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How do field margins contribute to the functional connectivity of insect-pollinated plants?

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Abstract

Context Habitat fragmentation generates a loss of functional connectivity detrimental to the persistence of biodiversity. The French agricultural intensification initiated in the 1950s has caused a decline in field margins.

Objectives As field margins may facilitate species dispersal while providing socio-economic benefits, it is of interest to assess their contribution to the functional connectivity of insect-pollinated plants in agro-ecosystems. This will help develop appropriate management strategies mitigating fragmentation.

Methods We addressed this issue by studying the links between landscape structure and the patterns of abundance and pollen dispersal (using fluorescent dye particles) for two contrasted insect-pollinated plants occurring in field margins (*Crepis sancta* and *Euphorbia serrata*). We investigated the influence of field margins quality and of the surrounding matrix on

pollen dispersal and compared the relevance of the least-cost algorithm with a straight-line approach to depict pollinators' movements.

Results The influence of landscape structure on plant abundance is species and scale-specific. Pollen dispersal decreases with distance from the source. For *E. serrata*, it was preferentially dispersed via field margins, confirming the relevance of the least-cost algorithm, while *C. sancta* dispersal followed a straight-line.

Conclusions *Euphorbia serrata*, which grows strictly on field margins with a greater dispersal ability and a more diversified pollinator guild than *C. sancta*, is less affected by land-use changes. Our study demonstrates the contrasting contributions of field margins to pollen dispersal as they may act as functional corridors favouring pollinators' movement depending on the species of interest.

Keywords Landscape connectivity · Fluorescent dye particles · Gene flow · Mediterranean agro-ecosystems · Least-cost algorithm

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Introduction

Habitat destruction and fragmentation undermine a species capacity to withstand environmental, demographic, and genetic stochasticity due to reduced population sizes and constraints on individual movement that

can lead to reduced gene flow and ultimately local extinction (Young et al. 1996; Leimu et al. 2006; Honnay and Jacquemyn 2007) but fragmentation still leads to controversial results (Fahrig 2003; Ethier and Fahrig 2011). In this context there is a need for further investigations on species response at the landscape-scale. Landscape connectivity—‘the degree to which the landscape facilitates or impedes movement of organisms among resource patches’ (Taylor et al. 1993)—is a useful concept to aid the formulation of effective management strategies ensuring the persistence of spatially-structured species (Calabrese and Fagan 2004). Particularly relevant is the functional dimension of landscape connectivity that accounts for organisms’ perception of the landscape (Tischendorf and Fahrig 2000).

Classically, assessing functional connectivity relies on the estimation of resistance values that index the ease of movement through each landscape feature (Ferrerias 2001). These resistance values can be expert-based or more rarely calibrated via an empirical approach (Zeller et al. 2012). Landscape resistance together with the least-cost algorithm can be used to quantify inter-patch effective distances (Adriaensen et al. 2003). Contemporary studies largely emphasise the superiority of the least-cost algorithm over a straight-line distance to predict the influence of landscape structure on species dispersal (Chardon et al. 2003; Sutcliffe et al. 2003; Stevenson et al. 2013; Etherington et al. 2014). In plant species, gene flow is a key process mediated by both seed and pollen dispersal. Petit et al. (2005) have showed however that at landscape level, pollen dispersal is the major driver for gene flow and may thus be a key element for investigating the functional connectivity of insect-pollinated plant species (e.g. Van Geert et al. 2010). Although knowledge of pollen dispersal would be essential to the design and management of networks such as ‘green-veining’ (Grashof-Bokdam and Langevelde 2005), it remains an understudied aspect of the functional connectivity of common plant species. Functional connectivity has indeed been much more explored for animals than for plants especially by means of resistance modelling (but see empirical studies by Tewksbury et al. 2002; Townsend and Levey 2005).

Landscape structure management is of central interest for agro-ecosystems. Indeed, the emergence of post-1950s French intensive agricultural policies has resulted in crop homogenisation and a wide loss of natural and semi-natural habitats like agro-ecological infrastructures (e.g. hedgerows; Le Roux et al. 2008)

leading to a strong decline in farmland biodiversity (Benton et al. 2003; Tschardt et al. 2005). Among agro-ecological infrastructures, field margins are particularly interesting regarding functional connectivity as they may act either as shelters or as links for dynamic processes (Marshall and Moonen 2002) and thus facilitate pollen dispersal (Van Geert et al. 2010), a major agro-ecosystems service (Klein et al. 2007). Field margins represent here the uncultivated strips of shrubby or herbaceous vegetation located at the interface between a field and another landscape feature (a field, a road or a path). In the Luberon Regional Natural Park (south-eastern France), where land-managers aim to reconcile a sustainable economic development with biodiversity conservation, the future of field margins and their typical plant associations remains uncertain due to increasing pressures from agricultural intensification and urban sprawl (Meyer-Vale 2012).

In this study, we combine an experimental protocol using fluorescent dye particles as pollen analogues and a modelling approach in order to disentangle the contributions of field margins and the matrix on the functional connectivity of common insect-pollinated plant species. From a preliminary analysis on species assemblages and functional traits we selected two representative species of typical functional groups encountered in field margins within the Luberon Regional Natural Park, *Crepis sancta* and *Euphorbia serrata*. We address the four following questions: (i) To what extent does landscape structure modulate plant species abundance within field margins?, (ii) Does insect-mediated pollen dispersal preferentially occur via field margins?, (iii) Does field margins quality and matrix heterogeneity influence pollinator movements? and (iv) What are the challenges in modelling functional connectivity for insect-pollinated plants? We finally discuss the implications of our findings on the abundance and dispersal patterns of common plant species for land-managers in agro-ecosystems.

Methods

Study site and species

Study site

The study site is located in the southern area of the Luberon Regional Natural Park (5°30′35.68″E,

43°44'1.853"N; Fig. 1) at the interface between the intensive agricultural systems of the Durance valley and the traditional farming systems of the Luberon massif (Guende and Olivier 1993). The study site extends over 24 km² including urban, natural and agricultural areas.

The landscape is dominated by viticulture (48 %) and woodlands, which are meso-Mediterranean formations under the influence of the Mediterranean climate (19 %), while cereal fields (12.5 %), buildings (7.7 %) and olive groves (2 %) occupy a smaller proportion. Three small villages and one medium-sized dynamic city, Pertuis (population growth rate of 0.5 % per year during the period 2007–2012, equal to the rate for the metropolitan France; Biau and Chauvot 2014) also surround the study site. Within agricultural areas, we identified two main types of practices: 30 % of unploughed fields (perennial fields such as vineyards and olive groves in which no ploughing occurred before and during our field surveys thus enabling the development of *C. sancta*) and 70 % of ploughed fields (ploughing occurred before our field surveys in some perennial fields and in all cereal fields thus preventing

the development of non-cultivated plants within them). From the observation of ortho-photos (cell size: 0.5 m, Coordinate system: Lambert 1993), we created two shape files in ArcGIS 10.2. (Esri 2013), one delineating land-use polygons and one depicting field margins as polylines. Then, during our field surveys in March 2014, we (i) informed each polygon according to its effective land-use type (buildings, fallow lands, pastures, paths, ploughed fields, roads, unploughed fields, water or woody habitats), (ii) manually geo-rectified the drawing of the field margins network and (iii) specified the typology of the field margin (a 'field/field', a 'field/road' or a 'field/path' field margin). The field margins network extends over 293 km, accounting for 2545 field margins.

Study species

Our selection of study species was based on several criteria. First, we used the SILENE database (<http://flore.silene.eu/>) to identify the most frequent plant species at the study site, i.e. occurring in at least 90 relevés. Second, our choice was oriented towards

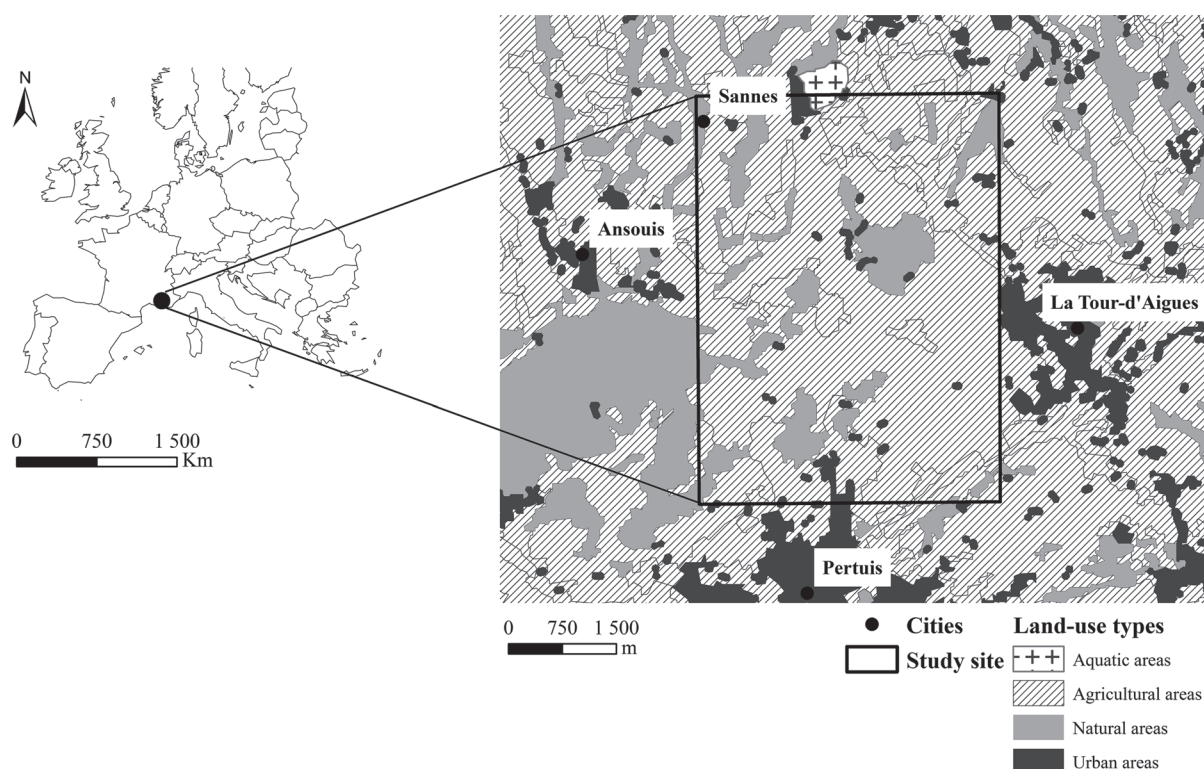


Fig. 1 Location of the study site (south-eastern France) and main land-use types

entomophilous plant species with spring flowering. Third, among the remaining species we identified the main contrasted functional strategies based on life-history traits, e.g. biological type, seed dispersal and major orders of pollinators. Finally, we checked for species representativeness in field margins. Two plant species fulfilled all of the above conditions: *C. sancta* L. Bornm (Asteraceae) and *E. serrata* L. (Euphorbiaceae). *Crepis sancta* is an annual herb with leafless flowering stems. It is insect-pollinated mainly by Apoidea such as *Panurgus dentipes* and *Apis mellifera* (C. Guiller, pers. obs.). It is a seed heteromorphic species with seed achene dispersed by anemochory and barochory (Imbert 2001). Conversely, *E. serrata* is a perennial herb with a thickened root, characterised by ovate-lanceolate leaves with finely toothed margins. Inflorescences are held in umbels containing nectar glands. It is mainly pollinated by Hymenoptera, e.g. *Athalia rosae*, *Macrophya montana* and *Tenthredo atra*, and Diptera, e.g. *Graphomya maculata* and *Sarcophaga carnaria* (C. Guiller, pers. obs.). Seeds disperse over short distances by projection coupled with myrmecochory (Baiges and Blanché 1991). According to the literature, both species occupy similar habitats such as disturbed sites, roadsides or grassy margins of vineyards (see Saatkamp et al. 2007), although we also recorded *C. sancta* in some unploughed fields. We can still consider from our field observations that field margins are the principal habitat for both species.

Species response to landscape structure

We assessed the influence of landscape structure, and particularly field margin configuration, on the distribution and abundance of *C. sancta* and *E. serrata*. For each species, we allocated a degree of abundance to each of the 2545 geolocated field margins (0: absent; 1: rare; 2: regular; 3: abundant). We repeated the analyses at two spatial scales (windows of 250 and 500 m radius centred on the sampled field margins) in order to identify relevant spatial scales for these biological patterns. Furthermore, to avoid overlaps between windows, we sampled a subset of field margins among the 2545 recorded ones as follows: (i) one field margin was randomly selected, (ii) a buffer of 250/500 m was applied around the selected field margin, (iii) the next central field margin was randomly selected beyond this buffer, and finally steps (ii) and (iii) were repeated until

the study site was completely covered by buffers around selected field margins. It represented respectively 30 (250 m scale) and 15 (500 m) windows. To depict the availability and quality of suitable habitats, we initially selected seven landscape indices reflecting both landscape composition (i.e. proportion of unploughed fields, proportion of ploughed fields, proportion of pastures and fallow lands) and configuration (i.e. landscape heterogeneity, interspersion-juxtaposition index, number of connections per field border, density of field margins in m/ha). Landscape heterogeneity (Burel and Baudry 1999) is measured via the Shannon formula. The interspersion-juxtaposition index (McGarigal et al. 2012) evaluates patch adjacencies; the higher this index is the more interspersed patch types are. Furthermore, the number of connections per field margin ‘*i*’ is defined as the total number of field margins ‘*j*’ that intersect with ‘*i*’. These indices were estimated through the *Chloe* software (Boussard and Baudry 2014), with the exception of the interspersion-juxtaposition index calculated with FRAGSTAT (McGarigal et al. 2012) and the number of connections via ArcGIS. Pairwise correlations on these seven landscape indices at each spatial scale (‘*cor.test*’, *Ade4* R-package; see Electronic supplementary material) allowed selecting four uncorrelated indices, common to both spatial scales, i.e. the landscape heterogeneity, the density of field margins, the proportion of unploughed fields and the proportion of pastures and fallow lands). We performed generalised linear models (‘*glm*’, *Ade4* R-package) with a probit link to relate landscape indices with the degree of abundance of each species (ordinal variable converted into proportional data ranging from 0—‘absent’ to 1—‘abundant’). To identify the best model, we operated a removal procedure based on a full model including the four explanatory variables, until all the combinations of variables had been tested. Following Burnham et al. (2011), we explored the support from empirical data for each model using the corrected Akaike information criterion (AICc), Akaike weights (ω_i) computed by *AICcmodavg* R-package and the evidence ratio, i.e. ratio of Akaike weights of model *i* and *j* (evidence ratio = ω_i/ω_j).

Pollen dispersal via fluorescent dye particles

In order to understand the link between landscape structure and pollen dispersal, and to check whether

pollinators preferentially follow field margins to move between floral resources, we used an experimental tool, i.e. the fluorescent dye particles analogues to pollen flow (Van Geert et al. 2010). Our experimental protocol involved four steps reiterated for both species. First, we identified two 1000 m radius non-overlapping experimental areas centred on a ‘source’ field margin per study species, defined as a field margin with the highest plant abundance (*C. sancta* or *E. serrata*). We ensured that the two experimental areas were representative of the study site (similar in terms of proportions of land-use). Second, fluorescent dye particles were installed at the optimum of the flowering period (March–April), on a single day without any wind or precipitation (between 8:00 and 10:00 a.m.). In each experimental area, we identified a 5 m segment on the source field margin within which we applied pink fluorescent particles (RADGLO JST®) on five randomly-selected plants and five randomly-selected mature inflorescences per plant (thus 25 inflorescences). Third, 48 h later, we sampled inflorescences in field margins following a ‘Step-by-step’ protocol (Fig. 2), i.e. sampling from the source over classes of geometrical distances following the network of field margins (5–10; 15–20; 35–40; 75–80; 155–160; 315–320; 635–640; 1275–1280 m). We collected a maximum of five mature inflorescences per plant on five randomly selected plants (depending on availability), for each distance class. Samples were individually stored in airtight bags. We accounted a total of 72 sampling points for *C. sancta* and 96 for *E. serrata*, representing 773 and 1869 collected inflorescences respectively. Fourth, the occurrence of the fluorescent dye particles was observed under a UV lamp for each collected inflorescence.

Measuring permeability from field observations

Defining permeability values for each landscape feature (i.e. the fraction of organisms traversing a given landscape feature; Adriaensen et al. 2007) is a prerequisite to apply the least-cost algorithm. Following the recommendations of Zeller et al. (2012), we used our empirical data to calibrate permeability values proper to the pollinators guilds of *C. sancta* and *E. serrata*. We assessed the ‘frequency that a given landscape feature (e.g. road, building, fallow land, field margin) is traversed by pollinators’ to obtain a ‘landscape permeability map’. We considered two

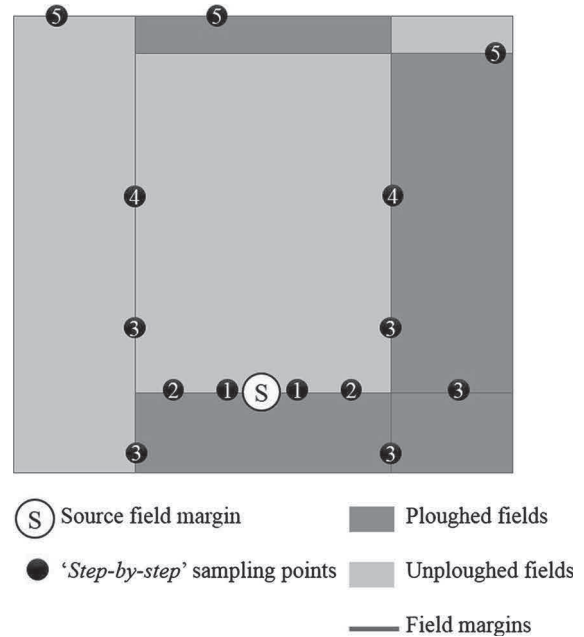
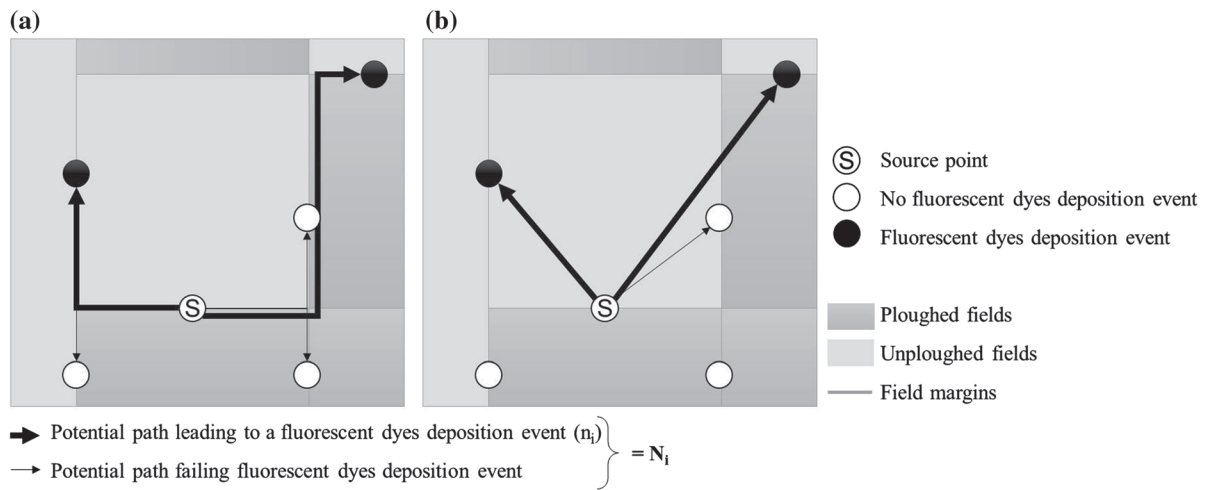


Fig. 2 Details of the ‘Step-by-step’ protocol at the scale of classes of geometrical distances: 1 (5–10 m), 2 (15–20 m), 3 (35–40 m), 4 (75–80 m) and 5 (155–160 m) up to 1275–1280 m

types of potential paths to help assigning the permeability of each landscape feature: (i) pollinators follow field margins (Fig. 3a) or (ii) pollinators move in a straight-line throughout the matrix (Fig. 3b). We defined a potential path as a series of displacements from the source (i.e. centre of the field margin receiving fluorescent dyes) to a destination point (i.e. ‘Step-by-step’ sampling points) via multiple landscape features. The permeability of the landscape feature ‘*i*’ is given by:

$$\text{Permeability} = n_i/N_i, \quad (1)$$

where ‘ N_i ’ denotes the total number of potential paths traversing at least once the landscape feature ‘*i*’ (leading or not to a deposition of fluorescent dye particles) and ‘ n_i ’ denotes the number of potential paths traversing at least once the landscape feature ‘*i*’ that actually led to a deposition of fluorescent dye particles at the destination point (Fig. 3). We obtained a value of permeability for each type of field margin and each type of polygon within the matrix, ranging from 0 (not traversed) to 1 (highly traversed by insect pollinators). The analysis was restricted to all sampling points encompassed within species dispersal distance to mimic the extent of pollinators’ perception.



(a) *Via* the field margins

Calculating permeability for ‘unploughed field/ploughed field’ field margins:

$N_i = 5$; $n_i = 2$; Permeability $_i = 2/5$

(b) *Via* the matrix

Calculating permeability for ‘unploughed fields’ polygons:

$N_i = 3$; $n_i = 2$; Permeability $_i = 2/3$

Fig. 3 Details on the elaboration of the permeability values assigned to each type of landscape features **a** via the field margins and **b** via the matrix. n_i Sum of potential paths traversing a landscape feature ‘ i ’ and leading to a deposition of

fluorescent dye particles at the destination point; N_i total number of potential paths along which ‘ i ’ is encountered; *Permeability* $_i$ the permeability of a landscape feature ‘ i ’

Finally, to apply the least-cost algorithm with ArcGIS 10.2., we transformed the permeability maps into resistance maps that depict the ecological costs of landscape features imposed on dispersers (Baguette et al. 2012), following:

$$\text{Resistance (landscape feature 'i')} = 101 - (100 \times \text{Permeability}_i) \quad (2)$$

Theoretically resistance maps can range from 1 (lowest resistance for pollinators’ movement) to 101 (the highest resistance thus impeding dispersers to move; See Electronic supplementary material).

Modelling functional connectivity

Importance of field margins

To examine whether pollinators’ movement preferentially occurred along field margins or via the matrix, we computed two types of distances between the source and each ‘*Step-by-step*’ sampling points, following a *straight-line* model versus a *field margins*

model, i.e. considering pollinators will not take shortcuts throughout the matrix.

In the context of the least-cost algorithm, we expressed these two extreme models according to the distances associated with the least-cost paths, i.e. minimal cumulative cost of moving to reach a target patch (Adriaensen et al. 2003). Hence, for the *straight-line* model, we set all resistance values to 1, identifying a uniform landscape. Contrastingly, for the *field margins* model, we allocated a resistance value of 1 to field margins (as well as to roads and paths that were not barriers to dispersal according to our field observations) and of 101 to any other landscape features. We obtained a matrix homogeneously impermeable to pollinators’ movement. From these two resistance maps, we applied the ‘*Cost distance*’ tool (ArcGIS 10.2.) to assess the minimal cumulated cost-distance between the source (i.e. centre of the field margin receiving fluorescent dyes) and any destination (i.e. ‘*Step-by-step*’ sampling points). Then, we implemented both distances (*straight-line* and *field margins*) into the ‘probability of dispersal’ (Bunn et al. 2000;

Urban and Keitt 2001), a classic negative exponential dispersal kernel (e.g. Hanski 1994) between the source ‘*i*’ and a destination point ‘*j*’ separated by a distance ‘ d_{ij} ’, following:

$$p_{ij} = \exp(-d_{ij} \times \theta) \quad (3)$$

‘ θ ’ reflects species dispersal ability and is parameterised considering that a probability of dispersal of 0.01 is achieved for the maximum dispersal distance observed in situ. Hence, we converted observed maximum dispersal distances to meet the assumptions of the two tested dispersal patterns, and we obtained for *C. sancta*: 155 m (*field margins*) and 135 m (*straight-line*) while for *E. serrata*: 635 m (*field margins*) and 623 m (*straight-line*).

Finally, we confronted the proportion of inflorescences with fluorescent dyes observed in situ to the modelled probability of dispersal via generalised linear models (probit link). We used AICc values, AICc weights (ω_i) and the evidence ratio in accordance with Burnham et al. (2011) to select the best model (*straight-line versus field margins*).

Influence of the surrounding matrix and field margins quality

To refine our understanding of pollinators’ movement, we integrated the influence of the surrounding matrix and field margins quality, defined as the relative abundance of *C. sancta* or *E. serrata*, by comparing the performance of alternative models to our reference models. The reference models are the ones obtained from the *straight-line* and *field margins* distances. We derived each alternative model from our empirical resistance maps (see 2.4.). The *straight-line with heterogeneity* model refines the *straight-line* model by assuming that landscape heterogeneity may influence pollinators’ movement. We combined resistance values of both field margins and other landscape features (values ranging from 1 to 101). The *field margins with heterogeneity* model refines the *field margins* model by presuming that pollinators follow field margins which differ in their permeability, depending on the surrounding matrix. Hence, we extracted resistance values for field margins only, ranging from 1 to 101. The resistance of other landscape features was set to 101 (impermeable to dispersers). Finally, with the GIS procedure described in “[Importance of Field Margins](#)” section, we obtained two new effective distances

(d_{ij}) from the *straight-line with heterogeneity* and *field margins with heterogeneity* resistance maps, between pairs of source and destination points that were integrated into Eq. 3. Additionally, we made further refinements to test whether the quality of field margins influences the movement of pollinators by attracting them into areas of higher floral resources. To do so, we weighted p_{ij} , calculated for both the reference and alternative models, by the relative abundance of *C. sancta* or *E. serrata* at the destination:

$$p_{ij}^* = a_j \times p_{ij} = a_j \times \exp(-d_{ij} \times \theta), \quad (4)$$

where ‘ a_j ’ denotes plants abundance for a given destination point divided by the highest level of abundance ($=3$), thus standardizing p_{ij}^* from 0 to 1. Ultimately, we performed generalised linear models linking the proportion of inflorescences with fluorescent dyes with p_{ij} and p_{ij}^* , to compare the statistical relevance of alternative models to reference models.

All statistical analysis previously mentioned were implemented in R 3.1.2. (R Development Core Team 2013).

Results

Species response to landscape structure

Overall, *C. sancta* and *E. serrata* occur in respectively 41.4 and 34.4 % of the 293 km field margins network. The model selection highlights that various landscape indices best predict the abundance pattern, depending on the spatial scale and the study species (Table 1). Regarding *C. sancta* at the 250 m scale, the two best models include the proportion of unploughed fields with or without the proportion of pastures and fallow lands. Given the very low Δ AICc, the weak evidence ratio ($=2.14$) and the fact that the proportion of pastures and fallow lands is not significant ($P > 0.1$), we keep the simplest as the best one (model B; explained deviance = 21.33 %). At the 500 m extent, the proportion of unploughed fields is also the variable best explaining the abundance of *C. sancta* (explained deviance = 11.05 %). This model was only 2.3 times more plausible than the null model.

Contrastingly, at 250 m, the abundance of *E. serrata* is mainly explained by the density of field margins (explained deviance = 11.65 %) alone or in combination with landscape heterogeneity ($P > 0.1$; evidence ratio = 2; Table 1), while at 500 m, it is

Table 1 Results from generalised linear models comparing the ability of landscape structure models to predict the abundance of *Crepis sancta* and *Euphorbia serrata* at the field border for two spatial scales (250/500 m)

Species	Scale (m)	Rank	Model	Np	AICc	Δ AICc	ω_i	Evidence ratio	Explained deviance (%)
<i>Crepis sancta</i>	250	A	Ab ~ P(PFL) + P(unploughed fields)	3	62.96	0.00	0.47		28.39
		B	Ab ~ P(unploughed fields)	2	64.46	1.50	0.22	2.14	21.33
		C	Ab ~ heterogeneity + P(unploughed fields) + density of field margins + P(PFL)	5	67.22	4.26	0.06	7.8	31.73
		D	Ab ~ 1	1	74.08	11.13	0.00		0
	500	A	Ab ~ P(unploughed fields)	2	55.32	0.00	0.32		11.05
		B	Ab ~ 1	1	56.91	1.59	0.14	2.3	0
		C	Ab ~ P(PFL) + P(unploughed fields)	3	57.42	2.10	0.11	2.9	12.40
		D	Ab ~ heterogeneity + P(unploughed fields) + density of field margins + P(PFL)	5	62.97	7.65	0.01	32	16.67
<i>Euphorbia serrata</i>	250	A	Ab ~ density of field margins	2	75.64	0.00	0.38		11.65
		B	Ab ~ density of field margins + heterogeneity	3	77.1	1.46	0.19	2	13.93
		C	Ab ~ P(PFL) + density of field margins	3	77.68	2.04	0.14	2.7	13.03
		D	Ab ~ 1	1	80.14	4.50	0.04	9.5	0
		E	Ab ~ heterogeneity + P(unploughed fields) + density of field margins + P(PFL)	5	82.53	6.89	0.01	38	14.40
	500	A	Ab ~ P(PFL)	2	50.68	0.00	0.58		19.45
		B	Ab ~ P(PFL) + density of field margins	3	52.85	2.17	0.20	2.9	20.49
		C	Ab ~ heterogeneity + P(unploughed fields) + density of field margins + P(PFL)	5	56.38	5.70	0.03	19.3	26.44
		D	Ab ~ 1	1	60.13	9.45	0.01	58	0

Selection of the four to five best models at each spatial scale

Ab abundance, P proportion, PFL pastures and fallow lands, Np: number of parameters, ω_i AICc weights

explained by the proportion of pastures and fallow lands (explained deviance = 19.45 %). The top-ranked model (model A) was 9.5 and 58 times more plausible than the null model at the spatial scales of 250 m and 500 m, respectively.

Inter-margin fluorescent dyes dispersal pattern and functional connectivity modelling

Importance of field margins

Experimental data reveal that for both species the proportion of inflorescences with fluorescent dyes rapidly decreases with the distance from the source field margin. Additionally, it follows well the negative exponential dispersal model (Eq. 3). The proportion of inflorescences with fluorescent dyes ranges from 0 to 0.96 for *E. serrata*, while varying from 0 to 0.36 for *C. sancta* (Fig. 4).

For *C. sancta*, the *straight-line* model (explained deviance = 86.7 %) performs better than the *field margins* model (Table 2; Fig. 4a and b) in explaining the proportion of inflorescences with fluorescent dyes. Regarding *E. serrata*, the *field margins* model (explained deviance = 37 %) exhibits the strongest correlation with the proportion of inflorescences with fluorescent dyes (Table 2; Fig. 4c and d). This model is around 50 times more plausible than the *straight-line* model.

Influence of the surrounding matrix and field margins quality

For *C. sancta*, the pattern of fluorescent dyes dispersal strongly correlates with *straight-line* model (Table 2). Accounting for landscape heterogeneity or for the quality of field margins does not lead to significantly better predictions of the empirical data. The top-

ranked model is around five times more plausible than the second-ranked model. Regarding *E. serrata*, effective distances via field margins coupled with field margins quality, are the best predictors of the pollen dispersal pattern (Table 2), though considering the quality of destination field margins only increased

the explained deviance by 2 %. Accounting more finely for landscape resistance (*field margins with heterogeneity* model) does not significantly improve the predictions. Overall, we detected better model fits for *C. sancta* (explained deviance >80 %) than for *E. serrata* (ranging from 21.1 to 39 %).

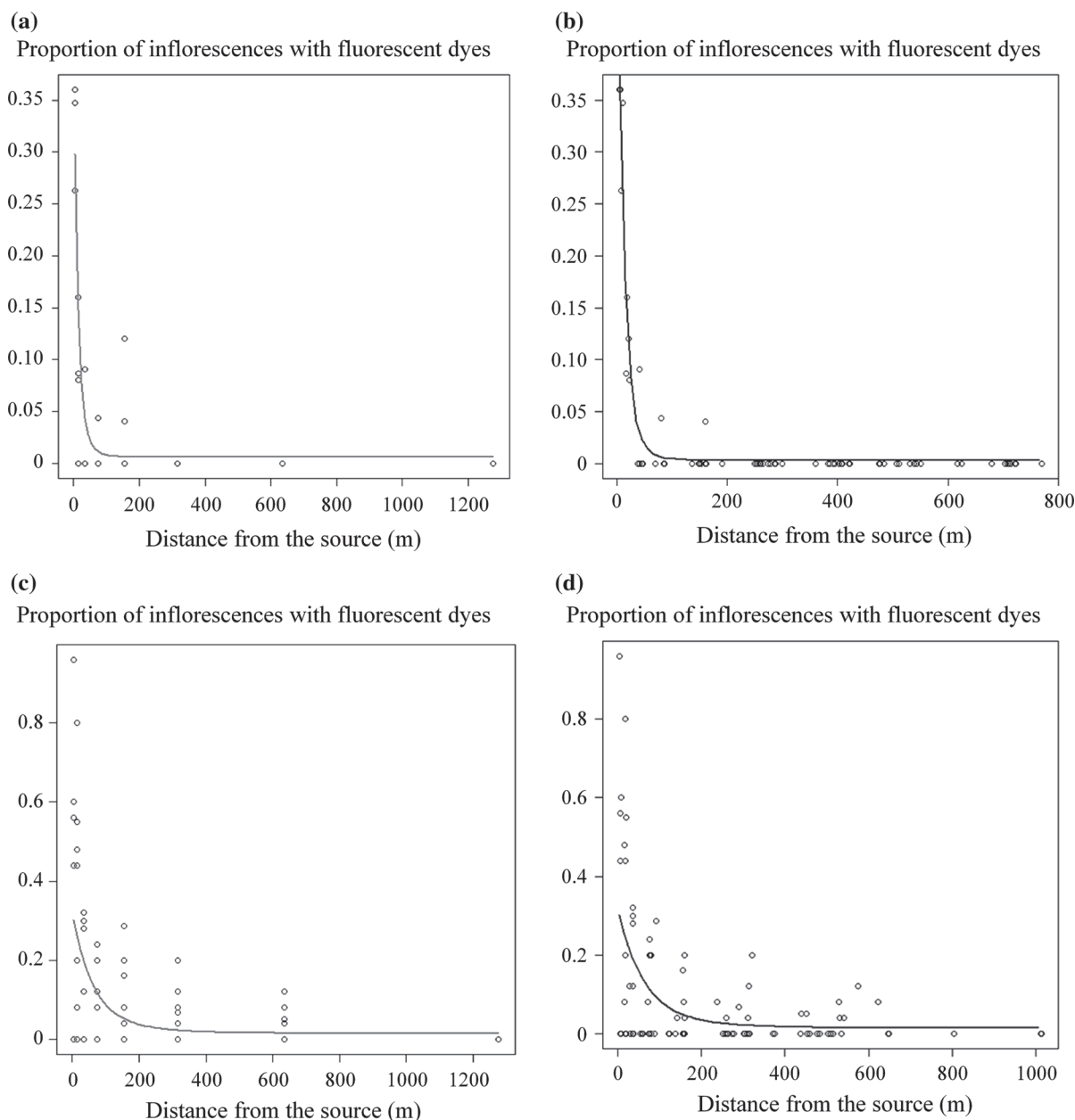


Fig. 4 Proportion of *Crepis sancta* and *Euphorbia serrata* inflorescences with fluorescent dye particles relative to the distance from the source per dispersal pattern. **a** Field margins model and **b** straight-line model for *Crepis sancta*; **c** Field

margins model and **d** straight-line model for *Euphorbia serrata*. The curves represent the distribution expected under the negative exponential dispersal kernel for the best-fitting parameters

Table 2 Results from generalised linear models comparing the ability of functional connectivity models to predict the fluorescent dyes dispersal pattern

	Species	Model	AICc	Δ AICc	ω_i	Evidence ratio	Explained deviance (%)
Field margins importance	<i>Crepis sancta</i>	P(inflorescences with dyes) $\sim p_{ij}(\text{straight-line})$	54.78	0.00	1.00		86.7
		P(inflorescences with dyes) $\sim p_{ij}(\text{field margins})$	70.14	15.36	0.00		75.8
		P(inflorescences with dyes) ~ 1	175.17	120.39	0		0
	<i>Euphorbia serrata</i>	P(inflorescences with dyes) $\sim p_{ij}(\text{field margins})$	491.81	0.00	0.98		37.0
		P(inflorescences with dyes) $\sim p_{ij}(\text{straight-line})$	500.03	8.22	0.02	49	35.0
		P(inflorescences with dyes) ~ 1	711.57	219.76	0		0
Influence of the matrix and the quality of field margins	<i>Crepis sancta</i>	P(inflorescences with dyes) $\sim p_{ij}(\text{straight-line})$	54.78	0.00	0.78		86.7
		P(inflorescences with dyes) $\sim p_{ij}^*(\text{straight-line})$	57.84	3.06	0.17	4.6	84.5
		P(inflorescences with dyes) $\sim p_{ij}(\text{straight-line with heterogeneity})$	60.95	6.17	0.04	19.5	82.3
		P(inflorescences with dyes) $\sim p_{ij}^*(\text{straight-line with heterogeneity})$	63.28	8.50	0.01	78	80.6
		P(inflorescences with dyes) ~ 1	175.17	120.39	0		0
		<i>Euphorbia serrata</i>	P(inflorescences with dyes) $\sim p_{ij}^*(\text{field margins})$	480.42	0.00	1.00	
	P(inflorescences with dyes) $\sim p_{ij}(\text{field margins})$		491.81	11.4	0.00		37.0
	P(inflorescences with dyes) $\sim p_{ij}(\text{field margins with heterogeneity})$		540.67	60.26	0.00		27.4
	P(inflorescences with dyes) $\sim p_{ij}^*(\text{field margins with heterogeneity})$		580.05	99.63	0.00		21.1
	P(inflorescences with dyes) ~ 1		711.57	219.76	0		0

P proportion, p_{ij} probability of dispersal between a source ‘ i ’ and a destination point ‘ j ’, p_{ij}^* probability of dispersal weighted by field margins quality, ω_i AICc weights

Discussion

Plant species abundance and dispersal patterns across a peri-urban agricultural landscape

Plant species abundance modulated by landscape structure

Following our first objective, little evidence was found of the influence of landscape structure on species abundance and we found a high degree of uncertainty

regarding the best models. However, our results confirm three main trends that have already been largely discussed for other types of organisms. We found that the relation between abundance and landscape structure is somewhat depending on both (i) the spatial scale and (ii) the species as previously demonstrated on animal species (Brennan and Schnell 2005; Barbaro et al. 2007). While the abundance of *C. sancta* was moderately determined by the proportion of unploughed fields (250 and 500 m spatial scales) the abundance of *E. serrata* slightly benefited from the

density of field margins (250 m) and the proportion of pastures and fallow lands (500 m). A possible explanation relates to species life-history traits. Indeed, perennial species (e.g. *E. serrata*) express a higher sensitivity to mechanical soil perturbations within fields (e.g. ploughing, which occurred in March and May for the ploughed and unploughed fields, respectively) than annual species, being thus restricted to less agriculturally disturbed habitats such as field margins (Saatkamp et al. 2007; Fried et al. 2009). Finally, our results emphasise that the heterogeneity of agro-ecosystems partly supports farmland species abundance within a fragmented peri-urban agricultural landscape (Benton et al. 2003; Vasseur et al. 2013). The heterogeneity of agro-ecosystems may indeed act as a lever of action to ensure an appropriate landscape management for plant species occurring in field margins. *Crepis sancta* responds to crop heterogeneity (no monoculture cover; e.g. unploughed fields) while *E. serrata* responds to between-fields heterogeneity (noncropped habitats; e.g. field margins, fallow lands). Landscape heterogeneity sensu Burel and Baudry (1999) did not affect species abundance. Indeed, similar profiles of heterogeneity encountered in randomly sampled buffers centred on field margins, led to less strength to identify significant statistical trends for *C. sancta* and *E. serrata*.

Influence of field margins and matrix heterogeneity on species dispersal

In view of our second and third objectives, our results give three main elements of response: (i) dispersal ability differs between *C. sancta* and *E. serrata*, (ii) the preferred pattern of pollen dispersal depends on the study species and (iii) field margins may facilitate pollinators' movement.

Regardless of the study species, our findings suggest that strongly-linked field margins (regarding functional connectivity) exhibit a high proportion of inflorescences with fluorescent dye particles. However, both species displayed contrasted maximum dispersal distances (*C. sancta*: 133 m and *E. serrata*: 635 m), thus emphasising the importance of a species-specific assessment of connectivity (Tischendorf and Fahrig 2000). We may impute such a difference to the contrasting composition of pollinators guilds. Indeed, among the 13 species of the *C. sancta* guild (*C. Guiller*, pers. obs.), Apoidea significantly contribute to

pollination. Bees foraging efficiency and behaviour proceed from distances between nesting sites and foraging habitats coupled with resources availability (Steffan-Dewenter and Kuhn 2003; Williams and Kremen 2007; Zurbuchen et al. 2010), hence they may preferentially visit profitable areas nearby their hives. If they do adopt this behaviour here, the lower dispersal distance of fluorescent dye particles is easily conceivable, considering the mass-flowering resources of *C. sancta* provided by unploughed fields adjacent to the source. Conversely, we described a more diversified guild for *E. serrata* (31 species; *C. Guiller*, pers. obs.), among which sawflies (e.g. *Athalia* sp., *Macrophya* sp., *Tenthredo* sp.) are known to be active dispersers with extended foraging areas (Nagasaka 1992; Liston et al. 2012).

Interestingly, our findings on functional connectivity indicate that *C. sancta* and *E. serrata* pollinators tend to use, on average, contrasted dispersal pathways. For *C. sancta*, analyses revealed a superior performance of the straight-line distance via landscape. Pollinators equally traversed field margins and the surrounding matrix. Moreover, dispersers were not specifically attracted by field margins with higher floral resource. Indeed, a particularly attractive resource of *C. sancta* provided by unploughed fields was available in the immediate vicinity of the source, within insect pollinators dispersal abilities. Hence, we can reasonably assume that this extensive floral resource modulates pollinators' movement, rather than floral resources in spatially restricted habitats such as field margins. However, note that we did not consider floral resources provided by other plant species that could as well influence insect foraging patterns.

Finally, we indicated that aside from offering suitable habitats, field margins may be valuable for species abundance and dispersal depending on species life-history traits in accordance with the findings of Van Geert et al. (2010) and Cranmer et al. (2012) on other agricultural linear elements.

Challenges of functional connectivity modelling for pollinated plants

Inconsistently with the dominant literature reporting that the matrix modulates connectivity between suitable habitats (e.g. Speckled wood butterfly (*Pararge aegeria*), Chardon et al. 2003; Red squirrel (*Sciurus*

vulgaris), Verbeylen et al. 2003; Natterjack toad (*Bufo calamita*), Stevens et al. 2006), we found little support for the least-cost algorithm and the concept of matrix heterogeneity regarding the pollen dispersal patterns of our two plant species. Ecological costs classically outperform the straight-line distance when modelling species functional connectivity because they integrate dispersers' perception of landscape structure (Chardon et al. 2003). Here, while one of our species (*E. serrata*) was better predicted by the *field margins* model, thus confirming the relevance of the least-cost algorithm, the other one (*C. sancta*) led to better predictions of the pollen pattern by straight-line distances. We may explain the latter pattern by three different reasons. (i) Given the low-contrast landscape contexts in the vicinity of the source points (low ratios of resistance values between adjacent landscape features) and the rapid distance decay of flower visitation (limited dispersal unlike usual animal dispersal distance; e.g. Stevens et al. 2006), we found similar performances of statistical models accounting for the heterogeneous matrix. (ii) *C. sancta* occurs in unploughed fields, which may lead pollinators to make intermediate stops between our sampling points. Additionally, it is pollinated by a generalist insect, *Apis mellifera* that may be attracted to a broader range of floral resources and thus be less affected by the apparent landscape heterogeneity, consistently with the findings of Foley and Holland (2010) on generalist flying beetles, known to travel straight between resources. (iii) Finally, the subtle contrasts pointed out between the alternative models integrating the heterogeneity of the matrix, and the reference models may proceed from the difficulty that we encountered in inferring the resistance values for each landscape feature. Indeed, inferring landscape resistance is a key stage for functional connectivity modelling, which classically involves expert opinions (Zeller et al. 2012) because tracking dispersers poses severe logistical challenges despite delivering accurate information about how organisms perceive landscape structure (Calabrese and Fagan 2004; Bélisle 2005). Here, it would have required a specific experimental design targeted on pollinator behaviour to accurately assign landscape permeability (e.g. Bélisle 2005; Hadley and Betts 2011; Bergerot et al. 2013). Although ecological costs allocated here did not derive from a subjective expert-based approach, our permeability elaboration may not be optimal to model pollen dispersal, and adds to our

range of permeability that was potentially not contrasted enough thus affecting the performance of the least-cost algorithm, as suggested by Rayfield et al. (2010) and Koen et al. (2012). Given the low-fits and statistical uncertainties, we should interpret our results with care and we do not preclude the potentiality that our landscape resistance could be improved.

Implication for land-managers facing changes in the agricultural practices within agro-ecosystems

Within the South of the Luberon Regional Natural Park, Meyer-Vale (2012) reports the existence of increasing agricultural pressures that aim at improving yields and facilitating the accessibility to the small sized fields (80 × 50 m on average in the study site). It means that arable fields may be grouped (Meyer-Vale 2012) and we can reasonably expect that intensive farming practices will be operated to meet higher yields thus impeding the development of flowering resources within arable fields (e.g. reluctance to widely let permanent inter-row vegetation cover or even reluctance to delayed ploughing due to competition for water resources in vineyards under Mediterranean climate that would affect yields; CETE 2013). Conversely, agricultural policies in the Luberon Regional Natural Park aim at maintaining natural and semi-natural habitats (Meyer-Vale 2012). From the preceding, and based on our results that underlined a positive relationship between the abundance of *C. sancta* and the proportion of unploughed fields, we expect that landscape disturbances may counteract the occurrence of *C. sancta*. On the other hand, *E. serrata* would be maintained within the network of field margins as its abundance mainly relates to the proportion of field margins. Our results overall suggest that the landscape structure affects both common plant species abundance and their pollination patterns. These elements are known to be the key components of robust plant-pollinator interactions and the warrant of their stability in the long term (Ghazoul 2005; Hadley and Betts 2011). Here, the occurrence of *E. serrata* into field margins, its extended dispersal distance (ability to rescue and recolonize distant habitats; Henle et al. 2004) coupled with its more diverse guild of pollinators likely to help maintaining its pollination in the long-term (e.g. Kremen et al. 2002) would thus enable pollen-

mediated gene flow under landscape disturbance such as intensive farming, as opposed to *C. sancta* (low dispersal ability and less diverse guild of pollinators to which would add the decline in the amount of suitable habitats caused by potential changes in farming practices). Although common plant species such as *C. sancta* and *E. serrata* are not currently threatened, they may be distinctly affected by future landscape disturbances given their life-history traits and how landscape structure modulates their contemporary abundance and dispersal patterns, and similarly for the functional groups they represent. Hence, our results have some implications for the planning of biodiversity management in agro-ecosystems. Indeed, our framework is a useful tool to identify which landscape features act as barriers or corridors for plant species dispersal. Based on species responses, we may formulate a few recommendations to enhance plant species abundance within field margins (e.g. delay ploughing in perennial fields, maintain or restore field margins for *C. sancta* and *E. serrata*, respectively) and to offer multiple dispersal routes for pollinators (e.g. adapt mowing in the field margins to the phenology of *E. serrata*, enhance floral resources within pollinators foraging areas, for both species).

Conclusion

In this study, we proposed to combine field observations, experimentations and a modelling framework for two plant species representing different functional strategies in the floral assemblages of Mediterranean agro-ecosystems. With such an approach we have shown how both abundance and dispersal patterns were contrasted between two plant species representing distinct functional groups in plant assemblages that are infested to field margins within low-intensity agro-ecosystems. We emphasised that landscape structure and particular landscape features, such as field margins, may play an essential role on these patterns as they may either offer suitable habitat and/or facilitate species dynamics (abundance and dispersal). Consequently, our results could help formulating management recommendations to optimise landscape connectivity via a dual action on the matrix and field margins and cope with the expected effects of agricultural intensification on the conservation of a subset of biodiversity which is not rare but still

constrained to specific semi-natural habitats. Finally, our framework could help bridge the gap between criticised agri-environment schemes aiming at limiting the impacts of agricultural intensification, and wide environmental policies sustaining landscape connectivity ('green-veining' policy).

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Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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