negatively correlated ( $r < -0.6$ ,  $P < 0.05$ ) across landscape maps. The influence of demographic parameters was not correlated with dispersal parameters, except that the influence of  $N_0^{\text{Ma}}$  was related to the influence of  $\omega^{\text{Ma,adult}}$  ( $r = 0.64$ ,  $P < 0.05$ ).

Concerning the link between the influence of biological parameters and landscape metrics computed at different distances around the central field, the response to landscape metrics differed between one group of demographic parameters ( $N_0$ ,  $\pi$ , and  $\delta$ ) and one group of dispersal parameters ( $\omega$ ,  $\tau$ , and  $\beta$ ) but the response of each parameter within one group was the same. In Fig. 5, we present two examples of parameters, one ( $\pi$ ) belonging to the group of demographic parameters and the other ( $\tau$ ) belonging to the group of dispersal parameters. The influence of  $\pi$  was positively related to the proportion of woodlands ( $r > 0.6$ ,  $P < 0.05$  in all cases) but only for buffer radii  $< 1,000$  m (Fig. 5a). The influence of  $\tau$  was negatively related to the proportion of oilseed rape and of previous oilseed rape in the landscape ( $r < -0.6$ ,  $P < 0.05$  in all cases) and positively related to the proportion of grasslands and woodlands in the landscape ( $r > 0.6$ ,  $P < 0.05$  in all cases) for buffer radii  $> 750$  m (Fig. 5b).

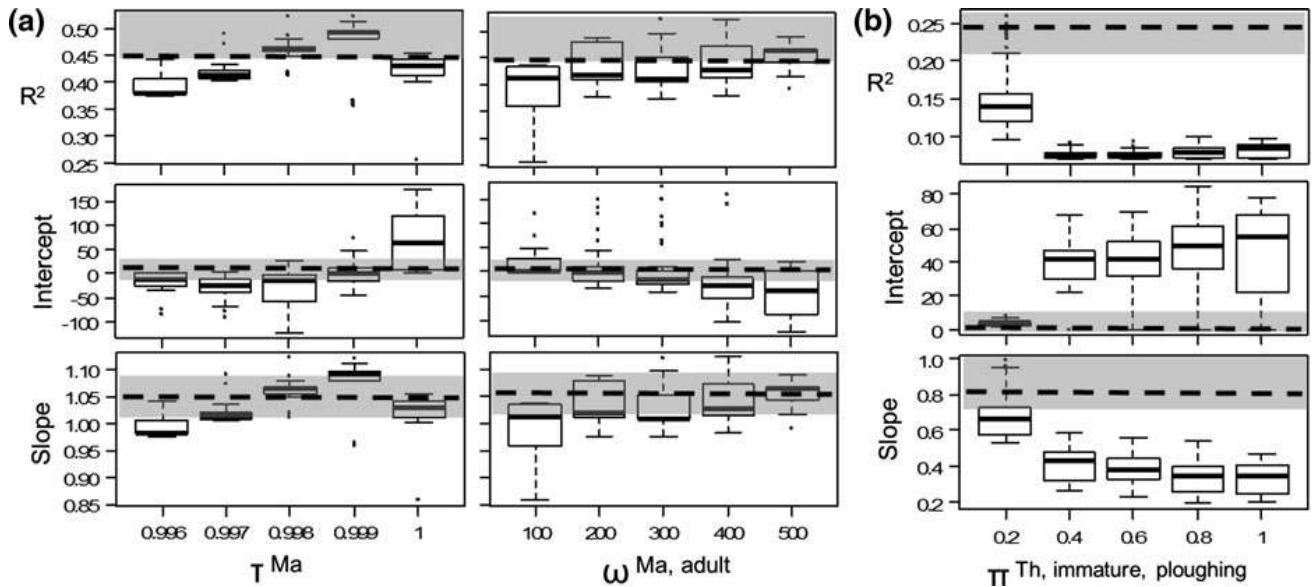
Given the large number of interacting parameters for parasitism rates, inertia analyses on the basis of PCAs were used rather than multiple Spearman's rank correlations to understand the relationships between groups of parameters and landscape composition. The first factorial plane of the PCA on the values of Morris'  $\mu^*$  accounted for 78.1 % of the total inertia. This indicates that the influences of demographic parameters of immature pollen beetles and parasitoids were highly correlated across landscape maps ( $r > 0.8$ ,  $P < 0.001$  in all cases), except for  $\delta^{\text{Ma}, 12}$  of the pollen beetle and  $\theta^{\text{Th,immature}}$  and  $\delta^{\text{Th,immature}}$  of parasitoids, which were correlated in a different group ( $r > 0.6$ ,  $P > 0.05$ ) (Fig. 6a). Dispersal parameters were also correlated in two distinct groups, one corresponding to



**Fig. 2** Box plots ( $n = 35$ ) for the values of the Morris **a**  $\mu^*$  and **b**  $\delta$  across landscape maps for pollen beetle densities. Only the six most influential parameters are presented (a most influential parameter was defined as one whose value for the Morris  $\mu^*$  was among the three highest for at least one map). Each *boxplot* contains the lower whisker, the lower hinge (first quartile), the median, the upper hinge (third quartile) and the extreme of the upper whisker. The whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box

pollen beetle parameters and one to parasitoid parameters ( $r > 0.6$ ,  $P < 0.001$  in all cases) (Fig. 6a).

Co-inertia analysis was significant ( $P = 0.005$ , based on 999 repetitions of Monte-Carlo simulations). The co-inertia analysis of the PCA of the values of Morris'  $\mu^*$  projected on the PCA of the *Landscape metrics* data set explained 76.3 % of the variability (Fig. 6a). The first factorial plane of the PCA on the *Landscape metrics* data set accounted for 59.2 % of the total inertia (Fig. 6b). Not surprisingly, landscape metrics describing the proportion of a given habitat at several buffer sizes were correlated among themselves.



**Fig. 3** Box plots of the coefficients of the linear model comparing observed and simulated data for **a** pollen beetle densities and **b** parasitism rates as a function of the values of selected biological parameters.  $n = 250$  (the total number of simulations per set of 35 maps divided by the five levels). The three parameters were chosen according to the sensitivity indexes on the linear model. Rectangles in grey indicate the range of coefficient values considered acceptable for selecting

the best linear model, i.e. that are non-significantly different from 1 and 0 for the slope and intercept, respectively, and that are higher than 20 % for the  $R^2$ . The dashed lines indicate the slope, intercept, and  $R^2$  of the best linear model. Each boxplot contains the lower whisker, the lower hinge (first quartile), the median, the upper hinge (third quartile) and the extreme of the upper whisker

For the relationships between the *Landscape metrics* data set and the values of Morris’  $\mu^*$ , it appeared that dispersal parameters of parasitoids ( $r > 0.6$ ,  $P < 0.05$ ) were related to grasslands whereas demographic parameters of pollen beetles were related to woodlands ( $r > 0.6$ ,  $P < 0.05$ ), except for three parameters ( $\delta^{Ma,12}$  of pollen beetle and  $\theta^{Th,immature}$  and  $\delta^{Th,immature}$  of parasitoids) (Fig. 6a, b). Two dispersal parameters of pollen beetles,  $\omega^{Ma,adult}$  and  $\beta^{Ma}$ , were linked to the proportion of previous oilseed rape fields at distances  $< 1,000$  m and to the proportion of oilseed rape fields at distances up to 750 m, respectively ( $r > 0.6$ ,  $P < 0.01$ ). Considering multicollinearities between buffers of a given habitat, no important distance effect was evident in the relationship between semi-natural habitats (woodlands and grasslands) and biological parameters.

**Discussion**

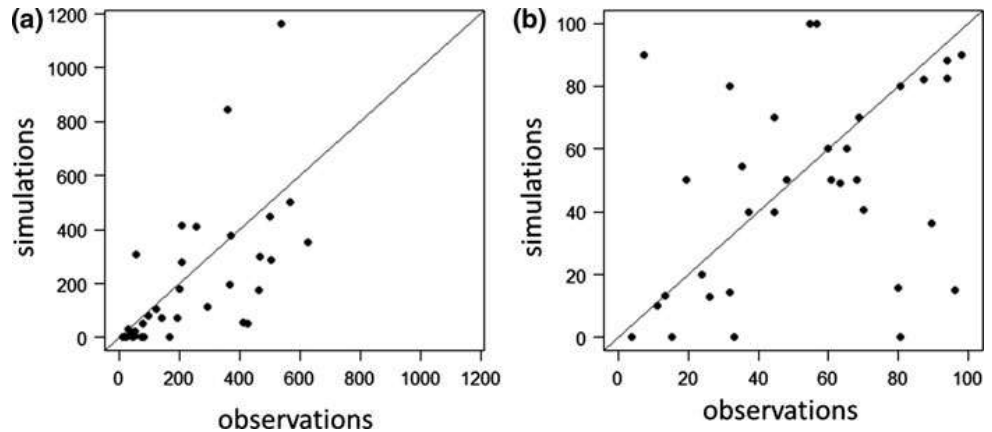
The Mosaic-Pest model integrates all the existing knowledge about the ecology of *M. aeneus* and *T. heteroceris* with regard to landscape effects. When

studying the relationships between simulated and observed values (Fig. 1, stage 2), we demonstrated that Mosaic-Pest is able to reproduce general trends of the system and of pollen beetle dynamics. The relationship between simulated and observed values was weaker for parasitism rates than for pollen beetle dynamics, and we therefore suspect that important processes need to be added in the model. As expected, the influences of dispersal parameters on model accuracy and precision were highly variable between the studied landscape maps because landscape composition affects distances between complementary and/or supplementary habitats. The effects of demographic parameters were also highly complex when they corresponded to processes occurring after dispersal events, such as duration of adult’s stage.

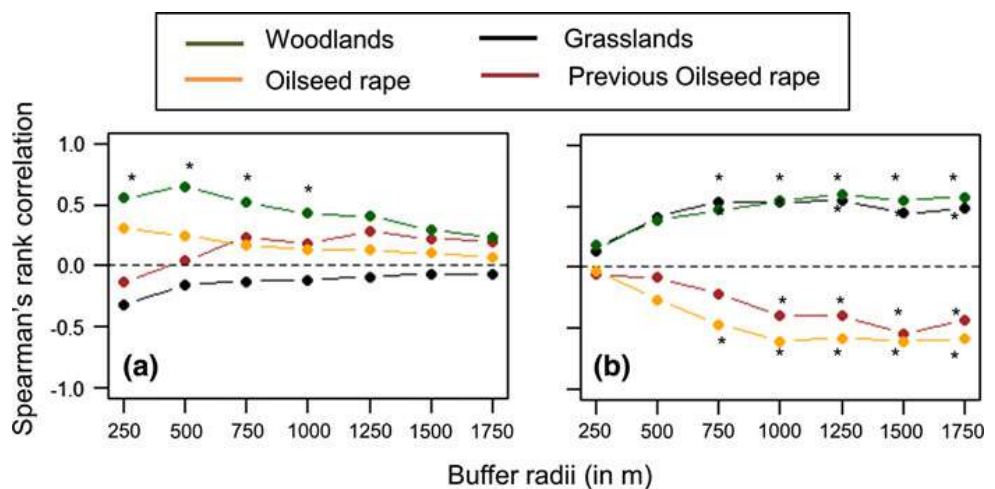
The sensitivity analysis of the Mosaic-Pest model highlights the importance of correctly specifying key parameters in studying the spatio-temporal dynamics of the pollen beetle. Among the 32 studied parameters, six and 19 greatly affect pollen beetle densities and parasitism rates, respectively. For example, the dispersal event before feeding is crucial and relies on parameters that should be re-examined. Moreover, the



**Fig. 4** Comparison of the predictions of the best parameter combination and the observation for **a** pollen beetle densities, and **b** parasitism rates simulated by the Mosaic-Pest model. *Solid line* indicates a perfect fit between observation and simulation



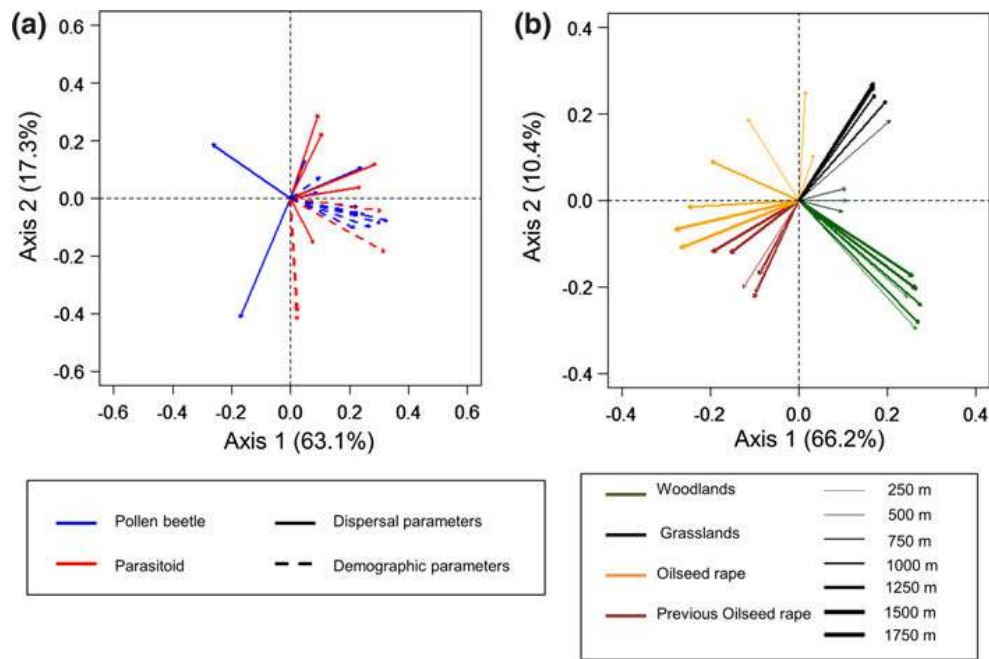
**Fig. 5** Spearman's rank correlation coefficient between the values for the Morris  $\mu^*$  and proportion of habitats between maps across buffer radii. Example of results for **a** Emergence and **b** FlightSurvival parameter of pollen beetles. *Stars* correspond to a Spearman's rank coefficient that is significantly different from 0 ( $P < 0.05$ )



proportion of adults able to emerge after overwintering is also a key parameter but is rather difficult to estimate despite recent studies on the overwintering period (Nilsson 2010). We found a higher number of influential parameters for parasitism rates than for density of pollen beetles because the former involved more processes. Moreover, the large size of box plots indicates that the value for Morris  $\mu^*$  was highly variable across landscape maps, which points out the importance of using several landscapes varying in habitat composition for sensitivity and validation procedures: the importance of parameters is greatly influenced by the landscape.

The use of multivariate analyses helps explain the influence of dispersal parameters in the system and their strong link with landscape composition. For pollen beetle densities, both proportion of individuals that survive per meter travelled and the decrease in habitat attractiveness with distance travelled depended

on the distance covered during dispersal. The influence of the proportion of individuals that survive per meter travelled was negatively related to the proportion of oilseed rape and previous oilseed rape in the landscape and was positively related to the proportion of grasslands and woodlands within buffer radii  $>750$  m. Two other dispersal parameters of pollen beetles, the maximum dispersal distance travelled by insects before feeding and the decrease in habitat attractiveness with distance travelled, were also linked to the proportion of previous oilseed rape fields. The results of co-inertia analysis suggest that an increase in the proportion of oilseed rape fields enhances the connectivity between fields and limits the importance of survival during dispersal. For example, the co-inertia analysis highlighted that dispersal parameters of parasitoids were related to grasslands, whereas demographic parameters of pollen beetles were related to woodlands. The effect of grasslands is reasonable



**Fig. 6** Projections on the first factorial plane of the co-inertia of **a** values for the Morris  $\mu^*$  for biological parameter and **b** landscape parameters. The output corresponds to parasitism rates. Results are issued from Mosaic-Pest model simulations

because grasslands enhance the spread of parasitoids in the landscape and consequently enhance parasitism rates. The influence of demographic parameters is related to woodlands because these habitats act as sources of pollen beetles, i.e., as hosts for parasitoids. This provision of resources is more important when distances are small.

These results indicate that dispersal parameters of parasitoids before feeding are crucial and that their estimates must be improved. This is especially the case for the quantitative link between the dispersal window of parasitoids and the proportion of grasslands in the landscape. Obtaining better estimates of how landscape affects parasitoid dispersal parameters should enhance the implementation of innovative pest management practices that affect demographic traits of pests and natural enemies because the efficiency of these practices will vary with landscape composition and structure, as pointed out by Tschamtko et al. (2005). The results on the relationship between parameter influence and landscape composition will help in identifying the landscapes in which a given biological parameter, e.g., density of overwintering insects or dispersal, will be the most important and will therefore enable researchers to focus on situations where the parameter is expected to show the greatest influence. For example, the Mosaic-

Pest model will help researchers select contrasting landscapes for calibrating dispersal processes. From a more applied perspective, knowledge of the relationship between landscape and parameter influence will facilitate the selection of a pest management strategy that focuses on a vulnerable part of the pest life cycle in a given landscape.

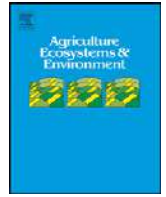
Studying the interaction between landscape composition and the influences of parameters on the output of a spatial model is novel and is important for understanding processes in landscape ecology. The co-inertia analysis helps us understand how the main effects of the model parameters on model outputs were affected by landscape composition. Co-inertia analyses are particularly suitable for studying ecological data tables in a symmetric way (ter Braak and Schaffers 2004); co-inertia analysis, for example, has been used to study the relationship between species composition and environmental variables sampled at the same location (Dray et al. 2003). We extended the use of co-inertia analyses to disentangle the complex links between landscape composition and ecological processes via a spatially explicit model. We hope that the new methodology presented here will help landscape modellers to go deeper in the understanding of the link between their model and landscape configuration.

The approach presented in our study, which combines Morris sensitivity analysis and variance decomposition techniques, provided useful results for our case study and could be part of the toolbox of inverse modelling techniques. The use of a given inverse modelling technique for calibrating model parameters is widely dependent on model computational time and number of parameters to assess. For example, Bayesian techniques (Martinez et al. 2011) or genetic algorithm (Stonedahl and Wilensky 2010) could be tested with success on some spatially explicit models with a low number of parameters. Global sensitivity analyses are the best techniques to calculate a synthetic measure of parameters influence, the parameters space uncertainty being explored via Morris method as presented in this paper, or latin hypercube sampling (Luxmoore et al. 1991) and a complete factorial plan (Beaudouin et al. 2008), depending on number of parameters evolved. For researchers interested in linking parameter influence to landscape metrics, different type of multivariate analyses could be found, depending as well on the number and the type of response variable to link (a complete review of the multivariate analyses could be found in Ramette 2007).

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## From IBM to IPM: Using individual-based models to design the spatial arrangement of traps and crops in integrated pest management strategies

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### ARTICLE INFO

#### Article history:

Received 11 April 2011

Received in revised form 5 October 2011

Accepted 7 October 2011

#### Keywords:

*Cosmopolites sordidus*

Banana weevil

Banana plantation

Crop residues

Pheromone trap

Movement

### ABSTRACT

The development of alternative pest-control strategies based on the spatial design of cropping systems requires a thorough understanding of the spatial links between the pest and its environment. Mechanistic models, especially individual-based models (IBMs), are powerful tools for integrating key behaviours, such as habitat selection and dispersal, with spatial heterogeneity. In this paper, we used an IBM calibrated and evaluated from real data to represent the spatial dynamics of the banana weevil in relation to the cropping system. We considered crop fragmentation and mass trapping as tools for suppressing pest numbers. Our simulation results showed that manipulating crop residues in the area surrounding each pheromone trap greatly improved trap efficiency. For an intensive banana plantation in fallow, traps were most effective when situated at the transition zone between banana area and fallow so as to maximize the trapping of weevils escaping the fallow. The model also showed that weevil numbers decreased when fragmentation of banana plantations was reduced.

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### 1. Introduction

Integrated pest management (IPM) strategies must consider key processes of insect behaviour, such as habitat selection, mating behaviour, dispersal, and predator–prey interactions (Petit et al., 2003; Roitberg, 2007). Habitat selection by insects is widely used in the “push–pull” control strategy in which pests are repelled (or “pushed”) from the crop and are simultaneously attracted (or “pulled”) by traps or a trap crop (Cook et al., 2007). Insect communication by sexual or aggregative pheromone is a widely used behaviour for mass trapping or mating disruption (Khan et al., 2008). The limited dispersal capacities of some insects are considered in a crop destruction strategy in which pests are unable to cross large areas of fallow to reach new habitats (Rhino et al., 2010). Perceptual ranges of insects are principal factors affecting predator–prey interactions (Bianchi et al., 2009). In banana agroecosystems, innovative IPM strategies are increasingly used to reduce the use of insecticides and herbicides. They may employ addition of cover crop (Duyck et al., 2011), inclusion of fallow in rotation sequences (Rhino et al., 2010), mass trapping (Rhino et al., 2010), and use of biological control agents (Akello et al., 2009; Padilla-Cubas et al., 2010). Understanding spatial ecology of pests

becomes necessary to develop and implement those innovative IPMs strategies.

Space has traditionally been ignored or treated as an implicit variable in pest-suppressive strategies (Kropff et al., 1995). With the recent emphasis on alternative methods of pest control, however, researchers have explicitly considered space as a means to link a pest to its environment (Potting et al., 2005). In the case of insect pests, alternative control strategies include those based on the spatial arrangement of traps (Yamanaka, 2007), of semi-natural habitats (Tscharrntke et al., 2007), or of alternative crops (Barari et al., 2005) in the landscape. Pheromone traps are used in mass trapping to maintain pest numbers within acceptable bounds (Witzgall et al., 2010). Beyond services provided by agroecosystems (Moonen and Barberi, 2008), semi-natural habitats (forests, hedgerows, field margins, fallows, and meadows) provide overwintering sites or alternative sources of pollen and nectar for insects and especially for parasitoids of pests (Musters et al., 2009), and these habitats therefore contribute to “top-down” pest control. Pheromone traps, semi-natural habitats, and alternative crops will greatly influence movements, egg-laying tactics, and mortality risks of insects and consequently their spatial distribution and related damages (Huffaker and Gutierrez, 1999). Because of its intrinsic complexity, the study of insect behaviour in spatially complex environments (i.e., in the real world) can benefit from spatially explicit, mechanistic models.

There is a growing interest in the use of such models as exploratory tools for the design of innovative cropping systems

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via spatial arrangement of resources (Kropff et al., 2001; Lo-Pelzer et al., 2010). These models, which consider landscape organization as a primary tool to suppress pest numbers, combine spatial processes in an integrated approach (Potting et al., 2005). They focus either on the population in “aggregated models” or on individuals in “individual-based models” (IBMs).

Aggregated models have been used to study the effect of landscape heterogeneity on insect spatial patterns (Vinatier et al., 2011b). Habitat fragmentation has been studied via metapopulation models (Banks and Ekblom, 1999), and the effect of orchard boundaries has been studied via reaction-diffusion models (Tyson et al., 2007). Parasitoid–pest interactions have been investigated using a lattice model (Lopes et al., 2010). Despite a synthetic formalism that makes them analytically tractable, aggregated models do not explicitly consider individual behaviour in response to environment, which is considered an important component of pest management (Choi et al., 2004; Roitberg, 2007).

IBMs are well suited for representing individual behaviours, such as mate-finding (Byers, 1991), attraction to pheromone traps (Byers, 1999; Yamanaka et al., 2003), or predator–prey interactions (Bianchi et al., 2009). They follow the principle that population properties will emerge from the representation of individual behaviours (Grimm and Railsback, 2005). In IBMs, each individual is explicitly modelled and acts according to a set of rules. IBMs are spatially explicit because exact locations of each habitat element and each individual are known. Recently, IBMs have been used to study the efficacy of agro-ecosystem diversification for pest control by enabling virtual modification of a landscape matrix (Potting et al., 2005).

Mechanistic, spatially explicit IBM models intended for the design of innovative IPM strategies that take into account habitat spatial organization have yet to be validated with real data. The IBM developed by Potting et al. (2005) is theoretical and based on arbitrarily chosen parameters. We think that a mechanistic approach with a strong reliance on data collected in the field will greatly improve the realism of the emerging properties of IBMs.

In this paper, we use a modelling approach to represent the spatial dynamics of an insect pest in relation to its environment. We took as a case study the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae), which lives in spatially heterogeneous banana agroecosystems. We chose an IBM that has already been validated by real data on this pest (Vinatier et al., 2009). Parameters of habitat preference based on a radiotelemetry data set measured on this pest (Vinatier et al., 2010) and estimated by Vinatier et al. (2011a) were added to this IBM. We considered crop fragmentation by fallow (Rhino et al., 2010) and mass trapping (Tinzaara et al., 2005b) as principal tools for suppressing pest numbers. We used the model to explore the effects on trap efficiency of (i) modifying the environment surrounding one trap, (ii) arranging multiple traps in a fallow surrounded by a banana plantation, and (iii) fragmenting a banana crop area with multiple fallows. The modelling study was performed to test how IBMs can contribute to development of innovative IPM strategies.

## 2. Materials and methods

### 2.1. The COSMOS model

The simulations described here are based on a modified form of the IBM developed earlier for this pest, called COSMOS. Weevil's and banana's individual traits values used in COSMOS can be found in Vinatier et al. (2009). COSMOS runs on a daily time step. The processes underlying the spatial pattern of the insect are explicitly modelled at the individual level. The environment is spatially explicit and represented by a grid of cells containing habitat

elements that are mutually exclusive (banana plant, crop residues, trap, ditch, or bare soil) and/or agents (insects, banana plants). A cell size of 1 m<sup>2</sup> was chosen to characterize the habitat variability, following Marzluff et al. (2004). The grid is considered as toroidal to avoid edge effects in the simulations, i.e. weevils that would disappear outside the map area reappear onto the opposite side of the map. Each agent passes through different stages: egg, larva, pupa, and adult for insects and maiden sucker, preflowering, post-flowering, and harvesting stages for banana plants. Insects act according to a set of rules that depend on the properties of their current location. Egg-laying, which occurs only on cells with banana plants, depends on the number of adults in the cell and on the stage of the banana plant. The development of plants, eggs, larvae, and pupae are temperature-dependent. The mortality of each insect stage is considered as a constant in the model.

In the previous model, movement was considered as deterministic and to occur only from plant to plant. In the model developed in this paper, the movement depends on the habitat features of each cell. At each time step, the probability that an individual will move from the current cell to a surrounding cell in the individual's perceptual range is assessed according to a potential given by a dispersal kernel and habitat quality of the cells (Vinatier et al., 2011a). An individual's decision to move to a new cell is based on a multinomial probit of all the potentials of the cells within the perceptual range (see Appendix A for more details on the calibration of the movement probabilities and Table A1 for values of dispersal kernel and habitat qualities).

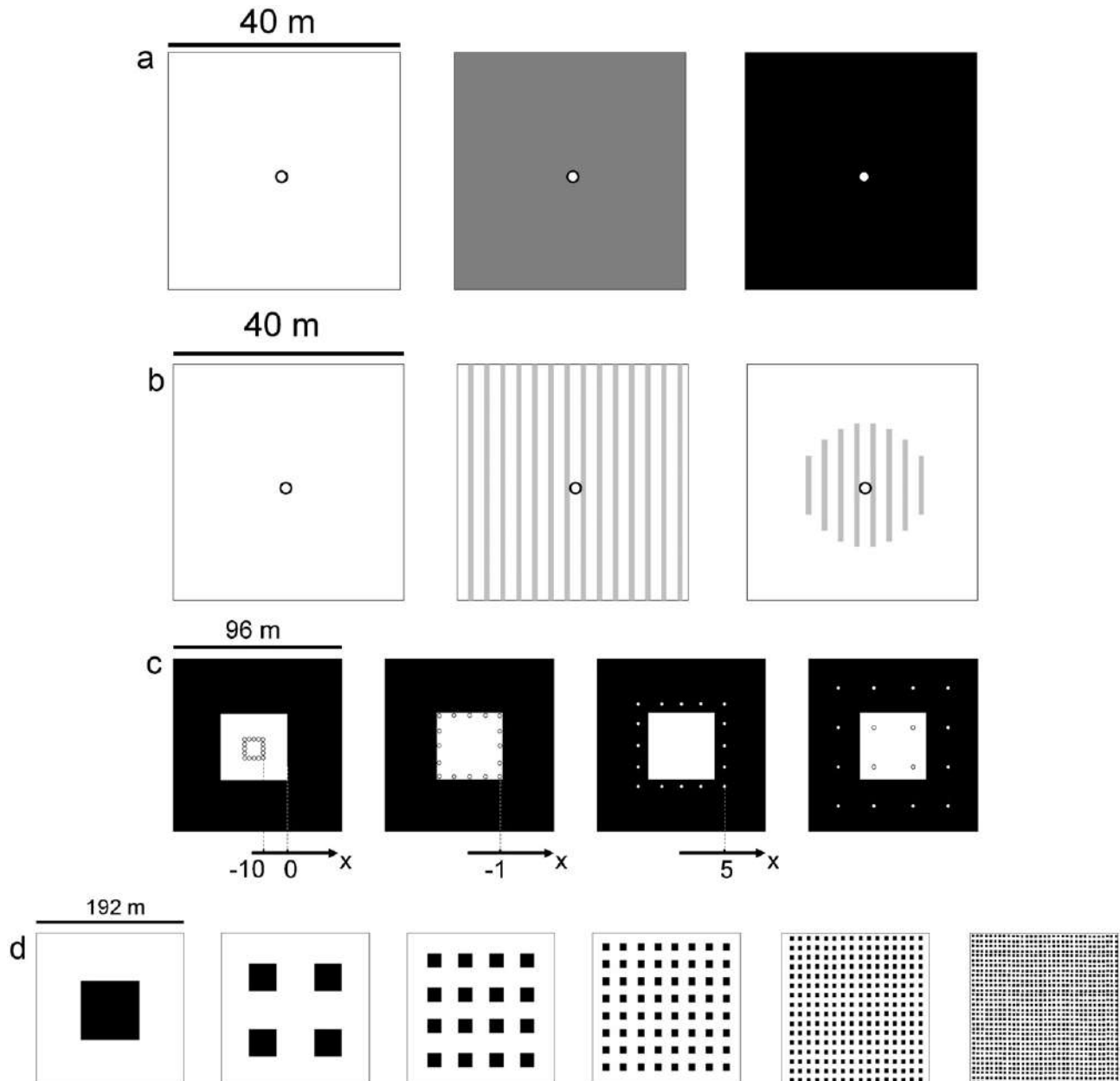
### 2.2. Crop system

Banana plants are considered to be semi-perennial, and plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner, 1994). Only one sucker per mat is selected by farmers. Banana leaves, trunks of harvested plants, and rejected suckers are regularly cut by farmers throughout the year and form a layer of crop residues. The duration of a banana plantation depends on the production areas. In the French West Indies, Costa Rica, and Brazil, plantations last about 5 years (i.e., for six successive cropping cycles) before replanting is required as a result of damage caused by insect pests and pathogens. In Africa and other areas, plantations last much longer than 5 years. In all cases, when the grower determines that a plantation (or part of a plantation) should be replanted, plants are killed by the injection of herbicides. After destruction, the treated area is left fallow for approximately 1 year before it is replanted.

### 2.3. Study species

The banana weevil *C. sordidus* is a walking insect whose activity is nocturnal and cryptic. *C. sordidus* occurs in all countries where its unique host plant, the banana, is present (Gold et al., 2001). Adults prefer moist environments and feed on banana plants or on their residues. Females lay eggs at the base of the host plant, and the larvae grow inside the corm. A plantation infested with banana weevils can be considered as a mosaic of different elements, each element having a potential effect on dispersal of adults. The elements of this mosaic include mats of banana plants, crop residues, bare soil, and ditches.

The control of *C. sordidus* populations is based on pheromone mass trapping (Rhino et al., 2010). Yellow pitfall traps containing an aggregation pheromone are buried in the soil. The chemical used in the traps is based on the aggregation pheromone sordidine, which is emitted by *C. sordidus* males and which attracts both males and females (Beauhaire et al., 1995). Despite the recent advances in the control of *C. sordidus* by the combination of fallow and mass



**Fig. 1.** Overview of the patterns used to test (a and b) environments surrounding the trap, (c) optimal spacing of traps in a fallow area surrounded by a banana plantation, and (d) fragmentation of a banana plantation. High density (2500/ha) of banana plants, low density (1100/ha) of banana plants, and fallow (bare soil) areas are in black, dark grey, and white, respectively. The trap is indicated by a white point. Vertical lines in light grey correspond to the lines of crop residues. (a) from left to right, one trap surrounded by: bare soil; a low density of banana plants; and a high density of banana plants. (b) from left to right, one trap surrounded by: bare soil; crop residues in continuous lines; and crop residues in continuous lines with incremental removal of residue from the perimeter. (c) from left to right, spatial arrangement of traps in a square at  $-10$  m, at  $-1$  m, or at  $5$  m from the border of the field, (according to direction indicated on the X-axis), and regularly distributed over the grid. (d) from left to right, fragmentation of a  $192 \times 192$  cell field of fallow in 1 patch, 4 patches, 16 patches, 64 patches, 256 patches, and 1024 patches of banana plants.

trapping (Rhino et al., 2010), additional information is needed on the best spatial arrangement of traps.

#### 2.4. IPM strategies tested using the COSMOS model

##### 2.4.1. The environment surrounding a trap

We hypothesized that trap efficiency should decrease when the trap is surrounded by attractive habitats, such as crop residues or banana plants.

Using the COSMOS model, we tested three environments surrounding one trap that was located at the centre of a  $40 \times 40$  cell grid (i.e.,  $1600 \text{ m}^2$  cells occupying  $0.16 \text{ ha}$ ): (i) bare soil exclusively, (ii) banana plants regularly planted at 2500 plants/ha ( $2 \text{ m} \times 2 \text{ m}$ ), and

(iii) banana plants regularly planted at 1100 plants/ha ( $3 \text{ m} \times 3 \text{ m}$ ) (Fig. 1a). At initialization, 100 adults were released into each cell of the grid, and the number of adults caught was recorded after 60 days of simulation. The probability of being caught at a given distance from the trap was recorded and averaged over 20 repetitions.

We also tested the spatial management of crop residues surrounding a trap located at the centre of the grid; this represented the case of a recently destroyed, fallow field. We compared the temporal dynamics of population on a  $40 \times 40$  cell grid surrounded by (i) bare soil (T0), (ii) crop residues in continuous lines, each line being separated by  $3 \text{ m}$  (T1), and (iii) the same configuration as in T1, with incremental removal of residues (we assumed that

weevils inside the crop residues fell on the ground when the residues were removed) from the border to the middle of the field such that the remaining residue occupied a circular area whose diameter was reduced by 3 m every week (T2). At initialization, 500 adults were randomly introduced all over the grid (Fig. 1b). The number of catches per trap was recorded at each time step during 130 days, averaged over 20 repetitions.

#### 2.4.2. Optimal spacing of traps in an intensive banana plantation in fallow

In areas of intensive production, banana plantations usually last 6–9 years before being destroyed by herbicide application, and the destroyed areas are then left in fallow for one year (Lassoudière, 2007). In the current study, the fallow area corresponded to one-ninth of the total area. The virtual banana field on which heterogeneity was manipulated was a  $96 \times 96$  cell grid ( $1 \text{ m}^2$  per cell, total area of the grid = 1 ha), with a fallow area in a central square of  $32 \times 32$  cells. This corresponds to a common situation in banana cropping systems in that fallow fields are frequently surrounded by planted fields (Lassoudière, 2007). As in real situations, banana plants were spaced at  $2 \times 2 \text{ m}$ , giving 2500 banana plants/ha.

Using the model field described in the previous paragraph, we tested a variety of permanent arrangements of mass trapping during 1 year. Trap density was set at 16/ha (a total of 16 traps in the grid), which is considered economically feasible for commercial plantations. The traps were arranged in a square of different sizes (the diameter ranged from 1 to 30 m) so that the distance from the perimeter of the square to fallow–banana interface ranged from 0 m (traps were at the interface) to  $-15 \text{ m}$  or to  $15 \text{ m}$ ; the negative distance indicates that the traps were in the area with planted bananas and the positive distances indicate that the traps were within the fallow area (Fig. 1c). In one additional arrangement, the traps were not arranged in a square but were arranged regularly over the entire grid (Fig. 1c). In all cases, adults of *C. sordidus* were randomly set all over the grid at a density of 1500 individuals/ha. The total number of adults on the grid and the number of adults captured per trap were recorded 1 month and 1 year after the beginning of the simulations and were averaged over 20 repetitions.

#### 2.4.3. Fragmentation and size effects in extensive banana plantations

In areas of extensive production, banana plants are regularly planted ( $2 \text{ m} \times 2 \text{ m}$ ) in patches of varying sizes (Lassoudière, 2007). We considered a grid consisting of banana plants and bare soil in the proportion 1:9. At initialization, the grid was composed of 2500 bananas/ha and 1500 weevils/ha. We tested the effect of varying patch fragmentation through six spatial patterns (from  $4^0 = 1$  patch to  $4^9 = 1024$  patches) for three different sizes of field ( $0.25 \text{ ha} = 48 \times 48$  cells,  $1 \text{ ha} = 92 \times 92$  cells, and  $3.7 \text{ ha} = 192 \times 192$  cells). Note that for each size of field, the proportion between banana area and fallow area was constant (Fig. 1d). Results were averaged over 20 repetitions.

#### 2.5. Statistical and modelling tools

The model was developed with Netlogo software (Wilensky, 1999). Maximum likelihood estimations of dispersal parameters were obtained with R software (R Development Core Team 2010) using package “stats4” (Appendix A).

### 3. Results

#### 3.1. The environment surrounding a trap

The probability that weevils were trapped increased with their proximity to traps and was higher when traps were surrounded

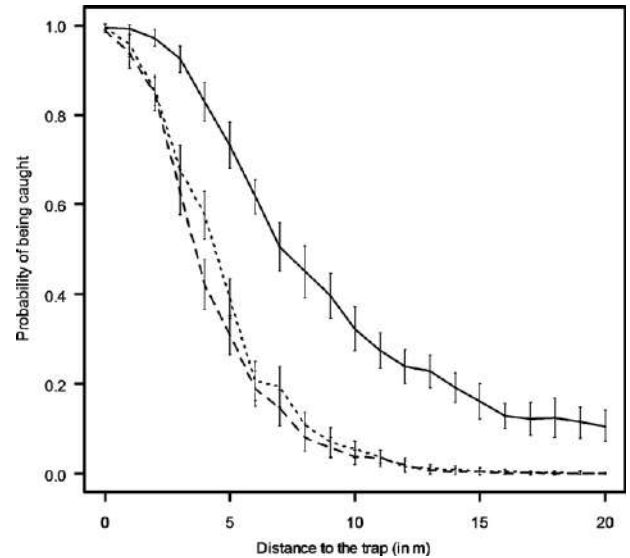


Fig. 2. Probability density curves generated by the COSMOS model of a  $40 \times 40$  cell grid with one trap located on the centre of the grid. The area is covered by bare soil (solid line), by bananas regularly planted at 1100/ha (dotted line), or by bananas regularly planted at 2500/ha (dashed line). Curves are issued from a loess spline on 20 repetitions. Vertical lines represent standard deviations with 20 repetitions.

with bare soil than with banana plants (Fig. 2; see Fig. 1a for trap and environment). Increasing the density of banana plants did not significantly modify the probability of being caught.

Fig. 3 shows the temporal dynamics of trap capture simulated by the COSMOS model for the three treatments: T0 (trap surrounded by bare soil); T1 (trap surrounded by residue in rows); and T2 (trap surrounded by residue in rows and with residue area decreasing over time) (see Fig. 1b for trap arrangement). The cumulative number of weevils trapped was always greater with T0 than T1, and the number trapped was similar for T1 and T2 until day 70. After day 70, the number trapped with T2 increased rapidly and surpassed that with T0. After day 70, the remaining area of crop residue in T2 contained almost all the uncaught weevils. The weevils were sufficiently close to the trap to be caught, so that the level of trap captures increased rapidly.

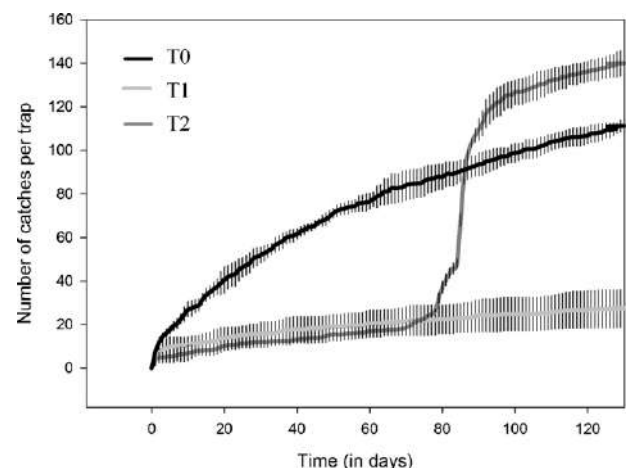
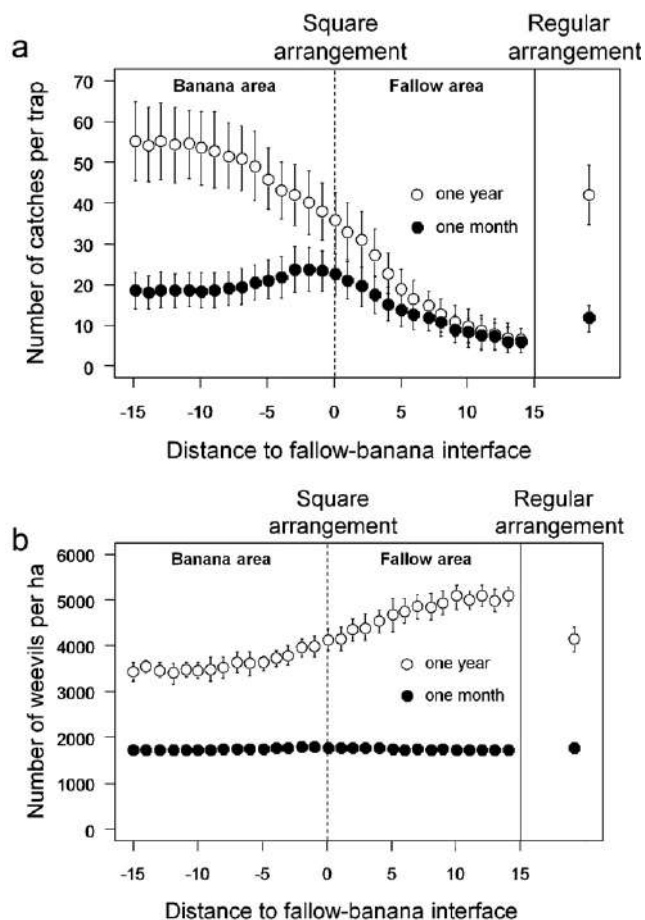


Fig. 3. Temporal dynamics of cumulative number of weevils caught per trap as simulated by the COSMOS model on a  $40 \times 40$  cell grid (adult number at initialization = 500). The trap is surrounded by: bare soil (T0); crop residues in continuous lines with 3 m between lines (T1); crop residues in continuous lines with 3 m between lines and with incremental removal of residues from the border to the middle of the field (diameter of residue circle was decreased by 3 m per week) (T2). Vertical lines represent standard deviations with >20 repetitions.

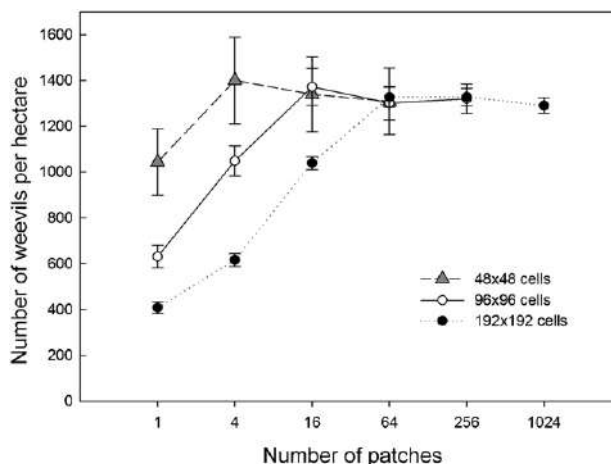




**Fig. 4.** Means (points) and standard deviations (bars) of (a) trap efficiency and (b) numbers of weevils per ha as a function of distance to the fallow–banana interface when traps were arranged in a square and as a function of a regular distribution of traps. Data are from 1-month (black point) and 1-year (white point) simulations using the COSMOS model. Standard deviations are based on 20 runs of the model.

3.2. Optimal spacing of traps in a fallow surrounded by a banana plantation

Fig. 4 shows the influence of the spatial arrangement of traps (see Fig. 1c for arrangement) on insect suppression and trap efficiency. For traps arranged in a square, both short- and long-term simulations (i.e. after one month and one year, respectively) indicated that the traps were more efficient and consequently the number of weevils per ha lower in the banana area than in the fallow area (Fig. 4a and b). In the fallow area, the low efficiency of traps distant from the fallow–banana interface was probably caused by the close proximity of traps resulting in competition between traps. Efficiency of regularly arranged traps (Fig. 4a) and the resulting population levels (Fig. 4b) were situated at the middle between cases of squared-arranged traps in banana and in fallow area. For traps regularly arranged and in comparison with traps in square, the lower level of trap competition in fallow area counterbalanced the lower number of traps in the banana area. After 1 month of simulation, trapping was highest when traps were located at the fallow–banana interface (Fig. 4a), because traps at this interface captured weevils that escaped the fallow area, as indicated by weevil residence time in each cell (data not shown). Effect of traps on weevil numbers was only pronounced for long-term simulations, as in short term simulations, the slight difference in number of caught weevils (almost 100 weevils) was negligible in comparison with the total number of weevils per ha (Fig. 4b).



**Fig. 5.** Simulated numbers of weevils per ha after 1-year as a function of fragmentation level and field size. At initialization of the COSMOS model, weevils were randomly distributed in the fields. Each cell is 1 m × 1 m. Vertical lines indicate the standard deviations for >20 runs of the model.

3.3. Fragmentation and size effects in extensive banana plantations

Fig. 5 shows the effect of fragmentation on weevil numbers after 1-year simulations. Weevil numbers increased with the level of fragmentation and levelled off when the number of patches exceeded 4, 16, and 64, for a field of 48 × 48 cells, 96 × 96 cells and 192 × 192 cells, respectively. For the same level of fragmentation, weevil numbers and variation in weevil numbers decreased when the size of the field increased (Fig. 5).

4. Discussion

4.1. The environment surrounding a trap

Our first objective was to study how the efficiency of individual traps could be improved through manipulation of the surrounding environment. According to the assessment of habitat attractiveness (Appendix A), the trap is about 100 times more attractive than bare soil and is the most attractive element in a banana plantation. Crop residues and banana plants, however, compete with traps for weevils.

When decreasing banana plant density was considered as a potential tool for increasing mass trapping efficiency, a two-fold decrease in the density of plants caused only a slight increase in trap efficiency. The small effect of this tool could be explained by the inter-plant distance, which was much shorter than the perceptual range of weevils in both high and low density plantations. Trap efficiency was significantly increased when the trap was only surrounded by bare soil, as experimentally demonstrated by Rhino et al. (2010).

Crop residues can be managed by farmers and are another potential tool for increasing the efficiency of mass trapping. The results showed that incremental removal of crop residues from the periphery to the trap location significantly improved trap catches in the absence of banana plants. This could be explained by the relative attractiveness of crop residues in comparison with bare soil. At each time when an outer ring of residues was removed, weevils located in the removed ring moved to the closest area of crop residues, i.e., they moved toward the trap.

The consideration of habitat arrangement as a possible factor affecting trap efficiency is relatively novel (Spurgeon and Raulston, 2006). Research on trap efficiency has generally concerned pheromone dose (Branco et al., 2006), climatic variables

(Tinzaara et al., 2005a), or trap features (Reddy et al., 2009). However, our spatial model demonstrated that the spatial arrangement and composition of habitat should be considered in mass trapping strategies.

#### 4.2. Optimal spacing of traps in a fallow surrounded by a banana plantation

Our second objective was to study the spatial arrangement of multiple traps in a fallow area surrounded by a banana plantation. The results of the simulation procedure indicated that traps should be located at the banana–fallow interface in the period immediately after the fallow is established. We suspect that weevils on bare soil escaped this unsuitable habitat to aggregate in the transition zone between the fallow area and the planted area. Oehlschlager et al. (1995) pointed out the importance of this zone in mass trapping strategies. Furthermore, locating traps along the perimeter of the fallow area increased the inter-trap distance and thereby reduced potential competition between traps, as emphasized by Bacca et al. (2006). Because trap relative attractiveness was calibrated in the absence of trap competition (see Appendix A), we considered no interference between traps, either positive or negative. For example, there is no additivity of trap attraction radii when trap radii are superposed. This formalism could lead to an underestimation of trap efficiency when traps are grouped but is the more tractable than the alternative in discrete-choice models. Very few spatial models simulate pheromone trap effectiveness (Byers, 1993; Yamanaka et al., 2003; Byers, 2009), and they only consider the dispersing stage of the pest population. Our model, by considering all insect stages, facilitates the understanding of the long-term effects of mass trapping strategies.

#### 4.3. Fragmentation and size effects in extensive banana plantations

The third objective of this study concerned patch fragmentation. Our results showed that weevil numbers increased with the fragmentation of the banana area. We suspect that a highly fragmented area of bananas results in high connectivity (shorter distances) between patches of banana plants. The randomly distributed weevils had a greater probability of locating and moving to a suitable patch when patches were small and abundant rather than when patches were large but few. At the field scale, this result contrasts with Haynes et al. (2007), whose experiments indicated no effect of micro-fragmentation on the density of flying insects (*Melanoplus femurrubrum*). At the landscape scale, Pichancourt et al. (2006) found with a modelling approach that numbers of a crawling insect (*Abax parallelepipedus*) were greater with a single large patch of wood than with several small patches of wood. The authors argued that highly fragmented landscapes allow insects to die more frequently when they move between patches. In our case, mortality does not depend on the habitat that is traversed; instead, the main source of population loss is due to individuals that fail to find a suitable patch.

For a given fragmentation level, the larger the size of the field, the larger the distance to cover between each fragment. In that way, increasing the size of the field with a given pattern limits weevil numbers, because a weak perceptual range prevents weevils from assessing large field patterns. This result can have important management implications in that low fragmentation of a banana plantation will cause greater suppression of the insect pest over a large area than over a small area. Our IBM has the advantage of explicitly simulating individual perceptual ranges of insects so as to elucidate

factors that determine insect numbers at the landscape scale. In doing so, the model aims at bridging the gap between individual behaviour and population processes (Grimm and Railsback, 2005).

## 5. Conclusion

Our study showed that, for the design of sustainable cropping systems for IPM purposes, IBMs are powerful tools because they consider three key points. First, IBMs simulate individual behaviour of insects and therefore are well suited for IPM strategies based on behaviour manipulation (Potting et al., 2005). Second, the explicit consideration of space allows IBMs to test various landscape arrangements including pheromone trap locations and crop development. Third, the IBMs can successfully use information from small-scale experiments collected at the level of the individual level to simulate pest dynamics at the field scale. We consider that models with a strong reliance on real data are better than theoretical ones for designing IPM strategies. Individual-based modelling provides a flexible way to extrapolate properties of plant–pest interactions to novel conditions and therefore helps in the design of innovative cropping systems.

## Acknowledgments

Authors thank two anonymous referees for helpful comments and suggestions on the manuscript and Bruce Jaffee for revising the English. Anne Vidie and Anaïs Chailleux are acknowledged for their assistance with fieldwork, as well as Dominique Arnaud, Jean-Claude Gertrude, Camille Hubervic and Gratient Theodose for technical assistance. This work is part of a Ph.D. of F.V. funded by the CIRAD.

## Appendix A.

The probability of moving from cell  $a$  to cell  $b$  in the grid within a temporal unit was a first-order Markov chain defined as:

$$Pr(a \rightarrow b) = \frac{\alpha_{h(b)} f_{\beta_{h(a)}}(d_{ab})}{\sum_{k=1}^m \alpha_{h(k)} f_{\beta_{h(a)}}(d_{ak})} \quad (1)$$

where  $\alpha_{h(k)}$  is the relative preference for habitat  $h$  of cell  $k$ ,  $d_{ak}$  the distance between cells  $a$  and  $k$ , and  $f(d_{ak})$  is the dispersal kernel depending on this distance of the form  $\exp(-\beta_{h(a)} \cdot d_{ak})$ .

The 10 unknown parameters ( $\alpha_h$  and  $\beta_h$  with  $h = [\text{trap, host plant, crop residues, bare soil, ditch}]$ ) were estimated via maximum likelihood estimation (Vinatier et al., 2011a) on the basis of a radio-tracking data set measured on this species (for more details on the tracking method, see Table A1 and Vinatier et al., 2010). Constraints were added in the model: the sum of alphas equals one, and each parameter is positive.  $\beta_T$  was fixed to 100 because the probability of escaping the trap is null. A complete version of this movement model and its evaluation can be found in Vinatier et al. (2011a).

The radio-tracking data set consisted of pairs of daily observations of approximately 800 males and 800 females of *C. sordidus* followed in experiments, in which the mosaic of habitats was experimentally manipulated. The data were collected on seven experiments (three are described in Vinatier et al. (2010), two in Vinatier et al. (2011a) and the two last come from unpublished data). Locations of insects and habitat elements were noted on a 1-m<sup>2</sup> cell grid that corresponded to the resolution of the model.

Table A1 shows that the trap was the most preferred habitat, followed by host plant and crop residue, which were equally preferred. Bare soil and ditch were the least preferred (Table A1). Regarding

**Table A1**  
Parameter estimates of the movement of *C. sordidus* in the individual-based model, based on the radio-tracking data set.

	Mean	Standard error
Relative habitat preference		
$\alpha_T$	0.86357375	0.0227554224
$\alpha_P$	0.07559439	0.0129049226
$\alpha_C$	0.05181051	0.0089547495
$\alpha_B$	0.0064581	Fixed
$\alpha_D$	0.00256325	0.0004704881
Parameter of the dispersal kernel		
$\beta_T$	100	Fixed
$\beta_P$	2.06518544	0.0368306669
$\beta_C$	2.09589287	0.0479089734
$\beta_B$	1.09817321	0.0253469307
$\beta_D$	0.72382497	0.1040634209

Note: the letters indicate the habitat type: T, trap; P, host plant; C, crop residue; B, bare soil; D, ditch.

parameter  $\beta$ , which defines the shape of the dispersal kernel, the higher the value of  $\beta_i$  for the current habitat  $i$ , the greater the probability that the individual will remain in habitat  $i$ . The value of  $\beta_i$  was highest for the host plant or the crop residue, intermediate for the bare soil, and lowest for the ditch (Table A1). Consequently, the movement rate was highest when the current habitat was ditch, was intermediate for bare soil, and was the lowest for crop residue and host plant.

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# Should I Stay or Should I Go? A Habitat-Dependent Dispersal Kernel Improves Prediction of Movement

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## Abstract

The analysis of animal movement within different landscapes may increase our understanding of how landscape features affect the perceptual range of animals. Perceptual range is linked to movement probability of an animal via a dispersal kernel, the latter being generally considered as spatially invariant but could be spatially affected. We hypothesize that spatial plasticity of an animal's dispersal kernel could greatly modify its distribution in time and space. After radio tracking the movements of walking insects (*Cosmopolites sordidus*) in banana plantations, we considered the movements of individuals as states of a Markov chain whose transition probabilities depended on the habitat characteristics of current and target locations. Combining a likelihood procedure and pattern-oriented modelling, we tested the hypothesis that dispersal kernel depended on habitat features. Our results were consistent with the concept that animal dispersal kernel depends on habitat features. Recognizing the plasticity of animal movement probabilities will provide insight into landscape-level ecological processes.

**Citation:** Vinatier F, Lescouret F, Duyck P-F, Martin O, Senoussi R, et al. (2011) Should I Stay or Should I Go? A Habitat-Dependent Dispersal Kernel Improves Prediction of Movement. PLoS ONE 6(7): e21115. doi:10.1371/journal.pone.0021115

**Editor:** Sharon Gursky-Doyen, Texas A&M University, United States of America

**Received:** March 11, 2011; **Accepted:** May 19, 2011; **Published:** July 12, 2011

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**Funding:** This work is part of a Ph.D study funded by the CIRAD (<http://www.cirad.fr>) with the contract number: 07-259/NH. Project SYBAN from the French Ministry of Ecology, Sustainable Development (grant n°CV070000779) and Project "sustainable cropping systems design" from E.U. FEFER (grant PRESAGE n°30411) have also funded the work. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

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## Introduction

Animals generally combine a wide variety of chemical, visual, and acoustic cues to assess the suitability of habitats for providing food [1], oviposition sites [2], or protection from predators [3]. The perceptual range of an animal, i.e., the spatial extent of the landscape for which information is available to drive decisions about movement, is a determinant of the dynamics and spatial distribution of animal populations [4]. An animal's perceptual range is directly linked to landscape connectivity, and analysis of perceptual range can help researchers understand how populations respond to habitat disturbance and fragmentation [5]. Perceptual range is a key parameter of the probability that animals successfully disperse in a landscape, and consequently of the existence and persistence of a fragmented population [6]. Perceptual abilities drive the foraging behaviour of predators with respect to a spatially and temporally varying distribution of prey [7] as well as the population dynamics of pests such as crickets [8]. Mechanisms of habitat selection by large mammals and birds are also quite related to their perceptual ranges [9–11].

Several spatio-temporal discrete models define the concept of perceptual range through the description of an individual's habitat preference and animal movement analysis [12,13]. In these models, the perceptual range of an individual represents an "information window" onto the surrounding landscape, where all potential habitats are given an availability coefficient either uniformly defined [9] or non-uniformly defined with a "dispersal

kernel". The dispersal kernel generally accounts for the relative cost of a movement (displacement) from one location to another in terms of the distance between locations and their ecological features [13,14]. The class of useful dispersal kernels is rich and may accommodate various shapes that can be fixed on the basis of some *a priori* knowledge [15]. Simple and interpretable kernels can be made very flexible by adjustment of parameters whose values govern important indices of the spatial distribution of individuals [16]. For example, "fat-tailed" distributions or kernels allow long-distance dispersal events and generally describe large-scale colonisation processes in accordance with a large perceptual range of individuals [17].

Although animal dispersal kernel is traditionally taken as species-invariant [4], observational evidence indicates that it can be variable [18]. Some of the factors that can cause variation in the dispersal kernel among individuals of a species or population are intrinsic characteristics such as sex, age, social status, and energy reserves; environmental conditions such as climate, season, and habitat quality; and ecological characteristics such as levels of competition, predation, and parasitism [7,19]. Other extrinsic environmental stimuli may also alter an animal's dispersal kernel [20]. Zollner and Lima [21] reported that the movement probabilities of white-footed mice significantly changes depending on whether they are released in bare fields or crop fields. In spite of its theoretical and practical significance [22,23], the plasticity of animal movement probabilities in landscapes remains an unexplored research area [4]. It clearly deserves more theoretical and empirical investigation because appropriate estimation of dispersal

kernel plasticity may lead to a better assessment of the functional connectivity of landscapes [24].

To assess whether and to what extent animal movement probability can be affected by spatial heterogeneity of habitats, we considered a data set of the locations of the insect *Cosmopolites sordidus* (coleoptera) within heterogeneous environments [25]. For that purpose, we used recent advances in radio-tracking techniques [26] to monitor the fine-scale movements of over 1000 individuals in five banana plots.

In this study, we assumed that the movement probability is defined by a negative-exponential kernel with a single parameter  $\beta$  that may account for the influence of the habitat features of the current animal location before a displacement. We then proposed a discrete space–time stochastic model of animal movement as a Markov chain in which the movement between arrival and departure locations depends on their geographic distance and possibly on their respective habitat characteristics. For our analysis, we considered the particular hypothesis  $H_0$  of a habitat-independent kernel ( $\beta$  independent of the habitat type of the departure cell) versus the general hypothesis  $H_1$  of a habitat-dependent kernel ( $\beta$  dependent on the habitat type of the departure cell). Using a radio-tracking data set of *C. sordidus* movements, we first tested the sub-model  $H_0$  against  $H_1$  with the likelihood ratio test. To reinforce our results, we then applied the pattern-oriented modelling (POM) approach [27] to compare the two hypotheses with spatially explicit simulations of the respective underlying individual-based models. POM is a general validation procedure that focuses on the analysis of pertinent variables, e.g., an animal's use of space. POM is based on the emerging recognition that population-level patterns may result from individual behaviours [28]. The POM procedure can thus help unravel the effects of different implicit or explicit assumptions underlying ecological models. In our study, POM is based on the simulation of the alternative models calibrated with their respective maximum likelihood estimates of parameters. Discrimination of the two models relies on testing their ability to reproduce the patterns observed in the studied plots with respect to two pertinent ecological variables [27], which are the proportion of non-moving individuals and the distribution of displacement lengths.

## Materials and Methods

### Materials: species, plots, and radio tracking

The banana weevil, *Cosmopolites sordidus*, is a walking insect with cryptic and nocturnal activities. It lives in all countries where its only host plant, the banana, grows [29]. Adults prefer moist environments and feed on banana plants or their residues. Females lay eggs at the base of the host plant, and larvae grow inside the corm. The movements of *C. sordidus* are not known to be socially organized or to be dependent on gender [25].

Daily radio-tracking data were collected for approximately 600 males and 600 females of wild *C. sordidus* that were caught with pseudostem traps from one banana field adjacent to the study site (Table S1). Insects caught were sexed and kept in laboratory approximately one week before release. They were tagged two hours before release using passive radio-tracking tags, released in five banana plots and followed for at least 10 days (for more details on the radio-tracking method, see [25]). Field studies were conducted according to the “Pôle de Recherche Agro-environnemental de la Martinique” permission. Each plot was depicted as a regular lattice of 800 to 2400 cells of 1-m<sup>2</sup>. This cell size was chosen because it was small enough to characterize resource variability [30] and large enough to match radio-tracking accuracy

[25]. Locations of individuals were rounded to one-meter grain and pinpointed at cell centres. Regular space–time agricultural practices on banana plots result in the occurrence of a structured mosaic of habitats (Figure S1). We distinguished four mutually exclusive types of habitat: (*P*) host plant, (*C*) crop residue, (*B*) bare soil, and (*D*) ditch. Types *P* and *C* are recognized as more suitable habitats for *C. sordidus* than *B* and *D*. Plots 3–5 contained a high proportion of suitable habitats while plots 1–2 contained a high proportion of unsuitable habitats (Figure S1).

### Methods: Discrete space–time stochastic modelling

To describe beetle movement in a plot, we chose a stochastic and discrete space–time formalism following an individual-based model developed earlier for this pest [31]. The spatial environment was represented by a lattice of  $n$  cells. Each cell  $i$  ( $i = 1, \dots, n$ ) was characterised by its centre coordinates  $c_i = (x_i, y_i)$  and its habitat type  $h_i$  ( $h_i = P, C, B, D$ ). Individual movements were considered as a Markovian random walk on the lattice centres. More specifically, we assumed that individuals moved independently from each other and that individuals had no memory of their previous displacements. We also assumed that the daily decision to remain in a cell or move from a cell was independent of time but depended on the habitat quality of this cell and on the attractiveness and closeness of other cells. With this time-homogeneous Markovian hypothesis, we considered *C. sordidus* walks as a first-order Markov chain whose states corresponded to cell centres and whose transition probabilities were defined with a dispersal kernel  $f_\beta(\mathbf{d})$ . An exponential form for the dispersal kernel,  $f_\beta(\mathbf{d}) = \exp(-\beta \mathbf{d})$ , was selected because of its simplicity and ease of interpretation. We allowed the shape coefficient  $\beta$ , however, to depend on the habitat type of departure cells. We expressed the daily probability of moving from the current cell  $c_i$  to an arrival cell  $c_j$  as:

$$p_{ij} = \text{Prob}(c_i \rightarrow c_j) = \frac{\alpha_{h_j} \exp(-\beta_{h_i} d_{ij})}{\sum_{k=1}^n \alpha_{h_k} \exp(-\beta_{h_i} d_{ik})} \quad (1)$$

where  $d_{ij} = d(c_i, c_j)$  is the Euclidean distance between centres of cells  $i$  and  $j$ . The parameters  $\alpha_{h_k}$ , which are non-negative and satisfy equality  $\alpha_P + \alpha_C + \alpha_B + \alpha_D = 1$ , can be interpreted as the relative attractiveness of habitat type  $h_k$  of cell  $k$ . The parameters  $\beta_{h_k}$  are non-negative and can be linked to the mean sojourn time in habitat type  $h_k$ , as explained below.

The Markovian hypothesis implies that the sojourn time  $\tau_i$  in a cell  $i$  has a geometric distribution with parameter  $p_{ii}$ . The mean sojourn time is a function of parameters  $\alpha$  and  $\beta$  and of all distances  $d_{ik}$  between cell  $i$  and other cells:

$$E(\tau_i) = p_{ii} / (1 - p_{ii}) = \alpha_{h_i} / \left( \sum_{k=1}^n \alpha_{h_k} \exp(-\beta_{h_i} d_{ik}) \right) \quad (2)$$

It implies that the probability of staying in a given cell (i.e.  $p_{ii}$ ) is different from one, especially for cells containing a good habitat, such as banana plants or crop residues. Ecologically, it means that animals located in good habitats move because they need to change place for egg-laying and/or mating during the study period.

To understand the intrinsic role of parameter  $\beta$ , we assumed that  $\alpha$  is constant and that the number of cells is large enough so that the following approximation can be used:

$$E(\tau_i) = 1 / \left( \sum_{k=1}^n \exp(-\beta_{h_i} d_{ik}) \right) \approx 1 / \left( \int_0^{\infty} \exp(-\beta_{h_i} r) dr \right) = \beta_{h_i} \quad (3)$$

### Likelihood formula

Because individuals were independent and individual movements were Markovian, the data likelihood within a single plot  $p$  consisted of the product of the daily movement probabilities according to equation [1] over all individuals released in this plot ( $m = 1, \dots, M$ ) and over all their daily moves  $c(m,t) \rightarrow c(m,t+1)$ ;  $t = 0, \dots, T_m - 1$  where  $T_m$  was the observation period of individual  $m$ :

$$L_p(\alpha, \beta) = \prod_{m=1}^M \prod_{t=0}^{T_m-1} \frac{\alpha_{h_{c(m,t+1)}} \exp(-\beta_{h_{c(m,t)}} d_{c(m,t),c(2m,t+1)})}{\sum_{k=1}^n \alpha_{h_k} \exp(-\beta_{h_{c(m,t)}} d_{c(m,t),k})} \quad (4)$$

and  $c(m,t)$  denoted the location (cell centre) of individual  $m$  at time  $t$ ,  $h_{c(m,t)}$  denoted its habitat type, and  $n$  denoted the number of cells of the plot. Actually, given the hypothesis that model parameters were independent of the five plots ( $p = 1$  to  $5$ ), the final likelihood is:

$$L(\alpha, \beta) = \prod_{p=1}^5 L_p(\alpha, \beta) \quad (5)$$

### Maximum likelihood estimation and hypothesis testing

First, we allowed the parameters  $\alpha_h$  and  $\beta_h$  to take distinct values for the four distinct habitats in what we called the general

model (denoted  $M_G^4$ ) and estimated the parameters by a maximum log-likelihood procedure of  $L(\alpha, \beta)$ . For that purpose, we used Nelder's Mead algorithm [32], which accounted for the parameter positiveness and the  $\alpha$ 's constraint ( $\alpha_P + \alpha_C + \alpha_B + \alpha_D = 1$ ). We also considered different sub-models (or hypotheses) in which some of the  $\alpha$ 's (respectively  $\beta$ ) parameters were set equal, e.g.,  $\alpha_P = \alpha_C = \alpha_{P+C}$  (respectively  $\beta_P = \beta_C = \beta_{P+C}$ ), which eventually amounted to the grouping of habitat  $P$  and  $C$  into a single type. We consequently denoted such sub-models as, e.g.,  $M_G^{3,(P+C)}$  and used the same procedure and algorithm for parameter estimation.

To test data fit of models  $M_G$  (with  $k_G$  parameters) and  $M_0$  (with  $k_0$  parameters, sub-model [nested model] of  $M_G$ ), we used the classical likelihood ratio statistic  $-2(\log(L(\hat{\alpha}_{M_0}, \hat{\beta}_{M_0})) - \log(L(\hat{\alpha}_{M_G}, \hat{\beta}_{M_G})))$ , which was expected to follow under  $M_0$  a  $\chi^2$  distribution with  $df = k_G - k_0$ . Within different habitat regrouping contexts, we might have tested a large number of nested hypotheses. For simplicity, we consider only the reasonable alternative hypotheses of habitat-independent moves ( $H_0$ :  $\beta_h$  is independent of  $h$ ,  $\alpha_h$  are distinct) versus habitat-dependent moves ( $H_1$ :  $\beta_h$  are distinct,  $\alpha_h$  are distinct).

### Pattern-oriented modelling

POM can be considered as a validation procedure for a specified model and is used to reproduce important patterns or statistical characteristics of a specific process [27]. POM consisted of developing and then simulating a spatially and temporally explicit individual-based model and assuming many mechanistic hypotheses. Some model outputs were then statistically compared to those of an observed data set. Discrepant results would indicate the irrelevance or omission of important working hypotheses.

**Table 1.** Modified log-likelihood  $[-2\log(L)]$  and parameter estimates for the different models.

		Dispersal kernel parameters $\beta_h$				Preference parameters $\alpha_h$				df	$-2 \cdot \log(L)$
<b>4 habitats</b>											
		$\beta_P$	$\beta_C$	$\beta_B$	$\beta_D$	$\alpha_P$	$\alpha_C$	$\alpha_B$	$\alpha_D$		
$M_0^4$	1.62					0.54	0.43	0.018	0.008	4	12991
$M_G^4$		2.01	2.11	1.14	0.71	0.54	0.40	0.036	0.014	7	<b>12394</b>
<b>3 habitats (grouping Host plant+Crop residue)</b>											
		$\beta_{P+C}$	$\beta_B$	$\beta_D$		$\alpha_{P+C}$	$\alpha_B$	$\alpha_D$			
$M_0^{3,(P+C)}$	1.63					0.95	0.01	0.04		3	12991
$M_G^{3,(P+C)}$		2.04	1.09	0.74		0.91	0.02	0.07		5	<b>12395</b>
<b>3 habitats (grouping Ditch+Bare soil)</b>											
		$\beta_P$	$\beta_C$	$\beta_{B+D}$		$\alpha_P$	$\alpha_C$	$\alpha_{B+D}$			
$M_0^{3,(B+D)}$	1.62					0.55	0.43	0.02		3	12993
$M_G^{3,(B+D)}$		1.97	2.14	1.08		0.56	0.41	0.03		5	<b>12422</b>
<b>2 habitats (grouping Host plant+Crop residue and Ditch+Bare soil)</b>											
		$\beta_{P+C}$	$\beta_{B+D}$			$\alpha_{P+C}$	$\alpha_{B+D}$				
$M_0^2$	1.63					0.97	0.03			2	13014
$M_G^2$		2.04	1.08			0.94	0.06			3	<b>12445</b>
<b>1 single habitat (grouping Host plant+Crop residue+Ditch+Bare soil)</b>											
		$\beta_{P+C+B+D}$				$\alpha_{P+C+B+D}$					
$M_G^1 = M_0^2$	1.89					0.25				1	14769

Parameter subscripts: P, host plant; C, crop residue (litter-covered soil); D, ditch; B, bare soil. P+C means that host plant and crop residue habitats are pooled in a single category.

Habitat-dependent (resp. habitat-independent) models with  $k$  types of habitat are denoted  $M_G^k$  (resp.  $M_0^k$ ).

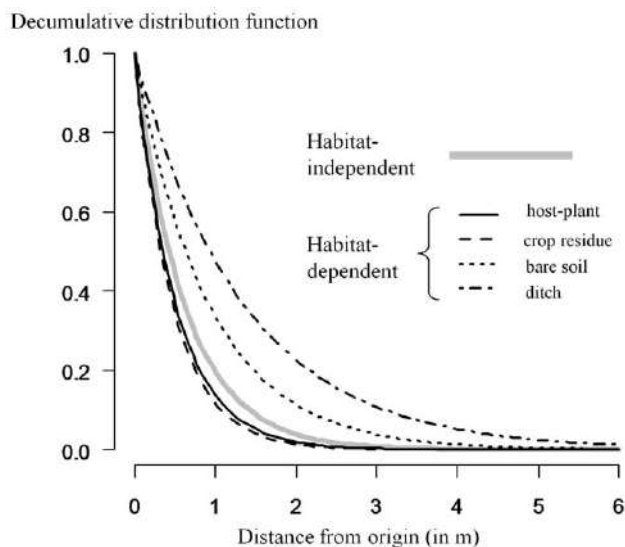
doi:10.1371/journal.pone.0021115.t001

In this study, we used the maximum likelihood estimates for model  $M_G^4$  (respectively  $M_0^4$ , see *Maximum likelihood estimation and hypothesis testing*) of a habitat-dependent (respectively independent) dispersal kernel to simulate 100 runs of the walk of the original *C. sordidus* population within the five plots. At each run and for each plot, all individuals of the population were spatially distributed according to their observed released position. The simulations covered 10 days. Data simulated from the two models were then compared to radio-tracking observations, with focus on two pertinent ecological variables of space use by animals. The first variable refers to the proportion of individuals remaining in their release cell throughout the study period. This variable might characterise the tendency of *C. sordidus* to be sedentary unless motivated to move by significant differences in environment suitability. The second variable describes the distribution of dispersal distances that characterise *C. sordidus* mobility and that depend on both soil roughness and habitat diversity. We restricted our analysis to two patterns able to discriminate between the two models. Other patterns such as direction of movements depend mainly on relative attractiveness of habitat and not on dispersal kernel, and mean squared displacement of movement is highly correlated to the distribution of dispersal distances.

Each simulated variable was represented by the mean of 100 runs, and the simulated and observed means were compared with the classical  $\chi^2$  test statistic for proportions and with the Kolmogorov-Smirnov test for distance distributions [33].

## Results

Regardless of the number of distinct habitats considered, the target habitat-preference estimates (the  $\alpha$ 's attractiveness coefficients) remained similar and their relative ranking remained very stable for the habitat-independent  $M_0$  and habitat-dependent models  $M_G$ . More specifically, host plant (P) and crop residue (C) habitats were always highly and equally preferred over bare soil (B)

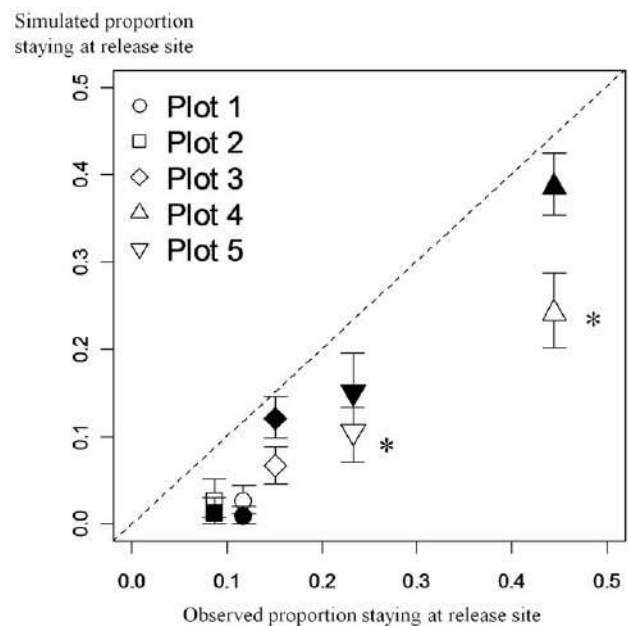


**Figure 1. The “decumulative” distribution function as a function of length of animal displacement ( $d$ ), i.e.,  $f(d) = \exp(-\beta \cdot d)$ .** Maximum likelihood estimates of exponential kernels are drawn for the habitat-independent (grey line) and the habitat-dependent (black lines) models. The slopes of the black curves depend on the estimated value of parameter  $\beta_h$  for the habitat type  $h$  of the individual's location before movement.

doi:10.1371/journal.pone.0021115.g001

and ditch (D) habitats (Table 1). When the four habitat types were dissociated, the log-likelihood of the habitat-dependent model  $M_G^4$  was significantly greater than that of the habitat-independent model  $M_0^4$  (Table 1,  $\chi^2_3 = 597$ ,  $p < 0.001$ ). When habitat types were pooled, the log-likelihood naturally decreased with parameter dimension for both models; note that Table 1 gives the opposite log-likelihood value. Also note, however, that the log-likelihood remained similar for the habitat-dependent models  $M_G^4$  and  $M_G^3$  (resp. the habitat independent models  $M_0^4$  and  $M_0^3$ ) when host plant (P) and crop residue (C) habitats were pooled ( $\chi^2_2 = 1$ ,  $p = 0.61$ ) (resp.  $\chi^2_1$ ,  $p = 0.5$ ). In all other cases, the embedded sub-models were significantly rejected ( $\chi^2_{1 \text{ to } 3}$  tests  $p < 0.001$ ). All habitat-dependent models  $M_G^k$  ( $k=3$  (P+C), 3 (D+B), 2) performed significantly better than the habitat-independent models  $M_0^k$  ( $M_{0/G}^{3,(P+C)}$ :  $\chi^2_2 = 596$ ,  $M_{0/G}^{3,(D+B)}$ :  $\chi^2_2 = 571$ ,  $M_{0/G}^2$ :  $\chi^2_1 = 569$ ,  $p < 0.001$  in all cases).

As indicated earlier, the  $\beta$  parameter values define the shape of the dispersal kernel assigned for each habitat feature and can be interpreted as the mean sojourn time in the current location when the attractiveness parameters  $\alpha$ 's of habitats are equal: the higher the  $\beta_h$  value for the current habitat  $h$ , the higher the tendency for the individual to remain in cells of habitat type  $h$ . Maximum likelihood estimators of  $\beta_h$  were high for the host plant (P) or the crop residue (C), intermediate for the bare soil (B), and low for the ditch (D) (Table 1). This means that the probability of movement was high if the current habitat was ditch (D), was intermediate if the current habitat was bare soil (B), and was low if the current habitat was crop residue (C) or host plant (P) (Fig. 1). Note the almost constant value of parameter  $\beta$  ( $\approx 1.62$ ) for all habitat-



**Figure 2. Proportion of individuals staying at their release site in the five banana plots (observed versus simulated by POM).** Means for each of the five banana plots and 95% quantile interval (vertical bars) were calculated for the habitat-independent (white) and the habitat-dependent (black) models with the respective maximum likelihood estimates based on 100 runs. The dotted line corresponds to ideal fit between observations and simulations. For each plot, an asterisk indicates a significant difference between the simulated and observed mean ( $\chi^2$  test,  $df=1$ ,  $P < 0.01$ ).

doi:10.1371/journal.pone.0021115.g002



independent models  $M_0^k$  regardless of how habitat types were grouped (Table 1).

Concerning the POM procedure, the habitat-independent model  $M_0^4$  significantly underestimated the proportion of individuals remaining in their release cells in plots 4 and 5 (Fig. 2). The habitat-independent model  $M_0^4$  overestimated the dispersal distances in all plots except plot 1 and 2, in which it underestimated the distance distribution (Fig. 3). In contrast, the habitat-dependent model  $M_G^4$  accurately reproduced the two characteristics of space use. The Kolmogorov-Smirnov test, however, rejected the hypothesis of equal distribution for observed and simulated dispersal distances in plots 1 and 5 despite the closeness of the two distributions (Fig. 3).

## Discussion

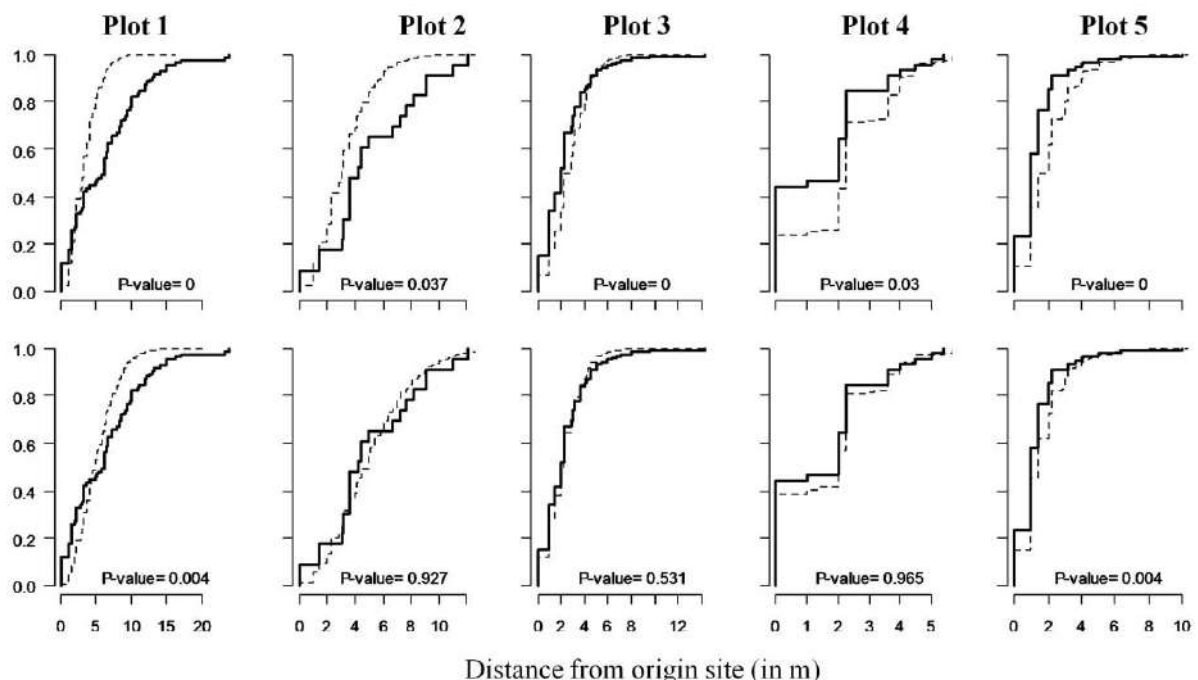
In this study of movement probabilities of the walking insect *C. sordidus*, we developed a stochastic Markov model to explore the effect of both target and departure habitats on an animal's decision to move or not to move. The ranking of "immigration attractiveness coefficients of habitats" (the  $\alpha_h$  parameters) was consistent with the *a priori* ordering of habitat quality for *C. sordidus*: the host plant is the most attractive for feeding and egg laying, and the litter-covered soil (crop residue) is the most attractive for protection against predators and feeding. Bare soil and ditch are less attractive because they are drier, provide no food, and offer no physical protection against predators. The ranking of the "habitat sedentariness coefficients" (the  $\beta_h$  parameters), which describe the cost of departure from a habitat, was similar to that of the  $\alpha_h$

coefficients. This concordance simply indicated that preferred habitats were those with high values for the coefficients  $\alpha$  and  $\beta$ , i.e., those which *C. sordidus* remained within or moved to.

Rhodes et al. [13] emphasized that animal movement probabilities could be usefully described as a function of habitat. Our results clearly support this view and showed that incorporating habitat dependency in dispersal kernels of spatially explicit models greatly improves our understanding of animal movements. Furthermore, the complementary POM approach showed that habitat-independent models failed to describe two pertinent statistical characteristics of animal space use. Introducing a habitat-dependent dispersal kernel was found to be useful and relevant because it enabled a reasonable statistical replication of the spatial and temporal behaviour of animals in habitats of both low and high suitability. Our study, therefore, provides elements to respond to the call by Olden et al. [4] for the development of spatially explicit models of animal movements that integrate the concept of context-dependent perceptual ranges.

Lima and Zollner [5] pointed out that perceptual range strongly depends on species and represents a key trait of mortality risk of dispersing animals. The authors reported that animals with high perceptual range are subjected to a higher risk of mortality because they spend more time searching suitable habitat. On the one hand, our results confirmed that individuals located in unsuitable habitats (bare soil or ditch) and experiencing a high risk of predation consequently "increase" their movement probabilities to perceive distant protective habitats such as host plant or litter-covered soil. On the other hand, the study also showed that individuals located in suitable habitats with a low mortality risk

## Cumulative probability density



**Figure 3. Dispersal distances in the five banana plots (observed versus simulated by POM).** Simulations were driven for habitat-dependent and habitat-independent models with the respective maximum likelihood estimates. Cumulative distribution plot of simulated distances (dashed line) versus observed distances (bold line) from (a) the habitat-independent model and (b) the habitat-dependent model. P-values correspond to the results of the Kolmogorov-Smirnov test of equal distributions for observed and simulated dispersal distances (based on >100 simulations).

doi:10.1371/journal.pone.0021115.g003

might “reduce” their movement probabilities and stay longer on these favourable sites. Our analysis emphasized that individuals adapt their displacements depending on their current locations. This is in accordance with Huffaker and Gutierrez [3], who argued that many insects adapt their movement traits to optimize their presence in favourable areas. However, using a simulation model, Zollner and Lima [34] found a minor role of landscape configuration on behavioural tradeoffs between perceptual range and predation risk. Authors concluded that the shape of the relationships between perceptual range and predation risk was the main factor affecting dispersal success of animals.

The use of simple mechanistic models like the one presented here might clarify complex processes such as the plasticity of movement. The dispersal kernel of *C. sordidus* appeared more extended in bare soil than in banana plants. Zollner and Lima [21] found the same result with white-footed mice, and they hypothesized that these forest mice might locate suitable habitats by mainly using vision: their perceptual range was large in bare fields, which lacked visual obstructions, but small in crop fields, which contained many visual obstructions. *Cosmopolites sordidus*, in contrast, would perceive its environment through semiochemical stimuli [29], and we might interpret that the alteration of its dispersal kernel on a banana plant habitat was due to a saturation of the environment by local attractive chemicals. Conversely, bare soils contained only low concentrations of local chemical attractants, and in such an environment *C. sordidus* might be more responsive to surrounding cues.

Our dispersal model relies on two substantial assumptions. The first assumption is that individuals have no social interaction and behave independently of each other. This assumption appears to be justified because the discrete choice model did not contain a social component but correctly described the distribution of observed displacement lengths. The second assumption is that daily moves of an individual are independent of each other. This is the Markovian property of our model and is generally called ‘first-order memory loss’. We might consider this assumption as reasonable because *C. sordidus* individuals rest during the day and move at night. In other contexts and for other species, animal walks are correlated, i.e., moves are sequentially related to each other [35]. For such cases, more complex (second- or third-order Markovian models) could be built to describe two or three consecutive displacements. Another refinement would be to model not only the length but also the direction (angle) of displacements when it is pertinent, e.g., in response to wind direction, sun light, altitude, etc.

Our results illustrate that likelihood- and POM-based approaches are complementary and can be used to increase the understanding of ecological processes. In most contexts, however, these approaches have different uses. Likelihood procedures are more suitable for comparing empirical and parsimonious statistical sub-models. POM procedures, in contrast, are more suitable for comparing mechanistic models based on their ability to simulate observed patterns. Models using POM procedures may contain numerous deterministic and stochastic mechanisms that cannot be handled by a statistical formulation. This perhaps explains why these complementary methods are rarely used by the same community of scientists [36]. The POM approach might be correctly considered as a way to validate a model by simultaneously addressing many characteristics of a complex process. The

dispersal model developed in this study is simple enough to enable a tractable statistical formalism and rich enough to allow the emergence of properties of space use at the population level. This illustrates the value of a trade-off between simplicity and complexity in ecological studies.

## Supporting Information

**Table S1 Characteristics of the radio-tracking data sets.** Adults of *C. sordidus* were trapped in the field near their release site. They were sexed and marked using passive RFID (radio-frequency identification) tags. A preliminary study in controlled conditions indicated that tags did not affect adult movement. After the adults were released in the plots, their positions were checked daily with a recapture rate ranging from 50 to 80% and a precision of the position of 30 cm. *C. sordidus* movement is highly variable between individuals and between days, and ranges from 0 to 900 cm in one night. We extracted only relocations separated by 1 day and during the first week for analysis. This led to 3388 pairs of radio-tracking locations. Locations defined in decimetres were rounded to the proximate meter in order to have each position located in the centre of a given cell of the raster grid.

(DOC)

**Figure S1 Plot-raster of the five habitats used for the *Cosmopolites sordidus* movement study.** Each cell is a 1-m<sup>2</sup> square. Plots 1 and 2 are composed mainly of bare soil. The proportions of host plant and crop residues are larger in Plots 3–5 than in Plots 1–2. Host plants are planted in staggered rows in Plots 3 and 4, with a cover of crop residues in Plot 3. In Plot 5, host plants are planted in 10 irregular double-rows, with an irregular cover of crop residues between host plants in each double-row. Banana plantations are composed of a matrix of heterogeneous habitats likely to influence *Cosmopolites sordidus* movements. Banana plants are considered as semi-perennial because plants are successively replaced by suckers emerging at irregular intervals from the lateral shoots of the mother plant, leading to almost 10 cropping cycles before destruction of the field. Each host plant is a mat consisting of a mother plant, a shoot, and an old plant. At the end of the first cropping cycle, banana leaves and other crop residues are cut and form a permanent litter cover on the soil. Ditches about 80 cm deep are formed to increase drainage. To characterize the environment of each plot, we considered that each plot consisted of a raster grid of 1-m × 1-m cells with the value of each cell representing the most common habitat in the cell.

(DOC)

## Acknowledgments

The authors thank the anonymous referees for helpful comments and suggestions on the manuscript; Anne Vidie and Anaïs Chailleux for their assistance with fieldwork; Dominique Arnaud for technical assistance. This work is part of a Ph.D. of F.V. funded by the CIRAD.

## Author Contributions

Conceived and designed the experiments: FV PT. Performed the experiments: FV PT. Analyzed the data: FV P-FD OM RS PT. Contributed reagents/materials/analysis tools: FV OM RS. Wrote the paper: FV FL PT P-FD RS.

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## Flux biotiques-abiotiques dans la matrice paysagère

- Rudi, G., Belaud, G., Troiano, S., Bailly, J., & [Vinatier, F.](#) (2020). Vegetation cover at the water surface best explains seed retention in open channels. *Ecohydrology* <https://doi.org/10.1002/eco.2263>
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## RESEARCH ARTICLE

# Vegetation cover at the water surface best explains seed retention in open channels

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## Funding information

Agropolis Fondation, Grant/Award Numbers: ID 1702-008/ ANR-10-LABX-001-01/ ANR-16-IDEX-0006, ANR-16-IDEX-0006

## Abstract

Hydrochorous dispersal through agricultural channels plays a role in structuring plant communities across agricultural landscapes. To date, research on seed retention in vegetated areas has mainly focused on vegetation types with simple architecture (often cylinders), which consequently do not represent real vegetation features. Here, we test the hypothesis that vegetation cover estimated at the water surface best explains floating seed retention in open channels. We therefore proposed an experiment to measure seed retention in a controlled environment across a large range of hydraulic conditions and vegetation architecture types. We used three types of artificial plants with contrasting morphotypes, and real seeds of *Rumex crispus*. Vegetation metrics were calculated on the basis of 3D plant models. We also tested the additivity of seed retention as a function of the length of vegetated area crossed by the seeds. We developed a semi-empirical formula for predicting seed retention. The main results of the experiment show that (i) the seed retention rate reacts differently to changes in density according to species, (ii) vegetation cover at the free water surface, potentially in contact with seeds, is a generic predictor of floating seed retention whatever the nature of the vegetated cover, and (iii) 95% of seed retention was reached for a large range of surface vegetation ratios and length of vegetation cover. The proposed formula could be used by stakeholders (farmers and ecologists) to estimate the amount of vegetation needed in a channel to limit or enhance seed dispersal.

## KEYWORDS

3D plant model, agricultural drainage networks, hydrochory, Propagule dispersal, *Rumex crispus*, vegetated channel, vegetation metrics, vegetation porosity

## 1 | INTRODUCTION

Hydrochorous dispersal plays a major role in structuring vegetation communities (Gurnell, Boitsidis, Thompson, & Clifford, 2006; Nilsson, Brown, Jansson, & Merritt, 2010; Nilsson, Gardfjell, & Grelsson, 1991; Ridley, 1930). In agricultural areas, some plant species are able to travel hundreds of metres via semi-natural waterways, such as ditches or irrigation channels (Rudi, Bailly, Belaud, & Vinatier, 2018; Soomers, Winkel, Du, & Wassen, 2010; Van Dijk, Van Ruijven, Berendse, & De Snoo, 2014). Plant dispersal can

therefore be favoured by a network-like organization of waterways, and propagules can readily travel through the agricultural landscape, either causing economic losses for farmers when the propagules compete with their crops (Petit, Boursault, Guilloux, Munier-Jolain, & Reboud, 2011), or contributing to the maintenance of community species richness and increasing genetic diversity in populations (Nilsson, Brown, Jansson, & Merritt, 2010). Plant richness in agricultural channels provides numerous microhabitat types and contributes to the connection of populations of mobile organisms, including amphibians, mammals and insects, which would otherwise be isolated in

intensively cropped areas (Dollinger, Dagès, Bailly, Lagacherie, & Voltz, 2015).

The interplay between propagule features, hydrodynamic characteristics and waterway properties drives propagule dispersal (Greet, Cousens, & Webb, 2012; Greet, Webb, & Downes, 2011; Hyslop & Trowsdale, 2012). The propagules' features, especially those determining the duration of buoyancy (Boedeltje, Bakker, & ter Heerdt, 2003; Carthey, Fryirs, Ralph, Bu, & Leishman, 2016; Riis & Sand-Jensen, 2006), are important factors for explaining the distance of transportation by water in natural ecosystems. The ability to float is mostly linked with the features of the propagules, such as density, size and shape. For floating propagules, the mean flow velocity (Defina & Peruzzo, 2010) and turbulent diffusion (White & Nepf, 2003) as well as hydrodynamic conditions at the water surface can be related to the rates of deposition in the channels (Merritt & Wohl, 2002). Other retention factors include the presence and abundance of vegetation (Chambert & James, 2009; Cornacchia et al., 2019; Defina & Peruzzo, 2010; Liu, Zeng, & Huai, 2019; Peruzzo, Defina, & Nepf, 2012; Peruzzo, Pietro Viero, & Defina, 2016) and vegetation type (de Jager et al., 2019), especially in narrow agricultural waterways, such as channels and ditches (Rudi et al., 2020; Rudi, Bailly, Belaud, & Vinatier, 2018; Soomers, Winkel, Du, & Wassen, 2010).

At the local scale, Defina and Peruzzo (2010) describe two mechanisms for temporary trapping of propagules in emergent vegetation: (i) wake trapping, in which the propagules are retained in the recirculation zone behind a plant (White & Nepf, 2003), and (ii) inertial impaction, in which the inertia of a propagule allows it to escape from the streamline and meet a stem (Palmer, Nepf, Pettersson, & Ackerman, 2004); and two possible mechanisms of permanent trapping: (i) net trapping, in which a bunch of stems or leaves forms a net-like structure and (ii) the 'Cheerios effect' (Vella & Mahadevan, 2005), which is explained by the deformation of the water surface linked with surface tension. For permanent propagule retention, note that the Cheerios effect is significant when the spacing between stems is greater than the propagule size and in slow-flowing conditions (Chambert & James, 2009). Some semi-empirical models have been developed to characterize propagule retention distances in vegetated media relying on channel experiments (Defina & Peruzzo, 2010; Liu, Zeng, & Huai, 2019; Peruzzo, Defina, & Nepf, 2012; Peruzzo, Pietro Viero, & Defina, 2016). These models have been mainly developed for slow flowing water and low to medium vegetation densities and focused mainly on the Cheerios effect. They described the probability of interaction and capture of propagules in vegetation. As described by Defina and Peruzzo (2012), the probability that a propagule reaches a specific distance depends on the propagule mean path length before permanent capture, the probability of interaction, the probability of permanent capture, and the mean centre-to-centre spacing between stems. In these experiments, the vegetation has usually been represented with rigid arrays, except in Defina and Peruzzo (2010, 2012), who used flexible plastic plants. The vegetation metrics used in the developed models are the mean centre-to-centre distance between stems, the mean spacing between adjacent cylinders (taking into account the stem diameter), and the density of plants

(Defina & Peruzzo, 2010, 2012; Liu, Zeng, & Huai, 2019; Peruzzo, Defina, & Nepf, 2012; Peruzzo, Pietro Viero, & Defina, 2016).

However, in field conditions, complex vegetation patterns are frequently observed. Vegetation exhibits a vertical variability, and consequently, the area of vegetation at the water surface that can potentially interact with propagules varies with the fluctuations in the water level. There is currently a lack of vegetation metrics and semi-empirical generic formulas able to predict the rates of propagule retention in the large range of hydrodynamic conditions observed in the field. Some attempts have been made to measure the percentage of plant cover at the water surface (Rudi, Bailly, Belaud, & Vinatier, 2018) or the plant cover 'porosity' (Vinatier et al., 2018) for real plant covers to characterize patterns of propagule deposition along agricultural channels. In these experiments, the tallest layers of vegetation hid the vegetation at the water surface and made it difficult to reconstruct the patterns of vegetation cover at the water surface. Moreover, as pointed out by Green (2005), the vertical heterogeneity of the vegetation profile needs to be taken into account in studies focusing on interactions between vegetation and fluxes of matter. Testing the importance of the specific vegetation surface permeability to propagules against other traditional metrics describing the vegetation cover seems necessary for a better comprehension of hydrochory.

The study was motivated by questions on the retention ability of terrestrial and semi-aquatic vegetation growing in agricultural channels and ditches in Mediterranean areas. One of the specificities of these patches is that they generally cover the total width of the channels and form a relatively homogeneous cover. As will be detailed below, the experimental setup therefore reflects the conditions commonly observed in these systems.

In this study, floating seed retention in vegetated channels is investigated, focusing on a large range of plant densities for three different types of emergent vegetation with complex architectures, representative of the types of vegetation that can be found in agricultural drainage or irrigation channels with medium velocity flow conditions. We hypothesized that vegetation cover estimated for the fine layer constituting the water flow surface is the best predictor of seed retention compared to other vegetation metrics. The specific purpose of the study was (i) to investigate seed retention rates in various artificial plant covers that closely reproduce the plant covers observed in the field, (ii) to test the hypothesis of additivity of seed retention according to the length of the vegetated area and (iii) to establish a semi-empirical retention function based on two components depending on plant metrics and hydrodynamic conditions to test the relevance of the vegetation cover at the surface to explain seed retention.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental channel design

The experiments were conducted in controlled hydraulic conditions in an experimental cement channel located at the *Institut Agro-Montpellier SupAgro* (Montpellier, France). The channel is rectangular

(9-m long and 0.66-m wide) (Figure 1). The slope is 0.0013 m/m. This channel was chosen because its dimensions were consistent with those of the channels and ditches found in southern France and with the morphologies of those channels, in which flows are generally sub-critical and turbulent. Commonly observed Froude and Reynolds numbers of these systems could be reproduced in the channel. The water inflow was regulated thanks to a control structure (constant level gate followed by baffle module weirs) ensuring a constant discharge ( $\pm 5\%$ ). Then, a flow tranquillizer followed by a 5-m reach ensured the formation of a well-established flow upstream of the channel. The downstream water level was controlled by a rectangular weir with a sill of 10 cm. At the end of the channel, a net was placed to collect seeds. The water was then filtered and recycled through the closed system.

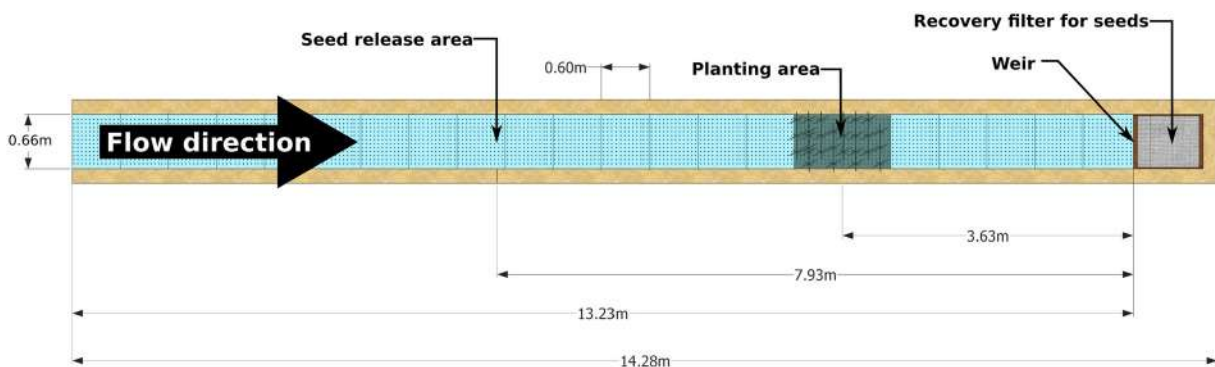
The selected steady-state flow rates varied from 10 to 40 L s<sup>-1</sup>, determined with an accuracy of  $\pm 5\%$  (Vinatier, Bailly, & Belaud, 2017). The range of variation in the discharges is based on the heights of the plants, in such a way that plants are never submerged.

## 2.2 | Plant material and its spatial arrangement

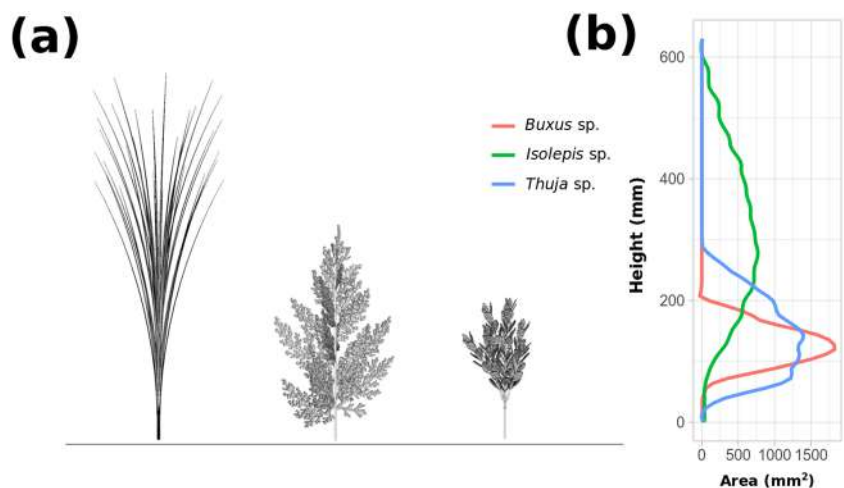
Three types of plastic plants of different architectures were chosen for the experiment: a Cyperaceae (*Isolepis* sp.), a Cupressaceae (*Thuja*

sp.) and a Buxaceae (*Buxus* sp.) (<https://www.artificielles.com>) (Figure 2). We chose these types of plants because they represented a diversity of architectural topologies characteristic of the plant diversity found in intermittent agricultural channels. The Cyperaceae morphotype represented by *Isolepis* sp. (thin and elongated) is similar to the grasses frequently encountered in channel banks, colonizing an intermediate ecological niche between terrestrial and wetland environments. The Cupressaceae morphotype (*Thuja* sp.) is characteristic of shrubby vegetation encountered in less well-managed channels. The Buxaceae morphotype (*Buxus* sp.) is similar to that of some Asteraceae found in the bottoms of channels, with a specific architecture consisting of a long stem surmounted by a vegetative spike. Table 1 presents the diversity of morphological characteristics of the studied artificial plants.

The plants were fixed on concrete panels (0.66 × 0.60 m) drilled with 144 holes, that is, approximately 362 holes per square metres, filled with screw anchors to fix the plants. Fourteen densities were established in a staggered pattern, representing the variability in natural plant densities found in ditches (Rudi, personal communication). A picture of the vegetated area with a medium density (36 plants per concrete panel) from above the channel for two panels is presented in Figure 3. The arrangement of plants in the channel for all the density configurations is provided in Appendix A.



**FIGURE 1** Schematic representation of the experimental channel



**FIGURE 2** (a) 2D representations of the three plants (*Isolepis* sp., *Thuja* sp. and *Buxus* sp., from left to right) used for the experiment and (b) the vertical profile of their surface area according to a horizontal plane

Variable	<i>Isolepis</i> sp.	<i>Thuja</i> sp.	<i>Buxus</i> sp.
Standing length (cm)	63	30	20
Ramification number	0	1	2
Number of branching stems	0	30	11
Volume (cm <sup>3</sup> )	241	230	147
Collar diameter (mm)	6	3	3
Leaf number	8	30	15
Projected surface area on horizontal plane (cm <sup>2</sup> )	162	40	52
Cumulative leaf surface area (cm <sup>2</sup> )	465	276	197

**TABLE 1** Characteristics of the studied artificial plants. The ramification number was based on the methodology detailed in Godin and Caraglio (1998)



**FIGURE 3** Picture of the vegetated area (*Isolepis* sp.) in the experimental channel (36 plants per concrete panel on two panels)

Note that for all the density configurations, the vegetation filled the channel width and was homogeneously distributed in the channel.

### 2.3 | Overview of the experiments

Two seed release experiments were conducted in the experimental channel. The first experiment aimed to characterize the retention rate of seeds in patches of vegetation with constant lengths (over the length of two concrete panels, that is, 1.2 m, with different plant density configurations, see Table 2) to assess the interactive effects of density per panel (D), species (SP) and discharge (Q) on seed retention. In the second experiment, the same plant density was planted on one to eight panels (i.e., 0.6 to 4.8 m) to characterize the effect of the length of the patch (where NB is the number of panels) on the seed retention and test the hypothesis of additivity of seed retention (Table 2). It is important to note that for the second experiment, discharge and density were chosen to explore the largest range of retention rates from one panel to eight panels and differed for each species. A trial without plants was conducted for each discharge tested in the experiment. Moreover, the results from these two experiments were used to calibrate the developed model of seed retention based on new vegetation metrics.

### 2.4 | Seed release and counting

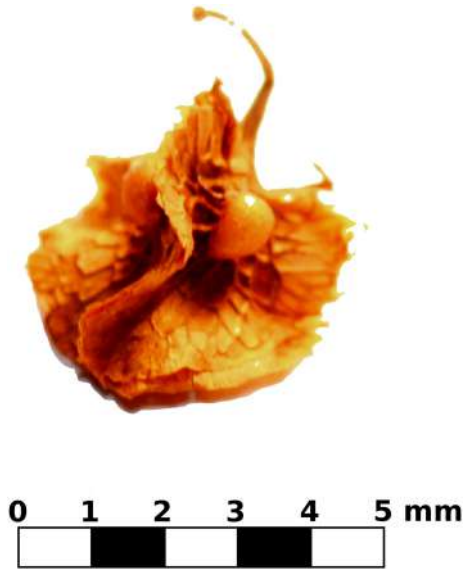
Seeds from curly dock (*Rumex crispus*) (Figure 4) were collected in Lattes (Hérault, France) in October 2018. This weed was chosen because it is common in rural areas, and its seeds have the potential to disperse via flow because they are contained in the calyx of the flower which has good buoyancy (Uva, Neal, & Ditomaso, 1997). The buoyancy of the collected seeds was assessed by immersing 200 seeds in 10 pots of water (20 seeds per pot) for 5 days. This experiment showed that 100% of the seeds were buoyant during the first 10 h of immersion (details of the experiment are provided in Appendix B). This was consistent with the results of Cavers and Harper (1964) and Favre-Bac, Mony, Burel, Seimandi-Corda, and Ernoult (2017), who classified *R. crispus* seeds as having long-term buoyancy compared to other species. The weight of the seeds (5.35 mg [ $\pm 0.68$  mg]) was estimated from the measurement of 10 lots of 10 seeds with a high-precision scale (Precisa XB 160 M; precision: 0.001 g; accuracy: 0.01 g). The seed diameter was measured as the average of 50 seeds (4.96 mm [ $\pm 0.76$ ], including the calyx) with a calliper.

During the experiment, following the Eulerian framework described in Defina and Peruzzo (2010), lots of 50 seeds were released at the head of the channel in the seed release area using a 60-cm long piece of metal. The lots were distributed



**TABLE 2** Summary of the experimental design. SP represents the species, Q the discharge, D the density of plants by panels of  $0.66 \times 0.60$  m and NB is the number of concrete panels filled with vegetation

SP	Q (in $L s^{-1}$ )	D	Density per $m^2$	NB
First experiment				
<i>Isolepis</i> sp.	10–25–40	0–144	0–361.9	2
<i>Buxus</i> sp.	10–20	0–36	0–90.5	2
<i>Thuja</i> sp.	10–20–30	0–96	0–241.3	2
Second experiment				
<i>Isolepis</i> sp.	10	36	90.5	1, 2, 4, 6, 8
	25	60	150.8	1, 2, 4, 6, 8
	40	60	150.8	1, 2, 4, 6, 8
<i>Buxus</i> sp.	10	9	22.6	1, 2, 4, 6, 8
	20	9	22.6	1, 2, 4, 6, 8
<i>Thuja</i> sp.	10	12	30.2	1, 2, 3, 4, 6, 8
	20	24	60.3	1, 2, 3, 4, 6, 8



**FIGURE 4** Picture of a curly dock (*Rumex crispus*) seed

homogeneously using this piece of metal, which covered the width of the channel. For each release, we counted the seeds that travelled to the end of the channel after a defined amount of time, depending on the length of the patch and the water discharge. The retention rate of seeds was calculated according to the following formula:

$$R_r(x) = \frac{N_{\text{release}} - N_{\text{out}}}{N_{\text{release}}} \quad (1)$$

where  $R_r(x)$  is the retention rate over a vegetated distance of  $x$  metres,  $N_{\text{release}}$  is the number of seeds in each release (50 for this experiment) and  $N_{\text{out}}$  is the number of seeds reaching the tail end of the experimental channel. Each release was repeated three times for one set of Q, SP and D.

Following Defina and Peruzzo (2010), we estimated that seeds were permanently trapped after a period equal to one order of magnitude above the mean travel time of a seed for the whole test section. For the first experiment (with two vegetated panels), this period was set at 2 min and 1 min 30 s for discharges equal to  $10 L s^{-1}$  and above  $10 L s^{-1}$  respectively, which is in accordance with the period of 2 min set in Cornacchia et al. (2019) and with preliminary tests showing that there was no seed release once these time limits were exceeded. For the second experiment, we adapted the period to the number of vegetated panels, by multiplying the length of the period according to the total number of vegetated panels, based on the periods chosen for two vegetated panels. For each release, when the time elapsed, we collected all the seeds trapped in the patch of vegetation before the next release. In total, 264 releases of 50 seeds were made in the first experiment and 111 in the second experiment, representing 18,750 released seeds in total.

## 2.5 | Characterization of the seed retention rates relative to the experimental variables

The effects of the experimental variables and their interactions on the  $R_r$  were analysed using a binomial generalized linear model with logit link function (analysis of deviance with binomial error). The experimental variables were Q, D, SP and NB. The significance of each variable was assessed via the change in deviance between the models with and without the variable. Overdispersion was accounted for using quasi-binomial instead of binomial models.

For each combination of SP  $\times$  Q for the first experiment (two panels, corresponding to a distance of 1.20 m), a sigmoid curve with the form

$$R_r(1.2) = \frac{1}{1 + e^{(-\text{slope} \times (D - D_{50}))}} \quad (2)$$

is fitted using the nonlinear least squares method to obtain  $D_{50}$  (the density needed to reach 50% seed retention) and the slope of the linear relation between  $D$  and  $R_r$ .

## 2.6 | Characterization of the vegetation metrics

Among the different metrics describing the influence of vegetation on ecohydrological processes are the proportion of surface area containing vegetation (Green, 2005), the percentage of submerged or emergent vegetation (Rudi, Bailly, Belaud, & Vinatier, 2018) and the porosity of the vertical section of a channel induced by vegetation (Vinatier et al., 2018); we reviewed all of these metrics to test the hypothesis that vegetation at the water surface is the best predictor of seed retention.

Because of the complexity of the architecture of individual plants, there are no simple measurements of the vegetation cover metrics, especially for the vegetation area in the thin slice corresponding to the water surface that can potentially interact with the floating seeds. Consequently, we constructed a three-dimensional model of each of the three artificial plants. This was made possible because of the homogeneity of the artificial plants and their repetitive elements.

A 3D model of each plant was realized by first establishing a master of all plant attributes. Each leaf of the artificial plant has been cut, numbered and scanned using a professional scanner (600 dpi resolution). Leaf thickness, stem diameters and spacing between the different stem portions were measured using a calliper. Orientations of leaves and stems were measured using a protractor. Then, meshes of all plant attributes were assembled using CloudCompare software (Girardeau-Montaut, 2014) to produce a continuous mesh for each plant.

After this step, different vegetation metrics were derived from the projection of the 3D plants on the horizontal plane of the channel (Figure 5):

- the projection of the whole plants on a horizontal plane, derived from the complete 3D model (basis for calculation of Metrics 1),
- the projected areas of the emergent and submerged vegetation (emergent and submerged vegetation on Figure 5) on a horizontal

plane, derived from the model cropped by a plane at the level of the water surface (basis for calculation of Metrics 2 and 3), and

- the area of the plant at the free surface of the water derived from the model sliced by two planes at 1 mm above and below the water level (basis for calculation of Metrics 4) (surface vegetation on Figure 5).

The different areas were calculated from (i) the product of each individual projected area by plant density for each experiment ('product' method) and (ii) a scene representing the 3D models arranged according to the spatial patterns found for each density ('scene' method). By construction, the overlapping surfaces of the high-density projections were summed in the 'product' method and were merged in the 'scene' method.

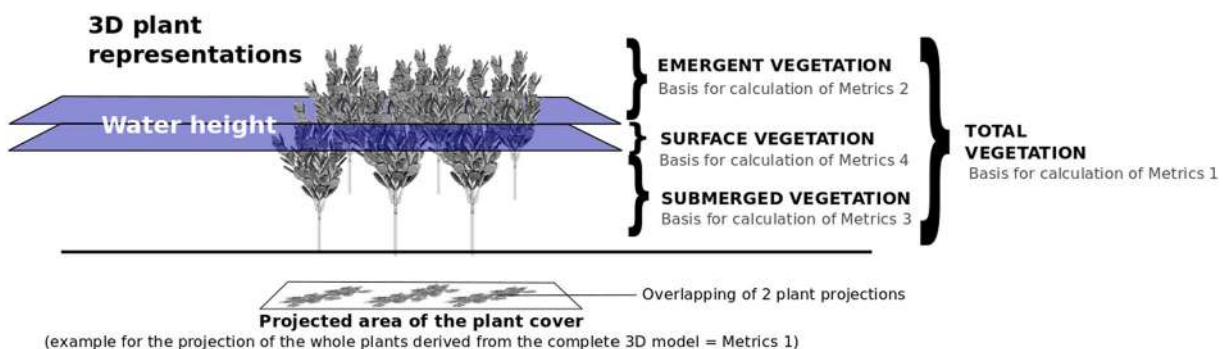
Then, we calculated the ratio of occupation of each vegetated area by dividing the area occupied by vegetation by the total planting area of the channel (on a horizontal plane) to obtain the four vegetation metrics, called  $Metrics_{veg}$ .

## 2.7 | Characterization of hydrodynamics

The literature survey suggests that the hydrodynamic conditions at the water surface, and especially the velocity at the water surface, largely influence the retention rates. More specifically, seeds are transported with the current, and we expect their probability to pass the vegetation filter to increase with turbulence. Therefore, we introduced the non-dimensional Reynolds number,  $\Re$ , to characterize the nature of the flow patterns:

$$\Re = U \times H / \nu \quad (3)$$

where  $U$  corresponds to the average velocity over a section in  $m\ s^{-1}$  ( $U = Q/(B \times H)$ ),  $H$  is the water height in m (corresponding to the characteristic length),  $B$  the width of the experimental channel in m, and  $\nu$  is the kinematic viscosity in  $m^2\ s^{-1}$ . Weakly turbulent flows (low Reynolds number) should result in high retention rates ( $R_r \rightarrow 1$ ) (in this case, surface tension will facilitate the capture by vegetation stems), while highly turbulent flows (large  $\Re$ ) should result in low seed



**FIGURE 5** Illustration of the different types of vegetation metrics for a group representing the plant arrangement for a given density

retention ( $R_r \rightarrow 0$ ). The range of the Reynolds numbers in our experiments was assessed between 15,000 and 60,000.

## 2.8 | The additivity effect

Based on a constant probability of capture on each panel, we tested the additivity of our model based on the following formula:

$$R_r(x) = 1 - \left(1 - \hat{R}_r(1.2)\right)^{\left(\frac{x}{l}\right)} \quad (4)$$

where  $x$  is the vegetated distance travelled by the seeds (in m),  $\hat{R}_r(1.2)$  is the mean experimental retention value for two vegetated panels, and  $l$  is the length of the two vegetated panels, that is, 1.2 m.

## 2.9 | The generic formula for seed retention

The relation linking  $R_r$  to  $Metrics_{veg}$  and  $\mathfrak{A}$  could be approximated by an exponential model of the form:

$$R_r(1.2) = 1 - e^{\left(\frac{-Metrics_{veg}}{a \times \mathfrak{A} \times 10^{-5}}\right)} \quad (5)$$

where  $a$  is a dimensionless parameter to estimate. The mathematical form respects the expected trends between  $R_r$  and  $\mathfrak{A}$ .

Combining Equations 4 and 5, we obtained the generic formula for seed retention:

$$R_r(x) = 1 - e^{\left(\frac{-Metrics_{veg} \times x}{a \times \mathfrak{A} \times 10^{-5} \times l}\right)} \quad (6)$$

Based on Equation 6, we tested what vegetation metrics best explained the seed retention rate ( $R_r$ ) from the two experiments on the basis of the  $R^2$  and the RMSE between the estimated and observed  $\hat{R}_r(1.2)$ .

## 2.10 | Software

All the statistical analyses were performed using R software (R Core Team, 2017). The processing of the 3D models was performed using dedicated R packages (Rvcg, Morpho and data.table).

**TABLE 3** Effect of discharge (Q), density (D), species (SP), and interactions between density (D) and species (SP) on the rates of seed capture in a generalized linear model (glm) with a binomial error distribution. Density and discharge were used as the continuous variables, and species was used as the categorical variable. The P value indicates the significance of the model

	d.f.	Deviance ( $\chi^2$ value)	Residual d.f.	Residual deviance	p Value
Q	1	654.4	253	7,047.3	<0.001
D	1	3708.3	252	3,339.0	<0.001
SP	2	718.16	250	2,620.8	<0.001
D × SP	2	440.5	248	2,180.3	<0.001

## 3 | RESULTS

### 3.1 | Effect of density, discharge and type of species on seed capture

The results of the statistical analysis (Table 3) show that the discharge, density or type of species significantly affects the rate of seed retention. The significant interaction between density and species means that the seed capture rate react differently to changes in density according to species. The results for the retention curves, as functions of plant density for each type of studied plant, are presented in Figure 6. Fitted parameters are presented in Table 4.

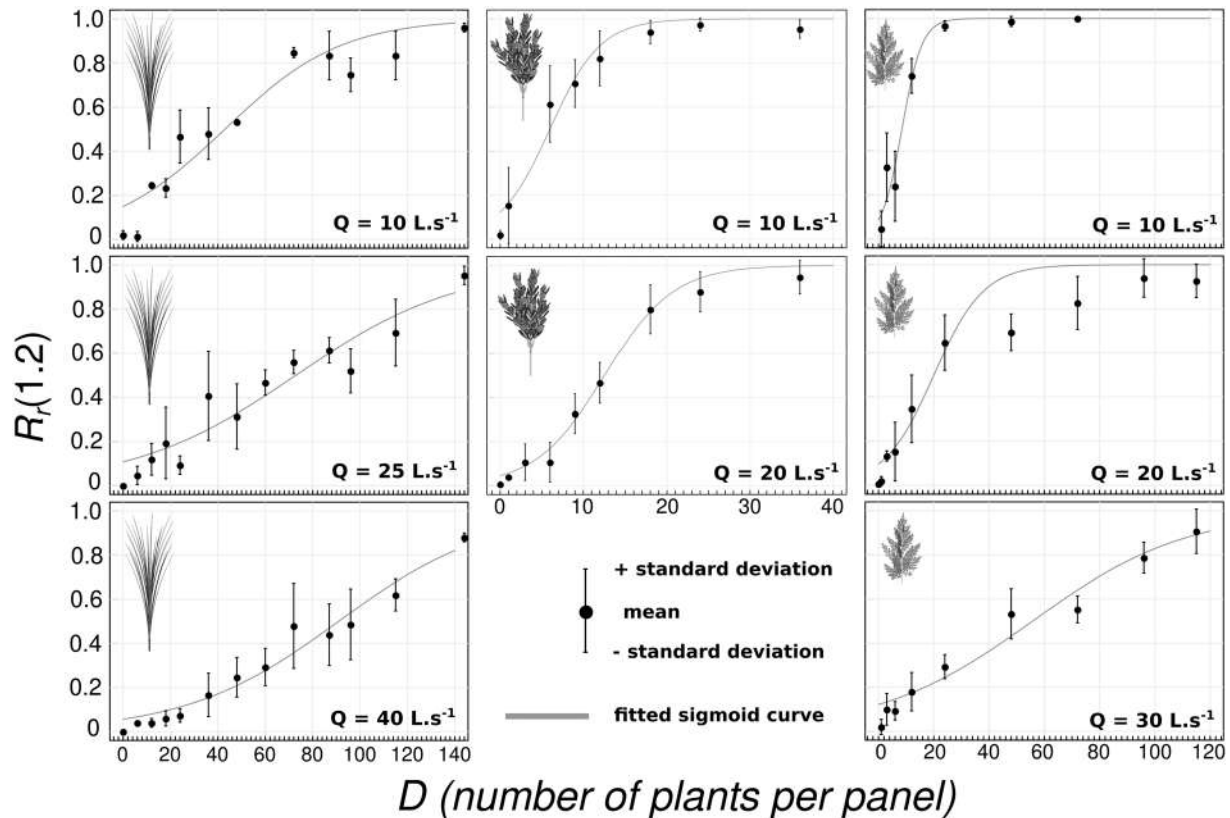
### 3.2 | Additivity of the seed capture rate as a function of vegetation patch length

We first tested the significance of the influence of the number of vegetated panels on water height. We found that in the conditions of the study, the number of panels had a non-significant influence on water height ( $p$  value = 0.123). This could be explained by the low density values tested for additivity (therefore, the vegetation did not significantly affect the hydraulic resistance). Consequently, we could neglect this effect in our experimental conditions.

The envelope of the additivity curve, extrapolated from the standard error of the  $\hat{R}_r(1.2)$ , generally encompasses the observed points for one, four, six and eight panels (Figure 7). The global  $R^2$  of the proposed model is 0.77 ( $\pm 0.16$ ).

### 3.3 | A generic formula for floating seed capture in differentiated plant covers

The calculated surface vegetation ratio was between approximately two-fold and 10-fold lower than the whole, submerged and emergent vegetation ratios. The Pearson cross product correlation test was significant between vegetation metrics ( $p < 0.001$ ). However, the correlation is low ( $0.2 < \text{cor} < 0.6$ ) between surface vegetation and the other metrics, and higher ( $\text{cor} > 0.6$ ) when comparing the metrics calculated by summing individual areas with the metrics calculated from a scene (Figure 5). The metrics calculated from the 'product' method



**FIGURE 6** Seed capture rates  $R_r$  as a function of plant density  $D$  (number of plants by panel) for *Isolepis* sp. (first column), *Buxus* sp. (second column), and *Thuja* sp. (third column). The solid line represents a sigmoid curve fitted using the nonlinear least squares method for each combination of SP and Q. Fitted parameters are given in Table 4

**TABLE 4** Parameters fitted to the sigmoid curves from Equation 2. Q is the discharge,  $D_{50}$  the density needed to reach 50% seed retention, and *Slope* the slope of the linear relation between the density ( $D$ ) and the seed retention rate ( $R_r$ )

Studied plant	Q (in $L.s^{-1}$ )	$D_{50}$	Slope	$R^2$
<i>Isolepis</i> sp.	10	43***	0.04***	0.86
	25	73***	0.03***	0.82
	40	91***	0.03***	0.88
<i>Buxus</i> sp.	10	6***	0.33***	0.90
	20	12***	0.24***	0.95
<i>Thuja</i> sp.	10	8***	0.28***	0.92
	20	20***	0.11***	0.85
	30	55***	0.04***	0.91

Note: Significance level of each parameter of the sigmoid curve fitted using non-linear least squares:

\*\*\*  $P < 0.001$ .

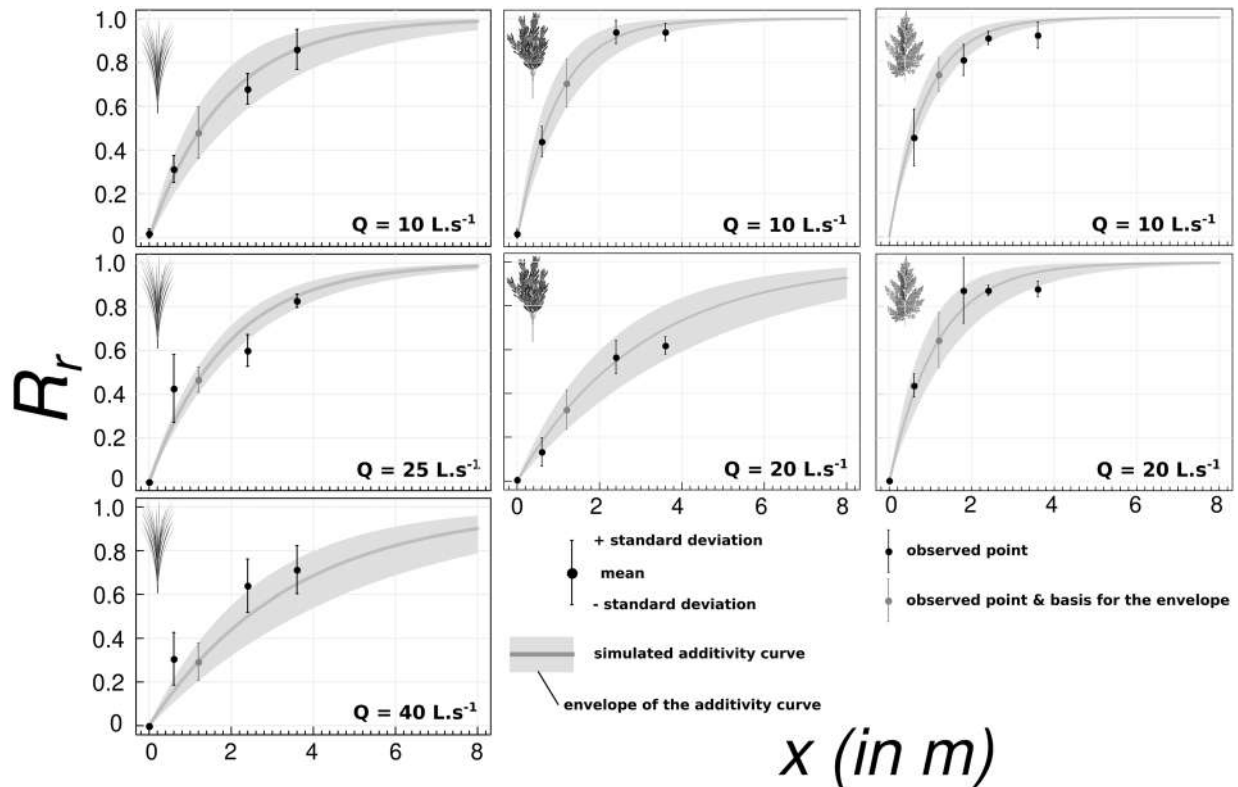
exceeded the total area of the channel, especially for the whole and emergent vegetation of *Isolepis* sp., due to the high degree of overlap observed for this species.

As shown in Table 5, the use of the surface vegetation ratio (Metrics 4) led to the best results ( $R^2 = 0.90$  and RMSE = 0.083 for

the 'scene' method, and  $R^2 = 0.58$  and RMSE = 0.178 for the 'product' method), regardless of how it was calculated. Considering a scene representing real spatial arrangements instead of the product of each individual plant area by density increased the performance of the models. The metrics calculated for the total vegetation (Metrics 1) and the emergent vegetation (Metrics 2) led to the worst results ( $R^2 < 0.30$  and RMSE > 0.25).

Regarding the seed retention rate in the best model corresponding to the scene method and use of 'Surface vegetation ratio' metrics (Metrics 4) ( $R^2 = 0.90$  and RMSE = 0.083), Figure 8 shows a homogeneous dispersion of the whole dataset across the fitted model. The data from the second experiment (additivity) were also included in the model, although they cover a lower range of vegetation metrics and hydraulic conditions. In Table 6, we observed that every studied plant was well fitted by the model.

Figure 9 indicates that 95% seed retention was reached for a large range of surface vegetation ratios and channel lengths (in hydrodynamic conditions allowing a Reynolds  $\Re$  of 32,000). Basically, with an  $R_r$  isoline equal to 0.95, channels of 10 and 20 m retained 95% of the seeds if the surface vegetation covered 5.3% and 2.5% of the water surface area, respectively.



**FIGURE 7** Comparison between the observed seed capture rates and predicted capture rates based on the additivity formula for the three plants (*Isolepis* sp. (first column), *Buxus* sp. (second column), and *Thuja* sp. (third column)). The mean and standard deviation (black points and arrays) values were calculated on the 3 repetitions of seed release experiment. The grey point and array are the mean and standard deviation for two vegetated panels, which served as a base for the calculation of the envelope (light grey)

**TABLE 5** Presentation of the results of the fitted generic formula across various  $Metrics_{veg}$  and  $\mathfrak{R}$  values

$Metrics_{veg}$	$\mathfrak{R}10^{-5}$		
	$R^2$	RMSE	$a$
Scene representing real plant arrangements ('scene' method)			
Total vegetation ratio (Metrics 1)	0.24	0.255	3.678
Emergent vegetation ratio (Metrics 2)	0.18	0.279	3.669
Submerged vegetation ratio (Metrics 3)	0.77	0.126	0.961
Surface vegetation ratio (Metrics 4)	0.90	0.083	0.464
Product of the projected area of individual plants by plant densities ('product' method)			
Total vegetation ratio (Metrics 1)	0.12	0.321	11.55
Emergent vegetation ratio (Metrics 2)	0.08	0.339	14.95
Submerged vegetation ratio (Metrics 3)	0.49	0.205	1.448
Surface vegetation ratio (Metrics 4)	0.58	0.178	0.654

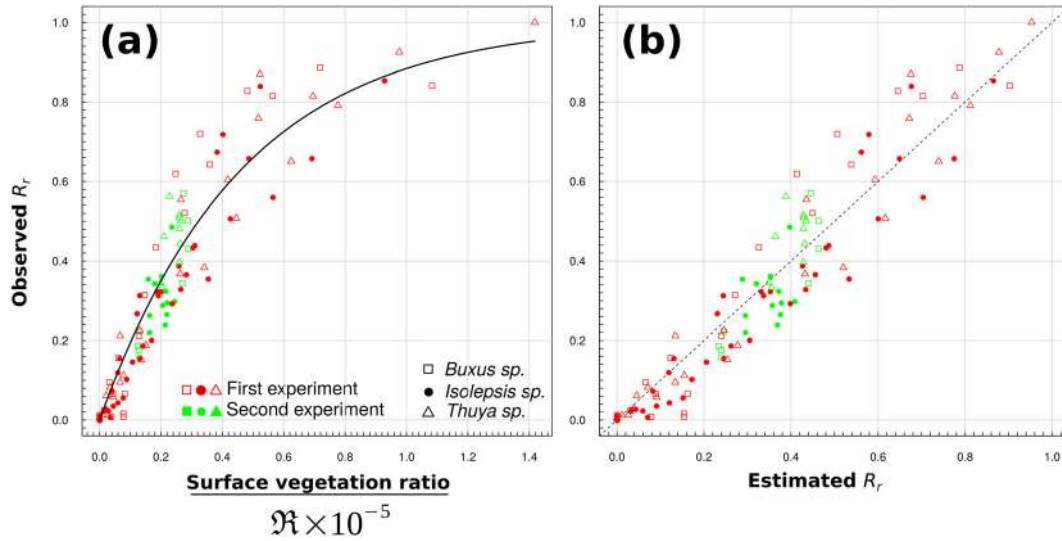
## 4 | DISCUSSION

### 4.1 | The area occupied by vegetation at the water surface is a relevant metric for seed retention prediction in a vegetated cover

This experiment showed the relevance of using the area occupied by vegetation at the water surface instead of the area calculated from

the total, emergent or submerged vegetation as a predictor of the seed capture rate in a vegetated channel. The use of the area occupied by vegetation at the water surface is interesting when focusing on plant covers with varied morphologies, because this metric is generic and works for the three types of vegetation covers tested.

In the experiment, the variations of discharge affected more the retention rates for *Thuja* sp. and *Buxus* sp. than for *Isolepis* sp. This is due to the fact that discharge affects directly water



**FIGURE 8** (a) Seed capture rate ( $R_r$ ) as a function of the best combination of vegetation metrics and Reynolds number. The solid line corresponds to the fit of the nonlinear model to the data. (b) Comparison between the observed and estimated  $R_r$  according to the model. The dashed line indicates a perfect fit between the observation and estimation

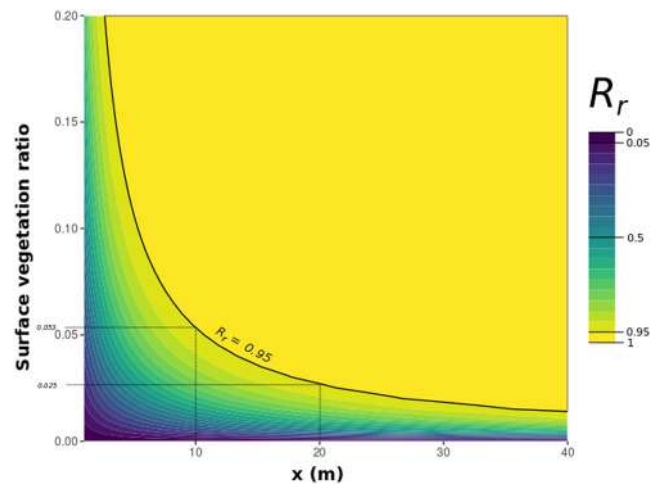
**TABLE 6** Estimation of the  $R^2$  and RMSE of the best fitted generic formula for the three studied plants

SP	Whole dataset	
	$R^2$	RMSE
<i>Buxus sp.</i>	0.83	0.26
<i>Isolepis sp.</i>	0.90	0.22
<i>Thuja sp.</i>	0.91	0.21

height in the channel, and the first two species display a greater variability of surface area according to water height than *Isolepis sp.* (see Figure 2b).

The additivity of the formula has been demonstrated on distances under 10 m with low vegetation densities. Higher vegetation densities would exert a significant influence on hydraulic conditions, especially height and velocity (Nepf, 2012), and the Reynolds number should be corrected as a consequence.

Our results reinforce the idea that representing vegetation cover as a porous media is an efficient approach for understanding water transport and particle transport in vegetated areas, as was highlighted in recent works focused on interaction between water transport and vegetation (see Rubol, Ling, & Battiato, 2018 and Vinatier, Bailly, & Belaud, 2017, for example). However, in this experiment, the spatial distribution of plants in the channel is relatively homogeneous. In configurations in which the vegetation is heterogeneously distributed, preferential transfers are observed (Cornacchia et al., 2019; Erktan, Cécillon, Roose, Frascaria-Lacoste, & Rey, 2013; Nepf, 2012). Indeed, the phenomena of flow divergence at the patch scale explain these preferential transfers, which could be susceptible to modifications in the relationship between the area occupied by vegetation and seed capture.



**FIGURE 9** Lattice plot based on the generic formula (Equation 6) and calibrated on the experimental data for a surface vegetation ratio between 0 and 20% and a channel length between 0 and 40 m, with the Reynolds value being fixed in the formula at 32 000 (which can correspond, for example, to a water height of 15 cm and an average velocity of  $0.21 \text{ m.s}^{-1}$ )

#### 4.2 | 3D representation of vegetation is an original and efficient method for characterizing plant cover at the water surface

The 3D representation of vegetation is an efficient approach, especially in contexts of high plant density or when plants are largely above the water level; in the latter case, techniques using photographs to reconstruct the area covered by vegetation from above have poor accuracy (because of the effect of sheltering), as revealed by our results. In situations in which we possess 3D models for each

type of plant encountered in agricultural channels, we could represent any vegetated cover and calculate the area at the water surface. Moreover, in the future, 3D plant models could help to calculate more evolved vegetation metrics commonly used in landscape ecology, such as core area or patch cohesion formed by the vegetation at the water surface.

However, the use of 3D plant models has limits. First, the production of 3D models is time consuming for real plants, and it would be even more time consuming if we wanted to create models for plants at different phenological stages. Moreover, in this study, the hydrodynamic conditions did not significantly modify the plant structure. However, plant reconfiguration has been observed under some hydrodynamic conditions (Vogel, 1996), and the degree of bending is usually a function of water velocity (Chapman, Wilson, & Gulliver, 2015; Luhar & Nepf, 2011) and height. The 3D models that we developed would be improved by being able to bend under flow drag forces. The integration of computational fluid dynamic tools, such as OpenFOAM ([www.openfoam.com](http://www.openfoam.com)) or Fluent ([www.ansys.com](http://www.ansys.com)), could allow the creation of this type of bowed plant model, but the amplitude of reconfiguration, the flex points and the representation of the streamlining of leaves as a function of water velocity still need to be characterized by further studies.

It will be necessary to test the effect of seed characteristics in the context of the main processes controlling vegetation and seed interactions. It has been shown that seed traits such as weight, size, density and shape influence interactions with vegetation when the Cheerios effect is the major mechanism of seed retention (Chambert & James, 2009; Liu, Zeng, & Huai, 2019; Peruzzo, Pietro Viero, & Defina, 2016), that is, when the water velocity is slow and the spacing between the stems of the vegetation is greater than the particle diameter (Chambert & James, 2009; Liu, Zeng, & Huai, 2019; Peruzzo, Pietro Viero, & Defina, 2016). In our hydrodynamic conditions, with net trapping being the major mechanism of seed capture, it is possible that seed features also influenced the rate of seed retention in our experiment. For example, de Jager et al. (2019) showed that large seeds were less affected by net trapping than smaller ones. The number of seeds released in the channel should also be considered. In our experiments, we observed that seeds sometimes formed clusters (due to the Cheerios effect) more susceptible to being captured by vegetation, especially when vegetation presented indented patterns, as for *Buxus* sp. and *Thuja* sp.

### 4.3 | Implications for the agroecological management of agricultural channels

It has been shown that agricultural channels could be significant dispersal vectors for weeds because they allow seeds to travel hundreds of metres in a few hours (Rudi, Bailly, Belaud, & Vinatier, 2018; Soomers, Winkel, Du, & Wassen, 2010). From a practical point of view, the developed formula provided an indication of the surface vegetation cover needed for a given channel length to reach a specified objective of retained seed rate. For portions of ditches of 10 m, it

would be necessary to have a surface vegetation ratio of 5.3% to retain 95% of seeds (with a Reynolds of 32,000, see Figure 9). Considering that the surface vegetation ratio is between twice and 10 times lower than the total vegetation ratio (see Section 3.3), vegetation coverage of 53% in the channel ( $5.3\% \times 10$ ) should be sufficient to retain 95% of the seeds transported by the channel. Previous studies of vegetation cover dynamics in agricultural channels (Dollinger, Vinatier, Voltz, Dagès, & Bailly, 2017; Levavasseur, Biarnès, Bailly, & Lagacherie, 2014) have revealed that management practices were a lever to control vegetation cover in space and time, and we should then be able to control hydrochorous seed dispersal through these management practices.

This work also confirms that water height variations, even moderate, play a role in the dispersal and subsequent establishment of plants in agricultural waterways, as observed by Engström, Nilsson, and Jansson (2009) and Cornacchia et al. (2019) in other aquatic ecosystems. Consequently, in agricultural channels, conserving a part of the vegetation that exceeds the maximal depth of the channel can guarantee retention and limitation of dispersal. In this sense, tall plants (i.e., taller than 50 cm) can play a preponderant role, because maximal depths in drainage channels and secondary/tertiary irrigation channels are generally approximately 50 cm in the studied ecosystems.

The developed prediction formula for seed retention is rather easy to use and can serve to assess the services of weed spreading limitation in agricultural landscapes or natural revegetation. Therefore, it is well adapted to be integrated in studies assessing benches of ecosystem services provided by vegetation of hydro-agricultural waterways such as ditches and channels (water transport regulation, weed spreading limitation or enhancement, and erosion limitation). Indeed, one of the drawbacks of multifunctional studies is the need to choose between indicator-based approaches (such as biomass, as a distant proxy for estimating the propagule retention capacity of vegetated channels) and physical approaches (e.g., using advection-dispersion equations, which need parameterization and substantial computing capacity and cannot be deployed when studying services on extended networks of channels) (Rudi, 2019; Rudi et al., 2020). Therefore, the developed formula in this research proposes a semi-empirical approach of medium complexity, process-based, to assess seed retention in agricultural channels.

## 5 | CONCLUSION

Seed dispersal by hydrochory through agricultural channels greatly influences weed spatio-temporal distributions at the landscape scale. Natural vegetation growing in these channels plays a major role in the retention rates of weed propagules, and these retention rates are greatly influenced by both vegetation features and hydrodynamic conditions. This research focused on the characterization of *R. crispus* seed capture rates in three different artificial vegetation covers (*Isolepis* sp., *Thuja* sp. and *Buxus* sp.) in an experimental channel. We compared the relevance of different vegetation metrics and showed that the cover of vegetation at the water surface, calculated from 3D

plants, was the best predictor of seed capture. We proposed a generic and semi-empirical formula to predict the seed capture rate in vegetated channels as a function of vegetation cover at the water surface and hydrodynamic conditions. This research supports the idea that the use of 3D plant models is an efficient way to understand water-plant-particle interactions in open channels. Our results have practical implications for the agroecological management of agricultural channels because they can inform on the relevant maintenance practices to manage vegetation according to the intended objectives of weed spreading limitation or natural revegetation through agricultural networks. Indeed, the choice between different options for vegetation management involves different vegetation dynamics along the year in terms of density or height of the cover (Dollinger, Vinatier, Voltz, Dagès, & Bailly, 2017; Levavasseur, Biarnès, Bailly, & Lagacherie, 2014). The proposed formula could be used as a basis for a wide variety of vegetation covers and extended to other types of floating seeds.

## ACKNOWLEDGEMENTS

The authors would like to thank Cédric Guillemain and Fabien Roudil for their help during the channel experiment. We would also like to thank first-year students from *l'Institut Agro (Montpellier SupAgro)* engineering programme (years 2017–2018 and 2018–2019) for performing the preliminary trials with us. This work (ID 1702-008) was publicly funded through ANR (the French National Research Agency) under the 'Investissements d'avenir' programme with the reference ANR-10-LABX-001-01 Labex Agro and coordinated by *Agropolis Fondation* under the frame of I-SITE MUSE (ANR-16-IDEX-0006). Inputs from two anonymous reviewers greatly improved the manuscript, and we are grateful for their recommendations.

## CONFLICT OF INTEREST

No conflict of interest was declared.

## DATA AVAILABILITY STATEMENT

The data that support the findings of the study will be available online (Rudi et al., 2020 - <https://doi.org/10.5281/zenodo.3947814>) from the date of publication.

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**How to cite this article:** Rudi G, Belaud G, Troiano S, Bailly J-S, Vinatier F. Vegetation cover at the water surface best explains seed retention in open channels. *Ecohydrology*. 2021;e2263. <https://doi.org/10.1002/eco.2263>

APPENDIX A.

Spatial arrangement of artificial plants in the channel according to the considered density

This appendix presents the spatial arrangement of the artificial plants in the channel for each tested density. Density is presented by number of plants by panel and by  $m^2$ . The water flowed from the right side to the left side of the vegetated panels (Figures A1–A15).

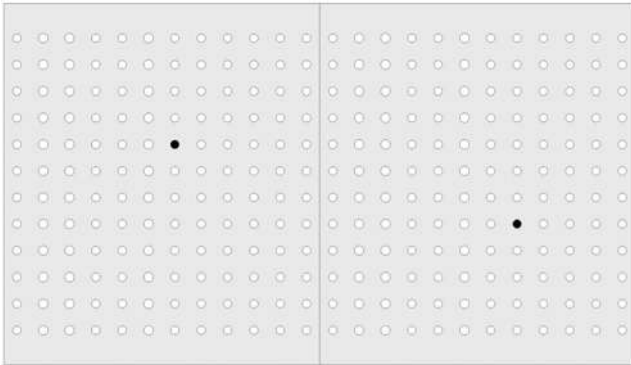


FIGURE A1 1 plant per panel (2.5 plants/ $m^2$ )

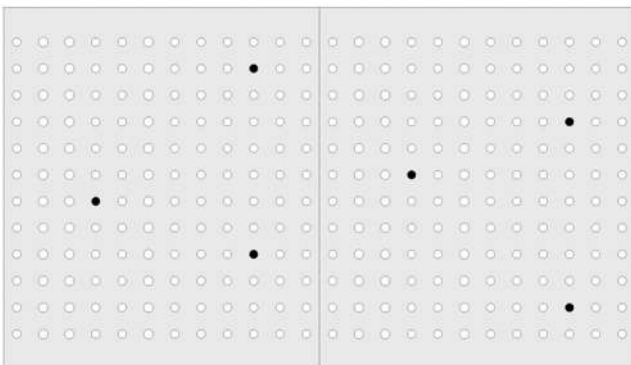


FIGURE A2 3 plants per panel (7.6 plants/ $m^2$ )

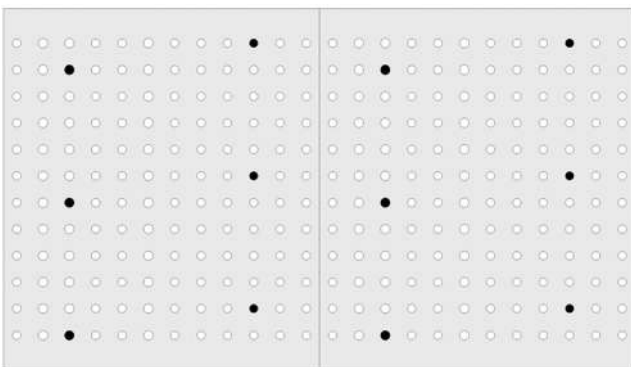


FIGURE A3 6 plants per panel (15.1 plants/ $m^2$ )

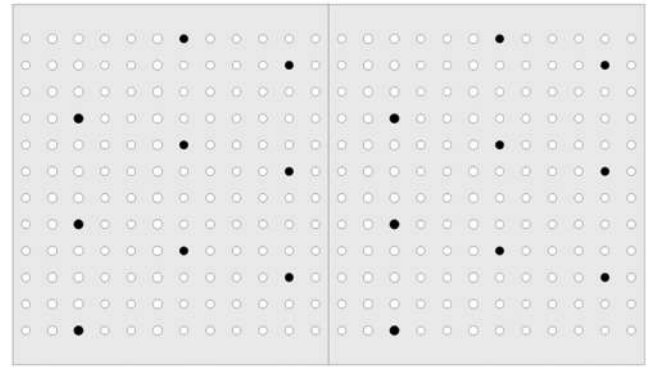


FIGURE A4 9 plants per panel (22.7 plants/ $m^2$ )

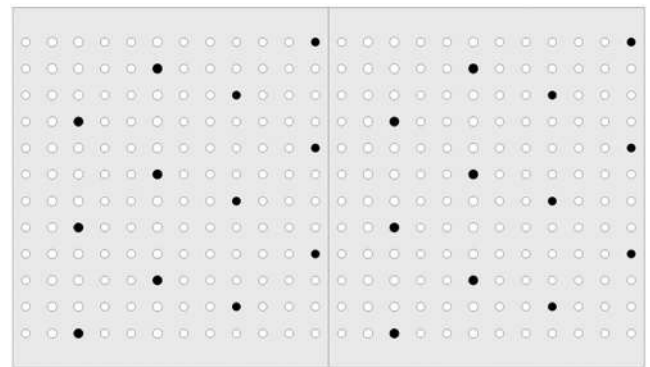


FIGURE A5 12 plants per panel (30.3 plants/ $m^2$ )

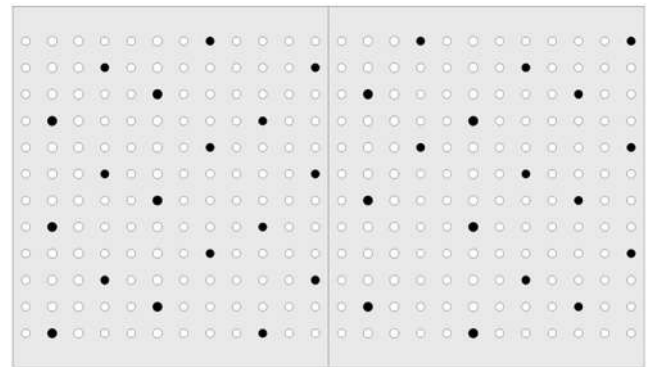


FIGURE A6 18 plants per panel (45.4 plants/ $m^2$ )

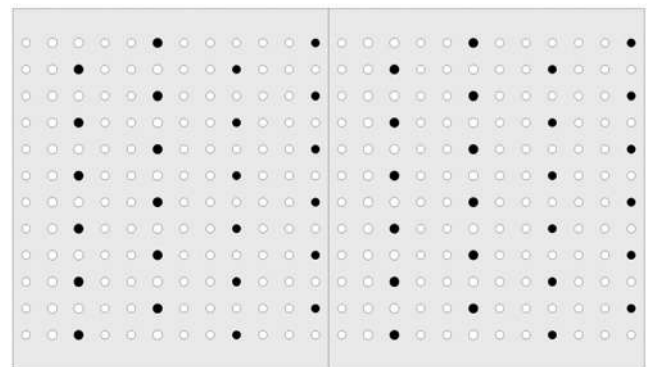
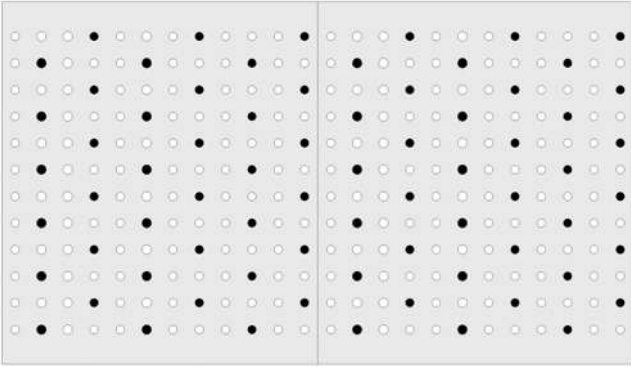
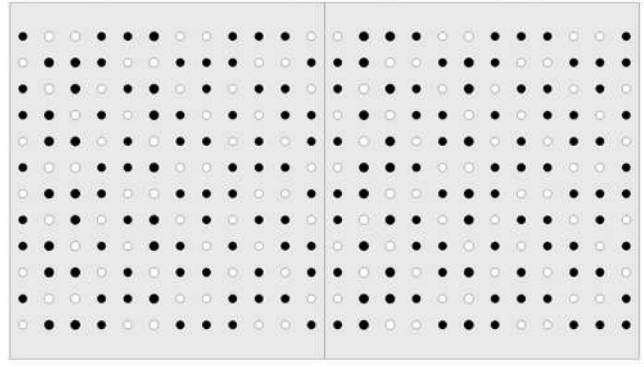


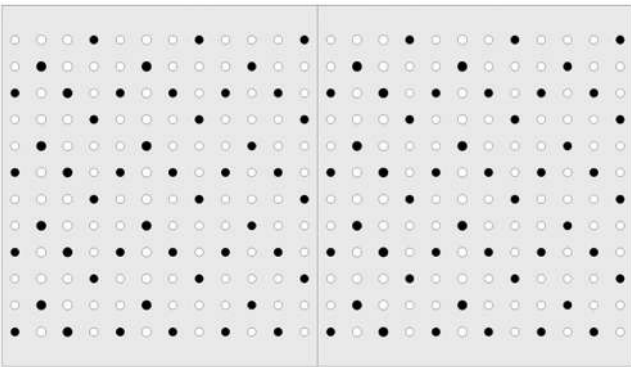
FIGURE A7 24 plants per panel (60.6 plants/ $m^2$ )



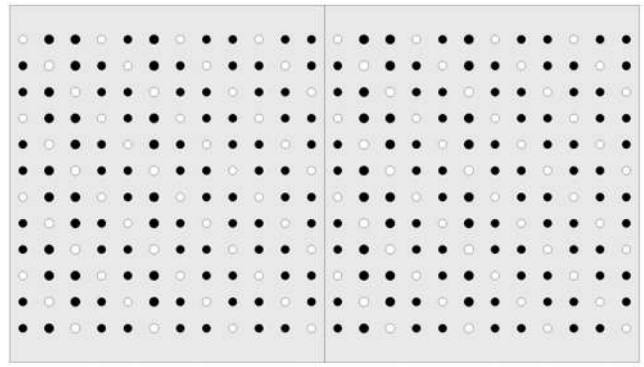
**FIGURE A8** 36 plants per panel (90.9 plants/m<sup>2</sup>)



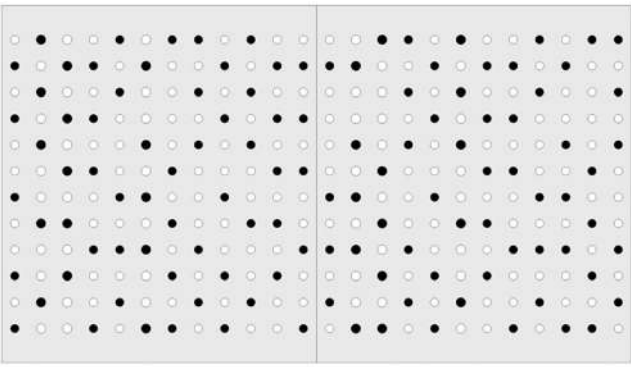
**FIGURE A12** 87 plants per panel (219.7 plants/m<sup>2</sup>)



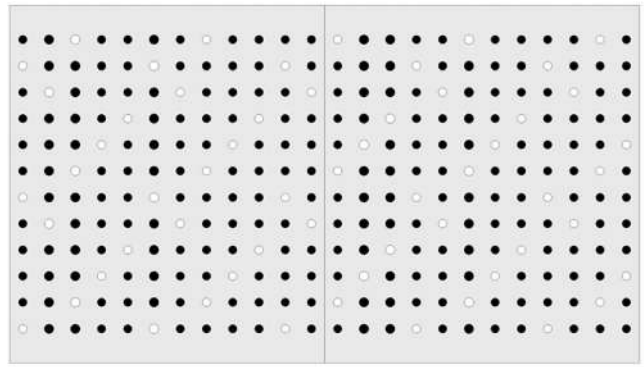
**FIGURE A9** 48 plants per panel (121.2 plants/m<sup>2</sup>)



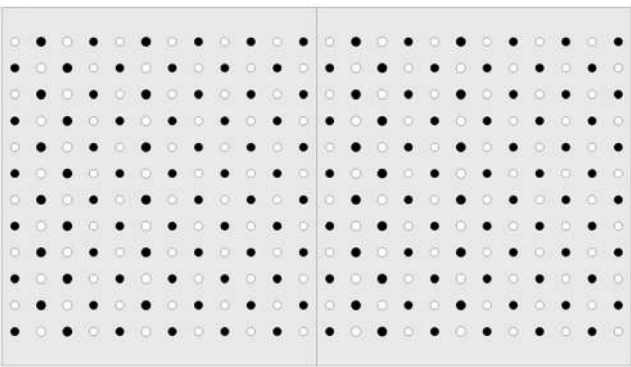
**FIGURE A13** 96 plants per panel (181.8 plants/m<sup>2</sup>)



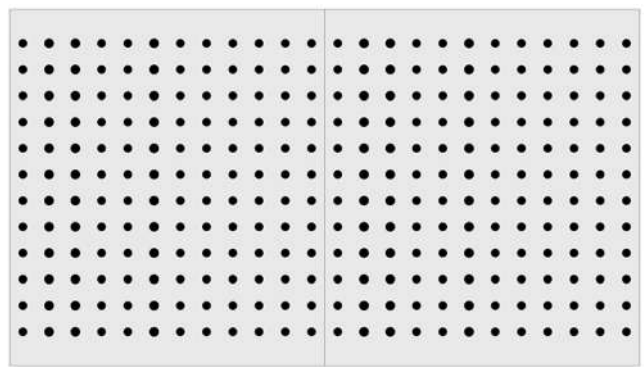
**FIGURE A10** 60 plants per panel (151.5 plants/m<sup>2</sup>)



**FIGURE A14** 115 plants per panel (290.4 plants/m<sup>2</sup>)



**FIGURE A11** 72 plants per panel (181.8 plants/m<sup>2</sup>)



**FIGURE A15** 144 plants per panel (363.6 plants/m<sup>2</sup>)

APPENDIX B.

Test of seed buoyancy duration for *Rumex crispus*

This buoyancy test was performed based on Boedeltje, Bakker, Bekker, Groenendael and Soesbergen (2003). We put 10 samples of 20 seeds in glass pots filled with tap water. We shook the pots during 5 s, and we counted the number of floating seeds immedi-

ately after shaking. Counts were realized every 4 min during the first hour, every 30 min during the four following hours, then hourly for the rest of the day, then twice a day until the end of the experiment (Figure B1, Table B1). After 3 days, some seeds started to germinate, and we stopped the experiment, as we were only interested about their behaviour at the scale of a few hours (time scale of our experiment).

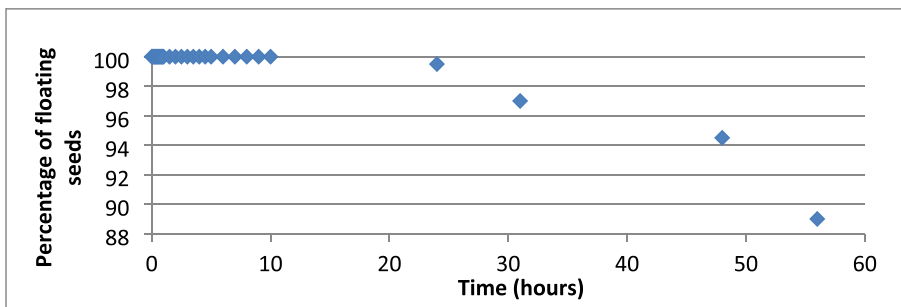


FIGURE B1 Evolution of the percentage of floating seeds over time

TABLE B1 Dataset of the evolution of the percentage of floating seeds over time with standard errors on the calculated percentage

Time	Percentage of floating seeds	Standard error
0 h	100.00	0.00
0 h 4 min	100.00	0.00
0 h 8 min	100.00	0.00
0 h 12 min	100.00	0.00
0 h 16 min	100.00	0.00
0 h 20min	100.00	0.00
0 h 24 min	100.00	0.00
0 h 28 min	100.00	0.00
0 h 32 min	100.00	0.00
0 h 36 min	100.00	0.00
0 h 40min	100.00	0.00
0 h 44min	100.00	0.00
0 h 48min	100.00	0.00
0 h 52min	100.00	0.00
0 h 56min	100.00	0.00
1 h	100.00	0.00
1 h 30min	100.00	0.00
2 h	100.00	0.00

(Continues)

TABLE B1 (Continued)

Time	Percentage of floating seeds	Standard error
2 h 30 min	100.00	0.00
3 h	100.00	0.00
3 h 30 min	100.00	0.00
4 h	100.00	0.00
4 h 30 min	100.00	0.00
5 h	100.00	0.00
6 h	100.00	0.00
7 h	100.00	0.00
8 h	100.00	0.00
9 h	100.00	0.00
10 h	100.00	0.00
24 h	99.50	1.58
31 h	97.00	4.83
48 h	94.50	5.50
56 h	89.00	7.75

Reference: Boedeltje, Bakker, Bekker, Groenendael, Soesbergen, (2003). Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. Journal of Ecology 91, 855–866 (<https://doi.org/10.1046/j.1365-2745.2003.00820.x>)

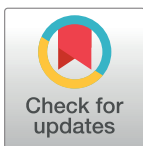
RESEARCH ARTICLE

# Using geomorphological variables to predict the spatial distribution of plant species in agricultural drainage networks

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## Abstract

To optimize ecosystem services provided by agricultural drainage networks (ditches) in headwater catchments, we need to manage the spatial distribution of plant species living in these networks. Geomorphological variables have been shown to be important predictors of plant distribution in other ecosystems because they control the water regime, the sediment deposition rates and the sun exposure in the ditches. Whether such variables may be used to predict plant distribution in agricultural drainage networks is unknown. We collected presence and absence data for 10 herbaceous plant species in a subset of a network of drainage ditches (35 km long) within a Mediterranean agricultural catchment. We simulated their spatial distribution with GLM and Maxent model using geomorphological variables and distance to natural lands and roads. Models were validated using k-fold cross-validation. We then compared the mean Area Under the Curve (AUC) values obtained for each model and other metrics issued from the confusion matrices between observed and predicted variables. Based on the results of all metrics, the models were efficient at predicting the distribution of seven species out of ten, confirming the relevance of geomorphological variables and distance to natural lands and roads to explain the occurrence of plant species in this Mediterranean catchment. In particular, the importance of the landscape geomorphological variables, ie the importance of the geomorphological features encompassing a broad environment around the ditch, has been highlighted. This suggests that agro-ecological measures for managing ecosystem services provided by ditch plants should focus on the control of the hydrological and sedimentological connectivity at the catchment scale. For example, the density of the ditch network could be modified or the spatial distribution of vegetative filter strips used for sediment trapping could be optimized. In addition, the vegetative filter strips could constitute new seed bank sources for species that are affected by the distance to natural lands and roads.

## OPEN ACCESS

**Citation:** Rudi G, Bailly J-S, Vinatier F (2018) Using geomorphological variables to predict the spatial distribution of plant species in agricultural drainage networks. PLoS ONE 13(1): e0191397. <https://doi.org/10.1371/journal.pone.0191397>

**Editor:** Paulo De Marco Júnior, Universidade Federal de Goias, BRAZIL

**Received:** February 1, 2017

**Accepted:** January 4, 2018

**Published:** January 23, 2018

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**Data Availability Statement:** The plant species survey, the Digital Terrain Model, the Digital Surface Model, and the explanatory variables derived from the Digital Terrain Model and from the Digital Surface Model, can be found on the open access repository Zenodo at the following address: <https://doi.org/10.5281/zenodo.837286>.

**Funding:** Authors are grateful to the INRA institution who partly funded the experimental work exposed in this paper within the 'Pari-Scientifique: Hydro-écologie des fossés agricoles' project (INRA-EA) to FV. This project was also funded by

Agropolis Fondation under the reference ID 1605-034 through the « Investissements d'avenir » programme (Labex Agro:ANR-10-LABX-0001-01) to FV. Lastly, the project was also supported by funds from a PhD grant provided by Montpellier Supagro and the INRA institution via the EcoServ metaprogram to GR. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing interests:** The authors have declared that no competing interests exist.

## Introduction

Agricultural drainage networks of headwater catchments are of high ecological value. They represent interfaces between anthropized and natural landscapes because they are mainly composed of linear hydro-agroecological infrastructures of anthropogenic origin [1] that are located at the boundary of fields and that are poorly constrained by crop technical operations. Their network design is generally in accordance with natural landforms and thalwegs [2]. They are also intermediary ecosystems between terrestrial and aquatic landscapes because they experience intermittent flooding and temporary waters [3] and are prone to upstream-downstream gradients. These drainage networks host various plant communities [3–5] that interact with biotic and abiotic components of the entire ecosystem [6,7]. Ditch vegetation may enhance ecosystem services including bank erosion mitigation [8], pesticide or nutrient retention [9–13], and groundwater recharge. On the other hand, the ditch vegetation may also provide disservices including the impairment of network water transport [14] and the enhancement of weed dispersal [15]. Estimating the services and disservices provided by drainage networks clearly requires the characterization of the spatio-temporal distribution of plant species along the networks.

Niche theory relies on the premise that plant species establish in specific environmental conditions [16,17]. These environmental conditions are sometimes called the fundamental niche [18]. Even when the niche is favourable for a species, other exogenous drivers such as niche accessibility [19] and human practices (especially in cultivated lands) [20–22] may impact the distribution of species.

In rain-fed agricultural headwater catchments under semi-arid climate, the factors that affect the occurrence of plant species in ditches indirectly depend on the local and landscape geomorphology. In this paper, we consider that the local geomorphology encompasses the close environment of the ditch, while the landscape geomorphology encompasses a broader environment surrounding the ditch. The local geomorphology, such as the slope in the ditches, and the landscape geomorphology, that determines the surface area drained by a section of ditch, impose varying hydraulic and hydrological conditions [23]. These variables determine the strength and duration of the exposure of plants to the water dynamics in surface and in the soil [24], which is crucial to explain the spatial distribution of species in water-limited ecosystems [25]. The strength of the association between geomorphology and plant spatial distribution is plant-specific, i.e., it depends on the facultative/obligate wetland nature of the considered species [26]. All hydrological and hydraulic processes in such systems are structured along an upstream-downstream gradient due to the growing surface area drained by the ditches from upstream to downstream and the dendritic structure of the drainage network. Consequently, the relative distance to the outlet may be an indirect indicator for describing the hydraulic conditions in a network. Moreover, in rivers and streams, geomorphology partly controls where sedimentation and erosion occur [27], and affects superficial bed soils by depositing or removing sediment layers. The same mechanisms are expected to take place in drainage systems in headwater catchments and the spatial distribution of valleys and ridges at different spatial scales in the catchment might determine the importance of deposited materials in the network. Lastly, the global sun exposure of the hillslopes and the solar radiation are known to affect the temperature conditions in streams and the plant responses to light [28]. Geomorphological variables were found to be good predictors of aquatic plant assemblages by Manolaki and Papastergiadou [29], who focused on the distribution of macrophytes in Mediterranean rivers. Maheu-Giroux and de Blois [30] emphasized that although the geomorphology of ditches may be a major factor explaining the spatial distribution of species, geomorphology is seldom considered in studies concerning linear hydro-agroecological infrastructures.

Niche accessibility is defined by the composition and spatial patterns of landscape features, and these composition and structure of landscapes may influence species richness [31,32]. In agricultural landscapes, the surrounding natural lands may represent significant propagule sources [33]. Van Dijk et al. [34] showed that the distance to natural reserves can influence community richness. In addition, roads may help transport plant propagules that may colonize roadsides and field boundaries [35] such as ditches. As is the case in rivers, niche accessibility in agricultural drainage networks is related to the surface area drained by the ditch and the length of the upstream network, because some plant propagules, whether hydrochorous or not, are transported along an upstream-downstream gradient [36]. When possible, niche accessibility should be analysed jointly with the dispersal abilities of the species because both define the connectivity between habitats for a given species. In agricultural landscapes, niche accessibility is therefore a major factor explaining plant patterns.

Compared to agricultural fields, ditches in agricultural headwater catchments are generally subjected to infrequent but regular management practices [14] but the practices may differ over time. In the long term, the effects of different practices may interact, because the effects of an agricultural practice can persist for several years [37]. The effects of some agricultural practices on plant distribution and richness have been investigated for field boundaries [4,38,39] but led to various conclusions. Additionally, little is known about how drainage networks might be managed to optimize the trade-offs between ecosystem services and disservices in Mediterranean agricultural areas.

Disentangling the influences of these different exogenous factors on plant distribution could facilitate agro-ecological engineering. The agro-ecological measures for this type of ecosystem might be of several types. Some authors [14,38] have shown that some local management practices, such as mowing for example, could modify the composition and distribution of the plant communities in the ditches in the medium term. Dollinger et al. [7] explained that the modification of the ditch morphological characteristics can have an impact on the abiotic properties of the ditches, and this could also have an impact on ditch communities. Cordeau et al. [40] determined that the establishment of sown grass strips had an impact on the spatial distribution of vegetation in field boundaries. Lastly, some other agro-ecological measures can be used to optimize ditch networks [41,42] such as restoring, creating or suppressing some ditches. This would result in changing the density of the network and modifying the surface area drained per section of ditch and the peak discharges [42]. Before applying any type of measure to control the occurrence of plant species, it is essential to know more about the factors that affect their spatial distribution in a whole network of ditches in a Mediterranean landscape. Indeed, it has been proven that years of agri-environmental measures (essentially local management measures) in the Netherlands was not totally successful in restoring the biodiversity on ditch banks [43]. This has led some authors to emphasize the role of other factors that have not been considered at first in the spatial distribution and composition of plant communities, such as connectivity or regional factors [33,43,44]. This example illustrates the importance of understanding how exogenous factors affect the spatial distribution of plant species in ditches under a Mediterranean semi-arid climate.

For the study of exogenous factors that structure plant community composition, models that predict the presence or presence/absence of species (spatial distribution models or SDMs) are often useful [45]. SDMs have often been used to identify areas where specific plants and invasive species have the capacity to develop [46]. SDMs are largely used in the literature on species distribution ecology [47] because of their increased predictive capacities, the possibility of cross-validation, and finally the use of non-categorical variables, in comparison to other recent multivariate approaches such as Permanova [48] or structural equation modelling [49].

This paper presents a catchment-scale analysis of plant patterns along an agricultural drainage network composed of ditches. Our hypothesis is that variables based on geomorphology and distance to natural lands and roads have the ability to predict the occurrence of plant species in a network of ditches in a semi-arid climate. Specifically, geomorphology could have an important effect due to the relationship between this geomorphology and the water regime under this type of climate. We also attempt to understand the origin of the part of the variability that cannot be explained by geomorphology and distance to natural lands and roads.

## Materials and methods

### Study area

The study area is a 6.4-km<sup>2</sup> headwater catchment named « Bourdic » in southern France, located northeast of Béziers city. The main towns of the area are Alignan-du-Vent and Roujan. Approximately 74% of the catchment is agricultural (mainly vineyards), and 26% is semi-natural (mainly woodlands and shrubs). The mean annual temperature is 14°C [23]. The catchment has a Mediterranean climate with heavy rainfalls causing significant Hortonian runoff [50]. The precipitation generally ranges from 600 to 800 mm per year [2], but some years can be drier. The rainfall regime is intermittent, with a dry period from April to October and heavy rainfalls in Autumn and Spring. Annual potential evapotranspiration is about 1100 mm [23]. Formally, the climate in the area is at the boundary between the sub-humid and the semi-arid climate, although the trends in the recent years tended to classify it as a semi-arid climate [51]. This is this last definition that we conserved for the study. The altitude ranges from 55 m a.s.l. at the outlet at the northeast to 128 m a.s.l. at the northwest. The following geomorphological units can be differentiated: an upstream-downstream succession of plateaus, steep slopes, and valley plains. Slopes up to 8% occur in the east, west and centre, and plains occur mainly in the north. The geomorphological units are associated with different soil typologies and sedimentary layers resulting from various erosion/redeposition mechanisms [52].

The man-made drainage network consists exclusively of agricultural and roadside ditches. The agricultural ditches were created over the centuries by farmers for the collection of water during intense rainfalls and for soil conservation. The network is 76 km long, and the density of the network is thus 119 m/ha. A survey in a subcatchment of 1 km<sup>2</sup> conducted by Levavasseur et al. [42] showed that 75% of the ditches had an upper width between 50 and 120 cm and a depth varying between 30 and 80 cm. The ditches form a directed hierarchical network (a dendritic structure). The drainage network is connected to a single outlet in the east of the study area. Note that in this paper, the word “ditch” refers to a homogeneous portion of network as regards with its properties (width, depth, sediment layer. . .), that can be variable in length, as defined by Lagacherie et al. [53], while a “ditch section” refers to a subset of the ditch according to the resolution of the study (2 m x 2 m in our case).

The Mediterranean vegetation growing on the bed of ditches (vegetation along the banks was not part of the study) included herbaceous grasses and forbs, and shrubs. The ditches are managed by farmers or local authorities, and vegetation management includes burning, herbicide application, and mowing [14]. The ditches are dredged when the hydraulic capacity requires restoration [14]. The frequency of management is 1.3 times per year in the study area [23] but varies with typology of the practice, period, and location in the network.

The methods followed these three main steps: (i) a survey of the occurrence of ditch plants along the network and the characterization of the ditch network (ii) the assessment of the spatial autocorrelation of plant patterns using Moran indices and spatial sorting bias in order to select non-correlated samples (iii) the use of a generalized linear model (GLM) and of a species distribution model (Maxent) to predict the occurrence of each species.



### Plant species distribution survey

Free access to private properties located in agricultural areas is permitted by French legislation, although landowners can apply for an exception as described in Article 647 of the Civil Code.

The following 10 herbaceous species were surveyed along the network: wild asparagus (*Asparagus acutifolius*), sand-couch (*Elytrigia juncea*), common horsetail (*Equisetum arvense*), purple loosestrife (*Lythrum salicaria*), water mint (*Mentha aquatica*), round-leaved mint (*Mentha suaveolens*), shrubby blackberry (*Rubus fruticosus*), curly dock (*Rumex crispus*), round-headed club-rush (*Scirpoides holoschoenus*), and Johnson grass (*Sorghum halepense*). These species were selected mostly because they differ in their sensitivity to various water regimes, and consequently were expected to be predicted heterogeneously by the different geomorphological variables. They were also selected because of their relative abundance and relative ease of identification. The studied species were classified according to their niche characteristics (Table 1), using Julve [54].

The surveys were conducted in July–August 2013 according to a non-destructive sampling procedure using GPS with an Android self-developed application [55]; this enabled a location accuracy of 2 m. Agricultural ditches, including roadside ditches, were part of the study. Thirty-five kilometres of the drainage network (46%) were surveyed for presence/absence of the species. The remaining ditches were excluded from the analysis because surveying them was impractical or because recent management practices impaired the identification of the species. After the survey, the georeferenced data were exported in a shapefile data format with line features.

### Ditch network characterization

The Bourdic drainage network, which is mainly composed of ditches, was first digitized in 2008–2009 based on aerial images [23]; the information was regularly updated with field surveys during the 2012–2013 period. During these field surveys, the depths and the upper and

**Table 1. Ecological optima, spatial autocorrelation (SAC) critical distances, frequency of occurrence of the 10 species after consideration of SAC and spatial sorting bias (SSB).**

Species	Ecological optimum					SAC	Frequency after SAC			SSB after SAC
	Light	Soil moisture	pH	Texture	Organic matter		Moran critical distance (m)	Number of "presence" rasters	Number of "absence" rasters	
<i>Asparagus acutifolius</i>	5	3	6	5	2	14	159	2 165	6.8	0.8
<i>Elytrigia juncea</i>	9	5	7	5	1	22	416	1 101	27.4	0.9
<i>Equisetum arvense</i>	7	3	5	3	3	30	279	786	26.2	0.8
<i>Lythrum salicaria</i>	7	5	6	1	8	26	133	1 055	11.2	0.8
<i>Mentha aquatica</i>	5	6	5	1	8	26	25	1 158	2.1	0.6
<i>Mentha suaveolens</i>	8	5	6	2	8	22	135	1 246	9.8	0.8
<i>Rubus fruticosus</i>	5	4	2	3	5	18	787	1 266	38.3	0.9
<i>Rumex crispus</i>	7	5	5	1	8	10	147	3 026	4.3	0.9
<i>Scirpoides holoschoenus</i>	8	6	7	1	9	18	185	1 601	10.4	0.8
<i>Sorghum halepense</i>	8	4	7	4	3	14	65	2 237	2.8	0.6

Ecological optima are based on a 1–9 scale from a minimum to a maximum. Texture ranged from clay (1) to rocks (9). SAC distances were based on Moran indices. The frequency of occurrence of species was given after considering SAC.

<https://doi.org/10.1371/journal.pone.0191397.t001>

lower widths of ditch cross sections were measured at 675 locations. We assumed that the ditch cross-sections did not change significantly between survey times. Each ditch section was then assigned with the presence/absence of plant species and with cross-sections measures. The ditch network was finally rasterized on a grid with a resolution of 2 m; this resolution was selected based on the precision of the GPS used in the field survey and on the resolution of the digital terrain model (DTM).

### Plant species spatial autocorrelation

The spatial pattern of each species was analysed separately in order to determine the range of spatial autocorrelation (SAC); this was done to exclude samples that were spatially autocorrelated from further analyses and to build a proper sampling design for model estimation [56]. If spatially autocorrelated samples are not excluded, the importance of environmental variables can be overestimated [57]. This analysis was conducted with Moran indices [58] based on stream distances. For each of the presence rasters, a matrix was created by counting presence points in the neighbourhood at several ranges of distances (from 2 m to 100 m). The Moran index corresponds to the ratio between covariance for neighbouring points and total variance [59]. For each species, Moran indices were then converted to Z-scores, and the critical distance indicating a significant spatial autocorrelation was determined. Finally, we resampled the presence rasters in order to space them with the critical distance established from Moran indices and to exclude spatial autocorrelation effects from further analysis. Critical distances calculated from Moran indices and the number of presence and absence pixels for each plant species after considering SAC were reported in Table 1. The consideration of the critical distance calculated with Moran indices drastically reduced the number of presence and absence rasters for each species.

### Geomorphological variables and distance to natural lands and roads

The landscape geomorphological variables included the distance to the outlet (**Doutlet**), the drained surface area (**Drain**), the Multiresolution Index of Valley Bottom Flatness (**Mrvbf**), and the sun exposure of the slopes (**Northness**). The local geomorphological variables were the slope (**Slope**) and solar radiation (**Solar**). The difference between local and landscape geomorphological variables is that the local variables encompass the close environment of a ditch, while the landscape variables encompass a broader environment surrounding the ditch. Distance to natural lands (**Dnat**) and distance to roads (**Droad**) were also chosen as explanatory variables (Table 2).

The six geomorphological variables were all derived from 2-m-resolution Digital Terrain Model (DTM) grids and Digital Surface Model (DSM) grids obtained from LIDAR surveys

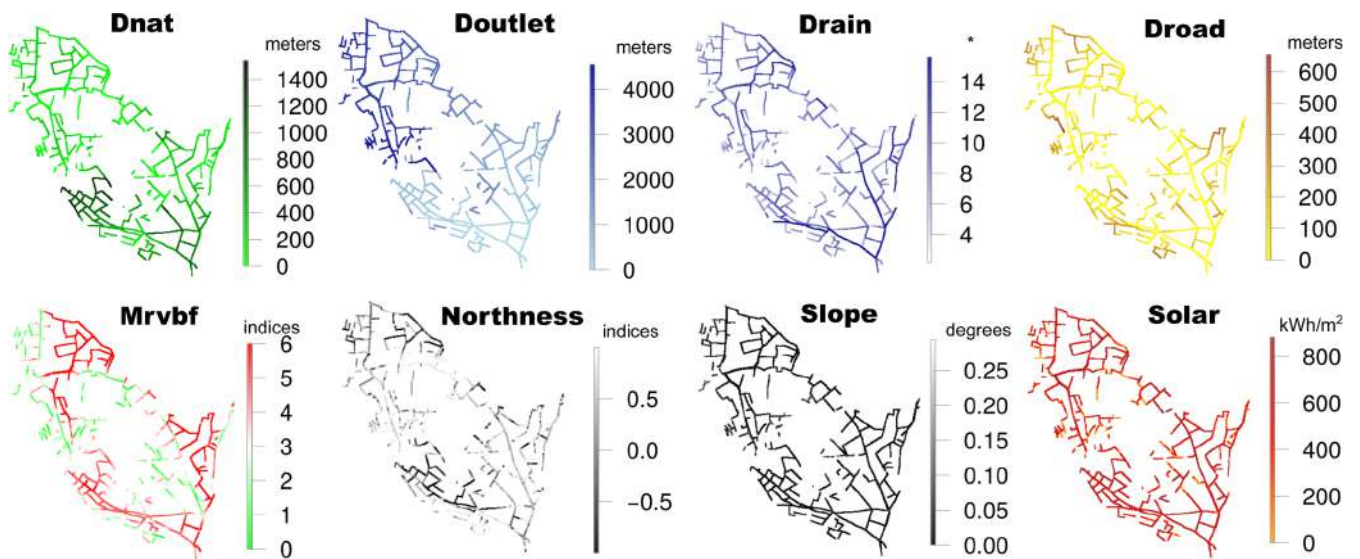
**Table 2. Summary of acronyms used for explanatory variables and type of variables.**

Variable	Acronym	Type of variable
Distance to Outlet	Doutlet	Geomorphological (Landscape)
Drained Surface Area	Drain	Geomorphological (Landscape)
Multi-resolution Valley Bottom Flatness	Mrvbf	Geomorphological (Landscape)
Northness	Northness	Geomorphological (Landscape)
Slope	Slope	Geomorphological (Local)
Solar Radiation	Solar	Geomorphological (Local)
Distance to Natural Areas	Dnat	Distance to Land-use
Distance to Roads	Droad	Distance to Land-use

<https://doi.org/10.1371/journal.pone.0191397.t002>

conducted in 2001 [60]. We considered that the geomorphology did not change significantly between 2001 and 2013. Indeed, the study area is mainly covered with vineyards and no major reorganization of the landscape took place between 2001 and 2013. The major driver of landscape reorganization in the region during this period was urbanization, and it was not significant in the study area. Regarding the morphology of the ditch network as such, the geometrical properties were updated in 2012–2013 with field surveys, as was described above. A “ditch section” consisted of a 2m\*2m section area (size of the pixel). A DTM pre-process consisted of stream-burning [61] the rasterized drainage network in the DTM and DSM in order to correctly force preferential water paths through the network of ditches. We hypothesized that the distance to outlet (**Doutlet**), the drained surface area (**Drain**) and the local slope of the ditch (**Slope**) accounted for the hydraulic and hydrological regimes, and also indirectly for soil hygromorphy, in a section of ditch. Indeed, the water regime is the major factor explaining plant spatial patterns in riparian areas [62,63] and then possibly explain the spatial distribution of plants in Mediterranean ditches. **Doutlet** was then calculated with 2-m accuracy, because it was computed as the shortest path via the gridded network from a ditch section to the outlet. **Drain** was the whole upstream area drained by a ditch section as computed with the usual D8 algorithm [64] on the stream-burned DTM. **Slope** represented the rasterized difference in elevation between ditch terminal nodes divided by ditch polyline lengths. **Mrvbf** is an indicator for soil composition and soil hygromorphy. More specifically, it is a topographic index that enables the mapping of valley bottoms at a range of scales [65]. **Mrvbf** is usually used to locate areas of water basins and deposited materials. **Mrvbf** index values < 0.5 indicate non-valley areas, values between 0.5 and 1.5 indicate steep valley bottoms, and values > 1.5 indicate large valley areas [65]. **Northness** and **Solar** accounted for sun exposure at different spatial scales. **Northness** was the global sun exposure in relation to an East-West reference axis. Solar radiation (**Solar**) was the direct potential incoming solar radiation. A solar constant of 1360.7 kWh. m<sup>-2</sup> was chosen based on the characteristics of the study area, and 70.1% was selected for the lumped atmospheric transmittance. The dust factor was 100 ppm. Direct Solar radiation was calculated over a 4-month period from March to June. Because **Solar** was calculated from the DSM, shade effects from vegetation were considered jointly with relief effects. The shade effect could be calculated for adjacent pixels but could not be easily calculated for the pixel producing the shade. Consequently, we attributed an incoming solar radiation value of 0 to pixels covered by tall vegetation, i.e., for pixels with an elevation difference of at least 1.5 m between DSM and DTM. We also hypothesized that distance to natural areas would be important because they are potential sources of seeds, therefore we included distance to natural areas (**Dnat**) in our analysis. Furthermore, distance to roads (**Droad**) was also included because roads are important seed dispersal vectors in agricultural landscapes and we hypothesized that they would be important for structuring plant communities in agricultural ditch networks. These variables were created from a land-use map established from a satellite image covering the study area in 2014. They were calculated as the shortest path between pixel centres located on a ditch and those located on natural lands or roads. Because some ditches were located on catchment boundaries, we extended the land use map footprint to 200 m in order to avoid edge effects. The spatial patterns and variability of the height variables are presented in Fig 1.

We tested the correlations between variables because multicollinearity implies that partial regression coefficients might be imperfectly assessed [66]. Because all variables could be considered continuous, a Pearson product-moment correlation test was used. No strong collinearity among variables was detected because all correlation coefficients were below to 0.6 [39,66].



**Fig 1. Spatial variability for each explanatory variable at the catchment scale.** Dnat is the distance to natural areas. Doutlet is the distance to the outlet. Drain is the Drained Surface Area. Droad is the distance to roads. Mrvbf is the Multi-resolution Valley Bottom Flatness. Northness is the exposure of slopes in relation to an East-West axis. Slope is the local slope of a ditch section. Solar is the direct potential incoming Solar Radiation. \* Drain is expressed in  $\log(\text{meters}^2 + 1)$ .

<https://doi.org/10.1371/journal.pone.0191397.g001>

### Data analysis

**Model selection procedure and importance of variables.** The occurrence of the 10 plant species in the ditch network was modelled using the 6 geomorphological parameters and the distance to natural areas and distance to roads as explanatory variables. We only selected prospected parts of the network where presence/absence had been determined. Because different models may differ in their performance depending on the application [67,68], we used two models: (i) a regression model, i.e., the GLM assuming a binomial distribution of values using a logit link [69]; (ii) a SDM, the non-linear maximum entropy model (Maxent) [70]. The GLM uses presence/absence data, but Maxent model uses presence-only data. We selected these models because they have been reported to be among the best distribution models [67,71]. The explanatory variables were rescaled between [0–1] to make their weights comparable during the modelling procedure.

For each plant species and each model, we performed a k-fold cross-validation ( $k = 4$ ). The number of presence data for each plant species in each learning and validation sample was greater than 10 pixels. Area under the curve (AUC) [72], a threshold-independent statistic, was used to assess the fitting of the different models for each validation sample and each species. A mean AUC value was calculated for the four validation samples. An AUC value  $\leq 0.5$  indicates that the model does not perform better than a random model; values between 0.5 and 0.7 indicate a low predictive ability; values between 0.7 and 0.9 indicate a good predictive ability; and values  $> 0.9$  indicate an excellent predictive ability [72]. The use of AUC in evaluating the performance of species distribution models has been criticized [73] and particularly because the AUC values are sensitive to the spatial extent used to select background points. To that end, we also calculated the "spatial sorting bias" (ssb), i.e. the difference between the distance from testing-presence to training-presence and the distance from testing-absence to training-presence points, for each species, following Hijmans [74]. A ssb close to 0 means a strong bias whereas a ssb close to 1 means an absence of bias. Before calculating the ssb, the data were spatially resampled to remove SAC by using Moran's autocorrelation indices calculated along the linear networks. Then ssb was calculated for each species after resampling. We

could not apply the pairwise distance sampling algorithm proposed by Hijmans [74] due to the specific structure of our dataset (network structure). We also added the accuracy measures derived from the confusion matrices, such as the Positive Predictive Value (PPV), the Negative Predictive Value (NPV) and the Overall accuracy, as proposed by Liu et al. [75]. The predicted values were thresholded using the maximum Kappa value [76] to calculate the confusion matrices. For each explanatory variable, we then determined its relative importance for Maxent, and the value of the coefficients for GLM (positive or negative) for each species. For GLM, because explanatory variables were all converted to a [0–1] scale, absolute values of regression coefficients also represented their relative importance. For GLM, only coefficients with p-values < 0.05 were displayed.

**Spatial patterns of false positive and false negative predictions.** The modelled distributions of species in the validation sample were calculated as continuous probability values. These probabilities were transformed into binary scores using a threshold value calculated from maximum Kappa values [76]. For Maxent, one map for false positive predictions and another map for false negative predictions, with compiled results for the 10 species, were created to identify areas with low prediction scores common to several species.

**Tools used for analysis.** Maps displaying spatial patterns of explanatory variables and false positive/false negative predictions were created using QGIS [77]. All analyses were conducted with R [78]. All explanatory variables were calculated using the RSAGA package [79]. The pre-modelling preparation of data relied on the R Spatstat package [80], R Raster Package [81], R Maptools Package [82], R Rgdal package [83], R sp package [84], R Rgeos package [85], R pbapply package [86], and R igraph package [87]. The R Dismo package [88] was used for the modelling step. Note that the Maxent model was run with the default features, i.e. the convergence threshold at 0.00001 and the maximum number of iterations at 5000.

## Results

SAC varied among species and ranged from 10 to 30 m (Table 1). The critical distances were largest for *E. arvense*, *L. salicaria*, and *M. aquatica*, and were smallest for *R. crispus*, *A. acutifolius*, and *S. halepense*. All ssb calculated after considering SAC (Table 1) were equal to or above 0.6, meaning that the spatial sorting bias was low in our case-study.

The mean AUC values were generally greater for Maxent models than for GLMs (Table 3). The order of species according to AUC values was roughly similar for the two models. Maxent

**Table 3. Mean area under the curve (AUC) values and three metrics derived from confusion matrices with GLM and Maxent model for each species.** Standard deviation issued from the cross-validation procedure were represented by values in brackets.

Species	AUC		Positive Predictive Value		Negative Predictive Value		Overall accuracy	
	Maxent	GLM	Maxent	GLM	Maxent	GLM	Maxent	GLM
<i>Asparagus acutifolius</i>	0.85 (0.03)	0.85 (0.04)	0.84 (0.04)	0.87 (0.05)	0.78 (0.07)	0.75 (0.05)	0.78 (0.06)	0.76 (0.05)
<i>Elytrigia juncea</i>	0.72 (0.03)	0.62 (0.02)	0.76 (0.08)	0.74 (0.04)	0.54 (0.05)	0.48 (0.06)	0.60 (0.02)	0.55 (0.03)
<i>Equisetum arvense</i>	0.89 (0.01)	0.79 (0.02)	0.84 (0.09)	0.75 (0.10)	0.86 (0.04)	0.79 (0.07)	0.85 (0.02)	0.78 (0.03)
<i>Lythrum salicaria</i>	0.90 (0.02)	0.86 (0.01)	0.80 (0.02)	0.90 (0.03)	0.85 (0.04)	0.72 (0.05)	0.85 (0.03)	0.74 (0.05)
<i>Mentha aquatica</i>	0.92 (0.03)	0.83 (0.09)	0.96 (0.09)	0.71 (0.16)	0.76 (0.12)	0.83 (0.17)	0.76 (0.12)	0.83 (0.17)
<i>Mentha suaveolens</i>	0.80 (0.02)	0.69 (0.04)	0.68 (0.10)	0.65 (0.07)	0.80 (0.08)	0.78 (0.05)	0.78 (0.06)	0.77 (0.03)
<i>Rubus fruticosus</i>	0.67 (0.01)	0.61 (0.03)	0.64 (0.21)	0.62 (0.16)	0.64 (0.21)	0.58 (0.18)	0.64 (0.05)	0.60 (0.05)
<i>Rumex crispus</i>	0.82 (0.03)	0.82 (0.02)	0.81 (0.05)	0.82 (0.02)	0.76 (0.08)	0.75 (0.03)	0.76 (0.07)	0.76 (0.03)
<i>Scirpoides holoschoenus</i>	0.86 (0.03)	0.82 (0.02)	0.80 (0.09)	0.74 (0.05)	0.82 (0.10)	0.81 (0.06)	0.82 (0.08)	0.80 (0.05)
<i>Sorghum halepense</i>	0.72 (0.11)	0.61 (0.05)	0.62 (0.12)	0.72 (0.12)	0.80 (0.09)	0.57 (0.18)	0.80 (0.09)	0.58 (0.17)

Mean AUC values, positive predictive values, negative predictive values and overall accuracy were obtained by k-fold cross-validation (k = 4).

<https://doi.org/10.1371/journal.pone.0191397.t003>

mean AUC values ranged from 0.92 for *M. aquatica* to 0.67 for *R. fruticosus*, and the standard deviations were moderate ( $\leq 0.05$ ) for all species models except for *S. halepense* (Sd = 0.11). Maxent species models with the highest mean AUC values ( $\geq 0.90$ ) were those for *M. aquatica* and *L. salicaria*. The only Maxent species model with a low mean AUC value ( $< 0.70$ ) was that for *R. fruticosus*. GLM mean AUC values ranged from 0.86 for *L. salicaria* to 0.61 for *R. fruticosus*, and the standard deviations were moderate ( $\leq 0.05$ ) for all species except for *M. aquatica* (Sd = 0.09). GLM species models with the highest mean AUC values ( $\geq 0.85$ ) were those for *L. salicaria* and *A. acutifolius*. GLM species models with the lowest mean AUC values ( $< 0.70$ ) were those for *R. fruticosus*, *S. halepense*, *E. juncea*, and *M. suaveolens*.

*M. aquatica* had the highest positive predictive value (0.96) and *S. halepense* the lowest (0.62) with the Maxent model (Table 3). *L. salicaria* had the highest positive predictive values (0.90) and *R. fruticosus* had the lowest (0.62) with the GLM model. *E. arvense* had the highest negative predictive value (0.86) and *E. juncea* the lowest (0.54) with the Maxent model. *M. aquatica* had the highest negative predictive value (0.83) and *E. juncea* the lowest (0.48) with the GLM model. For the Maxent model, the overall accuracy was then the highest for *E. arvense* and *L. salicaria* (0.85) and was low for *E. juncea* (0.6) and *R. fruticosus* (0.64). For the GLM model, the overall accuracy was the highest for *M. aquatica* (0.83) and the lowest for *E. juncea* (0.55) and *S. halepense* (0.58).

Based on Maxent and GLM models, the coefficients for each explanatory variable are presented in Tables 4 and 5. For each model, variables with high importance were considered those with coefficient values above the statistical median of the whole set of values attributed to the coefficients; the absolute value of the median was 9 for Maxent models and 2 for GLM.

Regarding the Maxent models, the importance was greater for **Doutlet** and **Mrvbf** than for the other variables for most of the 10 species. **Drain**, **Dnat**, and **Droad** were of secondary importance for Maxent models, and **Northness**, **Solar**, and **Slope** were of slight importance except for a few species. Geomorphological variables were then good explanatory variables for most species. **Mrvbf** was important for *A. acutifolius*, *E. arvense*, *L. salicaria*, *S. holoschoenus*, *M. aquatica*, *R. crispus*, and *S. halepense*. **Drain** was important for *L. salicaria*, *E. juncea*, *R. fruticosus*, *M. aquatica*, *S. halepense*, and *S. holoschoenus*. **Solar** was important for *A. acutifolius* and *R. fruticosus*, and **Northness** was important for *S. holoschoenus* and *M. aquatica*. **Slope** was important for *E. juncea* and *A. acutifolius*. Regarding distance to natural lands and distance to roads, **Dnat** was important for *R. fruticosus*, *E. arvense*, *M. aquatica*, *S. halepense*, and *R. crispus*. **Droad** was important for *S. halepense*, *M. suaveolens*, *R. fruticosus*, *E. arvense*, and *E. juncea*. **Dnat** and **Droad** had low importance for *S. holoschoenus*, *L. salicaria*, and *A. acutifolius*.

**Table 4. Results for Maxent models for each species.** Coefficients represent the relative importance of the explanatory variables (the sum of coefficients for each species is equal to 100). The more the coefficient is close to 100, the more the relative importance of the variable is high, compared to other variables.

Species	Doutlet	Drain	Mrvbf	Northness	Slope	Solar	Dnat	Droad
<i>Asparagus acutifolius</i>	18.1	0.9	43.9	0.4	9.2	17	5.8	4.6
<i>Elytrigia juncea</i>	42.4	13.7	4.8	2.0	9.2	7.2	8.9	11.8
<i>Equisetum arvense</i>	15.7	5.2	34.3	2.4	3.2	1.3	25.5	12.3
<i>Lythrum salicaria</i>	19.2	27.1	34.3	2.8	2.2	3.0	6.9	4.4
<i>Mentha aquatica</i>	35.8	11.2	16.4	9.8	1.2	1.7	21.4	2.5
<i>Mentha suaveolens</i>	58.1	5.8	4.6	1.7	2.6	4.8	4.9	17.5
<i>Rubus fruticosus</i>	17.5	13.2	2.4	2.5	6.0	16.7	29.3	12.4
<i>Rumex crispus</i>	46.3	8.9	16.4	1.7	2.4	5.3	11.5	7.5
<i>Scirpoides holoschoenus</i>	31.0	10.8	19.4	14.2	7.9	3.0	6.1	7.6
<i>Sorghum halepense</i>	33.1	10.8	9.9	4.0	3.8	1.1	18.6	18.6

<https://doi.org/10.1371/journal.pone.0191397.t004>

**Table 5. Results for GLM for each species.** Regression coefficients are presented; their absolute value indicate the relative importance of the explanatory variables because explanatory variables have been rescaled between [0–1] before modelling. Only coefficients with p-value>0.05 were presented.

Species	Doutlet	Drain	Mrvbf	Northness	Slope	Solar	Dnat	Droad
<i>Asparagus acutifolius</i>	-	-	-2.3	-	3.3	1.3	-3.3	1.3
<i>Elytrigia juncea</i>	-	0.7	-	-	-5.3	-	0.7	-1.2
<i>Equisetum arvense</i>	-	-	2.7	-	-7.8	-	-4.2	-1.7
<i>Lythrum salicaria</i>	-2.4	3.3	5.2	-	-	-	-1.7	-1.6
<i>Mentha aquatica</i>	-	3.1	3.2	-	-	-	-3.1	-
<i>Mentha suaveolens</i>	-3.0	-	0.8	-	-	-	-	-2.8
<i>Rubus fruticosus</i>	0.5	0.5	-	-0.3	-2	-0.8	-1.4	-0.8
<i>Rumex crispus</i>	-2.4	1.3	1.6	-	-	-	2.3	-2.0
<i>Scirpoides holoschoenus</i>	-1.7	2.9	1.3	-1	-	-	-	-4.2
<i>Sorghum halepense</i>	1.3	-	-	-	-	-	-	-3.7

<https://doi.org/10.1371/journal.pone.0191397.t005>

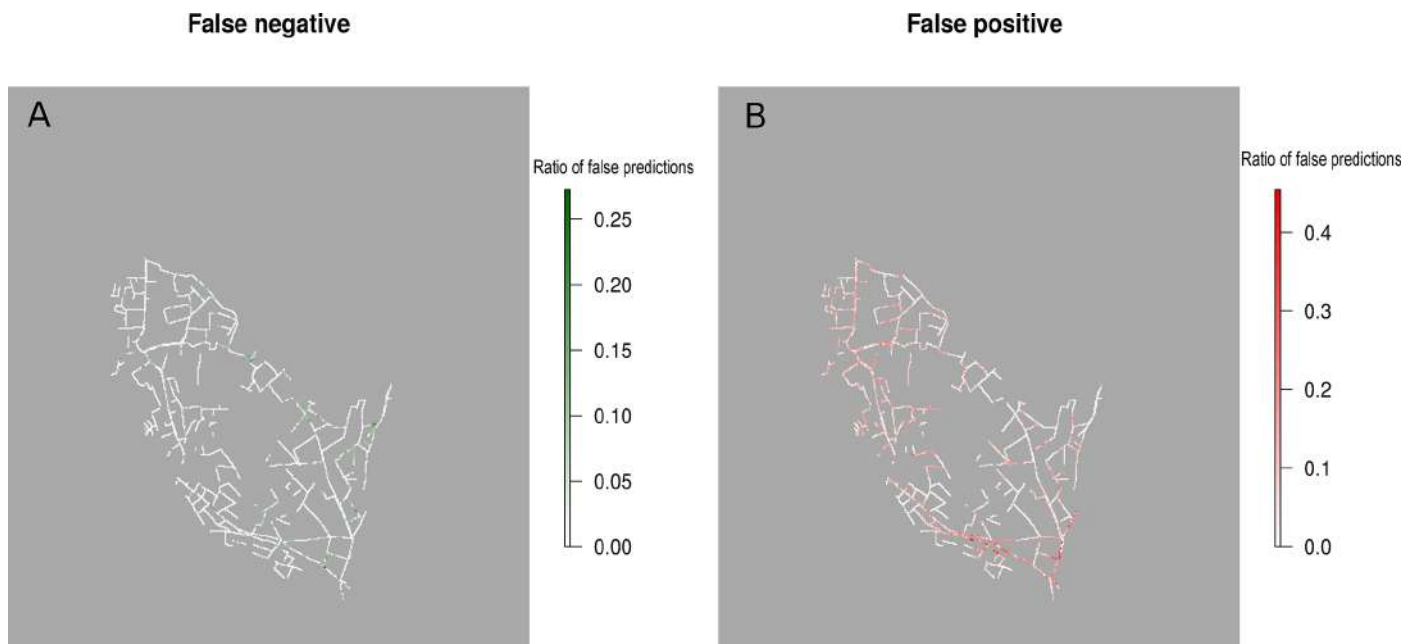
Regarding GLMs, **Droad**, **Dnat**, **Mrvbf**, and **Slope** were more important than the other variables for most of the studied plant species. **Doutlet** and **Drain** were of secondary importance for GLM models, and **Northness** and **Solar** were of low importance. Regarding correlations between geomorphological variables and species presence, **Mrvbf** was positively correlated with *L. salicaria*, *M. aquatica*, and *E. arvense* and was negatively correlated with *A. acutifolius*. **Slope** was negatively correlated with *E. arvense*, *E. juncea*, and *R. fruticosus* and positively correlated with *A. acutifolius*. **Doutlet** was negatively correlated with *M. suaveolens*, *R. crispus*, and *L. salicaria*. **Drain** was positively correlated with *L. salicaria*, *M. aquatica*, and *S. holoschoenus*. *S. halepense* occurrence was poorly explain by all of the geomorphological variables. Regarding distance to natural lands and roads, **Droad** was negatively correlated with *S. holoschoenus*, *S. halepense*, *M. suaveolens*, and *R. crispus*. **Dnat** was negatively correlated with *E. arvense*, *A. acutofolius*, and *M. aquatica* and was positively correlated with *R. crispus*. Geomorphological variables were then important to explain the distribution of all species with GLM, except for *S. halepense*.

The residual maps revealed false positive predictions along major road axes in the southern catchment (Fig 2B). No spatialized tendency was evident, however, for false negative predictions (Fig 2A).

## Discussion

### Effect of geomorphological variables and distance to natural areas and roads

That geomorphological variables greatly affect plant spatial distribution has been previously demonstrated in Mediterranean streams [29] and in wetlands [26], but has not been previously assessed in ditches. This is reasonable for ditches because geomorphological features control the water regime and consequently greatly influence the fluxes of sediments, nutrients, pesticides and plant propagules that reach the ditches. Additionally, the results of the current study showed that the landscape geomorphological variables were at least as important as local geomorphological variables for determining the spatial distribution of plants. In agricultural landscapes, weed dynamics have often been linked to local features, but as reported by Alignier et al. [89] for in-field weeds, the factors controlling plant distribution can involve several interacting spatial scales. The dependence of plant ditch communities on the landscape scale has been previously shown for a land-use mosaic [33] but not for landforms. The results of the current study also highlighted the upstream-downstream gradient of the communities in the



**Fig 2. Location of false negative (A) and false positive (B) predictions for Maxent model.** For each pixel, the value is the ratio between the number of false negative (2A), or false positive (2B) predictions for all species and the total number of species.

<https://doi.org/10.1371/journal.pone.0191397.g002>

network, in that **Outlet** was important for explaining the occurrence of all species. The weak ability of local geomorphological variables to predict species spatial distribution could also be explained by the expected greater error for local than for landscape variables, although the 6 geomorphological variables were derived from the DTM and DSM and calculated at the same resolution. Indeed, **Slope** calculation was based on the elevation difference between two points (at the beginning and end of the ditch) for which the uncertainty could be significant. Regarding **Solar**, due to the number of hypotheses we made (especially the fact that the pixel covered by vegetation was considered having no direct solar radiation), and due to the incertitude of measures of the geometrical properties of the ditch considered in the calculation, we can also expect it is less accurate than other variables calculated directly from the DTM and DSM.

In any case, the fact that landscape geomorphological variables, and especially **Drain**, **Outlet** and **Mrvbf** were important predictors, shows indirectly the role of the hydrological connectivity at the catchment scale to explain the distribution of plant species in the ditches. As the modification of the geomorphology of the catchment is not possible, agro-ecological measures aiming at controlling the occurrence of plant species in Mediterranean agricultural landscapes should consider modifying this hydrological connectivity, for example by changing the density of the ditch network. Indeed, it has been confirmed in Levvasseur et al. [42] that the modification of the density of the network would have consequences on the water fluxes (especially the drained surface area and the peak discharge at the outlet) at the catchment scale in rain-fed Mediterranean agricultural catchments. In addition, the fact that the **Mrvbf** is also an important variable gives credit to measures affecting the sedimentological connectivity of the catchment, such as the optimization of the spatial distribution of vegetative filter strips involved in sediment trapping [90], to manage the occurrence of plants species.

Previous studies have demonstrated that land use can influence plant distribution in field boundaries by acting as seed bank sources or vectors [30,33,39]. Van Dijk et al. [34] reported that the occurrence of most species decreased with distance to nature reserves. Similar results



were found in the present study as indicated by the negative correlation between **Dnat** and the occurrence of most species in GLM models. The strength of the association between the occurrence of species and the distance to seed sources or vectors was previously linked to the preferential dispersal strategy of the plant [33,34], but our data did not contain enough plant species to confirm this association. The effect of road proximity in our results was well-illustrated for *S. halepense*, which was previously shown to be dispersed with the movement of agricultural equipment [91]. These results illustrate the fact that measures based on the establishment of new seed bank sources such as vegetative filter strips (sown or not) along the ditches could be considered in order to enhance the occurrence of some species.

### Non-explained variability

The non-explained variability in spatial distribution varied greatly among the species in the current study. The selected explanatory variables were poor predictors of the spatial distribution for some species, especially for *R. fruticosus*, *S. halepense*, and *E. juncea*. The spatial variability of these species may be explained by factors that were not considered in our study. These factors could include biotic and abiotic variables and also the human activities involved in the maintaining of ditches.

Two main biotic factors that affect the spatial distribution of plants are dispersal processes and interspecific interactions such as competition and facilitation. Dispersal processes were indirectly taken into account in the current study by calculating the extent of spatial autocorrelation and by the choice of explanatory variables. However, competition and facilitation are rarely assessed in SDM studies [92]. These interactions are difficult to measure because variables that are considered to be biotic are sometimes micro-niche abiotic variables missing in the chosen pool of explanatory variables [93], and this may introduce collinearity effects between abiotic and biotic variables in the analysis [92]. Interactions would also be difficult to assess with the current data because they described the occurrence but not the abundance of the 10 selected species. Additionally, the influence of competition might be less important in drainage networks than in natural ecosystems because the networks are frequently disturbed [39,94]. However, these effects of competition and their importance can vary according to species. For example, Arnold et al. [95] showed that the perennial *S. halepense* had lower germination rates when the canopies of others plants were already developed, while the development of *R. fruticosus* was poorly impaired by the shading effects [96]. The consideration of these interactions represents a major challenge in the use of SDMs.

Abiotic variables from the environmental niche that could not be represented clearly by geomorphological variables were especially those linked with soil properties (e.g., pH, texture, structure, etc.). Firstly, the soil horizons in ditches have been formed over centuries when the geomorphology of the catchment was maybe slightly different. This could have implied different preferential places of deposition for sediments. The formation of the soils in the ditches was also influenced by the management practices led in the ditch network and in the plots of the upper catchment because agricultural practices affect the rates of transported materials [97]. Consequently, the current geomorphology partly controls where sediments are deposited today but soil formation in ditches was a long and multi-variable process, as was described in Needelman et al. [98], that is difficult to assess with static variables.

Another major challenge for SDM is the temporal variability of the explanatory variables. In the study area, the intermittency of rainfalls throughout the year and the inter-annual variability in the climate can create contrasted environmental conditions over time that could not be taken into account in our approach. This temporal variability can also affect plant interspecific relationships [99–100]. In some semi-arid landscapes, perennials create favourable or

unfavourable conditions for the growth of annuals [101] depending on the environmental conditions, and especially according to the water stress. The temporal variability in the explanatory variables is then a major challenge that could be partly solved taking into account the recent history of the explanatory variables, as was proposed in Alignier et al. [89] for management practices. However, for abiotic conditions, the problem of the temporal scales and types of indicators that we should use to take into account the recent history still needs to be solved.

The effects of ditch management practices have not been taken into account in this study. Yet, these management practices regularly disturb the ecosystem removing all the vegetation in place [14] and highly affect the local properties of the ditches [7]. It has been shown that both the type of practice and the time of the practice could affect the plant communities. In the Netherlands, a proper management of the ditch banks helped increase the richness of plant species [22]. It has also been shown that when there was a match between the period of the management practice and the seed maturity, the seed dispersal was optimal [38]. Consequently, for Mediterranean ditches, it would be interesting to know more about how these practices interact with plant species to understand better their spatial distribution.

The concentration of false positive predictions in the southern part of the study area and next to main roads remained unclear. These drainage networks are located near an urban area. In this suburban area, diffuse contaminants or non-agricultural maintenance practices may affect the spatial distribution of plants in ditches. Another explanation would be that these main roads would be less used by farm equipments, thus reducing the seed dispersal for species using this dispersal strategy.

These data on the sensitivity to explanatory variables could help guide the management of plants species in ditches in agricultural areas and in the suburbs of rural cities. For those species that are mostly explained by geomorphological variables, modifying the hydrological and sedimentological connectivity could be an effective way to manage their occurrence. For species mainly explained by distance to natural areas and distance to roads variables, supplementing seed bank sources on adjacent lands (by creating vegetative filter strips for example) would probably be effective. The factors that control the occurrence of species that were poorly predicted in this study need to be investigated. Future research should try to include the abundance of plants species, the whole community composition as well as management practices applied to the ditches.

### Performance of the Maxent model and GLM

Consistent with previous results [46, 67, 102], the Maxent model provided better spatial predictions for occurrence of plant species than the GLM model. The difference between Maxent and GLM performance was significant for the AUC but was slight for the other metrics. The stability of the predictions was correct because there was a moderate standard deviation (equal to or below 0.10) for all metrics after cross-validation, except for *S. halepense*, probably due to the small number of occurrence pixels after considering SAC or other explanatory variables that were not considered in the study, such as the sensitivity of some seeds to anthropogenic dispersion with agricultural equipment [103]. The ability of the Maxent model to consider interactions can also explain some of the differences in the identification of the main explanatory variables by the Maxent model vs. the GLM. Finally, the better performance of Maxent model than GLM may be explained by differences in data format. The GLM considers presence-absence data, while the Maxent model considers presence data compared against the entire region [71]. Although the sampling procedure of plant species was led at the whole catchment scale, the true absence of a plant species may be difficult to prove. Absence may reflect an unsuitable habitat or a suitable habitat that has not yet been colonized, as emphasised

by Jarnevič et al. [104]. Other reasons for the absence of a species could be linked with the timing of the dispersal events [38] that can be variable according to the years, the variability of the conditions needed for the germination and establishment of the species, interspecific interactions and the specific management practices of the area (for example, the practice of dredging removes all the seed bank contained in the superficial soils [7]). Additional surveys on several years would be necessary to confirm the true absence of a species.

## Conclusions

This study illustrates the importance of considering geomorphological variables and the distance to natural lands and roads in order to predict the occurrence of some plant species living in agricultural drainage ditches in a rain-fed Mediterranean catchment. The importance of the landscape geomorphological variables outlines the role of the landscape environment surrounding a ditch in explaining the occurrence of these plant species. Consequently, agro-ecological management in Mediterranean ditch networks should investigate measures based on the modification of the hydrological and sedimentological connectivity in the catchment, such as the modification of the density of ditches and the optimization of the spatial organization of vegetative filter strips. Moreover, these vegetative filter strips could constitute new seed bank sources for ditch plants because the distance to seed bank sources and the distance to seed dispersal vectors (roads) were also important predictors in the study.

## Acknowledgments

The authors thank Marie-Noëlle Moresmau, Jeanne Dollinger, Benoit Bellot, and Alexandre Bassini for their valuable field work. Marie-Noëlle Moresmau created the GIS application for the survey using App Inventor. We also thank Laurent Prévot and Guillaume Coulouma for their expertise and advice regarding the study area. Authors are grateful to the INRA institution who partly funded the experimental work exposed in this paper within the 'Pari-Scientifique: Hydro-écologie des fossés agricoles' project (INRA-EA). This project was also funded by Agropolis Fondation under the reference ID 1605–034 through the « Investissements d'avenir » programme (Labex Agro:ANR-10-LABX-0001-01). Lastly, the project was also supported by funds from a PhD grant provided by Montpellier Supagro and the INRA institution via the EcoServ metaprogram. Authors thank the three anonymous referees for helpful comments and suggestions on the manuscript, and Bruce Jaffee for the English revision.

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## RESEARCH ARTICLE

# From 3D grassy vegetation point cloud to hydraulic resistance: Application to close-range estimation of Manning coefficients for intermittent open channels

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**Funding information**

ONEMA; INRA

**Abstract**

The understanding of interrelations between biotic and abiotic processes in intermittent open channels is currently of primary importance to better assess the services and disservices they provide. A large body of literature attempts to characterize vegetation functional traits affecting hydraulic rugosity, through the introduction of the blockage factor of flow by vegetation. However, this factor has multiple definitions and is still difficult to assess in the fields with actual and diverse vegetation covers, especially for grassy plants of ditches. Our study aims at predicting flow resistance from 3D vegetation characteristics using a close-range laser scanner. Flow resistance and vegetation 3D characteristics were defined using Manning coefficient and blockage factors, respectively. We tested combined effects of flow discharge against plant species and densities characterizing intermittent channels in a channel flume. Our results showed a variability of Manning coefficient describing flow rugosity against species and densities, with a highest rugosity for sclerophyllous species than herbaceous ones. Different blockage factors were calculated on the basis of scan clouds linked to Manning coefficients using nonlinear equation. The best relationship ( $R^2 = .9$ ) was found for nonlinear equation relating Manning coefficients to a simplified blockage factor figuring the mean vegetation height deduced from the projection of the scan point cloud to the channel frontal area. The introduction of a coefficient to correct underestimated values issued from herbaceous species considering their reconfiguration under hydrodynamic loading is thus discussed.

**KEYWORDS**

3D, ditch, hydraulics, plant architecture, terrestrial Lidar scanner

**HIGHLIGHTS**

- We built a hydraulic experimental setup composed of real plants frequently found in Mediterranean ditches in a channel flume to analyze the effect of vegetation diversity and density on hydraulic resistance.
- We used a scanner laser to measure vegetation point clouds and estimate several blockage factor induced by vegetation cover.
- The blockage factor explained 90% of flow resistance deduced from the total head loss at the channel scale.
- The results we found allow the objective predetermination of resistance factors for intermittent grassy open channels (irrigation channels, drainage ditches) using close-range vegetation size estimation technics.

**1 | INTRODUCTION**

Intermittent open channels in cultivated landscapes consist of irrigation channels, roadside ditches, drainage ditches, and reshaped gullies that have been built for centuries (Lepart & Debussche, 1992) to convey water to plots or conversely, to catch the excess of water from plots or roads and convey them to rivers. They are mainly made of soft soil material where vegetation can grow, requiring channel vegetation management (Levavasseur, Biarnès, Bailly, & Lagacherie, 2014).

As a consequence, the vegetation of intermittent open channels and its dynamics could provide numerous ecosystem disservices and services (Dollinger, Dagés, Bailly, Lagacherie, & Voltz, 2015) by affecting the former channel hydraulic conveyance capacities, by trapping and transporting sediments, nutrients, and pollutants, making them

biogeochemicals hot spots in addition to be ecological hot spots (Herzon & Helenius, 2008).

In turn, intensities of these services and disservices result from complex interrelations between biotic and abiotic processes (Wiens, 2002; Thomas et al. 2014), governed by channel hydraulics (flow height, residence time, and flow velocity field) depending on plant functional traits (Kouwen, Unny, & Hill, 1969) such as the drag at the blade or plant scale, or integrated resistance factors at the patch or reach scales. The study of plant functional traits of interest (e.g., plant size and architecture) is usually carried out by agroecological insights (Colbach, Collard, Guyot, Meziere, & Munier-Jolain, 2014) but it also appears of primary importance to conduct researches at the interface between ecology and hydrology in order to study the diversity of plant functional traits against water flows (Nikora, 2010).

The link between vegetation and flow characteristics is the subject of many studies in ecohydraulics reviewed by Curran and Hession (2013); Nepf (2012); Vargas-Luna, Crosato, and Uijttewaal (2015). In particular, it was shown that vegetated channel flows could be approached with Nikuradse (1933)'s model, making the link between local shear stress and velocity distribution (Stephan & Gutknecht, 2002).

Many studies can be found in the literature, linking vegetation characteristics to local flow properties (Järvelä, 2005; Luhar & Nepf, 2013). Vargas-Luna et al. (2015) analyzed the performances of hydraulic models on 13 and 27 experimental studies linking flow resistance to real and artificial vegetation, respectively. Vegetation effects on flows were deduced from the rigid-cylinder analogy that considered a characteristic diameter, average height and distance between plant similar for each experiment.

Applying these concepts to real systems raises major issues, such as the characterization of vegetation properties, the effect of vegetation heterogeneity, or the upscaling from plant scale to reach scale (Folkard, 2011).

Advances have been done at plant scale by Weissteiner, Jalonen, Järvelä, and Rauch (2015) and Jalonen and Järvelä (2014), thanks to an original setup implying a towing tank and fully digitized riparian trees, they explored the plant reconfiguration under hydrodynamic loading. Cassan, Belaud, Baume, and Dejean (2015) could show the good correspondence between local shear stress and reach scale resistance, but vegetation properties could be estimated only indirectly through their effect on flow characteristics. Flows with emergent vegetation typical of intermittent channels were much less investigated, notably because of the difficulty to explore velocity fields within the vegetation (Pasquino et al. 2016), despite some advances in this field using numerical experiments (Boothroyd, Hardy, Warburton, & Marjoribanks, 2016).

Green (2005b) summarized the main concepts to calculate the resistance in the light of the nature and size of vegetation and obtained a nonlinear relationship between channel resistance and the proportion of the channel occupied by vegetation, suggesting its first-order effect on flow resistance.

However, the vegetation resistance cannot be observed directly: It is empirically calibrated and rarely defined at the reach scale. Green (2005a) identified the vegetation size parameters, usually resumed in a "blockage factor" included in different formulations of roughness estimation due to vegetation (Fisher, 1992). Blockage factor covers different vegetation size metrics and scales. It initially denoted at a given

abscissae of the reach, the cross-sectional blockage factor consisting of the proportion of the wetted cross section occupied by plant stands (Watson, 1987; Jalonen, Järvelä, Koivusalo, & Hyyppä, 2014). When sampled regularly along the reach, it corresponds at reach scale to the average punctual cross-sectional blockage factors (Champion & Tanner, 2000).

It results now multiple definitions of vegetation size metrics linked to resistance parameters at reach scale with different levels of difficulties to estimate it. This latter point lead Green (2005b) to conclude that surface area blockage factor had to be preferred, because measuring the vegetation size, especially at patch, stand or reach scale is a difficult task that depends on vegetation complexity. Recently, a large amount of literature attempted to approach the blockage factor using direct measures in the fields and in the laboratory, depending on plant type. The leaf area index or the leaf-to-stem area ratio was introduced as a vegetation density measure of the blockage factor (Jalonen, Järvelä, & Aberle, 2012; Jalonen & Järvelä, 2014) for woody vegetation. Jalonen et al. (2015) characterized the mixed floodplain vegetation in order to derive metrics for hydraulic analyses. They found that mean heights of vegetation were best related to their frontal areas for herbaceous vegetation, whereas a complete view of their 3D structure was necessary for woody plants.

The recent spread of terrestrial laser scanner (TLS) offers possible vegetation size estimations from in-field experiments for hydraulic applications (Jalonen et al. 2012; Jalonen et al. 2015; Boothroyd et al. 2016). The TLS helped characterizing the height distribution and the volumetric blockage factor of plant communities at channel scale (Jalonen et al. 2014; Jalonen et al. 2015), or the complete morphology of single trees (Boothroyd et al. 2016).

To our knowledge, although the empirical evidence of considering vegetation properties to infer flow transport (Vargas-Luna et al. 2015), and the potential of using TLS for predetermination of reach roughness parameters (Jalonen et al. 2015), there is no empirical study linking vegetation point clouds derived from TLS scans to open-channel roughness coefficients and especially for grassy plants that can be found in intermittent open channels of cultivated landscapes. Grassy plants have a small size and a large range of morphological variability and flexibility among species (Kattge et al. 2011), ranging from the herbaceous ones, very flexible, to the sclerophyllous plants that had hard leaves and/or stems.

This paper aims at investigating how different channel vegetation size metrics estimated from scanner laser point clouds may lead to the estimation of Manning roughness coefficient resulting from total head loss during steady flow. The study is based on original experiments using actual grassy plant material, both herbaceous and sclerophyllous, installed in a flume with controlled hydraulic conditions. The main originality of the paper comes from the attempt to link real grassy vegetation clouds to Manning roughness coefficients.

We first expose the factorial experimental setup regarding flow discharge, plant species and plant densities implemented on the channel bed. The different vegetation size metrics at the reach scale from scanner-laser data are then exposed. We finally test the statistical modelling between vegetation metrics and Manning coefficients. Results are then discussed in comparison to those obtained by Green (2005b), Jalonen et al. (2015), and Jalonen and Järvelä (2014).

## 2 | MATERIAL AND METHODS

### 2.1 | The experimental flume

Experiments were conducted in a channel with cement borders of length 13 m, width 0.67 m, and depth 0.40 m, located in the hydraulic laboratory of Montpellier, Supagro (43.62N, 3.85W; Figure 1). The channel was chosen according to its dimensions similar in terms of geometry and Froude number to agricultural ditches of the Languedoc vineyard area, avoiding scale effects. The downstream water level was imposed by a rectangular weir. Flow turbulencies were minimized using a flow tranquilizer located upstream (Figure 2). The channel bottom was covered with high-density polystyrene plates pierced at a density of 328 holes/m<sup>2</sup> arranged on a regular grid. Holes were filled with plastic dowels to facilitate plants push down and manipulation.

The channel slope  $S_b$  was 1.3/1,000. The discharge was maintained constant thanks to level control structures and baffle sluice gates located upstream of the flume. Discharges were checked by velocity integration on the wetted area (10 verticals, 5 points per vertical). Local velocities were explored using a current meter (Hydreka©M801). The two selected flow rates were 25.3 to 51.4 L/s, with an accuracy of 5%.

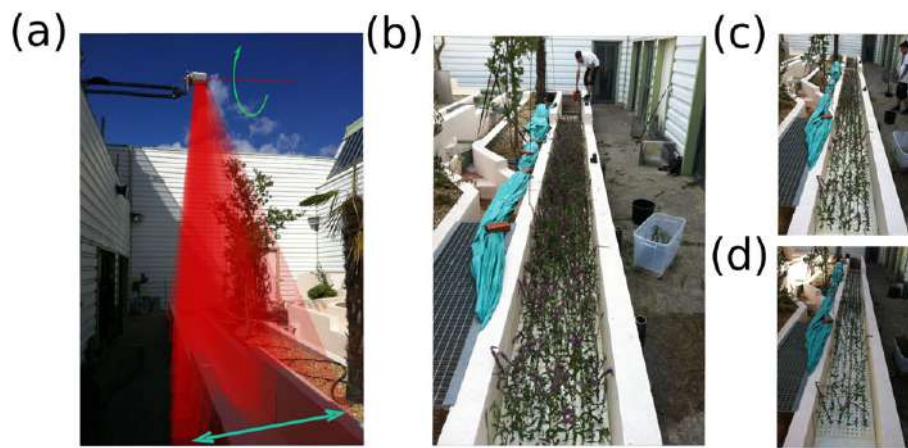
Water depth was measured using point gauges installed at the upstream end, the middle and the downstream end of the flume. Because uniform flow is hardly achievable in such conditions, roughness was obtained from the headloss in the channel. Therefore, the accuracy of the measured differences between upstream and

downstream levels was crucial. This accuracy is affected by the fixed error between the gauges (uncertainty estimated lower than 0.5 mm, thanks to precision levelling with still water) and by the reading of levels during experiments. The effect of water fluctuations was analyzed by different means: pressure level sensors (Keller 46X/0.1 bar, accuracy 0.01% of full scale in the range of the experiments) and digital cameras. The analysis showed that most uncertainties were due to water fluctuations ( $\pm 1$  mm) observed at the free surface. Because flows are clearly subcritical, these fluctuations were rather limited, but they induced an uncertainty between 1 and 2 mm on the measured headloss. The lowest uncertainties could be achieved by increasing the number of readings, which was essential for configurations with the lowest headloss (around 5 mm between most distant gauges). Water depths ranged from 18.9 to 26.7 cm over all experiments. Mean velocities ranged between 0.26 and 0.38 m/s. Manning roughness coefficient of the empty channel was estimated by removing all plants. A value of  $0.02 \pm 0.005 \text{ s/m}^{1/3}$  was obtained for both reference discharges.

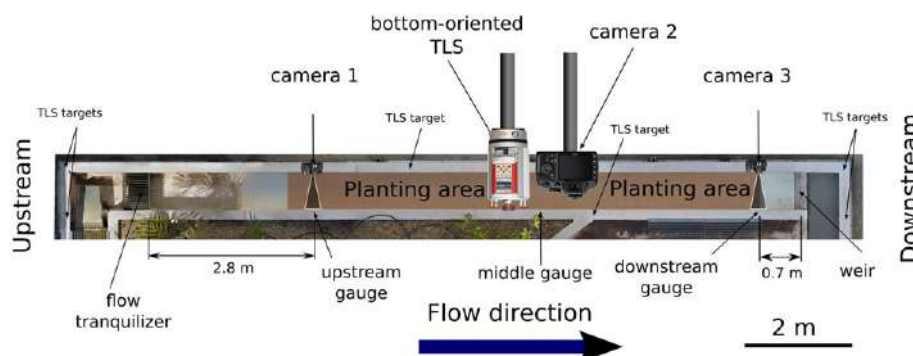
Six targets were fixed on channel curbstones to align TLS scans. Position of targets and gauges were precisely located using a tachometer at a 0.5-mm accuracy.

### 2.2 | Plant material

Four plant species were selected according to their hydrophilic behavior on a gradient from xerophyllous (*Asparagus acutifolius*) to



**FIGURE 1** Illustration of the experimental setup. (a) The laser scanner and its scanning view (in red) through the channel flume. (b), (c), and (d) An example of species planting (*Lythrum salicaria*) at densities of 41, 82, and 164 plants/m<sup>2</sup>, respectively



**FIGURE 2** Vertical view of the experimental setup. TLS = terrestrial laser scanner

hydrophyllous (*Lythrum salicaria*) that is in accordance with their upstream–downstream location in the drainage network, branching complexity, and their abundance in ditches of the Southern France landscapes (Marnotte & Carrara, 2006): *A. acutifolius*, *L. salicaria*, *Elytrigia repens*, and *Scirpoides holoschoenus*; these last two species being considered as herbaceous, whereas the two others can be considered as sclerophyllous (Figure 3). In order to get correct estimates of plant densities in real ditches, a sampling campaign was conducted in the Languedoc area (43.478N, 3.338W) in March 2013 to estimate the vegetation densities for all species in similar channels by counting total plant number per 0.48 m<sup>2</sup> quadrat in eight sites, leading to a density of  $170 \pm 100$  plants/m<sup>2</sup> (Benitou, 2013).

Approximately 1,600 plants of each species were collected in the Languedoc area just before experiments to prevent dessication and keep the initial roughness properties of plant material. Then each plant was cut at the basis to get calibrated  $40 \pm 5$  cm length replicates, that is, above the water depths of the setup, leading to a determination of flow resistance in case of non-submerged vegetation (Järvelä, 2004).

According to Jalonen and Järvelä (2014) & Weissteiner et al. (2015), properties of plants are described in terms of projected areas, architecture, and leaf-to-stem area ratios. Ten random samples of each plant were photographed laterally against white background in still air, and then area and stem parts were digitized from the scaled pictures to determine vegetation properties (Table 1). We conserved ramification variabilities occurring in the field. Only herbaceous plants were sometimes ramified, with a maximal axis order between 1 and 3 for *L. salicaria*

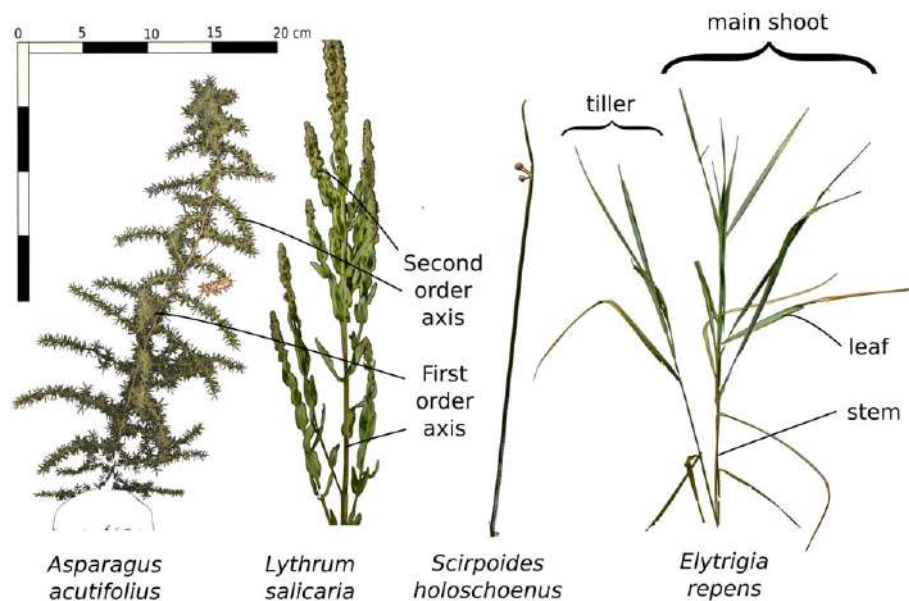
and between 2 and 3 for *A. acutifolius* (axis order is determined according to rules of the multi-scale tree graph formalism (Godin & Caraglio, 1998)). Each *E. repens* sampled consisted in one main shoot and one or two tillers, figuring herbaceous tillering. Each *S. holoschoenus* sample consisted in only one main shoot.

### 2.3 | Tested vegetation densities

Five increasing vegetation densities were settled at the channel bottom, with various plant densities for a regular pattern along channel width and staggered along channel length, varying respectively from 0 to 41, 82, 164, and 328 plants/m<sup>2</sup>. The corresponding nearest distances between plants varied from 14, 10, 7, and 5 cm, respectively, in line with the variabilities observed in the field.

### 2.4 | Estimation of plant reconfiguration in flow

According to Weissteiner et al. (2015), plant reconfiguration could be estimated by the underwater frontal projected area (FPA), giving deflected height and contracted width of the plant. Mounting cameras underwater at a distance preventing hydraulic artifacts and allowing plants observations under small water depths was not possible in our setup with small water depths. However, two cameras disposed on channel upstream and downstream borders and a third camera was located at nadir 6 m above the channel with vertical recording position



**FIGURE 3** Illustration of the shape of selected species for the experiments

**TABLE 1** Table representing the mean geometric characteristics of the plant species over 10 samples. Values in brackets correspond to the min–max. Note that the leaf-to-stem area ratio was not calculated for herbaceous species (indicated by a “-”)

Plant species	Basal stem diameter (cm)	Plant height (cm)	Plant width (cm)	FPA (cm <sup>2</sup> )	Leaf-to-stem area ratio
<i>Asparagus acutifolius</i>	0.28 (0.16–0.36)	41.5 (29–48)	25.2 (9–47)	172.1 (86–248)	2.45 (2.2–2.7)
<i>Elytrigia repens</i>	1.01 (0.9–1.2)	45.5 (35–57)	24.2 (16–35)	81.0 (50–157)	-
<i>Lythrum salicaria</i>	0.63 (0.4–0.8)	42.1 (37–45)	16.0 (8–20)	185.7 (26–366)	0.62 (0.2–1.1)
<i>Scirpoides holoschoenus</i>	0.47 (0.43–0.54)	40.6 (38–45)	5.7 (3–11)	19.4 (16–25)	-

Note. FPA = frontal projected area.

(cameras and gauge positions were illustrated in Figure 1). This allowed us to observe qualitatively if plant reconfiguration occurs during flow.

## 2.5 | Data clouds measure

Data clouds were measured in absence of flow using a 1,064-nm terrestrial Lidar scanner branded RIEGL®VZ400 located at nadir 5 m above the channel with vertical scan position at mid-length to prevent too high incident angles. The RIEGL®VZ400 a spot size of 4 mm, a scan rate up to 700,000 points per s, and a range up to 200 m. The selected field of view for the experiment was  $80^\circ \times 160^\circ$ , and the horizontal and vertical increments were both set to  $0.04^\circ$ , giving a scanning resolution of 7 mm at a distance of 10 m, corresponding to the range accuracy and precision of the scanner at this distance. TLS values were compared to manual measurements described in Table 1 only for vegetation height and FPA. The other variables cannot be accessed via the TLS clouds because cloud density was not high enough to identify a single plant architecture. Vegetation heights were directly issued from the cloud  $z$  values, whereas FPA  $\times$  planting density and FPA  $\times$  number of plants rows along channel width were deduced from the computation of  $Bf_1$  and  $Bf_2$ , respectively, as explained below.

We planted each combination of plant  $\times$  density, and we carried a first TLS scan. Then we opened the first sluice gate corresponding to a flow of 25.3 L/s. After the steady flow was reached, measurements were taken, then we repeated the operation for the second flow corresponding to 51.4 L/s.

## 2.6 | Blockage factor estimates

TLS scans were first exported in referenced XYZ point clouds using Riscan Pro®software. Data clouds issued from the scans were scaled in the same local projection system to get length and width of the channel along  $X$  and  $Y$  coordinates, respectively (see Figure 4 for definition of axes). Point clouds were first decimated using a mean nearest neighbor distance filter and then voxelized using a voxelization procedure illustrated in Figure 3 and similar to Jalonen et al. (2015) approach. We defined a voxel resolution (here  $1 \text{ mm}^3$ ) able to discriminate plant organs from TLS noise. Next,  $\mathbb{1}_{x,y,z}$  denotes the indicator function with 1 value when the TLS points are intercepted by the voxel, and 0 otherwise.

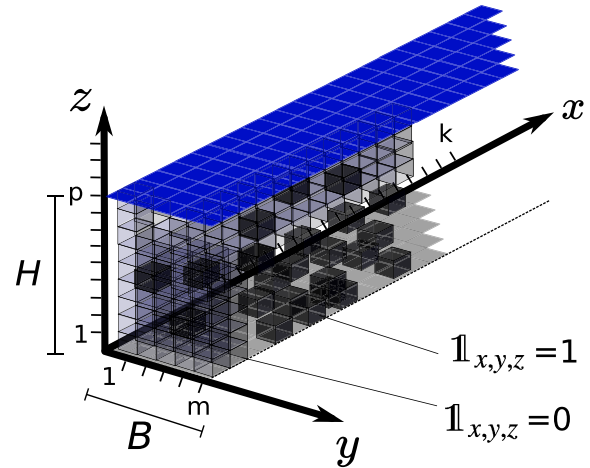
Then, we defined the density per voxel as  $d_{y,z}$  by summing each voxels along  $x$  axis, and we divided it by the total number of voxels along the channel length  $k$  to have a probability between 0 (no blockage) and 1 (complete blockage; Equation 1):

$$d_{y,z} = \frac{\sum_{x=1}^k \mathbb{1}_{x,y,z}}{k} \quad (1)$$

where  $x$  is the position index of the voxel along the channel length,  $y$  the position index of the voxel along the channel width, and  $z$  the position index of the voxel along the channel depth.

We derived from the calculation of  $d_{y,z}$  three possible definitions of the blockage factor  $Bf$ :

$Bf_1$ : the mean  $d_{y,z}$  in a cross section (Equation 2). This blockage factor corresponds to the volume blockage factor as defined by Fisher (1992).  $Bf_1$  is proportional to the FPA of each plant  $\times$



**FIGURE 4** Illustration of point cloud voxelization across the channel.  $H$  corresponds to the water level (in blue). Black and transparent voxels correspond to cubes that contained or not points issued from point cloud, respectively

planting density (Jalonen and Järvelä 2014).

$$Bf_1 = \frac{\sum_{z=1}^p \sum_{y=1}^m d_{y,z}}{m \times p}. \quad (2)$$

$Bf_2$ : the mean  $Bf_1$  thresholded in selected and nonselected pixels (Equation 3). The  $Bf_2$  is similar to the frontal projected area of Jalonen and Järvelä (2014) over the whole channel. In other words,  $Bf_2$  is proportional to the FPA of each plant  $\times$  number of plants rows along  $y$  axis.

$$Bf_2 = \mathbb{1}_{Bf_1 > s} \quad (3)$$

$Bf_3$ : the maximal height  $z$  of binarized  $d_{y,z}$  according to the threshold  $s$ , summed over the channel width (Equation 4).  $Bf_3$  is computed with all voxels beyond the canopy of the thresholded point cloud equal to 1.  $Bf_3$  is thus computed from the mean canopy height model.

$$Bf_3 = \frac{\sum_{y=1}^m z_{\max}(d_{y,z} > s)}{m \times p}, \quad (4)$$

where  $Bf_x$  denotes a given blockage factor metrics for point cloud;  $k$ ,  $m$ , and  $p$  denotes the number of voxels along  $x$ ,  $y$ , and  $z$  dimensions of the channel, respectively; and  $s$  denotes the threshold for  $d_{y,z}$  binarization.

Here, the threshold value  $s$  was fixed to the  $Q_{0.05}$  percentile of the  $d_{y,z}$  distribution. According to the usual Wald confidence level on parameters, we chose to eliminate 5% of the lower extreme value of  $d_{y,z}$  and considered the 5% percentile as the threshold for noise-free significant density.

## 2.7 | Estimation of water flow resistance

Manning coefficients were estimated from the measured total head loss between upstream and downstream ends of the vegetated reach. To do so, we considered the backwater curve equation, expressed in its differential form:

$$\frac{dH}{dx} = \frac{S_b - S}{1 - F^2} \quad (5)$$

with

$$S = \frac{n^2 Q^2}{B^2 H^2 R^{4/3}} \quad (6)$$

in which  $S_b$  is the bed slope,  $S$  is the friction slope,  $n$  is the Manning parameter,  $Q$  is the discharge,  $B$  the canal width,  $R$  the hydraulic radius,  $H$  the water height, and  $F$  the Froude number. Equation 5 was solved by imposing the downstream boundary condition with the measured value at the downstream gauge, and the Runge–Kutta fourth-order approximation. Manning  $n$  was obtained by minimizing the error between calculated and observed backwater curve.

### 2.8 | Relation between blockage factor and flow resistance

On the basis of nonlinear nature of Manning–blockage factors relationships (Green, 2005a), we linked the blockage factors  $Bf_x$  calculated to Manning coefficients using a simplified version of Nepf (2012) equation:

$$n = a \times (1 - Bf_x)^{-b} \times H^{(1/6)}. \quad (7)$$

Nonlinear Gauss–Newton fitting algorithm was used on Equation 7 to fit the  $a$  and  $b$  parameters.

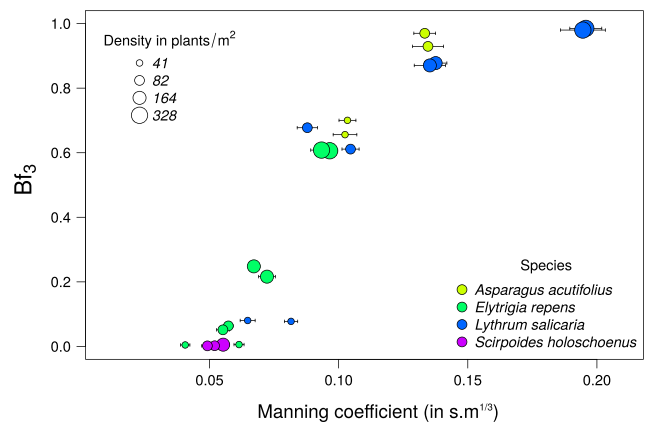
## 3 | RESULTS

### 3.1 | Blockage factor estimation at channel scale

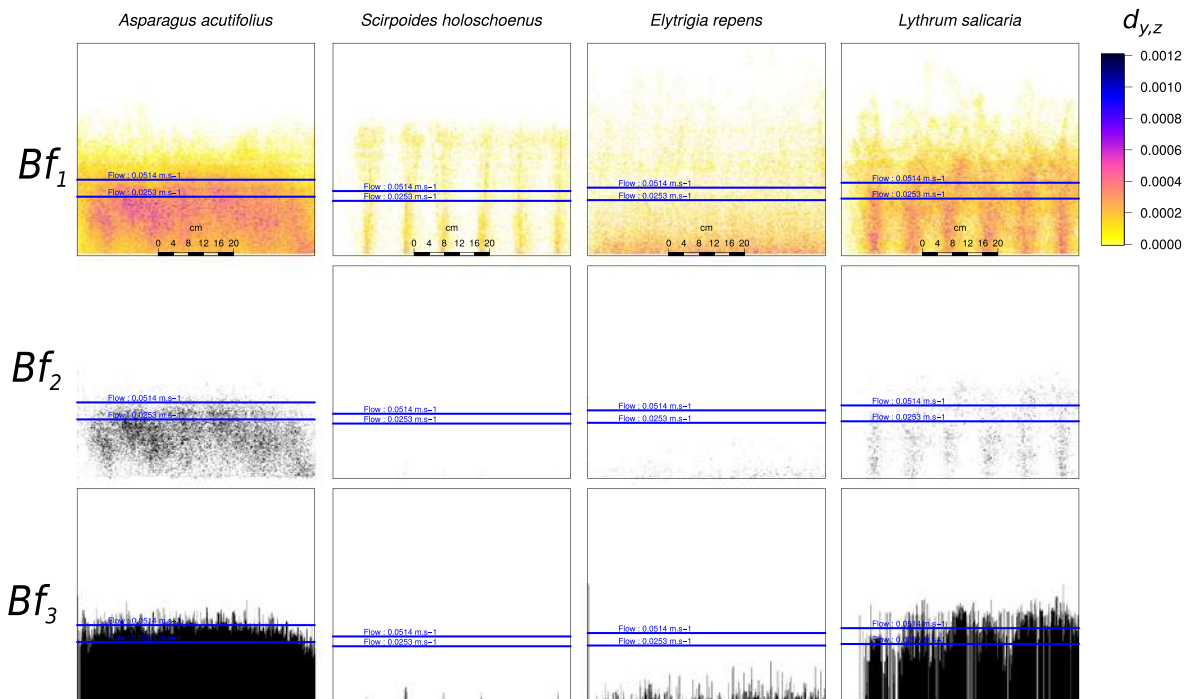
Considering each species individually (Figure 5), sclerophyllous plants such as *A. acutifolius* and *L. salicaria* had the highest levels of  $d_{y,z}$ . Herba-

ceous plants such as *E. repens* presented a vertical heterogeneity due to the presence of several blades from each plant sucker laying on the ground, unlike to *S. holoschoenus* that exhibited a higher rigidity level. Despite presenting occlusions for the sclerophyllous species due to a single scan position, TLS point clouds gave consistent images of expected  $d_{y,z}$  for each species. The threshold value  $s$  corresponding to  $d_{y,z}$   $zQ_{0.05}$  percentile was  $3.10^{-4}$ .

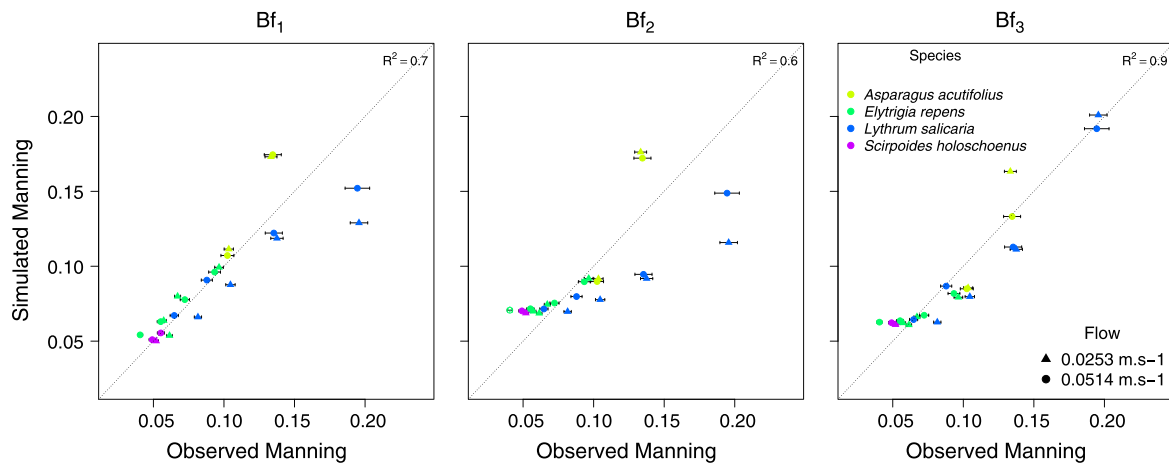
Mean vegetation heights issued from TLS scans were underestimated by 5% compared to manual measurements of each single plants. The range (min–max) of vegetation heights issued from TLS scans was similarly underestimated compared to manual measurements.  $Bf_1$  and  $Bf_2$  were correlated to FPA of each plant  $\times$  plant density and FPA of each



**FIGURE 6** Relation between the calculated Manning ( $n$ ) and calculated blockage factor  $Bf_3$  for all species. Color and point size indicate a species and its density, respectively. Estimated errors issued from water depth variations were represented by horizontal segments



**FIGURE 5** Description of calculated  $d_{y,z}$  issued from point clouds voxelization at  $1 \text{ mm}^3$  resolution. We illustrated the results for each species planted at  $82 \text{ plants/m}^2$ . Horizontal blue lines correspond to mean water level over the channel for the two different flows. First row corresponds to the illustration of  $Bf_1$  by pixel colors. Second and third rows correspond to the illustrations of  $Bf_2$  and  $Bf_3$ , respectively



**FIGURE 7** Comparison between observed Manning and its simulated value using Equation 7 according to calculation of blockage factors from vegetation point clouds. Colors indicated the species, and difference in flow values was symbolized by rounds and triangles. The dotted line corresponds to the perfect match between observations and simulations. Estimated errors issued from water depth variations were represented by horizontal segments

plant  $\times$  number of plants rows along  $y$  axis with a  $R^2 = .91$  and  $.79$ , respectively (linear model,  $p$  value  $< .001$ ,  $df = 12$ ). The  $p$  values of the intercepts of the linear models were both above 5%, indicating an absence of shift from TLS and manual measurements.

Video analysis from the three cameras revealed no reconfiguration of the plants, excepting the *E. repens* species that exhibited a blending of both main shoot and tillers of  $10^\circ \pm 2^\circ$  and  $40^\circ \pm 10^\circ$ , for first and second flows, respectively. This blending effect resulted in a deflected height reduction of 2% and 23%, respectively. We observed a small contraction of *E. repens* width with a bending of leaves toward flow direction, this qualitative observation being difficult to quantify regarding camera resolutions.

### 3.2 | Estimation of water flow resistance

The calculated Manning coefficients were highly dependent on plant species, with the higher values of Manning for sclerophyllous species such as *L. salicaria* and *A. acutifolius* (Figure 6). The herbaceous plants *S. holoschoenus* and *E. repens* exhibited lower values of Manning. This may be explained partly by branching complexity that is higher in sclerophyllous species (Figure 3).

The relation between Manning and  $Bf_3$  illustrated in Figure 6 was clearly nonlinear and was in accordance with the simplified Equation 7. The nonlinear relationship was also applied to the other calculated blockage factors. Plantation density was also positively correlated to Manning coefficient for all species, as shown in Figure 6. The error bars for  $n$  were obtained considering uncertainties on level and discharge measurements.

### 3.3 | Relation between blockage factor and flow resistance

Figure 7 showed that all Manning coefficients were well related to the blockage factors ( $R^2$  ranging between  $.6$  and  $.9$ ,  $p$  value  $< .05$ ).

**TABLE 2** Table representing the values of  $a$  and  $b$  estimated from nonlinear Gauss–Newton fitting algorithm on Equation 7

Blockage factor	Parameter	Estimate	SE	t value	Pr(>  t )
$Bf_1$ ( $0-2.10^{-4}$ )	$a$	0.06	0.01	8.93	> .0001
	$b$	5,492.28	693.77	7.9	> .0001
$Bf_2$ ( $0-0.24$ )	$a$	0.09	0.01	10.67	> .0001
	$b$	3.12	0.62	5.1	> .0001
$Bf_3$ ( $0-0.98$ )	$a$	0.08	0.00	18.14	> .0001
	$b$	0.27	0.02	13.5	> .0001

Note. Values in brackets correspond to the range of each calculated blockage factor  $Bf$ .

The models underestimated the highest values of  $n$  for  $Bf_1$  and  $Bf_2$  that corresponded to *E. repens* species.

All estimated parameters of Equation 7 were significant, with similar values for each calculated blockage factors, except for  $Bf_1$ , as denoted by Table 2. Value of parameter  $b$  was linked to the range of each blockage factor calculated with the highest value for  $Bf_1$ .

## 4 | DISCUSSION AND CONCLUSIONS

Combining laser scanner and hydraulic flume in the same experiments helped disentangling the link between vegetation architecture and resistance factor. The different calculations of the blockage factor were best suited to the point clouds derived from the observations and could be used for further experimental studies using real vegetation material. We deduced from point cloud analysis that plant traits related to blockage factor were branching complexity and height. Jalonen and Järvelä (2014) highlighted the importance of stem and leaf areas for the estimation of drag forces. Weissteiner et al. (2015) concluded as well that branching complexity had a major effect on plant reconfiguration under hydrodynamic loading, figuring that this plant characteristic may affect greatly plant porosity against flow.

We explored a small part of plant diversity, but we could extrapolate our primary results to the whole diversity by using global database of plant traits (Kattge et al. 2011).

By focusing on vegetation of Mediterranean ditches, we explored a research avenue that differed from previous studies on rigid and homogeneous plant species (Nikora et al. 2008; Whittaker et al. 2013), aquatic macrophytes, and shrubs or trees vegetation appearing in wide channels or rivers (Whittaker, Wilson, Aberle, Rauch, & Xavier, 2013; Weissteiner et al., 2015). Herbaceous and sclerophyllous plants in Mediterranean ditches have smallest size, different biomechanical properties compared to macrophytes and shrubs. We followed the work from Jalonen et al. (2015) on trees by using a voxelization procedure of point clouds at a finer resolution (millimeters) to get consistent results for our small plants.

Considering laws relating blockage factors to Manning coefficients (Equation 7), our results are consistent with preliminary studies on the subject (Green, 2005b) with an  $a$  value of .07 derived from Luhar and Nepf (2013). The consistence of Equation 7 with observed data, taking into account the nonlinear nature of the  $n-H$  and  $n-Bf_x$  relationships is in accordance with Green (2005b). The values of  $b$ , however, were substantially different from their estimated values .0239 given by (Luhar & Nepf, 2013).  $Bf_1$  appears too small, which explains why  $b$  must be set very large in this case.

The best model relating Manning coefficients to blockage factor were issued from Equation 7 applied to  $Bf_3$ . It indicated that a measure of mean vegetation height could be sufficient to capture the resistance factor induced by vegetation cover, in accordance with results from Jalonen et al. (2015), provided that vegetation was uniformly distributed along the channel. The blockage factor  $Bf_1$  that corresponds to the volume blockage factor of (Fisher, 1992) gave better results for the low Manning coefficients, that is,  $n < .1$ , than  $Bf_2$  and  $Bf_3$ , but failed to predict the high values of Manning. The threshold value  $s$  fixed at  $Q_{0.05}$  percentile of the total distributions of  $d_y$ ,  $z$  could explain that simulated Manning coefficients plateaued for values lower than .08.

The underestimation of Manning factors for herbaceous plants could be due to spatial plant reconfiguration against flow that limits friction factors (Whittaker et al. 2013; Poggi et al. 2009; Järvelä, 2005; Weissteiner et al. 2015). A further improvement of the blockage factor calculation should be to add a flexibility coefficient that reduced the potential blockage factor calculated without flow. This improvement could be adapted from observations in towing tanks from Weissteiner et al. (2015) on foliated trees, but with a reduced distance of underwater cameras from plants to get sufficient resolution level for deflection and contraction measures of plants.

## ACKNOWLEDGEMENTS

Authors are grateful to the ONEMA and the INRA institutions who both funded the experimental work exposed in this paper within the "Fossés Infiltrants et Pesticides" project (ONEMA) and the "Pari-Scientifique: Hydro-écologie des fossés agricoles" project (INRA-EA). Authors thank also David Combemale and Dénes Király for their help in the channel flume. Authors are grateful for reviewer constructive comments that considerably ameliorated the first manuscript draft.

The authors declare that there is no conflict of interest regarding the publication of this paper.

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**How to cite this article:** Vinatier F, Bailly J-S, Belaud G. From 3D grassy vegetation point cloud to hydraulic resistance: Application to close-range estimation of Manning coefficients for intermittent open channels. *Ecohydrol*. 2017;e1885. <https://doi.org/10.1002/eco.1885>