Landscape drivers of pests and pathogens abundance in arable crops

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EDITOR'S CHOICE

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Farmers' use of fungicides and insecticides constitutes a major threat to biodiversity that is also endangering agriculture itself. Landscapes could be designed to take advantage of the dependencies of pests, pathogens and their natural enemies on elements of the landscape. Yet the complexity of the interactions makes it difficult to establish general rules. In our study, we sought to characterize the impact of the landscape on pest and pathogen prevalence, taking into account both crop and semi-natural areas. We drew on a nine-year national survey of 30 major pests and pathogens of arable crops, distributed throughout the latitudes of metropolitan France. We performed binomial LASSO generalized linear regressions on the pest and pathogen prevalence as a function of the landscape composition in a total of 39 880 field × year × pest observation series. We observed a strong disequilibrium between the number of pests or pathogens favored (15) and disadvantaged (2) by the area of their host crop in the landscape during the previous growing season. The impact of the host crop area during the ongoing growing season was different on pests than on pathogens: the density of most pathogens increased (11 of 17, and no decreases) while the density of a small majority of pests decreased (7 of 13, and four increases). We also found that woodlands, scrublands, hedgerows and grasslands did not have a consistent effect on the studied spectrum of pests and pathogens. Although overall the estimated effect of the landscape is small compared to the effect of the climate, a territorial coordination that generally favors crop diversity but excludes a crop at risk in a given year might prove useful in reducing pesticide use.

Short abstract

We sought to identify general rules characterizing the impact of the landscape on the prevalence of pests and pathogens of arable crops. We showed that the host crop area is consistently correlated with increased pressure of the pests and pathogens the following growing season. Correlations of pests and pathogens with host crop areas in the same year or with semi-natural components of the landscape (grasslands, hedgerows and forests) are less consistent and depend on the functional traits of the organisms involved.

Keywords: crop pathogens, crop pests, crop protection, landscape composition

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Introduction

Yield losses of major arable crops due to animal pests and fungal pathogens are estimated at 20–30% worldwide (Savary et al. 2019). During the past decade, the growing awareness of environmental hazards associated with agricultural intensification (Kim et al. 2017, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2018) has motivated abundant studies on alternative agronomic levers to alleviate crop damage caused by pests (Altieri et al. 2018).

The focus of such research has progressively shifted from its historical focus on the field, to the landscape (Bianchi et al. 2006, Plantegenest et al. 2007) with an emphasis on the opposition between crop and non-crop components (Chaplin-Kramer et al. 2013, Karp et al. 2018, Martin et al. 2019, Sirami et al. 2019) to design integrated pest management strategies at the landscape scale (Tscharntke et al. 2005, 2016, Bianchi et al. 2006, Karp et al. 2018, Yang et al. 2019, Tamburini et al. 2020b). Complex tradeoffs between the impact of such landscape components on both the life cycle of animal pests and their natural enemies have often been pointed out (Woltz et al. 2012, Tscharntke et al. 2016, Perez-Alvarez et al. 2018).

Studies opposing cropland to semi-natural habitats have failed to define a general rule of thumb regarding the regulation of animal pest epidemics (Veres et al. 2013, Karp et al. 2018, Martin et al. 2019). No clear agreement emerges either for the management of crop pathogens, as empirical studies are scarce despite repeated calls for landscape-level assessments (Plantegenest et al. 2007, Yuen and Mila 2015). General principles to quantify the effect of crops and semi-natural spaces on the prevalence of pests and pathogens are yet to be defined (Bianchi et al. 2006, Tscharntke et al. 2016, Karp et al. 2018, Yang et al. 2019, Tamburini et al. 2020b).

Here we assume that it is possible to bring to light such general rules on landscape impact on the presence of pests or pathogens of arable crops by improving the description of landscape composition in several respects. First of all, the opposition between cultivated and uncultivated land must be refined by individualizing the crops that are susceptible to the pathogens or pests in question. Secondly, since both pests and their natural enemies have multiplication and possibly dilution dynamics in crops from one year to the next, it is necessary to distinguish between areas sensitive to a pest in the current year and the previous year (Schneider et al. 2015, Scheiner and Martin 2020). Semi-natural areas are less likely to change from one year to the next, but their impact in terms of both shelter and nutrition on pests and their natural enemies may depend strongly on their precise nature (forests, meadows, etc.) (Sarthou et al. 2014). These distinctions are also important for generating effective actionable knowledge and specifying the most effective semi-natural areas in terms of regulation.

Beyond the nature and temporality of landscape components, the difficulties encountered in identifying a coherent impact of the landscape on pests could also come from the small areas under consideration. The effects of different landscape components are frequently considered only up to a distance of 2 km or less (Bianchi et al. 2006, Karp et al. 2018, Scheiner and Martin 2020), yet insects, as well as pathogen spores, frequently have dispersal distances of several kilometers (Bianchi et al. 2010, Chaplin-Kramer et al. 2011). The consideration of much larger landscapes is therefore justified. Finally, to establish tendencies, a large number of pests and pathogens needs to be studied simultaneously and a large amount of data needs to be available for each one of them (Karp et al. 2018, Boinot et al. 2019).

French arable farming systems are particularly dependent on chemical treatments and two-thirds of the total pesticide value are used on cereals and industrial crops (Butault et al. 2011). In the following, we assessed in France the impact of the landscape composition on 30 animal pests and pathogens of six arable crops: wheat, barley, corn, oilseed rape, potato and sugar beet. The first four were the most cultivated in France during the studied years (Agreste 2019). Sugar beet and potato were added as they are the most chemically treated arable crops in France (Agreste 2019). On these crops, we selected the 30 most significant pests and pathogens as reflected by their frequency of observation in Vigicultures, one of the two databases of the national vegetal epidemic surveillance system. At the time of the analysis, this database gathered observations distributed over all latitudes of metropolitan France (Fig. 1) and over eight years (2009–2017).

To assess the impact of the landscape composition, we distinguished the host crop during the ongoing growing season (i.e. the growing season of the host crop of the pest or pathogen observed) and during the previous growing season. We also distinguished within semi-natural habitats the woodlands, scrublands, hedgerows and grasslands. The landscape composition up to 10 km from the pest observation points was obtained from official map data sets: Registre Parcellaire Graphique (RPG) from the Common Agricultural Policy (CAP) for crop fields and grasslands, BDTOPO from the French National Institute of Geographic, and Forest Information (IGN) for forests and hedgerows.

These data allowed us to test if for each of the considered landscape components there is a tendency toward negative or positive correlation among the considered pests and/or pathogens. We also test if such tendencies are different between pests and pathogens and finally compare the effect sizes of the different variables accounted for.

Material and methods

Overview of the analysis

For each landscape component, we considered four distances at which their influence can be exerted, that roughly correspond to potential management units: 200 m (the neighboring field), 1 km (the farm), 5 km (the village) and 10 km (the group of neighboring villages). Based on observations from the French epidemic-surveillance network (2009–2017), we

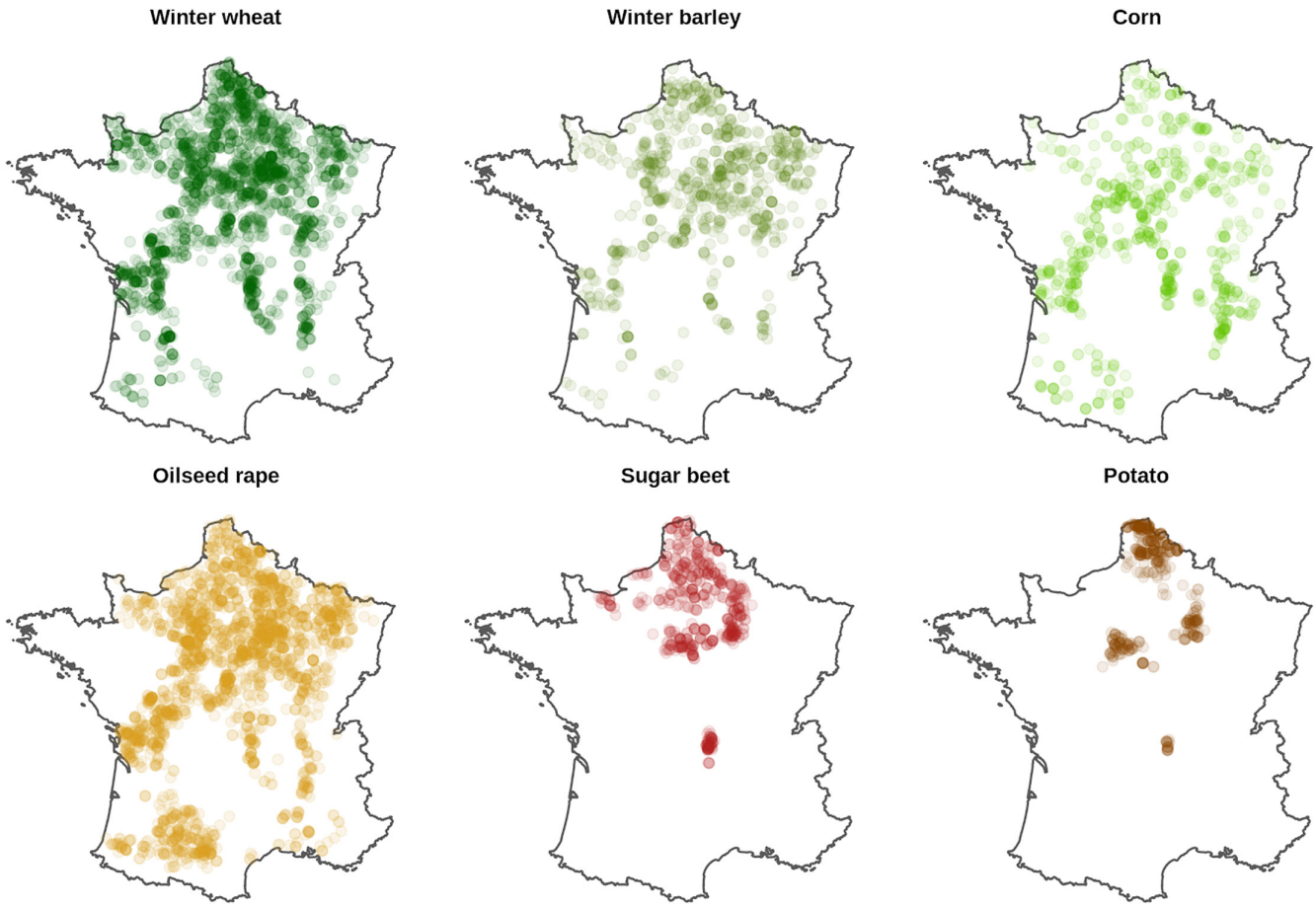

Figure 1. Spatial distribution of the monitored agricultural fields retained in the analysis for winter wheat, winter barley, corn, oilseed rape, sugar beet and potato. Each point represents an individual field surveyed any given year.

carried out bootstrapped binomial LASSO generalized linear regressions to describe the presence of pests and pathogens as a function of the landscape composition in a total of 39 880 observation series, each series corresponding to a field surveyed a given year for a given pest or pathogen (field × year × pest/pathogen) (Supporting information). In these regressions, we controlled for the effects of preceding crops on the observed field, and agroclimatic conditions. We also tested the robustness of our findings by comparing the results of alternative model specifications. Finally, we performed simple statistical tests on the results of the bootstrapped regressions to confirm the statistical significance of observed trends over pests and pathogens.

Pests and pathogens data

Since 2008, the French epidemiological services record and centralize observational data of crop pests and pathogens from arable field monitoring. In this study, we made use of two epidemiological information subsystems: Vigicultures (Sine et al. 2010) and VIGIBET (ITB – Sugar Beet Research Institute), that covered 17 of the 22 former French administrative regions including approximately two-thirds of the country over the 2009–2017 period. From these two databases, we extracted information for 30 pests or pathogens on six crops (winter wheat, winter barley, corn, oilseed rape, sugar beet, potato).

We eliminated from the data the observations for which the reported crop didn't match the crop indicated in the RPG data, considered here as the gold standard as they are tax data and have been successfully used to train automated detection of crops based on satellite imagery (Inglada et al. 2017). Depending on the crop, this could affect 5–30% of the field × year combinations in the database. Many of these observations also had little to no observations of pests or pathogens. We understand them as monitoring points entered by mistake and never really monitored.

Data from the surveys finally used in this study were structured by crop as follows: winter wheat (eight pathogens and four animal pests, 2246 fields × year), winter barley (two pathogens, 884 fields × year), maize (one insect pest, 745 fields × year), rapeseed (two pathogens and eight animal pests, 2617 fields × year), sugar beet (four pathogens, 572 fields × year) and potato (one pathogen, 411 fields × year). These crops are the top six most observed in the epidemic-surveillance database and cover 89% of the arable crop areas in France, the main missing crops being the sunflower and

the triticale, respectively 4.8% and 2.7% of the grain crops field areas in France (Agreste 2019).

Data were collected each year during the cropping season from weekly monitoring of georeferenced fields by technicians from various organizations and trained farmers (Supporting information). A different set of fields was monitored each year, freely chosen by the technicians performing the surveillance. It was requested that the fields be far enough apart to reflect the diversity of the territory for which the technicians are responsible, but practical access considerations were also taken into account. Possible issues with repeated measurements and auto-correlation in the data are discussed in the Supporting information.

All fields were conventional farming fields. The head of the observation network informed us that some observations were performed in non-treated spots but we could not account for the crop protection practices because the information was often missing in the database.

In each field, several observation types assessing the state of crop epidemics were retrieved through standardized protocols for each monitored pest and pathogen (e.g. damage severity scale on the plant for pathogens, relative or absolute organism abundance observed on the plant or in traps, amount of plants with symptoms, etc.). Not all the observation types were reported in equal numbers.

Here we kept for each organism considered only the observation type with the highest number of field × year observed to maximize the spatiotemporal extent of each pest or pathogen information. We also expected these widely used observation types to be relevant to describe the risk linked to the organisms as they are originally used to motivate pesticide applications. In total, data for 13 pests of winter wheat, corn and oilseed rape, and 17 pathogens of winter wheat, winter barley, oilseed rape, sugar beet and potatoes were analyzed. Detailed information on the pests and pathogens studied, observation periods and observation types we used can be found in the Supporting information.

Landscape composition data

The delimitation of all French agricultural fields subsidized within the framework of the European Common Agricultural Policy is provided through the 'Registre Parcellaire Graphique' (RPG). For annual crops, it is reputed to be nearly exhaustive. The geometry of the fields is described by farmers based on the aerial photographs of the BD Ortho, a departmental orthophotography of 50 cm resolution provided by the French National Institute for Geographic and Forestry Information (IGN) (Font 2018, ASP and IGN 2019). From 2006 to 2014, fields were described by islets, a group of contiguous fields, but 80% of them had only one type of crop. In each islet, the detailed areas were given by crop types (28 crop types for 329 crops registered). Here we used six of them: winter wheat, oilseed rape, winter barley, corn (including both silage and grain corn), other industrial crops (mainly and considered here to be beet) and flowering vegetables (mainly and considered here to be potatoes). From 2015 to 2017, the description of crops in the RPG was available by species (not crop type) and by field (not islet) and we used this more precise information.

The semi-natural components considered were woods, grasslands, scrublands and hedgerows. The RPG provided us with grassland delineations for the year of the observation (temporary and perennial grasslands are not distinguished here). The BD TOPO (vegetation layer ver. 2.2 2017), a vector map with a resolution of 1 m (IGN 2016) drawn from the BD ORTHO by the French National Institute for Geographic and Forestry Information, provided us with the geometry of the other components: woods, hedgerows and scrublands, considered to be stable over the studied years. From this database, we grouped as 'woodlands' the broadleaved, coniferous and mixed woodlands, with closed or open canopy.

Variables preparation and control variables

Pest and pathogen abundance measurements were not normally distributed, often rounded informally and sometimes distributed into categories. Also, the number of observations of a given pest or pathogen varied by field and year. As a result, we simplified the data into two counts per field and year: the count of observations above and under the median of the observations for all fields and years (Supporting information). For half of the organisms, only presence–absence data were available (Supporting information) we then used the counts of observations with or without the pest or pathogen among the observations of the year in a given field. In both cases (with/without or above/under median), the two counts have by construction, a binomial distribution and describe the risk of being above a threshold (presence or median), hereafter referred to as the risk.

We quantified the landscape composition by measuring the area (m^2) of semi-natural components and of the pest or pathogen host crop around each observation in buffers with radii of 200 m, 1, 5 and 10 km. As the abundance of a crop in the landscape could be correlated with its recurrence in the rotation at the field level, the field level rotation effect could be attributed by the regression models to landscape variables. To avoid such confusions we explicitly considered two crop rotation variables: the time elapsed in the observed field since 1) the host crop or 2) grassland, were cultivated. As only two years of RPG data were available before the first observations of pests and pathogens, we simplified these variables to three values: 1, 2 and 3 years or more. We discarded the points when the host crop or the grassland was not alone in the islet the last time it appeared.

To account for the potential effect of annual weather and the heterogeneity of crop management in different sub regions, we added two control variables to the pool of variables: first, a categorical variable by year and region based on a supra-regional zonation of agroclimatic conditions (Supporting information) aggregating French Départements (Lorgeou et al. 2012) and second, a sub-regional zonation of homogeneous farming systems (Supporting information), as

defined by the French technical institute for cereals Arvalis, Inst. du Végétal (Arvalis 2011).

Statistical analysis

Model fitting by LASSO and bootstrap

For each pest, we described the risk of exceeding the threshold by a generalized linear binomial model with a logit link (Guisan and Zimmermann 2000). The full model accounted for 28 variables (plus an intercept): the six landscape variables with four scales each: woods, scrublands, hedgerows, grasslands, host crop area the previous growing season and host crop area the ongoing growing season; the two field level variables: time elapsed since the host crop was cultivated in the field, time elapsed since grassland was present in the field; and two control variables: the year in a given agroclimatic region (77 levels at most) and the sub-regional homogeneous farming system units (124 levels at most). The two control variables were categorical, each level of these could count as a variable. As a result, the total number of fitted parameters, typically ranging from 100 to 200, depended on the spatial extent of pest or pathogen observations (Fig. 1). See the Supporting information for a description of the steps taken to elaborate this procedure and for a sensitivity analysis reflecting the diversity of models and variables tested.

Before the fit, as we used binomial regression with a logit link, we took the log of the variables (see the Supporting information for more details on the rationale and the impact of the transformation). Then, to allow comparison of the fitted coefficients between different parameters, we standardized them: we centered the values by removing the mean of the observations over all years and points for a given pest or pathogen and then divided them by their standard deviation. As we use linear models, this has no impact on the fitted models other than rescaling the estimated coefficients.

As the number of parameters was very large, standard linear regression could be difficult. In addition, the selection of relevant variables based on p-values is subject to multiple testing issues and has more generally been criticized by the American Statistical Association (Wasserstein and Lazar 2016), hence we relied on LASSO regressions (Tibshirani 1996) and a cross-validation procedure to select the most influential inputs. The LASSO regression selects the most relevant variables given a regularization parameter, the cross-validation procedure selects the regularization parameters parsimoniously based on the predictive ability of the model. Here, the LASSO Models were fitted by LASSO penalized regressions using the *glmnet* R package (Friedman et al. 2010). The value of the penalization factor was set conservatively by cross-validation (10 folds) keeping the prediction error within one standard deviation of the minimum standard error (lambda1se in the *glmnet* R package).

As the LASSO regression does not provide any quantification of the precision of the estimates and the selection can be inconsistent across replicates, the use of bootstrap with LASSO has been deemed essential by some authors (Bach 2008). To check the robustness of our results we hence performed a 1000 bootstrap replicates (Horowitz 2001) of the whole procedure: for each replicate and for a dataset of n observations, we selected n observations with replacement (duplicating some observations but losing others) and then as described above we evaluated the relevant penalization factor by cross-validation and retrieve the corresponding estimates. Hereafter, whenever we refer to quantiles, usually on values estimated on the replicates of the bootstrap, we refer to the default type (type 7) in the quantile function of the R 'stats' package.

Observation of tendencies in the sign and scales of correlations

To determine if there are tendencies over the spectrum of pests and pathogens, we counted the pests or pathogens whose median estimate for a variable over the bootstrap replicates is above, under or at zero (Fig. 2). For the landscape components, several scales can be selected by the LASSO for a pest or a pathogen. Here we considered the dominant scale to be the one with the largest median effect size over the bootstrap replicates. The normalization of the variables before the fit assured that the largest effect size corresponds to the largest effect on the variance of the dependent variable in the dataset. We used the coefficients of the dominant scales in the counts of positive versus negative correlations.

We used binomial two-sided tests to compare the counts of pests or pathogens negatively and positively correlated with a given landscape or field level variable. We also used binomial two-sided tests to compare the dominant scales for pests and pathogens: the numbers of correlations with dominant scale at 200 m or 1 km to the number of correlations with dominant scale at 5 km or 10 km. We did this test for all the landscape components together but also separately on host crop components and on semi-natural components.

We expected the spatial correlation with host crop areas during the previous growing season to happen on larger scales than spatial correlations with host crop areas during the ongoing growing season. We tested this hypothesis with a Fisher test on the count of correlations happening during the ongoing versus previous growing season at 200 m or 1 km versus 5 or 10 km.

We used Fisher tests throughout the interpretation of the results to evaluate the statistical significance of observed associations, for example, to test if positive correlations with landscape components are more common for pests rather than for pathogens.

We provide in the supplementary information (Supporting information) the median, 2.5% and 97.5% distribution of the counts of pests or pathogens positively, negatively or not correlated as well as the corresponding selected scales over the 1000 replicates of the bootstrap. This representation provides an alternate way to determine the statistical significance of the difference between the counts of pests or pathogens positively and negatively correlated based on the diversity in the replicates (see the Supporting information for more details).

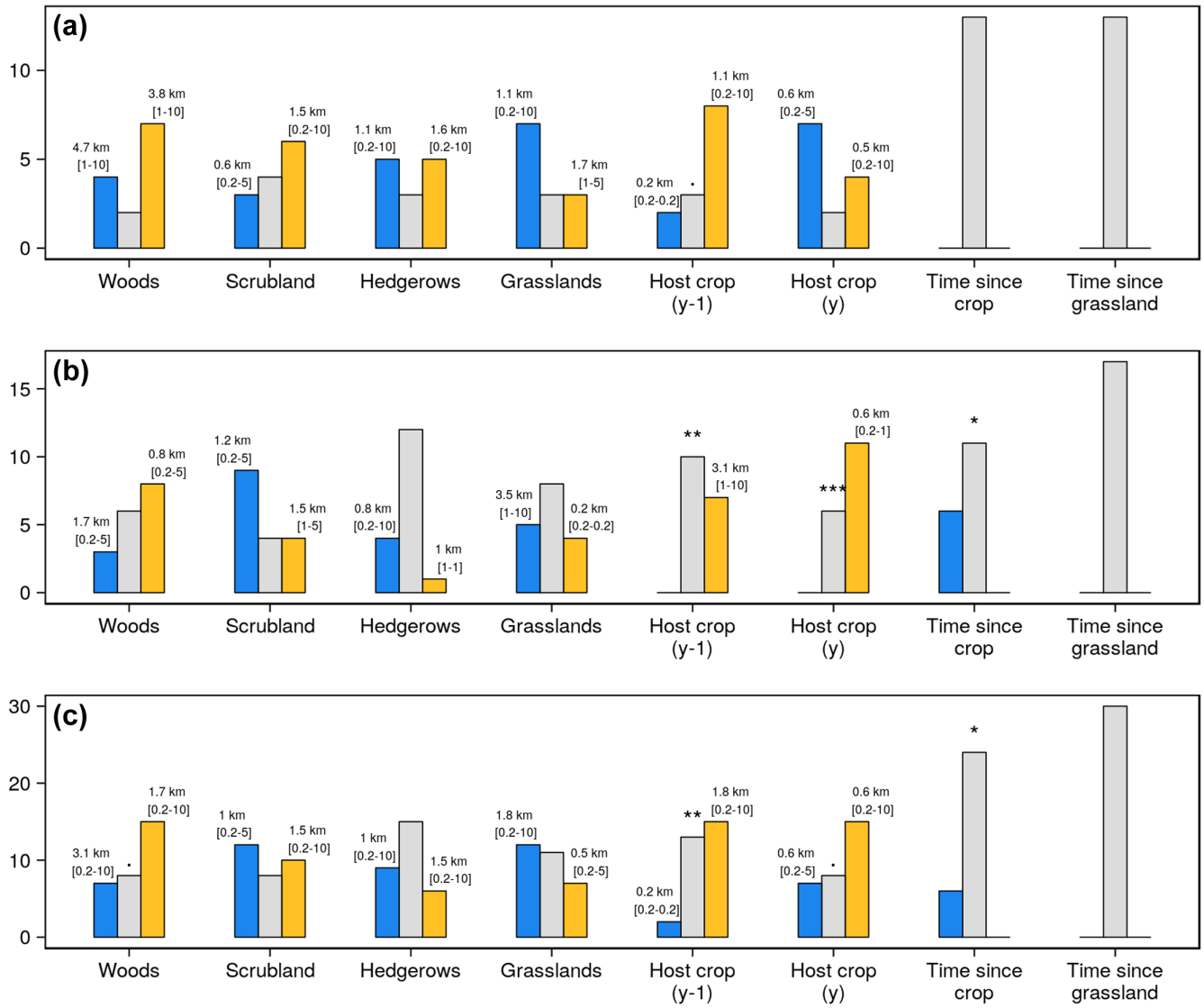

Figure 2. Number of organisms for which the risk of exceeding the abundance thresholds is correlated positively (orange), negatively (blue) and unaffected (grey) by each of the variables for (a) pests, (b) pathogens and (c) all organisms confounded (median over 1000 bootstrapped fits). Spatial variables (all but 'time since crop' and 'time since grassland') are assessed in four buffers: 200 m, 1, 5 and 10 km but only the dominant scale across replicates is accounted for. Host crop area (y) refers to the host crop area during the ongoing growing season of the observation, and (y − 1) refers to the previous growing season. Time since crop or grassland corresponds to the number of years (1, 2 or more) since the host crop or grassland was grown in the same field. The geometric average, the minimum and the maximum of the scales (buffer radii) with the highest effect size over the different organisms are indicated above the bars. p-value levels for the two-sided binomial test comparing the numbers of organisms positively and negatively correlated with a component are indicated by: '.': $p < 0.1$, '*': $p < 0.05$, '**': $p < 0.01$ and, '***': $p < 0.001$.

Individual pests or pathogens estimates

We provide in the supplementary materials the detail of the estimates for the dominant scale by pest and pathogen and by landscape or field level variable (Supporting information). For each variable, we provided the median and the quantiles 2.5% and 97.5% of the estimate (which might be corresponding to different scales of a landscape component for the different replicates). These variation intervals allowed us to distinguish components with a consistent positive or negative correlation with the pest or pathogen, but should not be understood as classical 'confidence intervals' of such estimates would anyway be problematic in a bootstrap of LASSO models (Chatterjee and Lahiri 2011). We distinguished four levels of evidence for a direction of the correlation: No support (null median of the estimates over the replicates), weak support (median not null but 95% variation interval including both positive and negative values), support for a direction of the correlation (median not null and 95% variation interval including zero but otherwise only positive or only negative), and strong support for a direction of the

correlation (95% variation interval strictly positive or strictly negative). Readers focusing on the results at the level of individual pests or pathogens should probably focus on the highest level of evidence. The median, 2.5% and 97.5% quantiles of the scales selected for each landscape component are also provided when the median estimate is not null.

Comparisons of effect sizes between explanatory variables

To compare effect sizes between landscape variables and with other variables, we calculated the standard deviations generated, according to the model, by variables or groups of variables. For each pest or pathogen, we first set the non-assessed variables to their mean over the observations. Second, we used the median of the coefficients, including the intercept, over all the bootstrap replicates to predict the risk with these transformed observations. Finally, we represented the standard deviation of these predictions over all the observations of the pest or pathogen. This allowed us not only to look at the strength of the estimate for a given variable but also at the strength of groups of variables, e.g. four scales of a landscape component, accounting for the possible correlations between variables.

Results

General observations

The variable selection left only 1 (*Helminthosporium* spp. on wheat) of the 30 considered organisms without any perceptible influence from a landscape component (median of the estimates over 1000 bootstrap replicates different from 0). The correlations with the landscape components are dependent on the pest or pathogen. The detail of the estimates for the scales with the most impact for each pest and pathogen is given in supplementary information (Supporting information).

When looking at the counts of pests or pathogens with at least weak support for correlation with each landscape or field level variable (Fig. 2) we noted that all landscape components were correlated with several pests, often in opposite ways. This highlighted the relevance of considering the impact of landscape composition over a large range of pests and pathogens.

In Fig. 2, we counted pests as correlated with a landscape feature when the median of the LASSO estimate over the bootstrap replicates is different from 0. In the supplementary materials, details are given by pest or pathogen on the distribution of the estimates over the bootstrap replicates (Supporting information). Using more stringent criteria to consider a pest correlated with a landscape feature (e.g. 95% of replicates with an estimate of the same sign) reduces quantitatively but not qualitatively the tendencies commented hereafter (Supporting information). These tendencies are also confirmed by the significance of the difference between the numbers of positively and negatively correlated pests over the bootstrap replicates (Supporting information).

We also found coherent results between models with different specifications (Supporting information). The detection of most landscape effects on pests and pathogens was only possible when climatic variability was accounted for (see Supporting information).

Directions and scales for the correlations in pest and pathogens models

To assess the coherence of the landscape composition impact over the pool of organisms studied, we compared the number of organisms positively and negatively impacted by each landscape component (Fig. 2).

Correlations with the host crops in the landscape

The risk of being above the abundance thresholds tended to be correlated with the host crop area the previous growing season for pests and pathogens together (two-sided binomial test: 15 to 2, $p < 0.01$, Fig. 2c) and to a lesser extent separately (two-sided binomial tests for pests: 8 to 2, test: $p = 0.11$, Fig. 2a; and pathogens 7 to 0, $p = 0.016$, Fig. 2b). For half of the organisms (Fig. 2c), epidemics were more likely to occur if the host crop was largely represented in the surrounding landscape the previous growing season. Two animal pests (*Sitobion avenae* and *Brevicoryne brassicae*) were nevertheless negatively correlated with the area of their host crop in the immediate neighborhood (200 m) during the previous growing season.

Host crop areas during the ongoing growing season showed contrasting results between pathogens, generally positively correlated (11 positively to 0 negatively, binomial test: $p < 0.001$, six not correlated Fig. 2b) and pests, often negatively correlated (7 to 4, binomial test: $p = 0.55$, Fig. 2a). This resulted in a statistically significant difference between pests and pathogens regarding the effect direction (Fisher test on pests less associated than pathogens with the host crop in the landscape the ongoing growing season OR = 0 [0, 0.42], $p = 0.004$). The selected distances for correlation of pests and pathogens with the host crops areas (ongoing or previous year) were smaller than expected by chance for pathogens (binomial test: 78% [0.52, 0.94] of the correlations at 200 m or 1 km, $p = 0.03$) and for pests (binomial test: 86% [0.64, 0.97], $p = 0.0015$), suggesting that underlying causal mechanisms usually play out at fairly local scales (< 5 km).

The average distance at which pathogens were most correlated with the host crop area was larger for the previous growing season (3.1 km range across pathogens from 1 to 10 km, 3 at 1 km, 4 at 5 or 10 km, Fig. 2b and Supporting information) than for the ongoing growing season (0.6 km range 0.2–1 km, 11 at 200 m or 1 km, none above, Fig. 2b and Supporting information); the corresponding Fisher test associating scales 200 m and 1 km with the host crop the ongoing growing season in contrast with distances 5 km and 10 km associated with the host crop the previous growing season yields (OR = 0 [0–0.71], $p = 0.012$). Such a difference was not observed for pests (Fisher test: OR = 1.94 [0.09, 130.77]) very local for both years, reinforcing the contrast between pathogens and pests in their response to the host crop areas in the landscape.

The six coleopteran tested (*Psylliodes chrysocephala*, *Phyllotreta nemorum*, *Ceutorhynchus picitarsis*, *Ceutorhynchus assimilis*, *Ceuthorhynchus napi* and *Meligethes aeneus*) which are univoltine species, were negatively correlated with the host crop area during the ongoing growing season. On the other hand, only one (*Brevicoryne brassicae*) of the four aphid species, also multivoltines, was negatively correlated with the host crop area during the ongoing growing season, one was positively correlated (*Rhopalosiphum padi*, also with short distances selected) and the other two were not correlated (*Sitobion avenae* and *Myzus persicae*). See Supporting information for the estimates and the detail of the pests and pathogens tested.

Correlations with the field level rotation

The time elapsed since the host crop was cultivated on the observed field consistently reduced the risk only for pathogens (binomial test: 6 to 0, $p = 0.03$, Fig. 2b). None of the organisms were affected by the time elapsed since grassland was present in the field. Overall, the variables related to the field level rotation were selected strikingly less often than the variables related to the host crop in the landscape. This was particularly true for pests (0 to 21, two-sided binomial test $p = 9.5e\text{-}7$), less for pathogens (18 to 6, two-sided binomial test, $p = 0.023$). Nevertheless, one should keep in mind that the four scales tested by landscape level variables increased the probability of selecting landscape level variables compared to the field level variables. The link between the six pathogens (*Oculimacula* spp., *Sclerotinia sclerotiorum*, *Gaeumannomyces graminis*, *Helminthosporium* on wheat, *Uromyces betae* and *Puccinia striiformis*) and the time elapsed since the host crop was cultivated in the same field should then be deemed very strong.

Correlations with semi-natural components

The area of semi-natural components in the agricultural landscape was very often correlated with the risk (Fig. 2c). At least one semi-natural component was selected by the bootstrapped LASSO procedure for all organisms but Helminthosporium on wheat with comparatively more relationships for pests (40 with, 12 without) than for pathogens (38 with, 30 without; Fisher test: $OR = 2.6$ [1.1, 6.5], $p = 0.021$). No trends emerged in the direction of these relationships other than a possible tendency of woods to increase the risk (15 to 7, two-sided binomial test: $p = 0.134$), a tendency more strongly supported by the test based on the bootstrap replicates (Supporting information) but that is reversed when not using the log of the areas in the models (Supporting information).

In contrast with distances selected for correlations with the host crop areas in the landscape, the correlations with semi-natural habitats were not significantly smaller than expected by chance both for pests (55% [0.38, 0.71], $p = 0.63$ of distances under 5 km, when it was 86% [0.64, 0.97] for crops) or for pathogens (66% [0.49, 0.8], $p = 0.07$ compared to 78% [0.52, 0.94] for crops).

Strength of the relationship between landscape components and organisms abundance

To compare the variations of the risk induced by the different variables according to the model, we looked for each pest or pathogen at the standard deviation of the predictions when setting all other variables than the ones of interest to their mean over the observations (Fig. 3, 4). The generated standard deviations were visually more variable between pests and pathogens for a given landscape component than between landscape components. The area of the host crop during the previous growing season and the area of woodlands had the most impact across the spectrum of organisms. The host crop during the ongoing growing season and the grassland area followed. Finally the hedgerows and scrublands induced only about half the generated standard deviation of the host crops during the previous growing season. The time elapsed since the host crop was cultivated in the observed field has the same average effect over the studied organisms as the scrubland area in the landscape. Though, for the small number of organisms impacted, the generated standard variations were comparable to the ones of woods or of the host crop during the previous growing season.

The risk diversity generated by the semi-natural components together (Fig. 3, SNH) was greater but comparable to the diversity generated by the host crop, whether accounting only for the host crop in the landscape or also accounting for the proximity of the host crop in the field rotation. Together, the landscape variables generated a diversity of risk larger but still comparable to the diversity generated by semi-natural habitats or the host crop alone. This indicates partial compensations between different correlated landscape factors.

We also compared the standard deviation generated by all the landscape components of the model to other types of variables and to the standard deviation in the data (Fig. 4). The average standard deviation generated by the landscape components in the model was about a tenth of the average standard deviation in the data, a third of the standard deviation generated by the full model and less than half the standard deviation generated by the Year-Region factor, the different years in a region, the different regions a given year or the farming system sub-regions. Our models in general explained only a fraction of the variability in the observations and the landscape variables explained only a small fraction of the variability explained by the models.

Discussion

Importance of the host crop in the landscape

The area allocated to the crop susceptible to a pest or pathogen in the year preceding the observation is the studied landscape component that had the most consistent impact across the spectrum of studied pests and pathogens. On average, it also had the strongest impact on pests and pathogens presence variability.

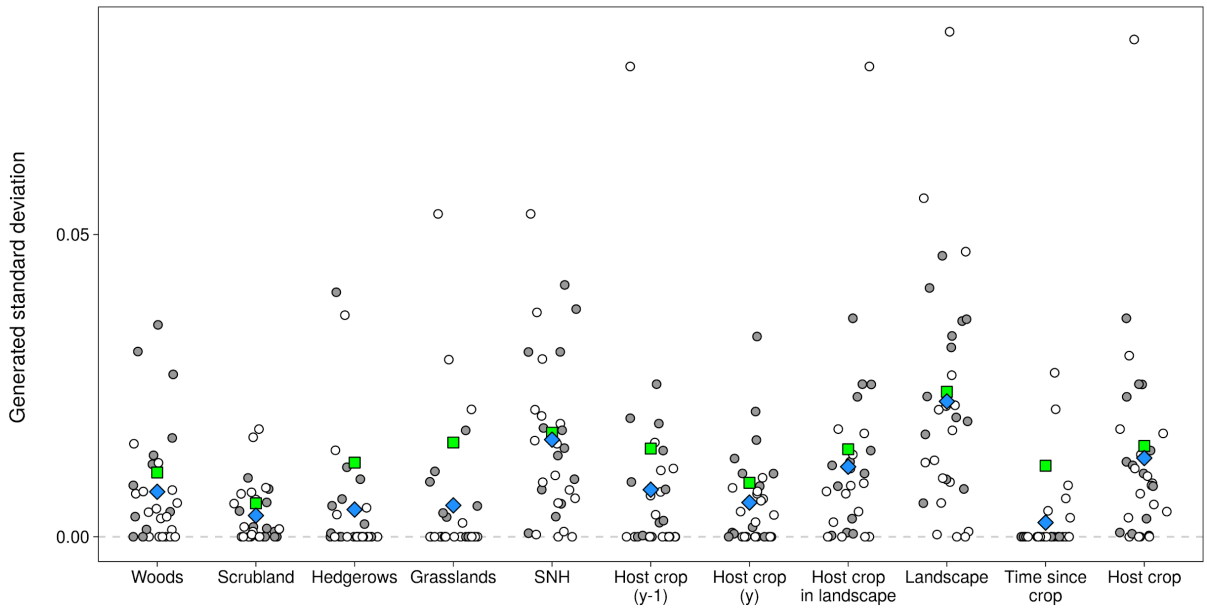

Figure 3. Standard deviation generated by landscape and field level groups of variables according to the fitted model. For each pest (grey dot, n = 13) and pathogen (white dot, n = 17), the standard deviation generated by a variable or group of variables corresponds to the standard deviation of the infestation predicted for the data by the fitted model when setting all other variables to their average value. When assessing the standard deviation generated by a landscape feature, all corresponding scales are kept to their original values. Blue diamonds are the means over all pests and pathogens. Green squares are the means over all pests and pathogens with generated standard deviations not null. Host crop: the area of the host crop of the organism during the same growing season as the observation (y) or the previous growing season (y − 1) or both variables (in landscape), time in years since the host crop was cultivated in the field of the observation (time since) or all three variables (y, y − 1 and time) if not specified. SNH: all the semi-natural habitats (woods, scrubland, hedgerows and grasslands) together. Landscape: All the SNH and host crops in the landscape variables. The x coordinates within each class are jittered for easier reading. The effect of grassland in the field rotation is always null and not represented here.

The dominant and positive effect of the host crop in the landscape the previous growing season suggests that, at the scale of the landscape, there is bottom–up control by the resource – here specifically by the host crop, a substrate for pathogens and often both food and habitat for animal pests. More specifically, it suggests a dominance of bottom–up control over top–down control for herbivores of arable crops, contrary to what has been observed more generally for herbivores (Vidal and Murphy 2018). Nevertheless, two aphids (*Sitobion avenae* and *Brevicoryne brassicae*) were negatively correlated with the host crop area during the previous growing season. This could be interpreted as an occasional top–down regulation by previously attracted natural enemies, particularly as the dominant scale of this negative correlation was very small (200 m). The clear and consistent response of animal pests to the host crop the previous growing season may seem contradictory with the absence of consistent response to the area of cultivated crops in the landscape in former studies (Veres et al. 2013, Karp et al. 2018), nevertheless, such studies did not usually account for the area of the host crop specifically nor did they usually differentiate the year before the observation and the year of the observation. The presence of the animal pests tended to be negatively correlated with the host crop area during the ongoing growing season while the opposite was observed for pathogens. This contrast may be explained by two mechanisms. First, pests can be active in their dispersal, enabling them to cluster in the fields of their host crop (Thies et al. 2008). Second, some pests only perform one life cycle per growing season, preventing epidemic propagation within the growing season (Jourdheuil 1960, Eickermann et al. 2014). Here the univoltine coleoptera species were negatively correlated with the host crop area in the landscape in a given year, suggesting dilution in the resource (Scheiner and Martin 2020). This dilution was less clear or there might even be concentration for the multivoltine aphids, and the pests with an uncertain number of cycles per year: the slugs and the European corn borer *Ostrinia nubilalis*. Such modulations of the abundance by concentration and dilution mechanisms are also characteristic of a bottom–up control of the pests (Root 1973, Grez and González 1995). It is also strikingly similar to an independent study on a complex of pests of cabbage, showing a dilution effect of areas of the host crop on coleopteran and lepidopteran leaf-chewing insects while aphids were not affected (Scheiner and Martin 2020). The orange wheat blossom midge *Sitodiplosis mosellana* might be the main exception to this bottom–up control of the pest by the host crop in our study as it is univoltine and nevertheless positively correlated with the host crop area during the ongoing growing season.

Pathogens cannot be diluted in the resource as they only rely on passive dispersal and are often multivoltine, allowing epidemic propagation facilitated by the abundance of the

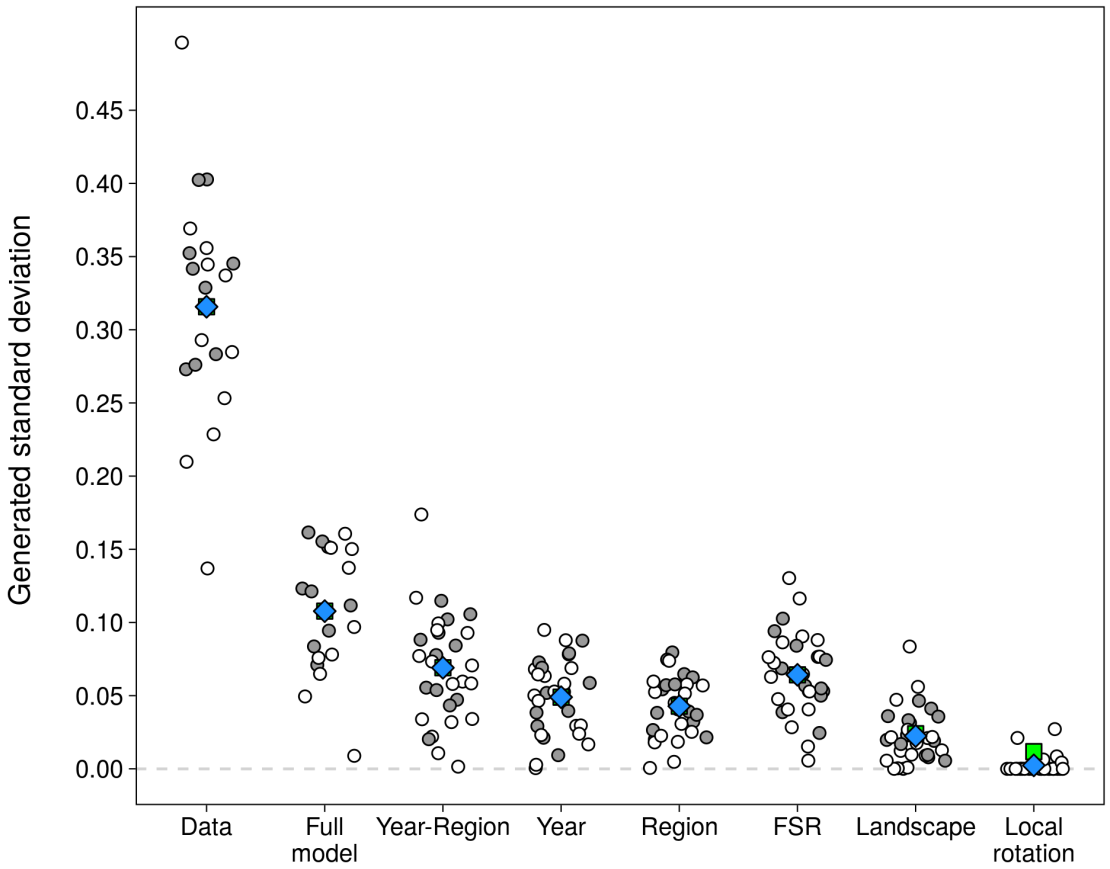

Figure 4. Standard deviation generated by different types of variables according to the fitted model. For each pest (grey dot, n = 13) and pathogen (white dot, n = 17), the standard deviation generated by a type of variable corresponds to the standard deviation of the infestation predicted for the data by the fitted model when setting all other variables to their average value. When assessing the standard deviation generated by the landscape variables, all corresponding scales are kept to their original values. Blue points are the mean standard deviations over all pests and pathogens. Green squares were the means over all pests and pathogens with generated standard deviation not null. Data: standard deviation in the observed rate of observations above the threshold. Full Model: standard deviation in the prediction of the full models. Year–Region: uses all the Year × Region factor levels. Year: uses a transformation of the Year × Region coefficients to focus on the effect of the year: in each agroclimatic region, we took the predicted standard deviation of the Year × Region factor over the years then we averaged over the regions before taking the standard deviation. Region: focus on the effect of the agroclimatic region doing the reverse of the Year transform. FSR: Farming system region, uses all factor levels corresponding to the farming system regions. Landscape: uses all the SNH and host crop variables (same as in Fig. 3 for the sake of comparability). Local rotation: uses the time since the host crop was cultivated in the same field and the time since grassland was cultivated in the same field.

resource during the ongoing growing season. When correlated with the host crop area during the ongoing growing season, the correlation was always positive. This correlation occurred at smaller scales on average than the correlations with the host crop during the previous growing season. This was not observed for the pests, mostly correlated at short distances with the host crop both during the ongoing and the previous growing season.

As pathogens propagate in space with time, their correlation with the host crop during the previous growing season was expected to be maximal for larger distances than for the host crop during the current growing season. It came more as a surprise that the correlation of pests with the host crop area was maximal at the same distance for the current and the former growing seasons. However, the correlations of the pests with the crop area of the current growing season, was negative and not positive like for pathogens. This would in particular be expected for a pest population coming directly, without reproduction or overwintering in a distant habitat, from crop fields of the former growing season and diluting in the crop fields of the current growing season. In this case, it is the same colonization event, hence over the same distance, which leads to positive correlation with crop areas during the former growing season and negative correlation with the host crop during the current growing season. The focus on landscapes within 2 km in former studies on the influence of landscapes on animal pests (Bianchi et al. 2006, Karp et al. 2018, Scheiner and Martin 2020) seems justified by the dominance of small scales for animal pests. This might not be enough though to correctly account for the effect of

semi-natural habitats on pests or pathogens nor to account for the impact on the host crop during the previous growing season on pathogens.

Despite the complexity of the systems studied, the main trends that emerged were easily understandable and are probably applicable to other pests and pathogens of annual crops accounting for the nature of the pest or pathogen and their life cycle. Our study also makes it possible to propose hypotheses to be explored on the life cycles of poorly known pests and pathogens, particularly on the role of semi-natural spaces that may shelter part of the cycle. For example, *Ceuthorhynchus assimilis* and *C. picitarsis* are positively correlated with the presence of woods, in a similar way to *M. aeneus*, another coleopteran for which such a relationship is well-known due to its need to overwinter in the leaf litter inducing a clear spatial dependency to the proximity of woods (Rusch et al. 2012, Juhel et al. 2017).

Our results should not be extrapolated too quickly to perennial crops as the areas of the host crops are largely stable over the years. The opposite effects of the host crop's area during the previous and during the ongoing growing season make the sign of the net effect of the crop area on the pests unpredictable. This is all the more so as the stability of the resource favors the development of natural enemies if they are not massively eliminated by insecticides (Lechenet et al. 2017). Nevertheless, pathogen dynamics, influenced in the same direction by crop area in the previous and current growing seasons, should generally be enhanced in perennial crops with increasing host crop area.

Semi-natural habitats are not a universal solution against pests

The importance of the correlation with the host crop component in the landscape calls into question the emphasis placed on the importance of semi-natural habitats as a source of regulation for the control of pests and pathogens at the landscape level (Bianchi et al. 2006, Tscharntke et al. 2016, Karp et al. 2018, Martin et al. 2019, Yang et al. 2019, Tamburini et al. 2020b). The semi-natural components were often correlated or anti-correlated with the risk but without a consistent trend across pests and pathogens. This observation already made on animal pests (Veres et al. 2013, Tscharntke et al. 2016, Karp et al. 2018, Yang et al. 2019) was here extended to pathogens. Theoretical research on pathogens showed that these areas can serve as barriers but can also present wild hosts facilitating transmission (Plantegenest et al. 2007, Ratnadass et al. 2012). For pests, some reviews have suggested an increased presence of the natural enemies with semi-natural habitats (Bianchi et al. 2006, Rusch et al. 2016, Tscharntke et al. 2016) though a more recent meta-analysis did not find such an effect with semi-natural areas but only with edge densities (Martin et al. 2019). In any case our results, as well as the most recent research (Karp et al. 2018, Martin et al. 2019, Yang et al. 2019), suggested that semi-natural components could be just as much a needed resource for pests as for their natural enemies. The result may highly depend on species functional traits (Martin et al. 2019, Tamburini et al. 2020a) but our results suggest that semi-natural elements should not a priori be considered as a protection of crops against pests and pathogens. In addition, the variability induced by semi-natural habitats, alone or together, is limited compared to the variability induced by the host crop alone. Given the relative stability of the semi-natural components considered and the low and inconsistent impact they have across the spectrum of pests and pathogens, it would seem reasonable, at the landscape scale, to focus on the management of the host crop.

The impact of the landscape is limited but may be underestimated

The consistency of the response of pests and pathogens to landscape composition could be used to limit the impact of pests and pathogens on arable crops. In the current state of agriculture in France, the landscape components seemed on average to have more impact on the variability of the studied pests and pathogens than field level crop rotation. Nevertheless, the risk variations induced by the landscape seemed on average sizably smaller than those induced by weather conditions (year and regional effects) or the farming system sub-regions. These control variables might nevertheless not be exempt from landscape effects as they may account for aspects of the landscape not accounted for in our analysis like field margins.

The estimated effect sizes were likely suboptimal as the data were heterogeneous (quality of the positioning, multiplicity of the experimenters) and the models were simple (neither interactions nor non-linear effects). In particular, though we scanned the data for inconsistencies, some localization errors might remain in the dataset, limiting the ability to assign the observed variability in pest presence to landscape components. As a consequence the real impact of the landscape on the pests might be underestimated here. Lack of statistical power might prevent us from observing some correlations for the pests and pathogens of the less abundant crops (beet and potato), particularly affecting the selection of lower importance landscape-related variables. Weather conditions might also have reduced the abundances during the studied period below thresholds where correlations with the landscape could be observed. Finally, the generalized use of pesticides in France as in many developed countries (Lechenet et al. 2017) might further mask correlations and even modulate the equilibrium between pests and natural enemies.

Limitations

The causality of the observed correlation was not explicitly addressed in our study. In particular, even if the correlations were causally related to the dispersal, it might be due not only to intrinsic dispersal capacity but also to passive dispersal by anthropic activities (Aubertot and Robin 2013). Partially repeated measurements and autocorrelation in the data might

have reduced the effective sample size of our data (Supporting information). We believe that the uncommonly large size of our dataset and the robustness of our results to alternate specifications of the models (Supporting information) make our qualitative results fairly immune to such potential issues.

Despite the cross-validation strategy adopted (Friedman et al. 2010), the number of tested features increased the risk of selection of spurious correlation or at least errors in the selection of the most correlated spatial scales for any of the 30 individual organisms. We have therefore focused on interpreting significant trends across organisms, rather than organism specific correlations (Fig. 2, 3) and the results by pest or pathogen (Supporting information) should be interpreted with care, especially regarding the absence of an effect.

A species level analysis could benefit from a better consideration of organism functional traits. In particular, one might consider the diversity of host crops of generalists such as *Rhopalosiphum padi* here observed on wheat but a pest of most cereals (Chiverton 1987, Dong et al. 2020). More advanced models could on one hand improve the description of the landscape by considering interactions between landscape components as well as their configuration (Martin et al. 2019, Haan et al. 2020). The lack of information on other landscape components, in particular flower strips, prevented us from accounting for these features though they might play an important role in pest regulations (Albrecht et al. 2020).

Implications for arable crop management

Could the trends we identified be used to reason the protection of arable crops at the landscape level? Early warning tools based on this approach may modulate risk estimates at the field level and thus limit the systematic use of preventive treatments (Lacasella et al. 2017). As for active landscape design, the management of host plant areas seems both the most influential and the easiest aspect to handle (Schneider et al. 2015). The first operational answer could be to diversify the crops to make them less recurrent in space and time. This is difficult as it requires a modification of the entire storage and downstream processing chain (Meynard et al. 2018) but it would also benefit biodiversity in the agroecosystems (Sirami et al. 2019). Beyond increasing the diversity of cultivated crops in the landscape, a rising pest or pathogen pressure on a crop might be answered by excluding the crop during a growing season over a large area (several kilometers of diameter). Such dynamic recommendations of a 'blank' year without a specific crop should not be confused with landscape-scale rotations on all crops that could have catastrophic effects on non-pest biodiversity (Rusch et al. 2016). Organizing at such scales all the stakeholders who often mismatch in terms of objectives and perceptions regarding potential benefits of ecosystem services (Kleijn et al. 2019) is a demanding challenge but not without precedent. Taking it up could for example benefit from the experience gained in watershed supply management to improve the quality of drinking water (Grolleau and McCann 2012, Hellec et al. 2013).

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Author contributions

Thomas Delaune: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Software (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (supporting). **Malick S. Ouattara**: Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Remy Ballot**: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal). **Christophe Sausse**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Project administration (supporting); Resources (equal); Supervision (supporting); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Irène Felix**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Fabienne Maupas**: Conceptualization (supporting); Investigation (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (supporting). **Mathilde Chen**: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Investigation (equal); Software (equal); Writing – original draft (supporting). **Muriel Morison**: Conceptualization (equal); Funding acquisition (supporting); Investigation (supporting); Project administration (supporting); Supervision (supporting); Validation (supporting). **David Makowski**: Conceptualization (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Supervision (supporting); Validation (supporting); Writing – original

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Data availability statement

Data used for the modeling is available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.w3r2280r5> (Barbu et al. 2021).

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