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Species traits elucidate crop pest response to landscape composition: a global analysis

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Recent synthesis studies have shown inconsistent responses of crop pests to landscape composition, imposing a fundamental limit to our capacity to design sustainable crop protection strategies to reduce yield losses caused by insect pests. Using a global dataset composed of 5242 observations encompassing 48 agricultural pest species and 26 crop species, we tested the role of pest traits (exotic status, host breadth and habitat breadth) and environmental context (crop type, range in landscape gradient and climate) in modifying the pest response to increasing semi-natural habitats in the surrounding landscape. For natives, increasing semi-natural habitats decreased the abundance of pests that exploit only crop habitats or that are highly polyphagous. On the contrary, populations of exotic pests increased with an increasing cover of semi-natural habitats. These effects might be related to changes in host plants and other resources across the landscapes and/or to modified top-down control by natural enemies. The range of the landscape gradient explored and climate did not affect pests, while crop type modified the response of pests to landscape composition. Although species traits and environmental context helped in explaining some of the variability in pest response to landscape composition, the observed large interspecific differences suggest that a portfolio of strategies must be considered and implemented for the effective control of rapidly changing communities of crop pests in agroecosystems.

1. Introduction

The intensive use of agrochemicals to control crop pests in modern agricultural systems has dramatically impacted the environment, representing a risk for human health worldwide [1,2]. Effective and environmentally friendly crop protection strategies are urgently needed to meet global food demands while limiting the negative effects of agriculture on biodiversity. For over two decades, ecologists have encouraged the maintenance and restoration of semi-natural habitats surrounding crop fields to enhance biological control of pests and reduce the need for pesticides [3,4]. Landscapes rich in semi-natural habitats are generally expected to boost

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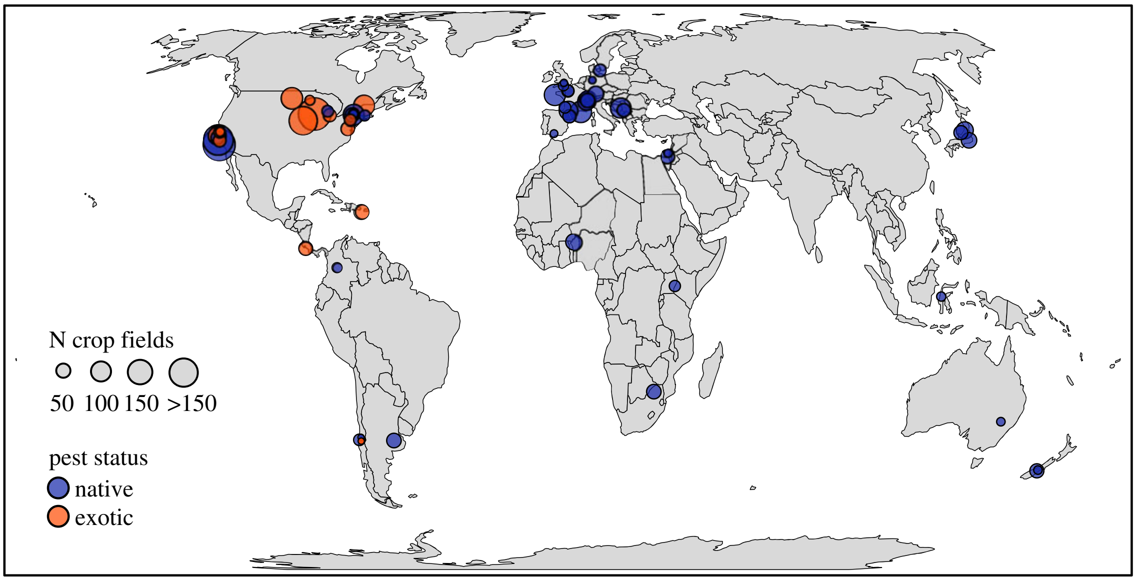

Figure 1. Map showing the location and the sample size (number of crop fields sampled) of the 59 studies included in the dataset (further details of studies are given in electronic supplementary material, appendix S1). (Online version in colour.)

natural enemy populations by providing supplemental food resources, shelter and overwintering sites [5,6]. For example, high edge density has been shown to support abundant natural enemy communities and to improve pest control across European landscapes [7]. Nevertheless, recent global syntheses have highlighted inconsistent responses of both natural enemies and pests to landscape complexity [8–10], imposing a fundamental limit to our capacity to plan sustainable crop protection strategies to reduce yield losses to insect pests. Species-specific characteristics (i.e. species traits), such as diet and habitat requirements or exotic status, shape organisms' response to environmental predictors [7,11]. However, whether species traits can shed light on the mechanisms driving pest responses to landscape composition remains largely unknown.

Semi-natural habitats can positively affect pest populations by providing important resources such as alternative hosts, food, shelter and overwintering sites [12–15]. Pest species able to feed on a broad range of host plants and that can use resources in non-crop habitats during their life cycle are expected to be even favoured by semi-natural habitats because of the abundant resources and nesting opportunities [16]. For instance, the cotton bollworm (*Helicoverpa armigera*) or the spotted wing drosophila (*Drosophila suzukii*) are generalist pests that appear to thrive in semi-natural habitats [17,18]. On the contrary, crop specialists that complete their life cycle within fields such as the coffee berry borer (*Hypothenemus hampei*) and the western corn rootworm (*Diabrotica virgifera*) mainly depend on local habitat quality and host availability across the landscape [7,19]. The positive effect of semi-natural habitats on biocontrol is hence expected to be stronger for crop specialists than for more generalist pests.

Semi-natural habitats are also expected to contribute to pest control by favouring natural enemy populations [3,20]. However, pest populations are not always regulated by natural enemies, even when enemies are abundant across the landscape [15]. In particular, the exponential increase of international trade has facilitated the spread of crop pests around the globe [21,22]. The success of exotic pests (i.e. pest species introduced from another continent) in their introduced range is often warranted by the abundance of host plants, reduced competition for resources and absence of co-evolved enemies that regulate their population dynamics in the native range [23]. Controlling exotic insects through landscape management might be challenging due to their often-unknown use of and response to semi-natural habitats, considering the lack of their specialist natural enemies in the newly invaded territories [24,25]. Even though native predators and generalist parasitoids may shift their diet towards exotics [26], outcomes are unpredictable and may be insufficient to provide satisfactory pest control [27]. Therefore, the positive effect of semi-natural habitats on biocontrol is expected to be stronger for native than for exotic pests.

Here, we used a global dataset composed of 59 studies encompassing 4550 agricultural landscapes (figure 1), 48 insect pest species of economic importance and 26 crop species [10] to test whether pest response to landscape composition is driven by species traits. We hypothesized that increasing surrounding semi-natural habitats would benefit (i) exotic over native crop pests (trait: exotic status), (ii) pests that feed on a broader number of host plants over host specialists (trait: host breadth) and (iii) habitat generalist pests that use semi-natural habitats for shelter, nesting or overwintering sites over crop specialists (trait: habitat breadth). We also considered the environmental context, including in our analysis a set of variables that could have affected pest response to semi-natural habitats such as crop type, the range of the landscape gradient explored in each study and climatic region. The results will elucidate key factors that modify pest response to landscape composition, and, by doing so, help explain the large variability in pest responses to landscape composition reported in previous studies [10–12].

2. Methods

(a) Pest dataset

To test the effects of species traits on pest responses to landscape composition, we used the publicly available dataset published by Karp *et al.* [10]. This dataset represents the largest collection to date of studies measuring pest abundance in crop fields across landscapes of varying composition. The original dataset was composed by studies that included pest control observations collected in at least five distinct sampling locations, all within crop fields and across a gradient of surrounding landscape composition. Information on species taxonomy, sampling dates, sampling methods (pan trap, pitfall trap, sweep net, etc.), and the number and duration of censuses were collected for each study. Sampled organisms were classified by data contributors as a dominant (economically damaging) pest, secondary pest, predator or parasitoid. Data from sampling methods that contributed less than 5% of the total observations (across sampling methods) were discarded, since some sampling methods are ineffective for particular taxa (e.g. sticky traps for epigeal predators).

For the present study, we selected only the studies in which dominant pest species were considered, pest abundance was estimated, and pests were identified to species. We obtained 59 studies for a total of 48 pest species (figure 1; electronic supplementary material, table S1, appendix S1). The majority of studies were performed in Europe (21 studies) and North America (20 studies), with six in Asia, four in South America, two in Central America, three in Africa, and three in Oceania. Twenty-six crop species were investigated. The most studied crop species were wheat (*Triticum aestivum*, 12 studies) and soya bean (*Glycine max*, six studies). Other important crops worldwide were present in our dataset such as corn (*Zea mays*, four studies), cotton (*Gossypium* sp., four studies), oilseed rape (*Brassica napus*, three studies) and rice (*Oryza sativa*, three studies). In 69% of the studies, pests were sampled in more than 20 focal crop fields (min = 6, max = 2110, mean = 77.1, s.d. = 280.1) selected along gradients in semi-natural habitats. The maximum number of dominant pest species recorded in one study was five (two studies), whereas the focus in 81% studies was on one pest species. The majority of pest species belonged to the order of Hemiptera (19 species) and Lepidoptera (14 species) followed by Coleoptera (7), Diptera (6), Heteroptera (1) and Hymenoptera (1). The English grain aphid (*Sitobion avenae*) and the soybean aphid (*Aphis glycines*) were the most frequently studied pests (seven and five studies, respectively), whereas the majority of pest species (31 species) were present in one study only. If multiple measures within 1 year were included in a study, we summed the pest abundance per site and per year. We then divided this value by the number of sampling rounds to standardize the sampling effort. If the study included a paired experimental design (pairs of fields sampled within each study site in order to test the effects of local factors; five studies), we averaged the pest abundance for each site. We thereby reduced the number of observations from 13 865 to 5242. Pest abundance was first log-transformed to abide by model assumptions (normality and homoscedasticity) and then standardized within each study (mean = 0, s.d. = 1) to increase comparability across studies [10]. When the study was carried out for more than 1 year and/or multiple sampling methods (e.g. both funnel and sticky traps), we standardized the log-transformed pest abundances within the year and sampling method.

(b) Pest traits

Each pest species was classified according to three traits expected to influence pest responses to landscape composition: exotic status, host breadth and habitat breadth (electronic supplementary material, table S1). We defined traits for all pest species according to the available literature and specialized online datasets (electronic supplementary material, table S1; see electronic supplementary material figure S1 for publication selection procedure). First, we determined whether pest species were exotic or native in the sampled region (exotic status, categorical). We considered as exotic the species introduced from another continent. This trait may dictate pests' interactions with potential native, coevolved competitors for resources and natural enemies. We acknowledge that this classification overlooks important characteristics such as species cosmopolitanism and time from the first introduction. However, the small number of exotic species present in our dataset did not allow further hypotheses to be tested within the category. Second, we derived the number of host plant families that each species can feed on (host breadth, numeric). Third, we categorized pest species according to the types of habitats they exploit during their whole life cycle for shelter, nesting opportunities and overwintering (habitat breadth, categorical). Crop specialists were dependent exclusively on crop habitats, whereas habitat generalists were able to use both crop and non-crop habitats. Host and habitat breadth traits are related to pests' ability and/or need to access resources provided by semi-natural habitats. Dispersal ability is another trait expected to modify pest responses to landscape composition and it is often considered in studies regarding natural enemies [7]. However, dispersal information was seldom available for crop pest species, and it was therefore not considered.

Forty insect species in our dataset were classified as native pests (46 studies, 2551 observations), 19 of which were crop specialists and 21 habitat generalists. Host breadth of native pests spanned from one to 55 host plant families (mean = 11.7, s.d. = 13.9). The remaining eight species were exotic pests (15 studies, 2691 observations), three of which were crop specialists and five habitat generalists. Host breadth of exotic pests spanned from one to 45 host plant families (mean = 10.6, s.d. = 14.8). In general, different combinations of species traits presented similar ranges of host plant families.

(c) Landscape composition

For each study site, landscape composition was quantified by Karp *et al*. [10] using a consistent classification at multiple spatial scales. High-resolution land-cover maps were provided by data contributors, when available. Otherwise, regional maps or, as a last resort, a 30 m global land-cover product were used. When possible, land-cover maps were chosen so that they matched the dates that samples were collected. Maps were then classified into seven land-use categories within a buffer of 2 km radius around each sampled field: forest and tree plantations, grassland, shrubland, annual cropland, perennial cropland, urban areas and other. Landscape composition was quantified through a distance-weighting procedure. First, the area (m^2) of each land-cover class was calculated in 20 concentric rings around each study site, with outer radii at 100 m intervals between 100 m and 2 km. Next, a Gaussian decay function was applied to assign weights to each ring, where rings closer to the focal site were weighted more than those further away:

$$W = \exp\left(\frac{-O^2}{2 * d^2}\right),$$

where W is the weight, O is out the outer edge distance of the ring and d is a decay rate that determines how rapidly weightings decline with distance. Three decay rates were identified (250, 750, 1250 m) to later assess landscape composition at multiple spatial scales. Weightings were then used to calculate a weighted sum for the total area of each land-cover class, which was then divided by the weighted sum of all land covers to ultimately obtain a proportional representation of each land-cover class around each study site. We quantified the proportional representation of semi-natural habitats (from now on: proportion of semi-natural habitats) by summing the weighted proportional cover of the grasslands, forests and other semi-natural habitats. We then quantified the proportional representation of arable land (from now on: proportion of arable land) by summing the weighted proportional cover of annual and perennial crops. We standardized the landscape variables at different spatial scales within each study (mean = 0, s.d. = 1). The proportion of semi-natural habitats and of arable land were highly correlated within and across studies at all spatial scales (electronic supplementary material, table S2) and their effects on pest populations were therefore analysed separately.

(d) Environmental context

We further gathered information on factors potentially influencing pest response to landscape composition: crop type, the range of the landscape gradient explored in each study and climatic region. First, we determined whether crops were herbaceous or woody (crop type, categorical). Second, we calculated the range in the proportion of semi-natural habitats in the landscape explored in each study (semi-natural habitat range, numeric). Studies considering larger gradients are expected to find stronger pest response to landscape composition. Third, we determined whether studies were performed in tropical or temperate regions (climatic region, categorical) [28]. Latitude can in fact influence biological control processes such as predation [29]. Local management is also expected to strongly influence pest abundance potentially modifying pest response to landscape composition (e.g. pesticide application and tillage [30,31]). However, this information was seldom available across the studies included in the present analysis, and it was therefore not considered.

Forty-seven studies in our dataset focused on herbaceous crops and 12 on woody crops. Range in the proportion of semi-natural habitats in the landscape spanned from 10.6 to 97.5% (mean = 59.3%, s.d. = 24.9%). Thirty-one studies were performed in temperate regions and 28 in tropical regions.

(e) Statistical analyses

We used an information-theoretic approach to evaluate alternative competing models exploring pest abundance response to landscape composition, pest traits and local context [32]. We used general linear mixed-effects models (GLMMs) to estimate model parameters (maximum-likelihood method). Because of the unbalanced occurrence of exotic and native pests in our dataset and the complexity of testing interactions between multiple variables, we adopted a multiple-step hierarchical methodology. We first used the full dataset to test whether exotic status and local context could influence pest response to landscape composition (*Model 1*, full dataset). We included the standardized proportion of semi-natural habitats or arable land, exotic status (categorical, exotic versus native), crop type (categorical, herbaceous versus woody), semi-natural habitat range (numeric, the range in the proportion of semi-natural habitat gradient explored in each study), climatic region (categorical, tropical versus temperate) and all the two-way interactions between landscape composition and the other predictors as fixed effects. Second, we explored the effects of host breadth, habitat breadth and local context on pest response to landscape composition, only for native species (*Model 2*, native pest subset). We included the standardized proportion of semi-natural habitats or arable land, host breadth (numeric, number of host families), habitat breadth (categorical, crop specialists dependent on crop habitats versus habitat generalists able to exploit both crop and non-crop habitats), the three environmental context variables and all the two-way interactions between landscape composition and the other predictors as fixed effect. We then further verified how exotic species respond to landscape composition (*Model 3*, exotic pest subset). We included the standardized proportion of semi-natural habitats or arable land as fixed effect. We did not include the other traits and local context variables, because predictor combinations coincided with single species identity (e.g. *Halyomorpha halys* is the only highly polyphagous, habitat generalist, exotic species sampled in a temperate region in the dataset; electronic supplementary material, table S1, appendix S1). All models included a crossed random structure since some pest species occurred in more than one study: (1 | Study ID) + (1 | Species). When multiple sampling methods were performed within the same study, we incorporated this information in the study ID (i.e. we fitted a random intercept for each study and sampling method combination). We used the whole dataset to assess the best-fitting landscape scale, running *Model 1* at the three different spatial scales for both the proportion of semi-natural habitats and arable land, using the maximum-likelihood estimation procedure. We then compared their fit using second-order Akaike's information criterion corrected for small sample size (AICc) and adopted the best model scale in further analyses.

With our information-theoretic approach, we compared the fit of all the possible candidate models nested within each of the three models presented above (global models, *Model 1*, *2* and *3*). In a set of n models, each model i can be ranked using its difference in AICc with the best-fitting model (ΔAICci = AICci–AICcMIN). A model in a set can be considered plausible if its ΔAICc is below 7 [33]. When there was more than one plausible model selected (*Model 1* and *2*), we calculated a model-averaged partial coefficient for each predictor, considering only plausible models. Parameter estimates obtained by model averaging are robust in the sense that they reduce model selection bias and account for model selection uncertainty [34]. Besides model-averaged coefficients, we also reported the list of all the plausible models with relative model weights in the electronic supplementary material.

To assess potential multicollinearity among the explanatory variables, we calculated the variance inflation factor (VIF) for all the global models without interactions. The highest VIF scores were below 2.2, indicating low collinearity in our dataset. [35]. Normality and homoscedasticity of the model residuals were validated graphically (electronic supplementary material figure S2). The multi-model inference analyses were performed using the 'lme4' and 'MuMIn' packages (Barton 2010) [36,37] implemented in R [38].

3. Results

Our multi-model inference analyses showed high model selection uncertainty for *Model 1* and *2* with 23 and 30 models with delta ΔAICc less than 7, respectively, whereas *Model 3* had one plausible model selected due to the inclusion of a single predictor (see electronic supplementary material, table S3 with all models listed). However, null models were never included in the sets of plausible models ($\Delta AICc < 7$) and several main effects and interactions were strongly supported. Pest abundance best responded to the proportion of semi-natural habitats and of arable land in the landscape at 250 m scale ($AICc > 7$; electronic supplementary material, tables S4 and S5). Below, we reported the effects based on the p-values obtained from the model-averaging procedure (conditional average).

When considering the whole dataset (*Model 1*), we found the abundance of exotic pests to increase with semi-natural habitats in the landscape, whereas natives overall displayed no response to the landscape gradient (exotic status×landscape interaction, figure 2*a*, table 1). Moreover, pest abundance in herbaceous crops increased with the proportion of semi-natural habitats in the landscape and it decreased in woody cropping systems (crop type × landscape interaction, figure 2*b*).

When considering only native pests (*Models 2*), we found species that feed on few host plant families slightly increase with the proportion of semi-natural habitats in the landscape, whereas highly polyphagous pests decrease along the landscape gradient (host breadth × landscape interaction;

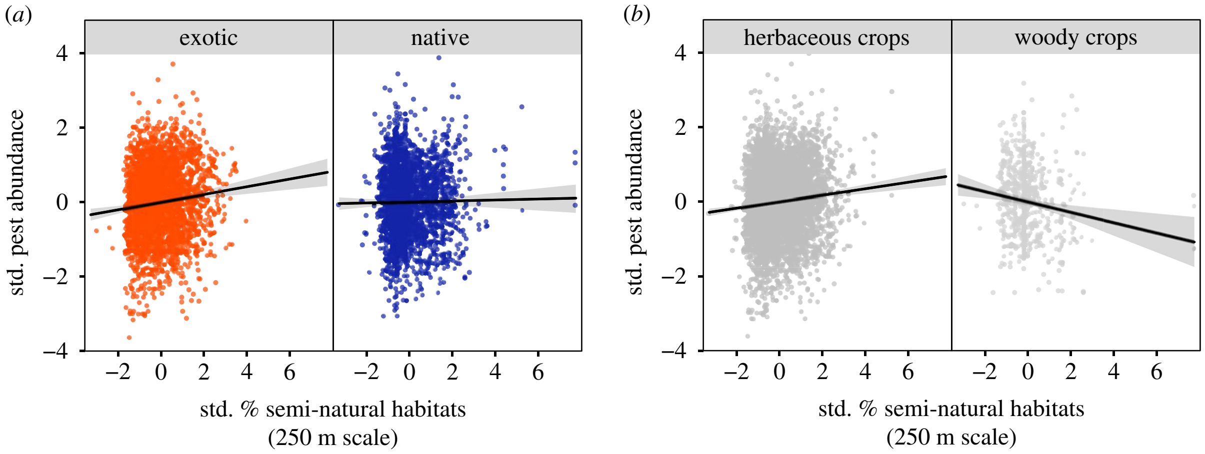

Figure 2. Partial residual plots depicting the effect of the proportion of semi-natural habitats in the landscape on pest abundance (*Model 1*) for (*a*) exotic versus native species and (*b*) for herbaceous versus woody crops. Pest abundance and landscape composition were standardized (mean 0 and s.d. 1) within each study. The area around model predictions represents 95% confidence intervals. Effect sizes (i.e. slopes) can be directly compared due to the variables' standardization. Plots were draws using the 'effects' package in R. (Online version in colour.)

figure 3*a*). Moreover, we found native specialists that only use crop habitats during their life cycle decrease with the proportion of semi-natural habitats in the landscape, whereas habitat generalists able to also exploit non-crop habitats did not respond to the landscape gradient (habitat breadth × landscape interaction; figure 3*b*). Finally, the abundance of native pests increased with the proportion of semi-natural habitats in the landscape in herbaceous crops and decreased in woody crops (crop type × landscape interaction, electronic supplementary material, figure S3).

Exotic pest abundance increased with semi-natural habitats in the landscape (*Model 3*; electronic supplementary material, figure S4).

Analyses considering different spatial scales and testing pest responses to the proportion of arable land in the landscape produced consistent results, i.e. opposite effects of arable land compared to that of semi-natural habitat cover (see electronic supplementary material).

4. Discussion

Our results show that species traits are important in understanding crop pest responses to landscape composition. Landscapes with more semi-natural habitat tended to house fewer native crop specialists and polyphagous pests, with small positive effects on native pests that also use resources outside crop fields and on native species with narrower host breadth. By contrast, the abundance of exotic species increased with semi-natural habitats in the landscape. Even though previous studies already suggested that native and exotic pests could exhibit contrasting responses to landscape processes [10,15], this is the first study to empirically test this hypothesis on the global scale. Moreover, pest abundance generally increased along the landscape gradient in herbaceous crops but decreased in woody cropping systems.

The abundance of native pests whose life cycles strictly depend on crop habitats decreased in landscapes rich in semi-natural habitats. One explanation for this trend is that specialist pests declined due to a decrease in crop host availability in surrounding fields [19]. Indeed, the resource concentration hypothesis posits that diverse polycultures suppress insect pests by disrupting visual and olfactory cues that trigger dispersal into the crop field. This concept, when extended to the landscape scale, suggests that landscapes with lower concentrations of a host crop will also be less likely to be plagued by severe pest outbreaks due to difficulties of specialized pests in locating host plants [39]. However, an alternative explanation is that semi-natural habitats support coevolved communities of natural enemies that contribute to the regulation of native pest populations in the field [3,7]. On the other hand, populations of native habitat generalists did not respond consistently to landscape composition. A possible explanation is that semi-natural habitats supported native habitat generalist pests through the provision of important supplementary resources, counterbalancing the expected increased top-down control by natural enemies [15].

Contrary to our hypothesis, highly polyphagous pests decreased with the proportion of semi-natural habitats. Landscapes with more semi-natural habitats likely harbour a higher diversity of host plants and were therefore expected to favour pests with wider host breadths [40]. However, it is also possible that polyphagous pests inhabiting complex landscapes are more likely to visit semi-natural habitat patches and to encounter natural enemies, being therefore more effectively controlled. More studies are needed to better understand pest movements across different habitats in agroecosystems.

We reveal differences in how exotic and native pests respond to landscape composition, suggesting that benefits provided by semi-natural habitats to exotic pests (i.e. alternative food, shelter, nesting and overwintering sites) probably outweigh the potential negative effects imposed by improved communities of native natural enemies [15]. Previous studies, not included in the present analysis, presented patterns similar to our findings. For instance, *Drosophila suzukii*, an exotic pest which severely impacts commercial fruit production worldwide [41], has been found to exploit multiple habitat types across agricultural landscapes and to cause greater crop damage in fields surrounded by forest-dominated landscapes [18,42]. Similarly, the abundance and spread of *Halyomorpha halys*, a highly polyphagous invasive pest, has been associated with the presence of non-crop habitats such as forests and

Table 1. Model-averaged coefficients (conditional average from model.avg() function in the MuMIn package for R) from the multi-model inference analysis of the GLMMs (*Model 1* and *2*) and results from GLMM (*Model 3*) testing the effects of standardized proportions of semi-natural habitats in the landscape (% SNH, 250 m scale), exotic status (native versus exotic), host breadth (number of host plant families), habitat breadth (crop specialists dependent on crop habitats versus habitat generalists able to exploit both crop and non-crop habitats), crop type (herbaceous versus woody), the range in the proportion of semi-natural habitats explored in the study (% SNH range) and the climatic region of the study area (tropical versus temperate) on standardized pest abundances measured in the focal field. *Model 1* includes both exotic and native pests (48 species, 5242 observations); *Model 2* includes only native pests (40 species, 2551 observations); *Model 3* includes only exotic pests (eight species, 2691 observations) and could test only the effect of SNH due to the small number of studies available. *p*-Values in italics are statistically significant ($p < 0.05$). The models were fit using a normal distribution and a crossed random structure.[a]

variables	estimate	s.e.	*z* value	*p*-value
Model 1: all species				
intercept	0.00	0.05	0.01	0.996
% SNH	0.14	0.07	1.93	0.054
exotic status	0.00	0.03	0.01	0.993
crop type	0.00	0.04	0.00	0.997
% SNH range	0.00	0.07	0.01	0.995
climatic region	0.00	0.04	0.00	0.999
exotic status × % SNH	*−0.08*	*0.04*	*2.08*	*0.038*
crop type × % SNH	*−0.22*	*0.05*	*4.63*	*<0.001*
% SNH range × % SNH	−0.14	0.08	1.69	0.091
climatic region × % SNH	−0.06	0.04	1.62	0.106
Model 2: native pests				
intercept	0.00	0.05	0.01	0.994
% SNH	−0.02	0.06	0.42	0.673
host breadth	0.00	0.02	0.00	0.997
habitat breadth	0.00	0.04	0.01	0.991
crop type	0.00	0.05	0.01	0.994
% SNH range	0.00	0.10	0.01	0.992
climatic region	0.00	0.04	0.00	0.998
host breadth × % SNH	*−0.04*	*0.02*	*2.01*	*0.045*
habitat breadth × % SNH	*0.13*	*0.04*	*2.86*	*0.004*
crop type × % SNH	*−0.19*	*0.05*	*3.59*	*<0.001*
% SNH range × % SNH	−0.09	0.10	0.86	0.389
climatic region × % SNH	0.05	0.05	0.89	0.371
Model 3: exotic pests				
intercept	0.00	0.02	0.00	1
% SNH	*0.11*	*0.02*	*5.61*	*<0.001*

[a]Crossed random structure using lme4 notation: (1|Study ID) + (1|Species).

wetlands [43,44]. Together, these results suggest that bottom-up forces might play a key role in driving the dynamics of exotic pests in recently invaded territories where their coevolved natural enemies are absent. However, the scarcity of empirical studies embracing the complexity of landscape effect on multi-trophic interactions still imposes a fundamental limit to our understanding of the mechanisms driving pest response to landscape features.

We found pest abundance in herbaceous crops to increase with the proportion of semi-natural habitats in the landscape and to decrease in woody cropping systems. Considering that most of the pest species included in our dataset feed on herbaceous plants, spillover from semi-natural patches to non-woody crops might be facilitated. However, the low number of studies performed on woody crops prompts more research on perennial systems. Finally, we found no effects of the range of the landscape gradient and of the climatic region.

The substantial variability observed in pest responses to landscape composition suggests some degree of context dependency not considered in the present study. First, other local factors such as pesticide application and landscape configuration, are expected to strongly shape pest dynamics potentially masking landscape influences [10,20,45,46]. Second, different pest species might depend on different subsets of semi-natural habitats. The use of a simple definition of semi-natural habitats, although widely adopted and straightforward from a management perspective, does not consider specific aspects of species ecology. Third, the majority of the studies on exotics included in the dataset were performed in North America on herbaceous crops (electronic supplementary

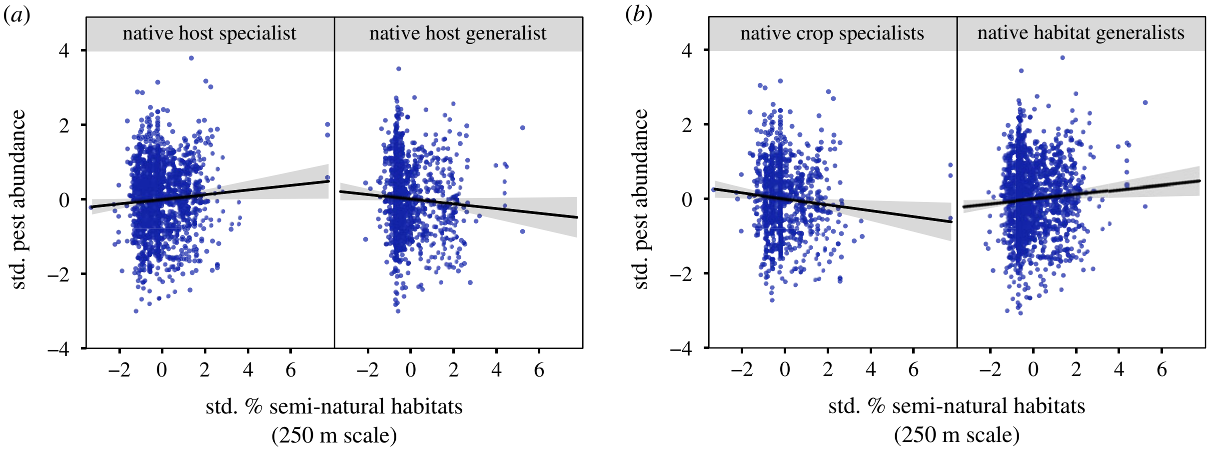

Figure 3. Partial residual plots depicting the effect of the proportion of semi-natural habitats in the landscape on abundance native pests (*Model 2*) for (*a*) different host breadth (number of host plant families pests feed on) and (*b*) different habitat breadth (i.e. crop specialists dependent exclusively on crop habitats versus habitat generalists able to use both crop and non-crop habitats). Pest abundance and landscape composition were standardized (mean 0 and s.d. 1) within each study. The area around model predictions represents 95% confidence intervals. Effect sizes (i.e. slopes) can be directly compared due to the variables' standardization. Plots were draws using the 'effects' package in R. (Online version in colour.)

material, table S1). The observed patterns might reflect specific characteristics of North American agricultural landscapes and crop production systems, and should therefore be interpreted with caution. Fourth, the lack of data on natural enemy populations prevents us from isolating their role in explaining the observed patterns.

At least two core findings resulted from our analyses. First, species traits are pivotal in understanding pest response to landscape composition. Second, semi-natural habitats surrounding crop fields have contrasting effects on pest species depending on their hosts, habitat requirements and exotic status. While the maintenance and restoration of non-crop habitats in agroecosystems remain of utmost importance to support biological control and to sustain farmland biodiversity [4,47], it is imperative to identify sustainable strategies to control the pests that seem to thrive in complex landscapes. Current efforts to control many economically damaging insects rely heavily on pesticide applications. However, the steady increase in insect resistance to pesticides and transgenic crops might compromise the efficacy of these crop protection strategies in the future [48]. Moreover, agrochemicals can disrupt biological control [30,49], imposing multiple negative environmental and societal externalities [1]. The identification of locally adapted sustainable farming practices (e.g. diversification of crop varieties, switch to perennial crops) might promote the biocontrol of both native habitat generalists and exotic pests [50–52]. As the threat of exotic species invasions is expected to increase with the intensification of international trade in the next decades [53,54], there is an urgent need to prevent or reduce establishment of new invaders and to develop innovative plant protection strategies for the control of emerging pests released from their coevolved antagonists. Our analysis suggests that a portfolio of strategies must be considered and implemented for the effective control of rapidly changing communities of crop pests in agroecosystems.

Data accessibility. Data are already publicly available [10].

Authors' contributions. L.M. conceived the study; D.K., R.C.K. and E.A.M. compiled pest and landscape dataset; G.S., M.P., T.K. and M.O.R. collated data on pest traits; G.T. and L.M. analysed data; G.T. wrote the first draft of the manuscript, and all authors provided substantial effort in ideas and revision of the manuscript.

Competing interests. We declare we have no competing interests.

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