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Applying generic landscape-scale models of natural pest control to real data: Associations between crops, pests and biocontrol agents make the difference

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ABSTRACT

Managing agricultural land to maximize the supply of natural pest control can help reduce pesticide use. Tools that are able to represent the relationship between landscape structure, field management and natural pest control can help in deciding which management practices should be used and where. However, the reliability and the predictive power of generic models of natural pest control is largely unknown. We applied an existing generic model of natural pest control potential based on landscape structure to nine sites in five European countries and tested the resulting values against field measurements of natural pest control. Subsequently, we added information on local level factors to test the possibility of improving model performance and predictive power. The results showed that there is generally little or no evidence of correlation between modeled and field-measured values of natural pest control. Moreover, we found high variability in the results, depending on the associations of crops, pests and biocontrol agents considered (e.g. *Oilseed rape-Pollen beetle-Parasitoids*) and on the different case studies. Factors at the local level, such as conservation tillage, had an overall positive effect on natural pest control, and their inclusion in the models typically increased their predictive power. Our results underline the importance of developing predictive models of natural pest control which are tailored towards specific associations between crops, pests and biocontrol agents, consider local level factors and are trained using field measurements. They would serve as important tools within farmers' decision making, ultimately supporting the shift toward a low-pesticide agriculture.

1. Introduction

The historic and current simplification of agricultural landscapes and the increase in the use of pesticides are one of the main reasons for the ongoing decline in insect biodiversity (Benton et al., 2021). This is reflected in a decrease in insect-provided ecosystem services, such as natural pest control (Dainese et al., 2019). As a consequence, homogeneous and intensively used agricultural areas become more vulnerable to crop losses due to pest outbreaks (Benton et al., 2021; Karp et al., 2018; Rosa-Schleich et al., 2019). For instance, at the European level, it was estimated that 15% of oilseed rape yield is lost by insect pests (Milovac et al., 2017) and that aphids are responsible for mean annual losses of 700,000 t of wheat (Wellings et al., 1989). Yield losses to insect pests are projected to increase due to climate change (Deutsch et al., 2018). The frequency of pest outbreaks is, in fact, expected to increase due to predicted shifts in temperatures and precipitation patterns (Ortiz et al., 2021; Pörtner et al., 2021; Skendžić et al., 2021). At the same time, global warming further exacerbates the decline in abundance of biocontrol agents and their effectiveness (e.g. due to desynchronized dynamics with pests) (Skendžić et al., 2021). The need to ensure the stability of agricultural production in the face of the increasing risk of pest outbreaks leads to an ever-increasing use of pesticides (Benton

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et al., 2021; Hassan et al., 2016; Seppelt et al., 2020), thus often creating pesticide resistance (Skellern and Cook, 2018). To break this vicious circle, it is necessary to reduce pesticide use, a goal defined, among others, by the European Union's (EU) Farm to Fork Strategy (EC, 2020a) and the Biodiversity Strategy to 2030 (EC, 2020b) under the newly promoted EU Green Deal. Managing agricultural landscapes to support populations of ecosystem service providers (i.e. biocontrol agents) and hence the supply of natural pest control is a key complementary strategy (Benton et al., 2021; Hassan et al., 2016). Benefits from natural pest control obviously help reduce external inputs (i.e. pesticides), and in many cases the applied measures also support other environmental objectives (e.g. improving soil and water quality, conserving farmland biodiversity, adapting to climate change) (Baaken, 2022; Beillouin et al., 2020; Tamburini, Bommarco et al., 2020). Natural pest control can be influenced by the management of agricultural land from the landscape level to individual fields and their surroundings (Petit et al., 2020) (Fig. 1). Complex landscapes, e.g. those with high proportions of semi-natural habitat (SNH), a low percentage of cropland, a high crop diversity and a high edge density between crop and non-crop habitats, generally have the potential to support source populations of natural enemies and to favor their spillover into crops (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Dainese et al., 2019; Fahrig et al., 2011; Martin et al., 2019; Zhang et al., 2020). However, these factors are not always related to an increase in natural pest control. While a positive relationship between the supply of natural pest control services and landscape complexity has been found in most studies (Dainese et al., 2019; Duarte et al., 2018; Martin et al., 2019; Palomo-Campesino et al., 2018; Rusch, Chaplin-Kramer et al., 2016; Zhang et al., 2020), this effect has also been found to be non-significant (Albrecht et al., 2020; Chaplin-Kramer et al., 2011) or highly variable (Bianchi et al., 2006; Holland et al., 2016; Karp et al., 2018; Petit et al., 2020; Tougeron et al., 2022; Veres et al., 2013; Zhang et al., 2020), depending on the specific parameters and species considered. At the local level, different factors, such as semi-natural habitats adjacent to target crops, in-field spatial and temporal diversification measures, conservation tillage or organic management, can have a positive effect on natural pest control by creating habitats for natural enemies at the soil surface or reducing disturbance to them, as well as acting on pests' life cycle or on plant resistance capacity (Garibaldi et al., in preparation; Hatt et al., 2018; Palomo-Campesino et al., 2018; Petit et al., 2020, 2021; Rosa-Schleich et al., 2019; Rusch, Bommarco et al., 2016).

Robust and reliable tools that are capable of representing the link between landscape and local land-use characteristics and the supply of natural pest control would help to better plan and manage agricultural landscapes in order to maximize service supply (Maes et al., 2012). Having reliable predictions would play an important role within farmers' decision making processes (e.g. Integrated Pest Management programmes). Farmers would be more prone to manage agricultural landscapes to preventively increase natural pest control, instead of relying uniquely on agrochemicals application when pests-related thresholds are exceeded, leading therefore to a transition towards low-pesticide agriculture. So far, however, models aiming to predict natural pest control (potential) suffer either from a lack of realism (i.e. generic models) or from a lack of generality (i.e. location-specific ecological models) (Alexandridis et al., 2021). These constraints strongly limit the applicability of such models as predictive management tools for stakeholders. Existing generic models are typically based on indicators of landscape composition or configuration (Alexandridis et al., 2021). For example, Zhang et al. (2020) used combinations of compositional and configurational metrics to develop three models at different spatial scales (from 250 to 1500 m radii) to analyze the responses of pest suppression in corn fields and grasslands in two locations in Midwest U.S. Similarly, Rega et al. (2018) used the composition and configuration of different types of SNH (i.e. herbaceous linear, herbaceous areal, woody linear and woody areal) within a radius of 500 m around target agricultural fields to develop a spatially-explicit, fine-resolution model for the European level that quantifies the potential of landscapes to support natural pest control by flying biocontrol agents (i.e. predatory flies of the family Syrphidae, Dolichopodidae and Empididae and parasitic wasps of the superfamilies Chalcidoidea, Braconidae and Ichneumonidae). Existing generic models are linking higher values of such indicators to higher expected values of natural pest control (Alexandridis et al., 2021). However, while complex agricultural landscapes can support high numbers of biocontrol agents, this cannot be automatically translated into agroecosystems that supply high levels of natural pest control service. For instance, the effects of landscape composition and configuration on pest suppression can be region-specific and scale-dependent (Zhang et al., 2020). Moreover, existing generic models hardly take into account the above mentioned local level factors, which may have an important impact on natural pest control. Unlike location-specific ecological models, they also do not account for differences among ecosystems and ecological processes (Alexandridis et al., 2021), failing to integrate the different trait-mediated responses of pests and biocontrol agents to the landscape context (Martin et al., 2019; Petit et al., 2020).

In this study, we used the model of Rega et al. (2018), here referred

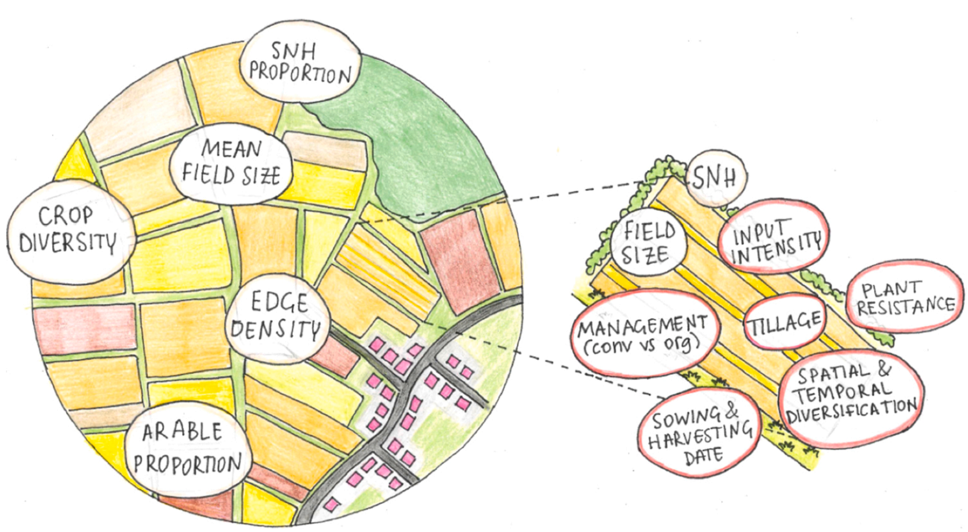

Fig. 1. Landscape (left) and local (right) level factors that potentially influence natural pest control (own illustration). Red-circled factors highlight in-field agricultural practices that influence landscape and local level complexity. SNH stands for Semi-Natural Habitats.

to as Pest Control Potential model, as an example of a generic approach, and we applied it to different regions in Europe in order to test (Q1) to what extent in-field measurements of natural pest control can be predicted by a generic model approach when applied at the local/regional level, and (Q2) whether model performance and predictive power are improved by adding information on local level factors (conventional or conservation tillage, conventional or organic management, presence or absence of SNH adjacent to crops). Hereby, we aim to further characterize the gaps between location-specific analysis and larger scale landscape-driven models, ultimately providing useful input for future generic models of natural pest control.

2. Materials and methods

We focused on nine case studies in five countries in Europe (Fig. 2 and Table S1), for which high-resolution land-use maps and field measurements of natural pest control were available (Martin et al., 2019). Each case study included a different number of sites (Fig. 2 and Table S2), so that the analysis was carried out at a total of 237 distinct sites, corresponding to points in target fields where field experiments (e.g. exclusion with cages, sampling plots) were conducted.

2.1. Case study database

From the synthesis of Martin et al. (2019) and from the individual case studies (Dainese et al., 2017; Sutter et al., 2018), we retrieved field-measured values for natural pest control at each site. The resulting database contained values for pest parasitism, pest predation, pest suppression and pest damage (hereafter called natural pest control indicators; Table 1 and Table S2). In some cases, more than one natural pest control indicator was measured (e.g. both aphid parasitism rate and aphid suppression index), giving a total of 346 measurements.

Depending on the indicator used, the relationship between the indicator and the level of ecosystem service provision was either positive (a high indicator value, e.g. high pest parasitism, corresponded to a high level of natural pest control) or negative (a high indicator value, e.g. high damage by pests, corresponded to a high pest pressure and a low level of pest control). The database also contained information on the crop type present in each site, together with the pest and biocontrol agents (species or taxa) observed (see Table S2 for details). Four case studies were characterized by cereal crops and one by cereal and legumes crops, whose main pest are aphids; two case studies were oilseed rape crops, whose main pest are pollen beetles; one case study was cherry orchards, infested by both aphids and herbivorous beetles; and one case study was tomato crops, infested by Lepidoptera tomato pests. The biocontrol agents sampled in the different case studies were parasitoids as well as ground-dwelling and vegetation-dwelling predators. In the case studies considered, flying biocontrol agents were always (but not only) sampled. Although the field-measured values for natural pest control could be explained also by non-flying biocontrol agents present in the same sites, this choice aims to get as close as possible to the results of the Pest Control Potential model. Based on this information on crop type and on the pest and biocontrol agents considered, we identified typical associations between crops, pests and biocontrol agents, which, together with the type of field measurements of natural pest control, we used to aggregate the case studies in seven different groups (Table 1).

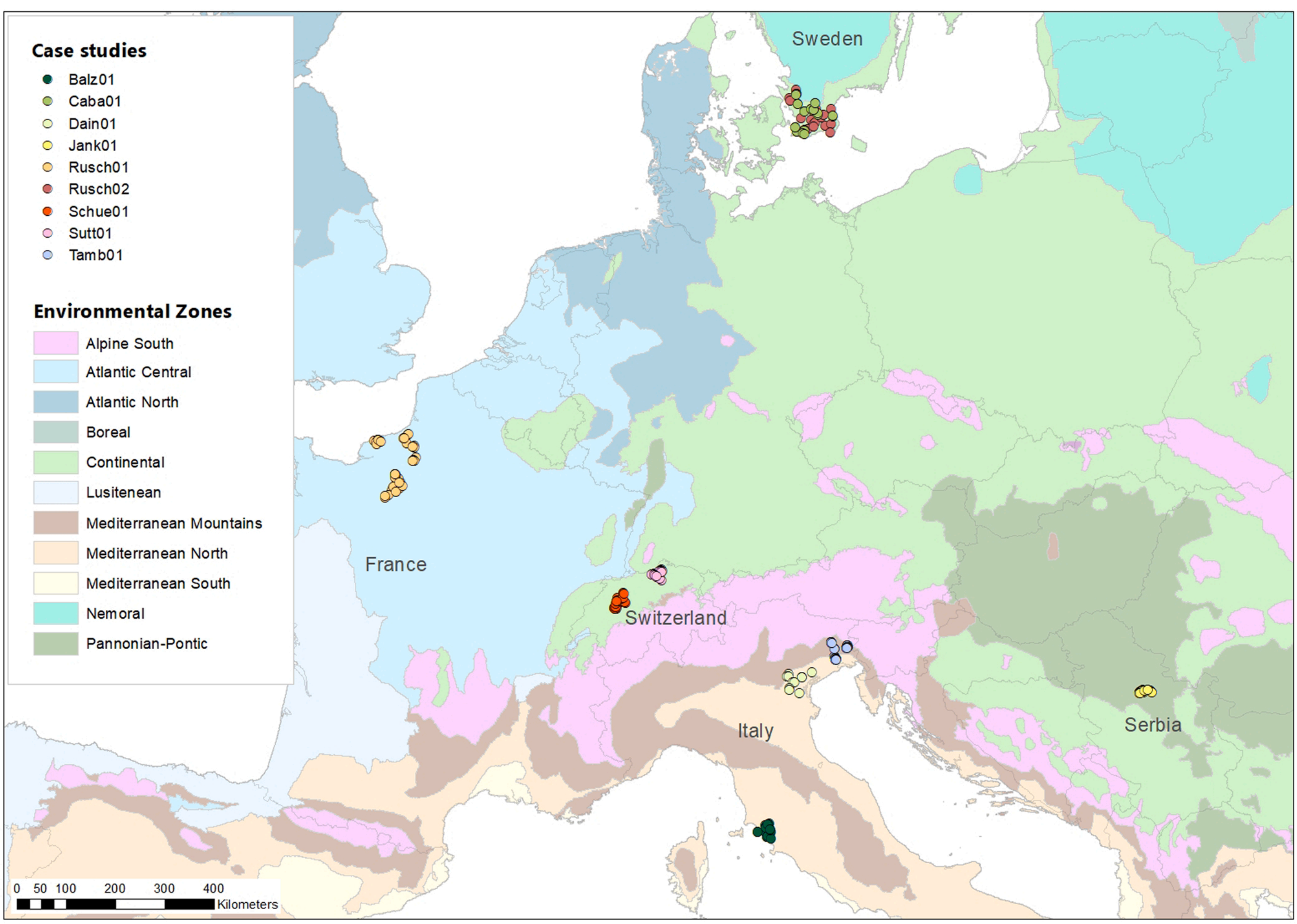

Fig. 2. Maps of case studies location. Each color corresponds to a different case study and each point to a different site. The different environmental zones are derived from the Environmental Stratification of Europe (Metzger, 2018), based on climate data, data on the ocean influence and geographical position (northing).

Table 1
Summary of the seven groups considered in this study, reporting the measured indicators and the corresponding type of measure of natural pest control (unit), the direction of the relationship between indicators and natural pest control service, the crop-pest-biocontrol agents associations and the number of case studies and sites for each of these groups, specifying the number of sites for which conservation tillage and organic management were recorded.

Indicator	Type of measure (unit)	Indicator - servicer relationship	Crop-pest-biocontrol agents associations	No. case studies	No. sites	No. sites conservation tillage	No. sites organic management
Pest parasitism	Parasitism rate (% or 0–1 range)	Positive	Cereals/legumes-Aphids-Parasitoids	5	127	26	30
			Oilseed rape-Pollen beetles-Parasitoids	2	60	0	0
Pest predation	Predation rate (%)	Positive	Oilseed rape-Pollen beetles-Natural enemies	1	18	unknown	0
Pest suppression	Aphid suppression index (0–1 range) (Gardiner et al., 2009)	Positive	Cereals/legumes-Aphids-Natural enemies	3	71	13	0
Pest damage	Damage rate (%)	Negative	Cherry trees-Aphids & Pollen beetle-Natural enemies	1	30	0	30
	Number of damaged fruit	Negative	Tomato-Lepidoptera-Natural enemies	1	20	0	0
	Number of galleries	Negative	Tomato-Lepidoptera-Natural enemies	1	20	0	0

Note: Parasitism rate was calculated as the proportion of aphids on plants that are mummies or as the proportion of pollen beetle larvae containing parasitoid eggs. Pest predation and pest suppression were estimated using exclusion experiments. Predation rate of pollen beetles was measured as the difference in numbers of pollen beetle adults emerging with vs. without exclusion of predators. Aphid suppression is the proportion of aphids remaining after 5 days in an open treatment vs. a closed cage treatment, calculated following (Gardiner et al., 2009). Damage rates were estimated as the percentage of leaf area lost by insects. The number of damaged fruit in the upper and middle part of the crop and the number of galleries on the fruits were used to estimate damage by Lepidoptera on tomatoes.

When available, we also gathered data from the original case studies on local level factors such as conventional/organic management, and conventional/conservation tillage (Table S1). Information on the (lack of) application of chemical pesticides and herbicides in the investigated fields was also reported when this was provided by the original case studies, but it was subsequently not used in the analysis as no differences in the use of pesticides were detected within each association, although it would been an important factor impacting effectiveness of biocontrol agents.

2.2. Geospatial data

For all sites, we obtained high-resolution land-use maps (i.e., minimum mapping units of ca. 4×4 m^2) from the data holders of the respective case study (see Martin et al., 2019 for details). The land-use maps covered an extent of 500–3000 m radius around the target fields and contained information on arable land, forests, semi-natural areas, urban areas and water bodies. The level of thematic detail was high enough for all sites to distinguish between the different types of SNH relevant for the application of the Natural Pest Control model: grassy margins, flower strips, unmanaged grassland and fallow land were considered herbaceous SNH, while hedgerows, shrubs, solitary trees, tree lines and forest were considered woody SNH. Linear and areal SNH were differentiated based on a perimeter-to-area ratio (P/A ratio) and the area of each feature (following Bartual et al., 2019 and Moonen et al., 2016), where P/A ratio > 0.125 and area > 150 m^2 correspond to linear features and P/A ratio $< = 0.125$ and area > 625 m^2 correspond to areal features. For woody areal features adjacent to non-woody land use classes, we also distinguished the edges of the features from their core, by creating an internal buffer of 12.5 m (Bartual et al., 2019; Moonen et al., 2016). For the differentiation amongst linear and areal SNH, as well as amongst edge and core of woody areal features, we used R version 4.0.5 (R Core Team, 2021) using the package *sf* (Pebesma, 2018). This process resulted in five SNH types (i.e. herbaceous linear, herbaceous areal, woody linear, woody areal edge and woody linear core) as indicated in Rega et al. (2018), themselves referring to Moonen et al. (2016).

Using the high-resolution maps, we also identified the sites for which SNH were adjacent to the target field, which we considered a local level factor influencing natural pest control. We created a buffer zone of 50 m around each site, as several studies (Albrecht et al., 2020; Boetzl et al., 2020; González et al., 2021) considered the effect of SNH adjacent to crops on natural pest control up to this distance. We recorded the presence or absence of SNH adjacent to the target field through binary values “yes”/”no”, depending on whether SNH fell within this 50 m radius area or not.

2.3. Model application

The Pest Control Potential model (Rega et al., 2018) uses a moving window of 500 m radius to calculate for each target cell a Pest Control Potential index (hereafter PCP) based on the amount of and type of SNH present in the neighborhood. For each of the SNH types, in fact, a score is assigned based on their potential to support flying natural enemies as estimated in Moonen et al. (2016) (i.e. herbaceous linear = 24.7; herbaceous areal = 26.8; woody linear = 34.4; woody areal edge = 45.6; woody areal interior = 20.7). These scores “do not have a meaningful absolute value, but rather assess the relative potential across SNH types and within-SNH location” as specified by Rega et al. (2018) in Table 1. The same scores are also used in this application. The contribution of SNH to the final index also depends on a distance-weighted decay function. PCP is calculated in each target cell as shown in Eq. 1:

$$PCP_x = \sum_{i=1}^{n} f(r_i) \sum_{j=1}^{5} SNH_{ji} * s_j \quad (1)$$

Where:

PCP_x = Pest Control Potential index in target cell x.
r_i = Euclidean distance between cell i (source) and cell x (target).
$f(r_i)$ = value of distance-weighted function at distance r.
n = number of cells surrounding cell x for which $f(r_i) > 0$.
SNH_{ji} = area share of the j_{th} SNH type in cell i.
s_j = score of the j_{th} SNH type based on its potential to support flying biocontrol agents.

For each case study, we used the SNH types derived from the high-resolution land-use maps (see Section 2.2.) as input to the model. Using R version 4.0.5 (R Core Team, 2021) and the packages sf (Pebesma, 2018) and terra (Hijmans, 2021), we calculated the PCP for an area within the original radius of 500 m, and for radii of 250 m, 750 m, 1000 m and 2000 m to test for possible differences in the results (see R code in Supplementary Material).

2.4. Statistical analysis

We used a linear modeling approach in order to assess the correlation between different in-field measurements of natural pest control and the PCP model predictions (question Q1). For each identified crop-pest-biocontrol agents associations (Table 1) we fitted linear models (LMs) considering the observed values as the response variable and the modeled values of PCP as an explanatory variable. For the associations characterized by multiple case studies (i.e. *Cereals/legumes-Aphids-Parasitoids* association, *Cereals/legumes-Aphids-Natural enemies* association and *Oilseed rape-Pollen beetles-Parasitoids* association), we fitted linear mixed-effect models (LMMs), with the different case studies considered as a random effect, including both random intercept and slope. We "log" transformed the indicators of pest control characterized by count values, and "logit" transformed the indicators characterized by continuous values between 0 and 1, in order to achieve normal distributions of the data. In the latter case, if the response variables included the extreme values of 0 and 1, we applied an adjustment factor to avoid proportions of 0 and 1 (Fox and Weisberg, 2019). As pest damage indicators are characterized by a negative relationship between indicator and natural pest control service (Table 1), these values were additionally reversed before running the linear models so that high values of the indicators also mean high values of natural pest control. To test for the additional effect of local level factors (i.e. conventional or organic management, conventional or conservation tillage and the presence of SNHs adjacent to the target field) on natural pest control (question Q2), we fitted the same LMs or LMMs using the local level factors and their interaction with the PCP as additional explanatory variables. We calculated AIC values in order to compare the nested (i.e. PCP only as explanatory variable) and complex (i.e. PCP and local level factor as explanatory variables) models. For all models, assumptions were checked using the graphical visualization tools recommended by Zuur et al. (2009). Absence of spatial autocorrelation was checked plotting the residuals vs. the longitude-latitude coordinates and calculating the Moran's I test (Fig. S1). We performed all statistical analyses in R using the packages *R Stats* (R Core Team, 2021), *lme4* (Bates et al., 2022) and *spdep* (Dependence and Schemes, 2022). In interpreting the results, we report the strength of evidence rather than significance, as recommended by Muff et al. (2022).

3. Results

3.1. Estimated Pest Control Potential index

In all case studies analyzed, the proportion of SNH followed a gradient from low to high. However, differences in the amount and predominant types of SNH were observed amongst the case studies (Fig. S2). *Jank01* and *Schue01* both presented a mean SNH proportion of 35% (Fig. S2a), and at some sites it reached up to 80% (Fig. S2b). The first case study is characterized by a very widespread presence of hedgerows and herbaceous vegetation at the field margins, while the latter case study is characterized mostly by forested areas (hence the prevalence of woody SNH types). On the other hand, several case studies had a mean SNH proportion of less than 10%, for example *Caba01* and *Rusch02* both located in Southern Sweden and *Dain01* and *Tamb01* both located in Northern Italy. *Rusch02* reached a value of up to 60% SNH for one site, but as with *Caba01*, no SNH were detected at most of the sites within the 500 m radius around the target field (Fig. S2b). SNH proportion in the *Dain01* and *Tamb01* sites never exceeded 30%, and they were only characterized by woody elements (Fig. S2b).

By applying the Pest Control Potential model, we obtained PCP values for all target fields, which we then normalized between 0 and 1 using a min-max normalization. Lower PCP values corresponded to agricultural landscapes characterized by a low occurrence of SNH or where SNH were present in a higher proportion but far from the target fields. The final PCP value was also influenced by the SNH type, which is expected to indicate the capacity to support the biocontrol agent's population (Bartual et al., 2019; Moonen et al., 2016). The values obtained varied among case studies, but were generally between 0 and 0.5 (Fig. S2b). An exceptions was in the *Caba01* case study, which had PCP values of 0.3 or less, and the Schue 01 and *Jank01* case studies, which had PCP values of 0.9 and 1, respectively. The latter cases are indeed the ones where the agricultural landscape is characterized by overall higher SNH proportions.

3.2. Correlation between Pest Control Potential index and field measurements

For most of the considered crop-pests-biocontrol agents associations, we identified little or no evidence that PCP at 500 m radius was associated with the in-field natural pest control measurements (p-value $>$ 0.1; Table 2 and Fig. 3). The only exception was given by the *Oilseed rape–Pollen beetles–Natural enemies* association, for which we observed weak evidence of a correlation between PCP and in-field pest predation (p-value $<$ 0.1; Table 2 and Fig. 3). The model input (PCP) explained very low percentages of the variation in the measurements of natural pest control for parasitism and suppression of aphids and for cherry tree damage (around 1%) (Table 2). These results remained constant also when considering larger or smaller spatial scales of analysis (Table S3). The model input (PCP) explained higher percentages of variation in the measurements of natural pest control for parasitism of pollen beetle (14%) (Table 2), but still we identified little or no evidence that PCP was associated with pollen beetle parasitism (p-value $>$ 0.1; Table 2 and Fig. 3). Within pollen beetle parasitism and aphid suppression associations, we found that the relationships between PCP and field measurements varied largely amongst case studies (Fig. 3). Differences amongst case studies were mostly random. However, we observed similar slopes in the *Cereals-Aphids-Natural enemies* association in the case studies *Dain01* and *Tamb01,* both belonging to the same environmental zone (i.e. Mediterranean north zone – Table S1). When considering predation of pollen beetles and tomato damage, the models were able to generate good predictions (low RMSE values) and explained higher percentages of the variation in natural pest control (17% and 10% respectively; Table 2). When considering larger spatial scales of analysis for these indicators, they reached values up to 32% and 21%, respectively. Moreover, for these indicators, we observed moderate evidence of a correlation between PCP and field measurements for 1000 and 2000 m radii (p-value $<$ 0.05, Table S3).

3.3. Model performance with local level factors

When adding the local level factors to the linear (mixed) models we observed that the complex models' input (PCP at 500 m radius and local level factors) generally explained comparatively higher percentages of variation in the measurements of natural pest control as indicated by higher R-sq and smaller RMSE values (Table 3). This improvement was

Table 2
Summary of LMs or LMMs for each group (combination of crop–pests–biocontrol agents association and field measurement of natural pest control) when considering only PCP at 500 m radius as explanatory variable. Underlined values indicate a weak evidence of the correlation between PCP and field measurements of natural pest control (p-value < 0.1).

Response variable	Explanatory variable	Estimate	Std. error	t-value	Pr (>|t|)	Df	R-sq	RMSE	AIC
Cereals/legumes-Aphids-Parasitoids association									
Parasitism rate	(Intercept)	-2.589	0.276	-9.393	< 0.001	123	0.01	0.83	334.83
	PCP	-0.422	0.478	-0.882	0.381				
Cereals/legumes-Aphids-Natural enemies association									
Aphid suppression index	(Intercept)	1.618	0.706	2.292	0.150	66	0.00	0.85	195.80
	PCP	-0.464	1.168	-0.397	0.726				
Oilseed rape-Pollen beetles-Parasitoids association									
Parasitism rate	(Intercept)	-1.827	1.049	-1.741	0.345	58	0.14	1.17	206.14
	PCP	3.186	2.233	1.427	0.411				
Oilseed rape-Pollen beetles-Natural enemies association									
Predation rate	(Intercept)	-1.978	-1.978	-8.316	< 0.001	16	0.17	0.45	28.07
	PCP	1.589	1.589	1.793	0.092				
Cherry trees-Aphids & Pollen beetles-Natural enemies association									
Damage rate	(Intercept)	1.092	0.264	4.140	< 0.001	28	0.01	0.73	71.91
	PCP	-0.397	0.678	-0.586	0.563				
Tomato-Lepidoptera-Natural enemies associations									
No. of galleries	(Intercept)	5.041	0.046	109.631	< 0.001	17	0.10	0.13	175.22
	PCP	0.387	0.247	1.567	0.136				
No. of damaged fruits	(Intercept)	3.701	0.060	61.984	< 0.001	17	0.11	0.16	134.25
	PCP	0.507	0.321	1.583	0.132				

strongest for the *Cereal-Aphids-Parasitoids* association, for which the percentages of variation in the measurements of natural pest control increased to 13% compared to the 1% without considering local level factors. Moreover, only for this association the AIC value decreased in the complex model compared to the nested one, thus indicating that adding local level factors as explanatory variables improved it significantly. For this association, in fact, we found moderate evidence of a positive correlation between conservation tillage and parasitism rate (p-value <0.05, Table 3), implying that aphid parasitism rate was higher in conservation than in conventional tillage. In this association, we also observed moderate evidence that field management (conventional or organic) modulates the correlation between PCP and field measurements of natural pest control. When a field was managed conventionally, parasitism rates remained constant with increasing PCP values, while parasitism rates decreased with increasing PCP values under organic management (Table 3).

For all the other associations, local level factors did not significantly improve the model performance (i.e. higher AIC values of the complex models compared to the nested ones), but we generally found a positive effect (as indicated by the positive estimates) of the presence of SNH adjacent to the target field on field measurements of pest control. Similar effect was also found for conservation tillage and organic management (when such information was available for the case studies considered) (Table 3 and Fig. S3).

4. Discussion

The Pest Control Potential model applied here had been designed to estimate the potential of a landscape to support natural pest control based on landscape complexity characteristics (i.e. presence and configuration of different SNH types). It focuses on flying biocontrol agents, and although we considered in this analysis only case studies in which flying insects were sampled, we are aware that the final measure of natural pest control in the field can also be explained by other species. When testing this estimate against actual natural pest control, our results showed that, with the exception of the *Oilseed rape-Pollen beetles-Natural enemies* association, there was generally no evidence of the correlation between PCP and in-field measurements of natural pest control. Overall, the models explained only a small percentage of the variation in the field measurements. The *Oilseed rape-Pollen beetles-Natural enemies* association, however, is represented by only one case study, making it difficult to confirm or reject the reliability of the model for this association type. For some associations (i.e. *Oilseed rape-Pollen Beetles-Natural enemies* and *Tomato-Lepidoptera-Natural enemies*), an improvement in model performance and moderate evidence of the correlation between PCP and in-field measurements were observed when the radius of analysis was extended to 1000 m and 2000 m. Indeed, it has previously been shown that responses of insect species to landscape context can differ based on the spatial scale of analysis (Alignier et al., 2014; Martin et al., 2016; Thies et al., 2003).

By adding local level factors, the models were able to explain the variation in natural pest control levels comparatively well for some of the associations. Although we found moderate evidence (p-value < 0.05) of a positive correlation between conservation tillage and parasitism rate only for the *Cereals-Aphids-Parasitoids* association, a positive effect of the presence of SNH adjacent to the target field and of conservation tillage and organic management was generally observed (as indicated by the positive estimates and the increasing R^2 values). Indeed, several recent meta-analyses (Albrecht et al., 2020; Beillouin et al., 2020; Petit et al., 2020; Rosa-Schleich et al., 2019; Tamburini, Bommarco et al., 2020) showed that SNH at the field boundaries positively contribute to pest suppression in adjacent crops. This is because SNH adjacent to the target field provide locally important resources (e.g. food, overwintering sites) for biocontrol agents. However, as Tscharntke et al. (2016) pointed out, SNH can also be a greater source of pests than of biocontrol agents, or SNH may be insufficient in amount, composition or configuration to support large enough populations of biocontrol agents. This can explain, for example, our results for the *Oilseed rape-Pollen beetles-Natural enemies* association, for which we found lower predation rates when SNH was adjacent to the target field. In contrast, the positive effect of conservation tillage may be associated with its reduced disturbance of biocontrol agents and especially to parasitoid larvae in the soil, which increases their survival rates until the next season, compared to the more intensive conventional techniques (Skellern and Cook, 2018).

When comparing different crop-pests-biocontrol agents associations, we found a negative slope of the correlation between PCP and field measurements for parasitism and suppression of cereal aphids and for damage to cherry trees. Variations in the trends of this correlation were also observed when comparing case studies belonging to the same association of crop-pest-biocontrol agents. Our results are therefore in line with other studies that have found highly variable relationships between

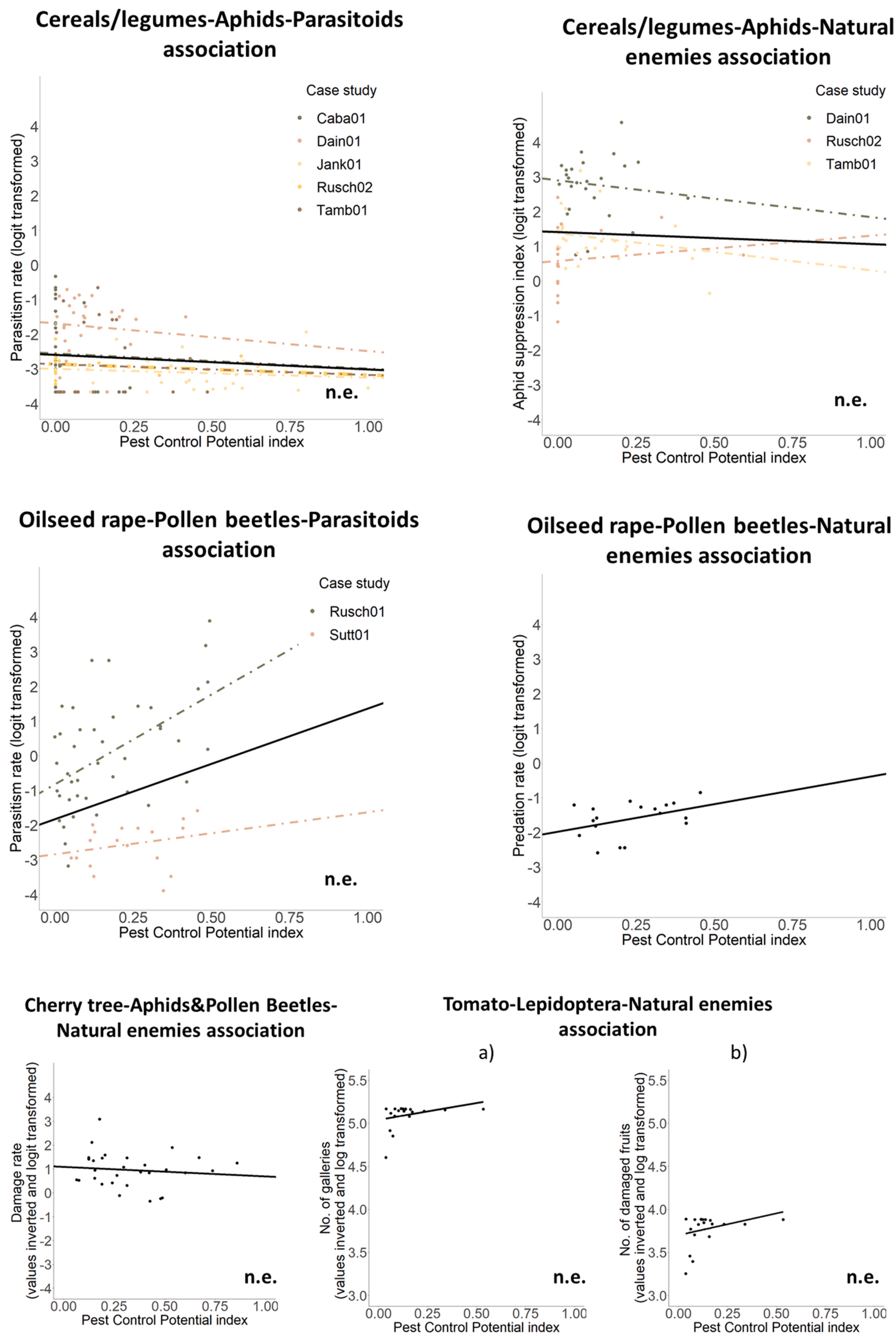

Fig. 3. Plot of in-field natural pest control values (transformed and inverted where necessary) and PCP values at 500 m radius for each considered group (combination of crop-pests-biocontrol agents association and field measurement of natural pest control). The black regression lines indicate the relationship between the two variables for each case study (considering only the fixed effect in the case of association characterized by multiple case studies). The colored dotted lines represent the regression lines for the different case studies within a crop-pest-biocontrol agents association. “n.e.” indicate weak or no evidence of the correlations between PCP and natural pest control measurements.

Table 3
Summary of LMs or LMMs for each group (combination of crop–pests–biocontrol agents association and field measurement of natural pest control) when considering PCP at 500 m radius and local level factors as explanatory variables. Underlined values indicate weak evidence of the correlation between PCP and natural pest control field measurements (p-value < 0.1), bold values indicate moderate evidence of this correlation (p-value <0.05). R-sq, RMSE and AIC of the nested model (i.e. considering PCP only) are given in brackets.

Response variable	Explanatory variable	Estimate	Std. error	t-value	Pr (>|t|)	Df	R-sq	RMSE	AIC
Cereals/legumes-Aphids-Parasitoids association									
Parasitism rate	(Intercept)	-2.859	0.391	-7.312	0.005	119	0.13	0.77	327.14
	PCP	-0.226	0.568	-0.397	0.698			[0.83]	[334.83]
	Presence local SNH	0.313	0.216	1.449	0.150		[0.01]		
	Conservation tillage	0.589	0.228	2.586	**0.011**				
	Organic management	0.489	0.843	0.580	0.607				
	PCP x Organic management	-5.079	2.090	-2.431	**0.017**				
Cereals/legumes-Aphids-Natural enemies association									
Aphid suppression Index	(Intercept)	1.540	0.662	2.327	0.144	64	0.02	0.83	198.34
	PCP	-0.814	1.434	-0.568	0.622				[195.80]
	Presence local SNH	0.459	0.282	1.627	0.109		[0.00]	[0.85]	
	Conservation tillage	0.094	0.353	0.265	0.792				
Oilseed rape-Pollen beetles-Parasitoids association									
Parasitism rate	(Intercept)	-1.906	1.109	-1.719	0.344	57	0.04	1.16	207.27
	PCP	3.063	2.429	0.871	0.449				[206.14]
	Presence local SNH	0.335	0.492	0.682	0.498		[0.14]	[1.17]	
Oilseed rape-Pollen beetles-Natural enemies association									
Predation rate	(Intercept)	-1.911	0.259	-7.383	< 0.001	15	0.20	0.44	29.46
	PCP	1.751	0.928	1.887	0.079				[28.07]
							[0.17]	[0.45]	
	Presence local SNH	-0.172	0.240	-0.718	0.484				
Cherry trees-Aphids & Pollen beetles-Natural enemies association									
Damage rate	(Intercept)	1.065	0.416	2.560	0.016	27	0.01	0.73	73.90
	PCP	-0.396	0.690	-0.573	0.571				[71.91]
	Presence local SNH	0.031	0.375	0.083	0.934		[0.01]	[0.73]	
Tomato-Lepidoptera-Natural enemies association									
No. of galleries	(Intercept)	5.002	0.055	91.777	< 0.001	16	0.18	0.12	175.47
	PCP	0.220	0.278	0.792	0.440				[175.22]
	Presence local SNH	0.091	0.070	1.325	0.204		[0.10]	[0.13]	
No. of damaged fruits	(Intercept)	3.654	0.071	51.525	< 0.001	16	0.18	0.16	134.70
	PCP	0.306	0.362	0.844	0.411				[134.25]
	Presence local SNH	0.111	0.090	1.232	0.236		[0.11]	[0.16]	

the supply of natural pest control and landscape complexity depending on the type of crops, pests and biocontrol agents considered in the studies (Alexandridis et al., 2022; Bianchi et al., 2006; Karp et al., 2018; Tamburini, Santoiemma et al., 2020; Veres et al., 2013) and the different locations of the case studies (Petit et al., 2020; Tougeron et al., 2022; Zhang et al., 2020). For example, a correlation of aphid parasitoid activity with landscape complexity was also not found by Hawro et al. (2015), who focused on cereal aphids in five locations in Europe. Instead, they observed a stronger correlation with agricultural intensification, specifically a weak tendency towards higher parasitoid species richness and parasitism rates in low-intensity cropland. Moreover, there is growing evidence that the density of cereal aphids' parasitoids is influenced by aphids' density itself rather than landscape factors (Bosem Baillod et al., 2017; Redlich et al., 2018). On the contrary, pollen beetle control appeared to be more dependent on landscape characteristics, such as SNH composition and configuration, but also on the proportion of oilseed rape, which can lead to a decrease in pollen beetle abundance due to a dilution effect (Berger et al., 2018; Skellern and Cook, 2018). In parallel, high plant density, high nutrient status and reduced or no tillage during the establishment of crops following oilseed rape have been found to reduce crop damage and enhance parasitoids' survival (Skellern and Cook, 2018). This highlights the importance of both landscape and local-level factors in understanding natural pest control (Berger et al., 2018; Rusch et al., 2011; Skellern and Cook, 2018) and thus in designing suitable models of natural pest control.

In addition to the factors considered, the parameters and structure of the model may play an important role in the final results. In our application, we used the same parameters of the original model (i.e. the scores assigned to the different SNH types), but in order to improve the correlation between modeled and measured values of natural pest control such parameters should probably vary according to the different species of biocontrol agents considered. Indeed, the contribution of SNH types to supporting biocontrol agents can vary depending on the insects' traits (e.g. insects that overwinter mainly inside crops vs outside crops, insects that prefer forested areas vs grassy strips). As can be seen from the results the radius of influence of SNH can increase for some biocontrol agents, suggesting that the maximum area around the site considered in the model should also be changed based on the considered association between crop, pest and biocontrol agents.

5. Conclusion

Shifting to agriculture that relies more on natural pest control than on the massive use of pesticides is an important step towards more sustainable agriculture that has a positive impact on biodiversity and ecosystem services (e.g. soil formation, purification of water, pollination) and is more adaptable to future scenarios related to climate change.

Robust and reliable natural pest control models can help achieve these results by supporting farmers' decisions on where and to what extent measures should be applied at the landscape and local level. The results of our study showed that generic models based only on SNH composition and configuration do not have sufficient predictive power. Further, landscape characteristics alone do not always explain natural pest control values. Considering landscape composition and configuration in different combinations in future applications could provide further insights into the effect of landscape complexity on natural pest control, as they may affect the service supply differently, for instance depending on the scale of analysis (Zhang et al., 2020). Factors at the local level had an overall positive effect on field-measured pest control, and including them in the models mainly increased their predictive power. Additional data would be needed to better test the effects of local level factors on different indicators of natural pest control, as, for example, information on conventional/conservation tillage and conventional/organic management was available only for a few crop-pests-biocontrol agents associations. Moreover, it would be interesting to consider other local management factors such as crop diversity and field size, which could not be calculated for all case studies with the available land-use maps. Similarly, it was not possible to test the effect of the (lack of) application of agro-chemicals, which could affect the presence and effectiveness of biological control agents and would therefore be another important factor to consider in future models. Although our results cannot provide conclusive evidence on the effect of local level factors on natural pest control for all considered associations, when combined with the existing literature, they suggest that considering local level factors in models of natural pest control is an important element. Moreover, within the frame of generic natural pest control models, different predictive tools should be developed for different associations of crop-pests-biocontrol agents, or at least the model parameters should be adapted according to the insects considered. This would allow us to account for the different trait-mediated responses of pests and biocontrol agents to the landscape, which are responsible for the variability of the results obtained also in this study. Alexandridis et al. (2022) already worked in this direction by using archetypes to group together pests-enemy systems typical of American and African agroecosystems that share the same traits (i.e. dietary, dispersal and overwintering strategies) and therefore also show the same responses to landscape characteristics and management. The potential of archetype modeling approaches is to maintain some model generality while capturing the ecological processes at play. Finally, although it has not been tested here, we believe that future models of natural pest control should also incorporate climate data, as shifts in temperature and precipitation patterns can influence pest outbreaks and the effectiveness of biocontrol agents.

The results of this study show that it is difficult to obtain effective generic tools for predicting natural pest control with sufficient explanatory power to support decision making for land users. However, our findings can still be used to stimulate discussion with local stakeholders on spatial planning of agricultural areas. Moreover, we hope that they will make a valuable contribution to the development of future generic predictive models that can successfully support the transition to low-pesticide agricultural systems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share the land-use maps. The field measurements of natural pest control are already publicly available. The R code is reported in the Supplementary Material.

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CRediT authorship contribution statement

All authors contributed to the conceptualization of the research. Ma. B. conducted the research including all data preparation and analysis steps, with M.S. contributing to the R coding. Ma.B. wrote the first draft of the paper and all authors contributed to review and editing.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108215.

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