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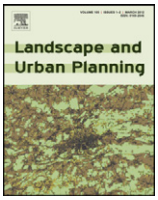

Using landscape indicators to predict high pest infestations and successful natural pest control at the regional scale

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ABSTRACT

Designing multifunctional landscapes requires accurate indicators to assess the effect of landscape structure on the provision on ecosystem services. Biological pest control relying on natural enemies is an important ecosystem service considered as a sustainable alternative to chemical control. The aim of this study was to measure and compare the accuracy of landscape indicators computed at various spatial scales to predict pollen beetle infestations and successful biological control in northwestern France. The sensitivity, specificity, and probability of correctly ranking fields were estimated for each indicator based on a survey of 42 fields using the receiver operating characteristic procedure. For pest infestation, the proportion of woodland and the proportion of semi-natural habitats were found to be informative indicators with good discriminatory abilities. For biological control, the proportion of woodland, the proportion of semi-natural habitats and the proportion of the previous year's oilseed rape fields with reduced soil tillage were found to be informative indicators with good discriminatory abilities. By using indicator values and optimal thresholds we were able to compute maps of areas at risk for pest infestation and those displaying successful biological control at the regional scale. This study provides tools that could help extension services, landscape planners, and policy makers in optimizing landscape structure according to the provision of a key ecosystem service. The results of this study also provide new grounds for understanding trophic interactions at the regional scale as well as the ambivalent effect of landscape complexity on pest and natural enemy populations.

1. Introduction

Agricultural intensification has an adverse impact on the environment and ecosystem services at various scales (Matson, Parton, Power, & Swift, 1997; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). More specifically, pesticide use poses a major threat for biodiversity and human health (Geiger et al., 2010; Koutros et al., 2009). Because pest management mainly relies on the intensive use of broad spectrum pesticides, there is now a need to design sustainable pest management strategies that better integrate ecological processes (Altieri, 1999; Gurr, Wratten, & Luna, 2003).

Biological pest control that relies on natural enemies such as predators or parasitoids is an important ecosystem service considered as a sustainable alternative to chemical control (Gurr et al., 2003; Letourneau, Jedlicka, Bothwell, & Moreno, 2009). There are two different, complementary strategies for promoting natural pest control in agroecosystems: crop management practices at the field scale, such as increasing within-field diversity or reducing soil tillage, and landscape management measures such as optimizing the spatial configuration between crop and semi-natural habitats (Landis, Wratten, & Gurr, 2000; Rusch, Valantin-Morison, Sarthou, & Roger-Estrade, 2010). However, despite the increasing body of evidence suggesting the strong influence of landscape context on population dynamics and trophic interactions, there is a lack of practical guidelines for landscape planning to optimize ecosystem services (Rusch et al., 2010).

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Designing multifunctional landscapes requires simple and accurate indicators to assess the impact of landscape structure on the provision of specific functions and in turn to help in the decision-making process (de Groot, 2006; Steingrover, Geertsema, & van Wingerden, 2010; Termorshuizen & Opdam, 2009). Indicators are widely used in agro-ecology to assess farming systems or the effects of agri-environmental policies (Lovell et al., 2010; Makowski, Tichit, Guichard, Van Keulen, & Beaudoin, 2009). The development of applicable landscape measures integrating landscape functioning also need to produce knowledge about which critical values best provide the services decision-makers have designated as important (Opdam, Steingrover, & van Rooij, 2006). Landscape measures to improve the pest control function in agroecosystems should be built upon the relationship between landscape structural characteristics and functioning. For instance, an increasing number of studies have demonstrated that the proportion of semi-natural habitats (i.e. landscape complexity) strongly influences biological pest control, with more complex landscapes generally leading to higher predation or parasitism rates (Bianchi, Booij, & Tscharntke, 2006). However, even though there is an increasing concern about the relationships between landscape features and biological control, the accuracy of landscape indicators to correctly categorize fields according to their risks of pest infestations or to their probabilities of successful biological pest control has not been investigated before.

The pollen beetle (*Meligethes aeneus* F.) (Coleoptera, Nitidulidae) is one of the most important insect pests in winter oilseed rape (OSR) (*Brassica napus* L.) in Europe, implying important amounts of insecticides sprayed over fields. Due to this intensive pesticide pressure, insecticide-resistance in pollen beetle populations has been an increasing and rapidly spreading phenomenon in many European countries (Detourne, Ballanger, & Delorme, 2008). Therefore, there is a need to develop alternative pest management strategies. After emergence from overwintering areas, adults migrate onto OSR fields to feed on pollen and oviposit in buds thereby inflicting severe yield losses. Pollen beetle larvae develop within buds and flowers and drop to the ground to pupate. The new generation of pollen beetle emerges a few weeks later, in early summer, and rapidly searches for overwintering sites. In Europe, univoltine parasitoids are major biological control agent of pollen beetle (Ulber, Williams, Klukowski, Luik, & Nilsson, 2010). Parasitoids emerge from the previous year's OSR fields and search for pollen beetle larvae during the flowering of the crop (i.e. in April and May) to lay their eggs. Then, the parasitoids overwinter as diapausing adults within their host cocoons to emerge the following spring from the previous year's OSR fields.

Pollen beetle infestations in winter oilseed rape are known to be increased by landscape complexity (Rusch, Valantin-Morison, Sarthou, & Roger-Estrade, in press; Zaller, Moser, Drapela, Schmoger, & Frank, 2008). However, parasitism rates of pollen beetle have also been found to be positively affected by landscape complexity (Rusch, Valantin-Morison, Sarthou, & Roger-Estrade, 2011-b). Moreover, host abundance has no effect on parasitism rates (Thies, Steffan-Dewenter, & Tscharntke, 2003) indicating that both pest and natural enemy populations seem to benefit from an increase in landscape complexity. This ambivalent effect of landscape complexity has also been reported in others studies on aphid populations (Roschewitz, Hucker, Tscharntke, & Thies, 2005; Thies, Roschewitz, & Tscharntke, 2005) and highlights the need to take into account all trophic levels if we are to optimize landscape structure so that it enhance biological pest control.

This study aims to measure and compare the accuracy of individual landscape indicators computed at various spatial scales to predict pest infestations and successful biological control in winter OSR using receiver operating characteristic (ROC) methodology. Based on this analysis we identified optimal thresholds of accurate landscape indicators to discriminate landscapes according to pest infestation and biological control levels. Finally, we computed posterior probabilities of high pest infestations and successful biological control for a given field based on landscape indicators values and produced maps at the regional scale. Using logistic regressions, we also investigated the interest of combining several individual landscape indicators to predict pest infestations and successful biological control.

2. Material and methods

2.1. Study area and data collection

A set of 42 winter OSR fields (23 fields in 2008 and 19 fields in 2009) located in the Haute-Normandie region of France was monitored for pollen beetle infestations and parasitism rates of pollen beetle larvae during 2008 and 2009. Fields were selected in order to build a gradient in landscape complexity ranging from simple and open landscapes, with less than 3% of semi-natural habitats, to more complex and closed landscapes, with more than 58% of semi-natural habitats (within a 2000 m radius around each field). For each year, non-overlapping landscapes were used to ensure spatial independence between fields. The landscape of this region is mainly characterized by little areas of semi-natural habitats such as small woodlots, hedgerows and grasslands and scattered among agricultural areas. The main crops are: cereals (75% of the arable land area), OSR (15%), sugar beet (4%), potato (2%), and high protein crops (2%).

Between bud development stage (Growth Stage GS 50) and flowering stage (GS 65) of OSR, pollen beetle infestations were measured by counting the number of adults on 50 randomly chosen plants along a transect. Parasitism rates of pollen beetle larvae were assessed at the end of flowering by sampling 150 larvae on 30 plants randomly selected along a transect. The larvae were dissected under a microscope to check for parasitism. Parasitoid species were identified according to Osborne (1960). Pollen beetle larvae were sampled at the end of flowering in order to provide an estimation of maximum parasitism rates by all possible parasitoid species.

Based on aerial photographs (BD ORTHO®, IGN, 2004, pixel size: 0.5 m) and intensive field inspections, we manually digitized the land use around each field and quantified the total area of each habitat type using ArcGis software (Version 9.2, ESRI). Habitat types were classified into 22 categories: arable land (16 different crop types), grassland (meadow and fallow), hedgerow, woodland, water area, and settlement. Because previous results have demonstrated the strong influence of semi-natural habitats and the fact that most landscape indexes are highly correlated, we chose to compute a few simple landscape indicators. Hence, the proportion of woodland, the proportion of grassland, the total proportion of semi-natural habitats, and the Shannon index of habitat diversity in the landscape around each field were calculated within eight different nested circular sectors with radii ranging from 250 m to 2000 m (see Appendix A for correlation matrices among landscape variables).

Because it has been found that pollen beetle abundance were negatively related to the area of OSR within the landscape, we also computed the proportion of OSR in each landscape at all given radii (Zaller et al., 2008). We also computed the proportion of the previous year's OSR fields with reduced soil tillage as these variables have been found to influence parasitoid survival and parasitism rates of pollen beetle larvae (Nilsson, 1985; Rusch et al., 2011-b). Each of these landscape indicators were first individually evaluated for accuracy in categorizing situations according to (i) pollen beetle infestation levels and (ii) larval parasitism rates (see below).

Logistic regression was then used to study the value of combining individual indicators (see below).

2.2. Receiver operating characteristic (ROC) curve analysis

For each type of dependent variable (i.e. pest infestation (P), or parasitism rate (B)), fields were divided into two groups depending on whether the variable exceeded a predefined threshold (noted P_{th} and B_{th}) or was below that threshold (Makowski et al., 2009). In the case of pest infestation, the two groups were defined according to an economic threshold, with pollen beetle densities over this threshold indicating high infestations and economic losses, and with population densities below this threshold indicating low pest infestations. Based on a recent survey of the various economic thresholds used in European countries (Williams, 2010), we categorized fields according to three different thresholds: $P_{th1} = 2$ pollen beetles per plant at growth stage 51; $P_{th2} = 6$ pollen beetles per plant at growth stage 55; $P_{th3} = 15$ pollen beetles per plant at growth stage 55. These thresholds are variable between countries because they are subjected to the economical context as well as climate and farming practices (Williams, 2010).

For parasitism rates, the two groups were defined according to a successful control threshold above which the pest population is assumed to be controlled and below which pest population is not or little affected by parasitoids. Several studies have provided strong evidence that successful biological control is associated with relatively high rates of parasitism and that probability of success increases with parasitism rates (Hawkins & Cornell, 1994; Hawkins, Thomas, & Hochberg, 1993; Kean & Barlow, 2000). In a modelling approach Kean and Barlow (2000) found that a host population can be impacted by 50% when parasitism rates were about 80%. Because the exact value of this control threshold is not known for pollen beetles, we investigated three thresholds above which biological pest control is assumed to be successful: $B_{th1} = 70\%$, $B_{th2} = 80\%$ and $B_{th3} = 90\%$. Let us remark here that the control exerted by parasitoids a given year impact the pest population that will attack oilseed rape fields the following year. Therefore, if we assume no migration between pest populations, high parasitism rates a given year are expected to limit pest infestation the following year.

Receiver operating characteristic (ROC) analysis was used to evaluate the ability of each landscape indicator to discriminate fields according to either infestations or parasitism rates, based on the given threshold values. A ROC analysis was performed separately for each landscape indicator at each spatial scale and for each value of P_{th} and B_{th}. The values of each landscape indicator at each spatial scale were then calculated for each field. Each indicator value (I) was compared to a decision threshold (I_{th}). These results were used to calculate the true positive proportion (TPP; sensitivity) and the true negative proportion (TNP; specificity). TPP is defined as the number of fields with $I > I_{th}$ in the group of fields with $D > D_{th}$ divided by the number of fields in that group; and TNP as the number of fields with $I \leq I_{th}$ in the group of fields with $P \leq P_{th}$ (or $B \leq B_{th}$) divided by the number of fields in that group. ROC curves show the relationship between the true positive proportion (TPP; sensitivity) and the false positive proportion (FPP; 1-specificity) across all possible values of I_{th} and for a given value of P_{th} or B_{th}. In the context of this study, sensitivity is therefore the probability of having an indicator predicting high pollen beetle infestation or high parasitism rates when the true infestations or parasitism rates are above the given thresholds. Similarly, specificity is the probability of having an indicator predicting low pollen beetle infestation or low parasitism rates when the effective infestations or parasitism rates are below the true infestations or parasitism rates. For each indicator at each spatial scale, ROC curves were thus created by plotting TPP against FPP.

To evaluate and compare the accuracy of each indicator, the area under the ROC curve (AUC) of each indicator was calculated. The AUC summarizes ROC plot with a measure of the overall accuracy of an indicator independently of a particular threshold. It can be interpreted as the probability that the indicator values for two randomly selected fields of positive and negative events will be correctly ranked (Makowski et al., 2009). Traditionally, prediction accuracy is considered not to be better than random for AUC values ≤ 0.5, poor when they fall within the 0.5–0.7 range, good if within the 0.7–0.9 range, and excellent for AUC values ≥ 0.9 (Swets, 1988). Thus, an indicator that provides no discrimination of whether pest or natural control is below or above P_{th} (or B_{th}) will have a ROC curve that follows the no-information line (the straight line between points (0,0) and (1,1)) and a AUC value equal to 0.5. An indicator with a good discriminatory ability will have a ROC curve that passes close to the point (0,1) and a AUC value close to 1 as it means that it will have a high sensitivity and a high specificity.

2.3. Optimal threshold

In practice, it is necessary to know the best cut-off point of an indicator to use as an operational threshold for decision-making. Various methods can be used to compute the best cut-off value of an indicator, e.g. Kappa-maximized threshold, Youden's index-maximized threshold, maximized sum of sensitivity and specificity (Zweig & Campbell, 1993). When the objective is to minimize the overall error, then the threshold approaching the coordinate (0,1) is considered as the optimal threshold, i.e. the point that is furthest to the non-informative line and which corresponds to a maximized TPP and TNP. As a general rule, a good classifier needs to minimize the false positive and negative proportions or maximize the true negative and positive proportions. The threshold that minimizes the difference between sensitivity and specificity is thus defined as the optimal threshold. This threshold corresponds to the point where both sensitivity and specificity curves crossed (Makowski et al., 2009). We thus determined the optimal threshold for every pest and parasitism thresholds of all informative indicators.

2.4. Posterior probability

Sensitivity and specificity values can be used to compute posterior probability of $P > P_{th}$ (or $B > B_{th}$) and $P < P_{th}$ (or $B < B_{th}$) for a new field depending on the indicator value obtained in this new field (Makowski et al., 2009). For a given indicator I and a decision threshold I_{th}, the probability of $P > P_{th}$ conditional to $I > I_{th}$ is defined by:

$$Pr(P > P_{th}|I > I_{th}) = \frac{Se(I_{th})Pr(P > P_{th})}{Se(I_{th})Pr(P > P_{th}) + [1 - Sp(I_{th})][1 - Pr(P > P_{th})]}$$

$\Pr(P > P_{th})$ is the prior probability of $P > P_{th}$ which can be estimated from our data set as the proportion of fields with $P > P_{th}$ for each threshold, and $\Pr(P > P_{th}|I > I_{th})$ is the posterior probability when $I > I_{th}$ in a new field. $Se(I_{th})$ and $Sp(I_{th})$ are respectively the sensitivity and the specificity for a given threshold I_{th} and are derived from previous ROC analysis (Makowski et al., 2009). We computed posterior probabilities for the indicator "proportion of woodland at the 2000 m scale" but it can be applied to other indicators and with other pest or parasitism thresholds. All computations were performed using the statistical software R 2.11 (R Development Core Team, 2010) and the ROCR package (Sing, Sander, Beerenwinkel, & Lengauer, 2005).

2.5. Maps

Based on the accuracy of landscape indicators to discriminate negative and positive situations for pest infestation and

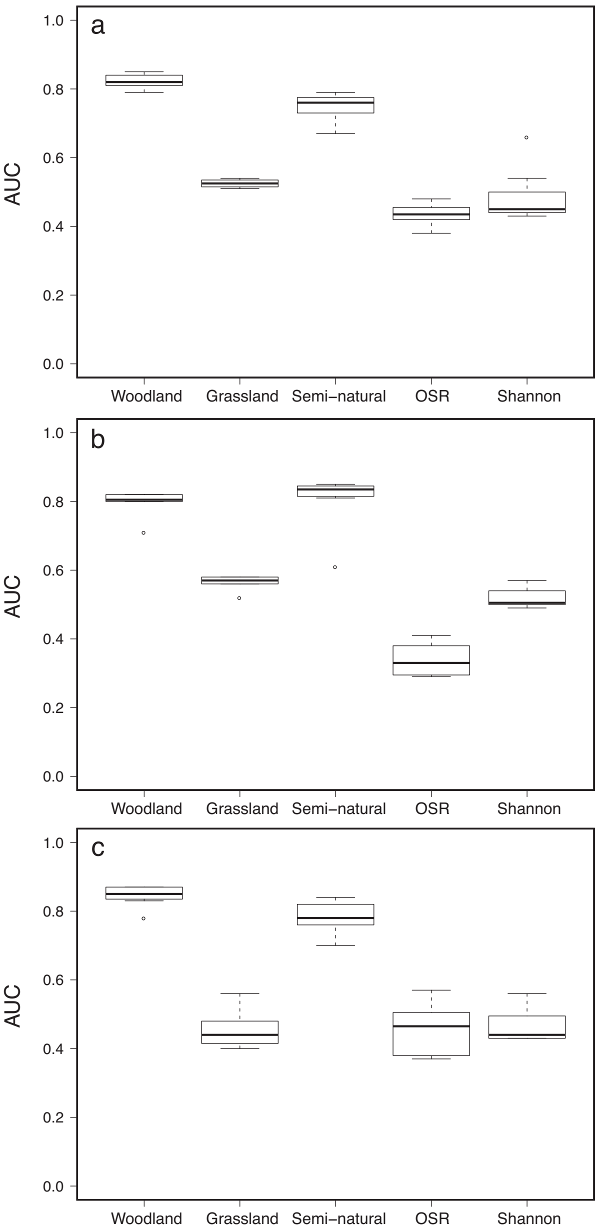

Fig. 1. Values of the area under the ROC curves (AUC) for each individual indicator considering all spatial scales for high pollen beetle infestation in function of threshold values P_{th1} (a), P_{th2} (b) and P_{th3} (c). The box-plots show median (horizontal line in the box) AUC value per indicator computed for each of the eight spatial scales. The bottom and top of the box are the first and third quartiles. The whiskers represent the minimum and the maximum value. Observations outside the range of the whiskers are plotted individually.

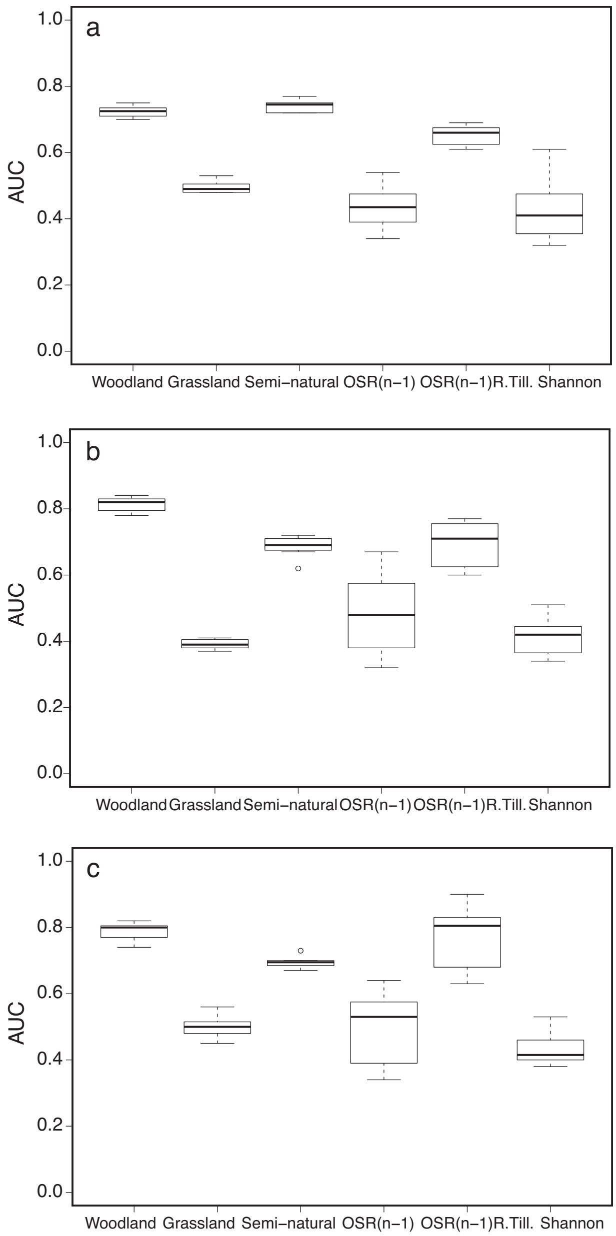

Fig. 2. Values of the area under the ROC curves (AUC) for each individual indicator considering all spatial scales for high parasitism rates in function of threshold values P_{th1} (a), P_{th2} (b) and P_{th3} (c). The box-plots show median (horizontal line in the box) AUC value per indicator computed for each of the eight spatial scales. The bottom and top of the box are the first and third quartiles. The whiskers represent the minimum and the maximum value. Observations outside the range of the whiskers are plotted individually.

biological pest control, we mapped landscape situations over the entire region. Based on the optimal thresholds identified for individual landscape indicators, we were able to produce binary maps with and without structural risk for pollen beetle infestations and with or without successful pest control according to the indicator value. The value of each indicator was calculated for each point of the raster layer (cell size = 100 m × 100 m) using the CORINE Land Cover data base and the ArcGis software (Version 9.2, ESRI), and compared it to the optimal threshold. This approach gave us general and simple predictions of arable land running a risk of high pollen beetle infestation and a risk of unsuccessful natural control according to the indicator values. Some examples of maps are presented in the results section.

2.6. Logistic regression

Using logistic regression, at each spatial scale, different landscape indicators were combined to predict the probability of high pollen beetle infestation and successful biological control according to the given thresholds. Logistic regression was used to examine the interest of using several indicators computed at the same spatial scale to predict the probability of high pest infestation or successful biological control for each threshold (Barbottin et al., 2008). For pollen beetle infestation, we used the proportion of woodland, the proportion of grassland, the proportion of OSR, and the Shannon index of habitat diversity. For parasitism rates, we combined the proportion

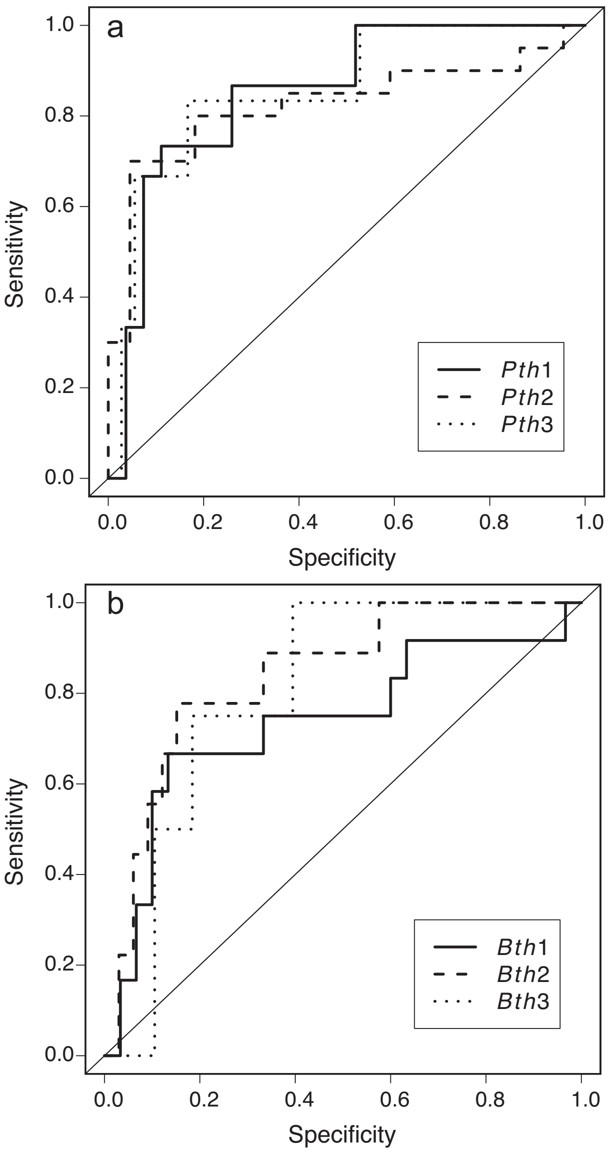

Fig. 3. ROC curves of the indicator "proportion of woodland within the 2000 m spatial scale" for high pollen beetle infestation (a) and high parasitism rates (b) obtained respectively with thresholds P_{th1}, P_{th2}, P_{th3} and B_{th1}, B_{th2}, B_{th3}. The straight line between points (0,0) and (1,1) represents the no-discrimination line.

of woodland, the proportion of grassland, the proportion of the previous year's OSR fields with reduced tillage, and the Shannon index of habitat diversity. We used Akaike Information Criterion (AIC) and multimodel inference for parameter estimations and calculated the relative importance of each variable (Burnham & Anderson, 2002). For a set of indicators at a given spatial scale, the multi-model inference approach considers all the possible models obtained from linear combinations of the indicators. Each model was then ranked according to its Akaike weight, and parameter estimations were computed by a weighted average of parameter estimates from models in which a given variable is explicitly present (Burnham & Anderson, 2002). As previously, for each logistic regression at each scale, the discriminatory ability of each model was assessed using ROC curve analysis and AUC. AUC values for logistic regressions were computed using leave-one-out cross validation to limit the risk of the underestimation of model errors (Primot, Valantin-Morison, & Makowski, 2006).

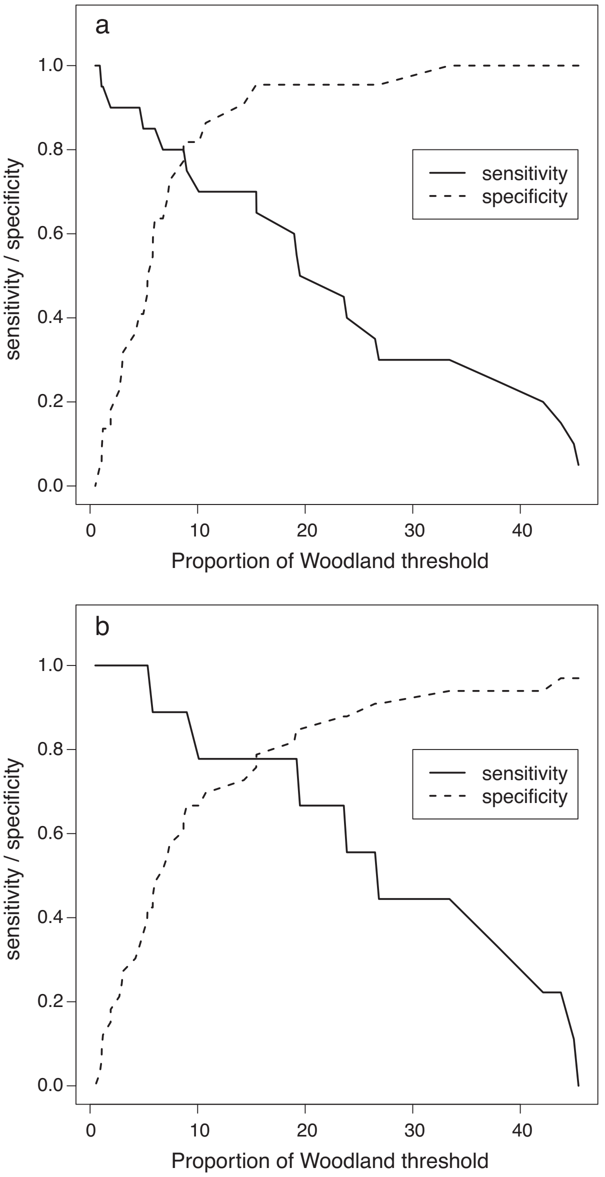

Fig. 4. Sensitivity and specificity of the indicator "proportion of woodland within the 2000 m spatial scale" for pollen beetle infestation above P_{th2} (a) and parasitism rates above B_{th2} (b) as a function of the indicator value.

3. Results

The mean number of pollen beetles in a field at GS 51 ranged from 0 to 26.92 adults per plant and the mean number of pollen beetles at GS 55 ranged from 0.84 to 27.56 adults per plant. Parasitism rates of pollen beetle larvae ranged from 0% to 98%. Pollen beetle density was above P_{th1} in 35.7% of the fields, above P_{th2} in 47.6% of the fields, and above P_{th3} in 14.2% of the fields. The parasitism rate of pollen beetle larvae was above B_{th1} in 28.5% of the fields, above B_{th2} in 21.4% of the fields, and above B_{th3} in 9.5% of the fields.

3.1. AUC values of individual indicators

AUC values obtained from ROC curves of each indicator at a given threshold are presented in Table 1 for pollen beetle infestation, and in Table 2 for parasitism rates of pollen beetle larvae. Proportion of woodland and proportion of semi-natural habitats in the landscape were informative indicator of pest infestations as shown by their

Table 1
Values of the area under the curve (AUC) of each individual indicator computed at various spatial scales and of the logistic models combining several landscape indicators computed at the same spatial scale for high pollen beetle infestation. AUC values have been calculated for three different thresholds: P_{th1} = 2 pollen beetles per plant at growth stage 51; P_{th2} = 6 pollen beetles per plant at growth stage 55; P_{th3} = 15 pollen beetle per plant at growth stage 55. AUC was estimated by cross-validation for logistic models.

Pest thresholds	Indicators	Spatial scale							
		250 m	500 m	750 m	1000 m	1250 m	1500 m	1750 m	2000 m
P_{th1}	Prop woodland	0.82	0.83	0.81	0.79	0.81	0.82	0.85	0.85
	Prop grassland	0.51	0.52	0.51	0.54	0.54	0.54	0.53	0.52
	Prop semi-natural habitats	0.67	0.76	0.72	0.74	0.76	0.77	0.79	0.78
	Prop OSR	0.38	0.41	0.43	0.47	0.48	0.44	0.44	0.43
	Shannon index of habitat diversity	0.66	0.54	0.46	0.45	0.45	0.44	0.43	0.44
	Logistic regression	0.79	0.80	0.79	0.77	0.76	0.78	0.83	0.84
P_{th2}	Prop woodland	0.71	0.80	0.81	0.80	0.80	0.82	0.82	0.82
	Prop grassland	0.52	0.58	0.58	0.56	0.56	0.57	0.57	0.58
	Prop semi-natural habitats	0.61	0.81	0.82	0.83	0.84	0.84	0.85	0.85
	Prop OSR	0.41	0.41	0.35	0.34	0.32	0.29	0.29	0.30
	Shannon index of habitat diversity	0.56	0.57	0.52	0.49	0.50	0.50	0.50	0.51
	Logistic regression	0.64	0.79	0.80	0.81	0.81	0.82	0.84	0.87
P_{th3}	Prop woodland	0.78	0.83	0.84	0.85	0.87	0.87	0.86	0.85
	Prop grassland	0.56	0.48	0.48	0.44	0.40	0.41	0.42	0.44
	Prop semi-natural habitats	0.70	0.78	0.75	0.75	0.78	0.80	0.83	0.84
	Prop OSR	0.45	0.57	0.53	0.48	0.48	0.38	0.38	0.37
	Shannon index of habitat diversity	0.49	0.56	0.50	0.45	0.43	0.43	0.43	0.43
	Logistic regression	0.63	0.82	0.81	0.82	0.85	0.86	0.86	0.78

high AUC values irrespective of thresholds (Table 1 and Fig. 1). For these indicators, the AUC values ranged between 0.61 and 0.87. The mean AUC value at all scales and all infestation thresholds was 0.82 for the indicator "proportion of woodland" and 0.77 for the indicator "proportion of semi-natural habitats", indicating that they are informative and that they have a good discriminating ability (see the example of ROC curves for pest infestation in Fig. 3a). When considering all infestation thresholds, these two indicators seem to have the best discriminating ability at larger spatial scales (Table 1). When considering all spatial scales for each infestation threshold, the indicator "proportion of woodland" is a more informative indicator than "proportion of semi-natural habitats" (Table 1).

The proportion of grassland, the proportion of OSR, and the Shannon index of habitat diversity were not informative indicators of pest infestations at any spatial scale (Table 1). The AUC values for the proportion of grassland ranged from 0.51 to 0.58 across all spatial scales for P_{th1} and P_{th2} and were lower than 0.50 at P_{th3} at all spatial scales except for the 250 m spatial scale (i.e. AUC = 0.56). The proportion of OSR always had AUC values lower than the non-informative line (AUC = 0.5) except for P_{th3} at the 500 m and the 750 m spatial scales when AUC values were of 0.57 and 0.53, respectively. The AUC values for the Shannon index for P_{th1} and P_{th2} revealed that this indicator was quite informative at the 250 m scale, whereas this was not the case for P_{th3} and for other scales.

For parasitism rates, the proportion of woodland, the proportion of semi-natural habitats and the proportion of the previous year's OSR fields with reduced soil tillage were informative indicator for all thresholds (Table 2 and Fig. 2). For these three indicators, the AUC values ranged between 0.60 and 0.90. The mean AUC value at all scales and all parasitism thresholds was 0.77 for the indicator "proportion of woodland", 0.70 for "proportion of semi-natural habitats" and 0.70 for the indicator "proportion of the previous year's OSR fields with reduced soil tillage". They had therefore a good ability to discriminate between negative and positive situations (see example of ROC curves for parasitism rates in Fig. 3b). When considering all spatial scales for each parasitism threshold, it seems that the indicator "proportion of woodland" is a more informative indicator than the other two, except for the proportion of the previous year's OSR fields with reduced soil tillage at the 2000 m scale. For the indicators "proportion of woodland" and

Table 2
Values of the area under the curve (AUC) of each individual indicator computed at various spatial scales and of the logistic models combining several landscape indicators computed at the same spatial scale for successful biological control. AUC values have been calculated for three different parasitism thresholds: B_{th1} = 70%; B_{th2} = 80%; B_{th3} = 90%. AUC was estimated by cross-validation for logistic models.

Biocontrol thresholds	Indicators	Spatial scale							
		250 m	500 m	750 m	1000 m	1250 m	1500 m	1750 m	2000 m
B_{th1}	Prop woodland	0.75	0.74	0.71	0.70	0.71	0.72	0.73	0.73
	Prop grassland	0.53	0.51	0.48	0.48	0.48	0.50	0.50	0.48
	Prop semi-natural habitats	0.72	0.77	0.72	0.72	0.74	0.75	0.75	0.75
	Prop previous year's OSR with reduced tillage	0.62	0.61	0.63	0.66	0.66	0.67	0.68	0.69
	Shannon index of habitat diversity	0.61	0.36	0.32	0.35	0.40	0.42	0.46	0.49
	Logistic regression	0.74	0.71	0.64	0.66	0.69	0.70	0.72	0.73
B_{th2}	Prop woodland	0.84	0.83	0.79	0.78	0.70	0.81	0.83	0.83
	Prop grassland	0.38	0.39	0.37	0.38	0.39	0.41	0.41	0.40
	Prop semi-natural habitats	0.62	0.71	0.67	0.68	0.69	0.69	0.71	0.72
	Prop previous year's OSR with reduced tillage	0.60	0.60	0.65	0.70	0.72	0.75	0.76	0.77
	Shannon index of habitat diversity	0.51	0.38	0.34	0.35	0.41	0.43	0.44	0.45
	Logistic regression	0.74	0.78	0.76	0.75	0.79	0.82	0.84	0.87
B_{th3}	Prop woodland	0.82	0.78	0.74	0.76	0.81	0.80	0.82	0.80
	Prop grassland	0.49	0.56	0.52	0.51	0.51	0.48	0.48	0.45
	Prop semi-natural habitats	0.70	0.73	0.70	0.70	0.69	0.68	0.68	0.67
	Prop previous year's OSR with reduced tillage	0.67	0.63	0.69	0.79	0.82	0.82	0.84	0.90
	Shannon index of habitat diversity	0.53	0.38	0.43	0.40	0.40	0.40	0.43	0.49
	Logistic regression	0.58	0.57	0.56	0.74	0.89	0.90	0.92	0.92

Table 3
Estimated parameters values, their standard errors (SE) and the relative variable importance for logistic models predicting the probability of high pollen beetle infestation (a) and successful biological control (b) using landscape indicators computed at the 2000 m spatial scale. For each dependent variable we used three different thresholds.

(a)

Pest thresholds	Prop OSR		Prop woodland		Prop grassland		SHDI	
	Estimated parameter values (SE)	Relative variable importance	Estimated parameter values (SE)	Relative variable importance	Estimated parameter values (SE)	Relative variable importance	Estimated parameter values (SE)	Relative variable importance
P_{th1}	0.18 (0.23)	0.59	0.15 (0.07)	0.99	0.09 (0.10)	0.66	0.43 (1.45)	0.31
P_{th2}	−0.001 (0.10)	0.34	0.18 (0.06)	0.99	0.08 (0.06)	0.79	−0.1 (1.12)	0.27
P_{th3}	0.01 (0.15)	0.3	0.11 (0.06)	0.96	0.02 (0.07)	0.33	0.93 (2.47)	0.34

(b)

Biocontrol thresholds	Prop OSR(n-1) Red Till.		Prop woodland		Prop grassland		SHDI	
	Estimated parameter values (SE)	Relative variable importance	Estimated parameter values (SE)	Relative variable importance	Estimated parameter values (SE)	Relative variable importance	Estimated parameter values (SE)	Relative variable importance
B_{th1}	0.31 (0.24)	0.78	0.07 (0.03)	0.95	0.01 (0.03)	0.39	0.54 (1.35)	0.34
B_{th2}	0.71 (0.35)	0.97	0.12 (0.04)	0.99	−0.006 (0.04)	0.28	1.46 (2.42)	0.46
B_{th3}	1.17 (0.68)	0.99	0.13 (0.10)	0.9	0.016 (0.09)	0.29	2.72 (5.26)	0.43

Prop OSR, proportion of oilseed rape; Prop woodland, proportion of woodland; Prop grassland, proportion of grassland; SHDI, Shannon index of habitat diversity; Prop OSR(n-1) Red. Till, proportion of previous year's oilseed rape fields with reduced tillage.

“proportion of semi-natural habitats”, the lowest AUC values were always obtained for the intermediate spatial scales (i.e. 750–1250 m), indicating better discriminating ability for successful biological control when these indicators were computed at small and large scales (Table 2). The AUC values for the indicator “proportion of OSR fields with reduced soil tillage” were always higher at larger spatial scales, indicating better discriminating ability for successful biological control when this indicator was computed at large scales (Table 2). The proportion of grassland and the Shannon index of habitat diversity were in no case informative indicators (except for the 250 m scale at B_{th1}) (Table 2).

3.2. Logistic regression models

Estimated parameter values and the relative variable importance obtained for logistic regressions revealed an important positive effect of the proportion of woodland on the probability of high pollen beetle infestation to occur for each pest threshold (Table 3a). We also found positive effects of the proportion of woodland and the proportion of previous year's OSR fields with reduced tillage on the probability of high parasitism rates for each parasitism threshold (Table 3b). AUC values estimated by leave-one-out cross validation for each logistic regression are given in Table 1 for pollen beetle infestation and in Table 2 for biological pest control. Considering all pest and parasitism thresholds, the mean AUC value was 0.79 (min.: 0.63; max.: 0.87) for pollen beetle infestation, and 0.75 (min.: 0.56; max.: 0.92) for parasitism rates. Thus, AUC values obtained from logistic regression for pollen beetle infestation and parasitism rates were generally not higher than their respective values obtained for the best performing individual indicator (Tables 1 and 2). For parasitism rates, AUC values obtained from logistic regression at B_{th3} with the landscape indicator computed at large scales were higher than the best performing individual indicator at the same scales (Table 2).

3.3. Optimal thresholds and posterior probabilities

The optimal thresholds have been calculated for the indicator “proportion of woodland” for pest pollen beetle infestation and biological pest control (Table 4 and Fig. 4), as it appeared to be the more informative and robust indicator across spatial scales for each pest and parasitism threshold. For instance, Table 4a and b shows the threshold that gives the best trade-offs between sensitivity and specificity of the indicator “proportion of woodland” for pest infestation and natural control, respectively. If we consider the 2000 m scale and the indicator “proportion of woodland” we found that the best trade-offs between sensitivity and specificity were obtained for the threshold 10.10%, 8.70% and 19.51% respectively for P_{th1}, P_{th2} and P_{th3} and for 10.10%, 15.46% and 19.20% respectively for B_{th1}, B_{th2} and B_{th3} (Table 4 and Fig. 4). These results reveal the potential ambivalent effect of the landscape where landscape structures at risk for important pollen beetle infestations are also able to achieve successful biological control. These thresholds all had a sensitivity and a specificity higher than 0.63 for both pollen beetle infestation and parasitism rates. Other optimal thresholds can easily be computed for other indicators such as for the proportion of semi-natural habitats.

We computed the posterior probability that pest infestation would be higher than P_{th1}, P_{th2} and P_{th3} or that parasitism rates would be higher than B_{th1}, B_{th2} and B_{th3} for a new field conditionally to the proportion of woodland measured in the surrounding landscape. The prior probabilities $\Pr(P > P_{th})$ and $\Pr(B > B_{th})$ for each threshold are estimated as the proportion of fields where $P > P_{th}$ and $B > B_{th}$ in our dataset (i.e. 0.35, 0.47 and 0.14 respectively for P_{th1}, P_{th2} and P_{th3}; 0.28, 0.21, and 0.09 respectively for B_{th1}, B_{th2} and B_{th3}). The probabilities that pest infestation would be higher than P_{th1}, P_{th2} and P_{th3} when the proportion of woodland at the 2000 m scale is respectively higher than 10.10%, 8.70% and 19.51% are 0.66, 0.79 and 0.44, and are thus higher than the prior probabilities. Similarly, the probabilities that parasitism rates would be higher than B_{th1}, B_{th2} and B_{th3} when the proportion of woodland at the 2000 m scale is respectively higher than 10.10%, 15.46% and 19.20% are 0.44, 0.50 and 0.25, and are thus higher than the prior probabilities.

3.4. Maps

Among individual indicators, the proportion of woodland computed at the 1750 m and the 2000 m scales showed the highest AUC values and the best trade-offs for predicting pollen beetle infestation and parasitism rates whatever the thresholds (Tables 1 and 2). Using the proportion of woodland at the 2000 m scale, we generated binary maps for the entire region according to the landscape's potential structural risk of pollen beetle infestation (Fig. 5a) and

Table 4
Optimal thresholds with sensitivity and specificity values of the indicator "proportion of woodland" obtained at various spatial scales for pollen beetle infestation and parasitism rates at each threshold (P_{th1} = 2 pollen beetles per plant at growth stage 51; P_{th2} = 6 pollen beetles per plant at growth stage 55; P_{th3} = 15 pollen beetle per plant at growth stage 55) and parasitism thresholds (B_{th1} = 70%; B_{th2} = 80%; B_{th3} = 90%).

Thresholds	Spatial scale											
	250 m			500 m			750 m			1000 m		
	Sens.	Spec.	Thresh.	Sens.	Spec.	Thresh.	Sens.	Spec.	Thresh.	Sens.	Spec.	Thresh.
P_{th1}	0.80	0.81	1.25	0.73	0.74	9.77	0.73	0.74	10.90	0.73	0.74	9.89
P_{th2}	0.70	0.68	0.18	0.63	0.65	7.00	0.75	0.72	7.09	0.75	0.72	8.59
P_{th3}	0.66	0.66	1.77	0.83	0.80	17.65	0.83	0.80	19.39	0.83	0.77	20.38
B_{th1}	0.66	0.66	1.10	0.66	0.66	9.77	0.66	0.66	10.90	0.66	0.66	9.89
B_{th2}	0.77	0.78	2.37	0.77	0.78	14.65	0.77	0.75	13.04	0.66	0.66	10.07
B_{th3}	0.75	0.71	2.37	0.75	0.76	17.65	0.75	0.76	19.39	0.75	0.76	21.84

Thresholds	Spatial scale											
	1250 m			1500 m			1750 m			2000 m		
	Sens.	Spec.	Thresh.	Sens.	Spec.	Thresh.	Sens.	Spec.	Thresh.	Sens.	Spec.	Thresh.
P_{th1}	0.73	0.70	8.66	0.73	0.70	8.24	0.80	0.77	9.33	0.73	0.74	10.10
P_{th2}	0.75	0.70	8.12	0.75	0.77	7.37	0.75	0.77	8.78	0.80	0.81	8.70
P_{th3}	0.66	75.00	20.98	0.66	0.75	18.52	0.83	0.80	18.68	0.83	0.83	19.51
B_{th1}	0.66	0.66	8.66	0.66	0.63	8.24	0.66	0.75	10.33	0.66	0.66	10.10
B_{th2}	0.66	0.66	9.77	0.66	0.66	9.78	0.77	0.72	12.57	0.77	0.78	15.46
B_{th3}	0.75	0.76	22.04	0.75	0.76	20.31	0.75	0.76	18.68	0.75	0.76	19.20

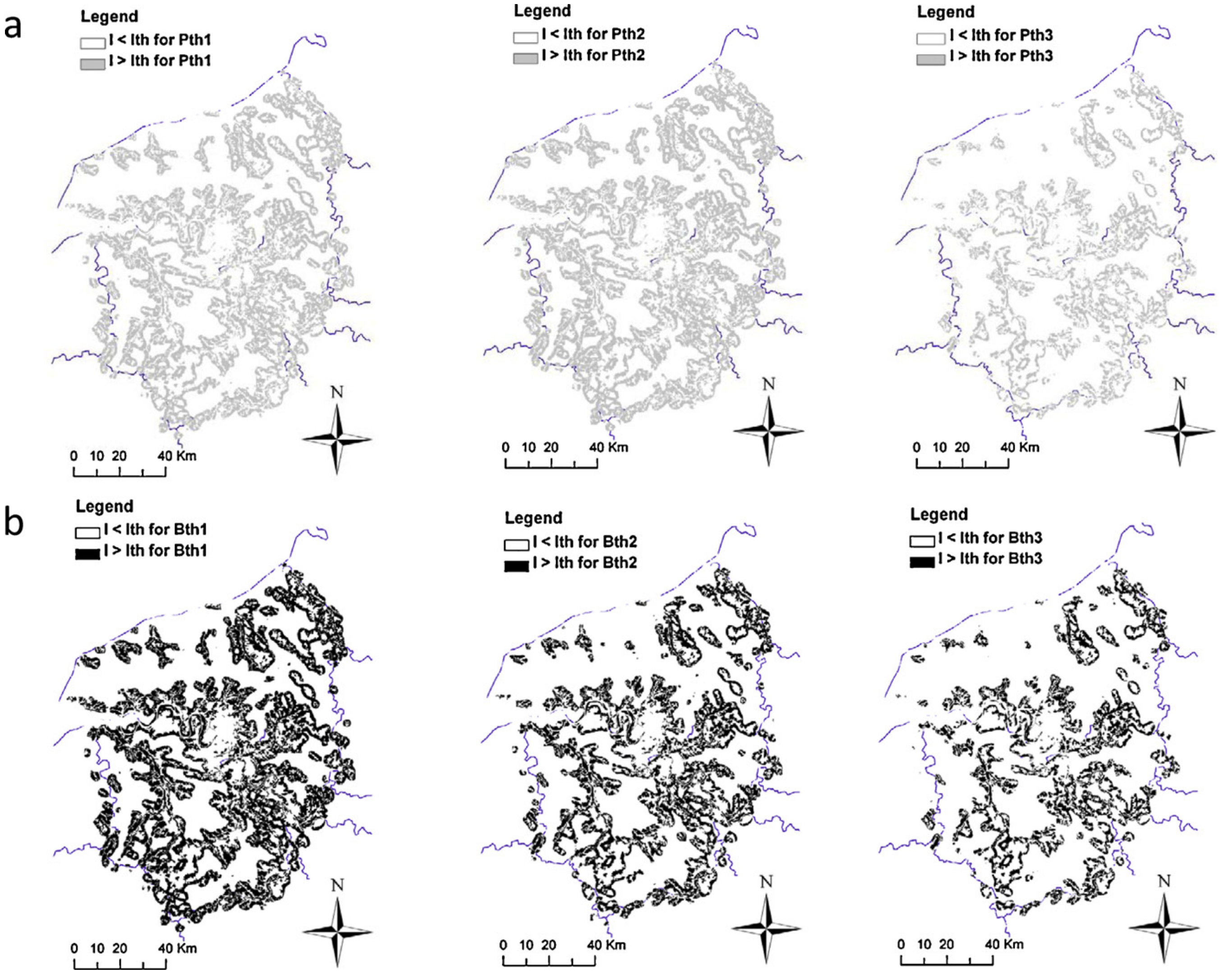

Fig. 5. Binary maps of the Haute-Normandie region based on the value of the indicator (I) "proportion of woodland in the 2000 m spatial scale" representing arable land with pollen beetle infestation above the three thresholds P_{th1}, P_{th2} and P_{th3} (a) and with parasitism rates above the three thresholds B_{th1}, B_{th2} and B_{th3} (b). For each map, white areas represent areas with an indicator (I) value below the optimal threshold (I_{th}) and the colored areas represent areas with an indicator value above the optimal threshold.

Table 5

Proportion between areas where the indicator "proportion of woodland within the 2000 m scale" indicated pest infestation above the thresholds P_{th1}, P_{th2} and P_{th3}, and areas where the indicator predicted parasitism rates above the thresholds B_{th1}, B_{th2} and B_{th3}. For instance, 46% of the area with pest infestation above P_{th2} is assumed to support parasitism rates above B_{th3}; 100% indicates that based on the indicator value there is total spatial synchrony.

Decision thresholds	B_{th1}	B_{th2}	B_{th3}
P_{th1}	100%	68%	51%
P_{th2}	90%	62%	46%
P_{th3}	100%	100%	100%

risk of unsuccessful biological control (Fig. 5b) for each of the thresholds. These maps are here to illustrate our findings and other binary maps could be computed using different infestations or parasitism thresholds as well as other landscape indicators. Based on this indicator, Arable land embedded in landscapes, where the indicator "proportion of woodland" was higher than the threshold identified on our dataset for pollen beetle infestation, represented 36%, 40% and 18% of the total area of the Haute-Normandie region respectively for P_{th1}, P_{th2} and P_{th3} (Fig. 5a). Similarly, arable land embedded in landscapes, where the indicator "proportion of woodland" was higher than the threshold for biological pest control, represented 36%, 25% and 18% of the total area respectively for B_{th1}, B_{th2} and B_{th3} (Fig. 5b). Other maps considering other pest or parasitism thresholds can be produced.

By taking into account areas with both a structural risk for pest infestation and a structural success for natural regulation, we defined zones of spatial synchrony (areas with high pest infestation and high parasitism rates) or asynchrony (areas with high pest infestation and low parasitism rates) between the pest and the parasitoid population (Fig. 6, Table 5). For instance, in the case of the indicator "proportion of woodland", we found that 10% of the area running the risk of high pollen beetle infestation was not successfully controlled for P_{th2} and B_{th1}. Similarly, we found that 54% of the area running the risk of high pollen beetle infestation was not successfully controlled for P_{th2} and B_{th3} (Table 5). Landscapes supporting unsuccessful biological control can be considered as spatial refuge for pest populations even at low adults densities.

4. Discussion

Our study showed that the accuracy of landscape indicators to correctly rank situations of high pest infestations and successful biological control were highly variable. For pollen beetle infestation, two individual landscape indicators (the proportion of woodland and the proportion of semi-natural habitats) were found to be informative and have a good discriminatory ability with AUC values above 0.7. For biological control, three individual landscape indicators (the proportion of woodland, the proportion of semi-natural habitats, and the proportion of the previous year's OSR fields with reduced soil tillage) were found to be informative and have a good discriminatory ability with AUC values above 0.6. The proportion of woodland was generally found to be a more informative indicator than the others. The other individual indicators appeared to be poor indicators of pest infestation and natural control as they did not perform better than random decision. The results of logistic regression revealed that the proportion of woodland always had positive effects on the probability of high pollen beetle infestation for each pest threshold. Both landscape complexity and the proportion of post harvest-soil tillage of OSR fields appeared to have positive effects on the probability of high parasitism rates of pollen beetle larvae. However, combining various landscape indicators through logistic regression generally did not improve prediction accuracy compared to the best individual landscape indicators for pollen beetle infestation and parasitism rates, except for B_{th3} when combining large scales indicators. The accuracy of local field management indicators such as plant density, nitrogen fertilization and field size have been examined for pollen beetle infestation and parasitism rates: they were always non informative indicators with AUC values < 0.5 (data not shown).

The good predictive accuracy of respectively two and three landscape indicators for high pollen beetle infestation and successful biological pest control may be explained by the life-cycle and the ecological requirements of both the pollen beetle and its parasitoids. Previous studies have demonstrated that pollen beetles overwinter in the soil of sheltered habitats (Müller, 1941; Rusch, Valantin-Morison, Roger-Estrade, & Sarthou, 2011-a). These habitats are able to provide protection against unsuitable climatic conditions by limiting winter mortality and favoring the number of pests the following spring. Thus, it was not surprising that we found a positive effect of the proportion of woodland on the probability of high pollen beetle infestation and that the indicator "proportion of woodland" was an accurate predictor of pollen beetle infestation in the field. However, because pollen beetle may overwinter in various habitats, it might be interesting to study the accuracy of such indicators in several regions contrasted in terms of habitat types and climatic conditions.

It has also been demonstrated that semi-natural habitats provide the natural enemies with key resources such as food resources, alternative hosts, and a refuge from disturbance which can lead to an increase in parasitoids fitness (Wäckers, van Rijn, & Bruin, 2005). Parasitoid populations have also been found to be negatively impacted by deep conventional soil tillage (Nilsson, 1985). These elements can explain the positive effects of the proportion of woodland and the proportion of the previous year's OSR fields with reduced soil tillage on the probability of successful biological control. They can also explain the capacity of these indicators to discriminate situations according to their level of biological control. Surprisingly, the proportion of grassland was found to be a non-informative indicator of successful biological control. This can be explained by the fact that we selected relatively high thresholds of parasitism rates and that in our dataset, very high rates of parasitism (>70%) were found in the same area characterized by large proportions of woodland. Moreover, grassland represent different habitat types, particularly due to various management, that were not taken into account by our land-use classification. Such variability in habitat types can also explain the poor discriminatory ability of the indicator "proportion of grassland".

The scales at which the accuracy of the indicators "proportion of woodland" and "proportion of semi-natural habitat" were the highest for both pollen beetle infestation and parasitism rates are in accordance with knowledge about pollen beetles and parasitoids. Indeed, it has been found that pollen beetle respond to landscape complexity at large scales whereas parasitoids seem to be influenced by landscape complexity at both small and large spatial scales (Rusch et al., 2011-b; Zaller et al., 2008; Zaller, Moser, Drapela, Schmoger, & Frank, 2009). However, the relative small variation in AUC values for a given indicator across spatial scales might be due to our binary classification of fields and to a relative constant proportion of each habitat types across spatial scales.

In our study, we used sensitivity and specificity of landscape indicators to determine their optimal thresholds. Hence, these optimal thresholds can be used as operational thresholds to categorize fields according to pollen beetle infestation and parasitism rates over the entire region. We found various optimal thresholds for the "proportion of woodland" (i.e. the more informative one) depending on the pest or parasitism threshold considered and on the scale at which the indicator is computed. For instance, if we consider a common economic threshold for pollen beetle infestations (i.e.

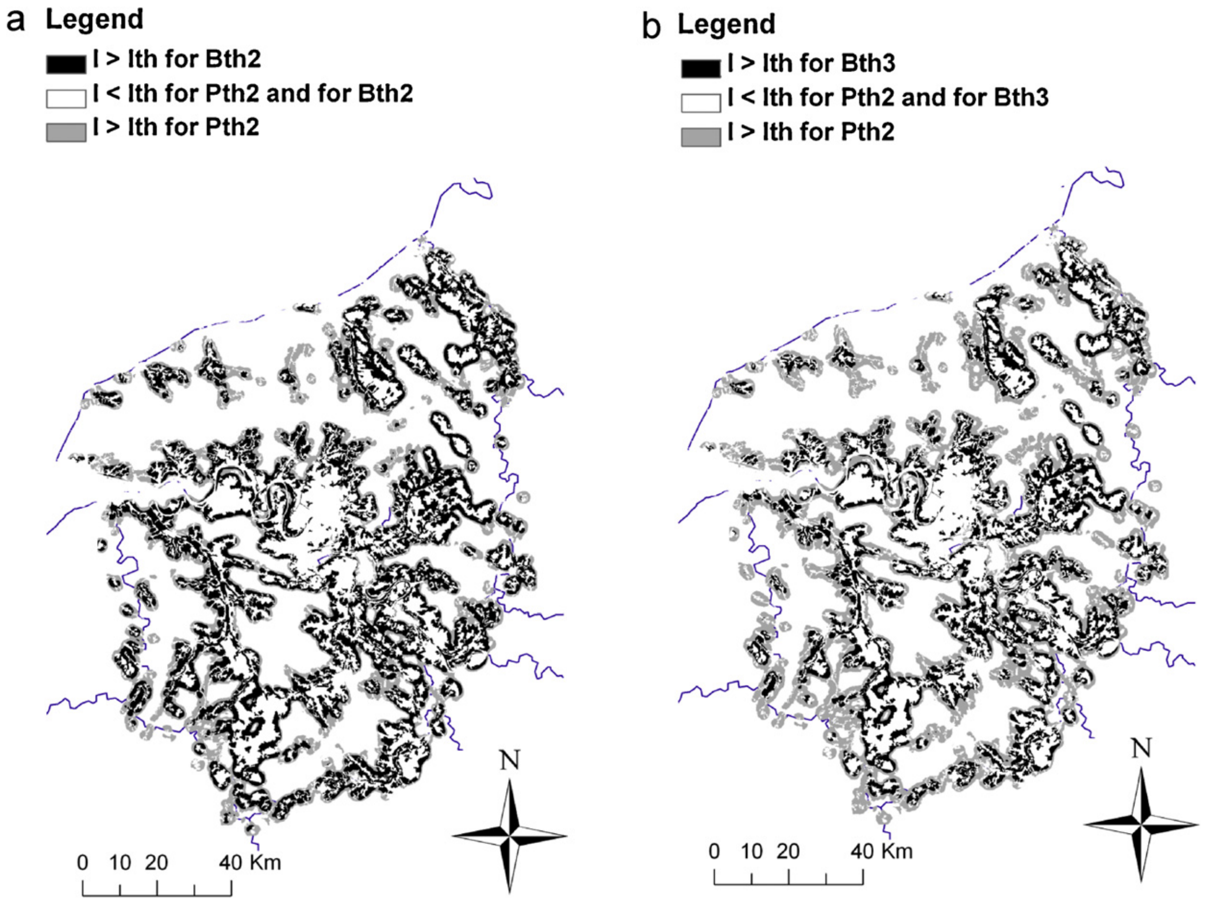

Fig. 6. Superposition of binary maps representing arable land with pollen beetle infestation above the thresholds P_{th2} and with parasitism rates above the threshold B_{th2} (a) according to the value of the indicator "proportion of woodland within the 2000 m spatial scale"; Superposition of binary maps representing arable land with pollen beetle infestation above the thresholds P_{th2} and with parasitism rates above the threshold B_{th3} (b) according to the value of the indicator "proportion of woodland within the 2000 m spatial scale". White areas represent areas with an indicator value below the optimal threshold for both pest infestation and biological control; black areas represent areas with an indicator value above the optimal threshold for biological control; grey areas represent areas with an indicator value above the optimal threshold for pest infestation.

P_{th1} = 2 pollen beetles per plant at GS 51), we found that fields surrounded by more than 10.10% of woodland within a 2000 m radius are assumed to favor pollen beetle infestation above P_{th1}. Similarly, if we considered that biological control is successful above the B_{th2} threshold (i.e. 80% of parasitism), we found that pest population in fields surrounded by more than 15.46% of woodland within a 2000 m radius are assumed to be successfully controlled a given year.

An increasing number of studies are exploring the relationships between landscape context and biological pest control (Chaplin Kramer, O'Rourke, Blitzer & Kremen, 2011), but to our knowledge none have assessed the accuracy of landscape indicators as well as determined their optimal thresholds for predicting levels of biological control. Our approach is therefore complementary to the correlative approaches usually developed in landscape ecology (e.g. Thies et al., 2003) as it assesses the accuracy of indicators and takes into account economical and biological control thresholds in a decision-making framework. However, the results of this study would need to be validated with independent and larger datasets from different regions and years to examine the robustness of landscape indicators.

The results and the approach developed in this study also provide new grounds for explaining the ambivalent role of landscape in the functioning of host–parasitoid interactions at the regional scale. Indeed, when considering spatial repartition of landscapes at risk for pest infestation and with efficient biological control for different realistic thresholds, we confirmed an ambivalent effect of landscape structure and highlighted potential zones of "spatial refuges" for the pest population. Spatial heterogeneity in the parasitoid attack rate is known to play an important role in the dynamics of host-parasitoid interactions as they influence pest mortalities and allow the host to benefit from enemy-free space (Berryman & Hawkins, 2006). In these refuges, pollen beetle larvae may have been parasitized but not to a sufficient degree to reach successful control thresholds. Such refuges may allow the persistence of pest populations as a major part of the population may escape the natural regulation exerted by their natural enemies. This part of the population could then supply new adults that would be able to colonize successfully controlled areas. For instance, simple landscapes are relatively poorly controlled areas providing new pollen beetles which are seeking semi-natural habitats for overwintering (Rusch et al., in press). Thus, new pollen beetles may disperse to complex landscapes to find suitable habitats. Such spatial pattern implying exchanges of populations among landscapes would allow the pest population to persevere at a larger scale.

This hypothesis is in accordance with the observed data on our region where landscapes with very high rates of parasitism a given year also support, in the spring of the following year, significant pollen beetle populations in woodland at emergence and same amounts of pollen beetles in OSR fields (data not shown). Indeed, this suggests immigration of the new generation just before overwintering from spatial refuges to areas where the majority of the local populations have been controlled by parasitoids the year before, i.e. with high rates of parasitism in these areas. Moreover, we found a negative relationship between female fecundity and adult densities in the spring (data not shown), confirming previous results from Hokkanen (2000). These results indicate that even areas with relatively low densities of adults in the spring may be able to provide non-negligible populations of the new generation which can act as sources of pollen beetle for the following year as no overwintering sites might be available in those landscapes. The hypothesis of spatial refuges for pollen beetles and long distance migration before overwintering is also in accordance with recent data on genetic diversity of pollen beetles (Kazachkova, Meijer, & Ekbom, 2007).

5. Conclusion

We found differences in accuracy for landscape indicators in predicting pollen beetle infestation and parasitism rates. More specifically, the proportion of woodland and the proportion of semi-natural habitats indicators appeared to be accurate ones for pollen beetle infestation. For parasitism rates of pollen beetle, the proportion of woodland and the proportion of semi-natural habitat indicators as well as the proportion of previous year's OSR fields with reduced tillage were all found to be informative indicators. The indicator "proportion of woodland" generally performed better than the others. Although our results necessitate further validation using independent datasets, we think that the approach developed in this study could help extension services, landscape planners, and policy makers for predicting landscapes running the risk of pest infestation or unsuccessful biological control. It should also help them to optimize spatial configuration to foster the biological control of pests. Indeed, computing maps at the regional scale makes it possible to readily compare and assess different scenarios of land use and thereby to optimize landscape configuration and services according to various pest or parasitism thresholds. Moreover, using landscape indicators can help in the understanding of biological control mechanisms by formulating new hypotheses about trophic interactions at large scales. For instance, our results highlight the potential existence of spatial refuges for pest populations. Hence, enhancing biological control through habitat and landscape management in these areas might be the key for the implementation of successful conservation biological control at the regional scale. In this study, we examined infestation of only one pest and its biological control through its specialized parasitoids. However, management at the landscape scale needs to take into account several objectives and services to achieve an optimization of land use. Thus, it should be interesting to study the effects of landscape context on a multi-species approach in order to find trade-offs in landscape management to optimize regulating services such as pollination and natural pest control.

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Appendix A.

Correlation matrix between variables at each spatial scale included in the logistic regressions for predicting the probability of (a) high pollen beetle infestations and (b) high parasitism rates.

(a)

Scale	Variables	Prop OSR	Prop woodland	Prop grassland	SHDI
2000 m	Prop OSR				
	Prop woodland	−0.32			
	Prop grassland	−0.62	−0.25		
	SHDI	−0.28	−0.12	0.38	
1750 m	Prop OSR				
	Prop woodland	−0.34			
	Prop grassland	−0.56	−0.27		
	SHDI	−0.22	−0.18	0.4	
1500 m	Prop OSR				
	Prop woodland	−0.36			
	Prop grassland	−0.51	−0.27		
	SHDI	−0.18	−0.22	0.42	
1250 m	Prop OSR				
	Prop woodland	−0.34			
	Prop grassland	−0.49	−0.24		
	SHDI	−0.14	−0.21	0.41	
1000 m	Prop OSR				
	Prop woodland	−0.3			
	Prop grassland	−0.45	−0.21		
	SHDI	−0.09	−0.17	0.46	
750 m	Prop OSR				
	Prop woodland	−0.21			
	Prop grassland	−0.46	−0.18		
	SHDI	0.03	−0.1	0.42	
500 m	Prop OSR				
	Prop woodland	−0.02			
	Prop grassland	−0.43	−0.21		
	SHDI	−0.004	−0.04	0.32	
250 m	Prop OSR				
	Prop woodland	−0.16			
	Prop grassland	−0.47	−0.11		
	SHDI	−0.63	0.07	0.5	

(b)

Scale	Variables	Prop reduced tillage OSR(n-l)	Prop woodland	ProP grassland	SHDI
2000 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.02			
	Prop grassland	−0.09	−0.25		
	SHDI	−0.19	−0.12	0.38	
1750 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.02			
	Prop grassland	−0.12	−0.27		
	SHDI	−0.17	−0.18	0.4	
1500 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.03			
	Prop grassland	−0.18	−0.27		
	SHDI	−0.14	−0.22	0.42	
1250 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.09			
	Prop grassland	−0.24	−0.24		
	SHDI	−0.12	−0.21	0.41	
1000 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.21			
	Prop grassland	−0.31	−0.21		
	SHDI	−0.18	−0.17	0.46	
750 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.28			
	Prop grassland	−0.32	−0.18		
	SHDI	−0.28	−0.1	0.42	
500 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.24			
	Prop grassland	−0.25	−0.21		
	SHDI	−0.18	−0.04	0.32	

(b)

Scale	Variables	Prop reduced tillage OSR(n-l)	Prop woodland	ProP grassland	SHDI
250 m	Prop reduced tillage OSR(n-l)				
	Prop woodland	0.08			
	Prop grassland	−0.01	−0.11		
	SHDI	0.06	0.07	0.5	

Prop OSR, proportion of OSR fields; Prop woodland, proportion of woodland; Prop grassland, proportion of grassland; SHDI, Shannon index of habitat diversity; Prop reduced tillage OSR(n-1), proportion of previous year's oilseed rape fields with reduced soil tillage. Values are Pearson correlation coefficient.

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