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RESEARCH ARTICLE

Combined effects of area, connectivity, history and structural heterogeneity of woodlands on the species richness of hoverflies (Diptera: Syrphidae)

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Abstract

Context Hoverflies are often used as bio-indicators for ecosystem conservation, but only few studies have actually investigated the key factors explaining their richness in woodlands.

Objectives In a fragmented landscape in southwest France, we investigated the joint effects of woodland area, structural heterogeneity, connectivity and history on the species richness of forest-specialist hoverflies, and whether there was a time lag in the response of hoverflies to habitat changes, and tested the effect of spatiotemporal changes.

Methods Current species richness was sampled in 48 woodlands using 99 Malaise traps. Structural variables were derived from a rapid habitat assessment protocol. Old maps and aerial photographs were used to extract past and present spatial patterns of the woodlands since 1850. Relationships between species richness and explanatory variables were explored using generalized linear models.

Results We show that current habitat area, connectivity, historical continuity and the average density of

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tree-microhabitats explained 35 % of variation in species richness. Species richness was affected differently by changes in patch area between 1979 and 2010, depending on woodland connectivity. In isolated woodlands, extinction debt and colonization credit were revealed, showing that even several decades are not sufficient for hoverflies to adapt to landscape-scale habitat conditions.

Conclusions These findings emphasise the importance of maintaining connectedness between woodlands, which facilitates the dispersion in a changing landscape. Our results also highlight the benefits of using a change-oriented approach to explain the current distribution patterns of species, especially when several spatial processes act jointly.

Introduction

Forests are among the most biologically diverse ecosystems on the planet (Gosselin and Laroussinie 2004). Species richness and species composition are influenced by broad spatial-scale processes, forest area, habitat heterogeneity, the history of disturbances and resource continuity, and stochastic events, which can lead to local extinction, and connectivity, which enables recolonization, inter-specific competition, etc. (Ricklefs 1987; Huston 1994). Despite the fact that multiple factors are involved, most studies on forest biodiversity focus on only a few factors and are conducted mainly at the local scale. Quantifying the relative importance of each factor and the effect of the landscape on local species richness thus remains a challenge.

Centuries of management have changed both the structure of forest ecosystems and their biodiversity (Larsson 2001). Habitat loss and fragmentation are currently the primary causes of biodiversity decline (Fahrig 2003; Foley et al. 2005; Hanski 2005). Local extinction of populations may not be reversible by colonization because of increasing isolation and the reduction in habitat size. Conversely, the creation of new habitat patches or an increase in connectivity among habitats could facilitate species immigration. Some species react to landscape changes immediately

while others respond with a time lag (Hanski and Ovaskainen 2002; Nagelkerke et al. 2002; Lindborg and Eriksson 2004; Metzger et al. 2009; Krauss et al. 2010). A time lag in the response of certain species may lead to what is termed an extinction debt (Tilman et al. 1994; Cousins 2009; Kuussaari et al. 2009) or a colonization credit (Cristofoli et al. 2010; Piqueray et al. 2011).

Extinction debts have been reported in vascular plants in temperate regions (Helm et al. 2006; Krauss et al. 2010; Guardiola et al. 2013) but also in other species with higher dispersal ability, including pollinating insects (butterflies, hoverflies) and birds (Brooks et al. 1999; Ford et al. 2009). Colonization credits have also been reported in butterfly communities in wet heathland (Cristofoli and Mahy 2010) and in plant communities in calcareous grasslands (Piqueray et al. 2011). The mechanisms involved in the delayed responses of species remain unclear, but specialist species are expected to be more affected by habitat changes than generalist species (Cousins and Vanhoenacker 2011), because the latter can adapt more easily to new environmental conditions.

Empirical evidence of extinction debt is often based on the comparison of past and present habitat characteristics (Kuussaari et al. 2009). When past habitat variables explain current species richness better than the present ones, an extinction debt is assumed (Krauss et al. 2010). Although this comparison makes it possible to detect a potential extinction debt, "past" and "current" habitat characteristics are disconnected because the state of habitats is described without integrating patch history. The temporal trajectory of habitats is mostly ignored. Estimated colonization credit is often based on species-area relationships in equilibrium habitat patches, i.e. when the species richness of the patch is in accordance with their spatial characteristics (Cristofoli and Mahy 2010). A colonization credit is assumed when observed species richness in new habitats is lower than would be expected given the spatial properties of the habitat. This can be evaluated by defining groups of old and new patches and by comparing their species-habitat relationships, under the assumption that old patches are closer to equilibrium (Cristofoli and Mahy 2010).

Recently, some authors used a dynamic approach to detect extinction debt or to analyse the historical factors influencing species richness (Metzger et al. 2009) by considering habitat change as a cumulative

process (Ewers et al. 2013). Metzger et al. (2009) showed that including the rate of change in habitat area (i.e. the rate of relative change between two dates) and in connectivity for several taxonomic groups (tree, bird and frog species), in addition to the present habitat characteristics, considerably improved the explanation of species richness and abundance. The rate of landscape change could influence the ratio of colonization to extinction (Münzbergová et al. 2005).

Ouin et al. (2006) investigated the effects of landscape variables on the presence of hoverflies (Syrphidae) in a fragmented landscape in southwest France and showed that current woodland area explained roughly 30 % of the variability of forest species richness. Hoverflies are known to be quite mobile and are therefore sensitive to large-scale conditions (Smith et al. 2008). The Syrphidae family comprises a diverse group of species in terms of trophic and habitat requirements, including saproxylic species, and has been used as an indicator of disturbance or habitat quality (Sommaggio 1999). Hoverflies have also been used as bioindicators to identify forests for potential conservation (Good and Speight 1996). Larvae of saproxylic species are involved in recycling deadwood (Speight 1989), and adults of all hoverfly species are flower-visiting insects and probably provide pollination services for several trees and shrubs (Groot and Bevk 2012).

Despite the crucial role of hoverflies in ecosystem functioning, little is known about the factors which influence their contemporary patterns (Keil and Konvicka 2005). In this study, we investigated the species richness of forest hoverflies by combining the effects of current landscape, their past dynamics, and local structural heterogeneity. First, we assessed the relative importance of area, connectivity, structural heterogeneity, and the history of the woodland on the species richness of forest specialists. Lower species richness was expected in small isolated woodlands than in big and well connected ones. Nevertheless, a weak effect of connectivity was assumed due to the high dispersal abilities of hoverflies (Ouin et al. 2006). It was also assumed that the presence of tree microhabitats (hereafter called microhabitats) and deadwood provide favourable habitats for saproxylic species, which might also depend on the historical continuity of their resources. Thus, younger woodlands, especially isolated woodlands, would be expected to have fewer species than older woodlands. Second, we evaluated

the extinction debt or colonization credit of hoverfly communities. Recently, Bommarco et al. (2014) showed that specialist and generalist species richness was better predicted by past area than by current area. Here, we studied historical changes in area and connectivity of woodlands to identify indications of extinction debt and colonisation credit. In the case of a time-lag in response, extinction debt in patches with decreased area would lead to more species being present than expected, while colonization credit would lead to fewer species than expected in patches whose area had increased. The effect of change in area could be modulated by changes in connectivity, the number of species resulting from colonization-extinction dynamics (MacArthur 1967).

Materials and methods

Study area

The study site is located in southwest France (43°16′28″N, 0°51′11″E, WGS-84) and covers roughly 30,000 ha, including the Long-Term Ecological Research site "*Vallées et Coteaux de Gascogne*" (LTER_EU_FR_003) (Fig. 1). This is a hilly region (altitude 215–400 m asl.), dissected by north–south valleys. The climate is temperate with Pyrenean Mountain and slight Mediterranean influences. The forest cover is fragmented and accounts for only about 15 % of the area. The dominant tree species in more than 80 % of the woodland area are sessile oak (*Quercus petraea* Mattus), pedunculate oak (*Quercus robur* L.) and pubescent oak (*Quercus pubescens* Willd.) (IFN 2000).

Small privately owned forests are the most frequent type of woodland in this region. There is high spatial heterogeneity between woodlands owing to the absence of a forest management plan in approximately 90 % of the area. Owners generally only have empirical knowledge of forest management, which may strongly influence the spatial patterns of forest biodiversity (De Warnaffe et al. 2006; Andrieu et al. 2008).

Data collection

Biological sampling

Hoverflies (Diptera: Syrphidae) had been sampled by Ouin et al. (2006) in two one-month periods in
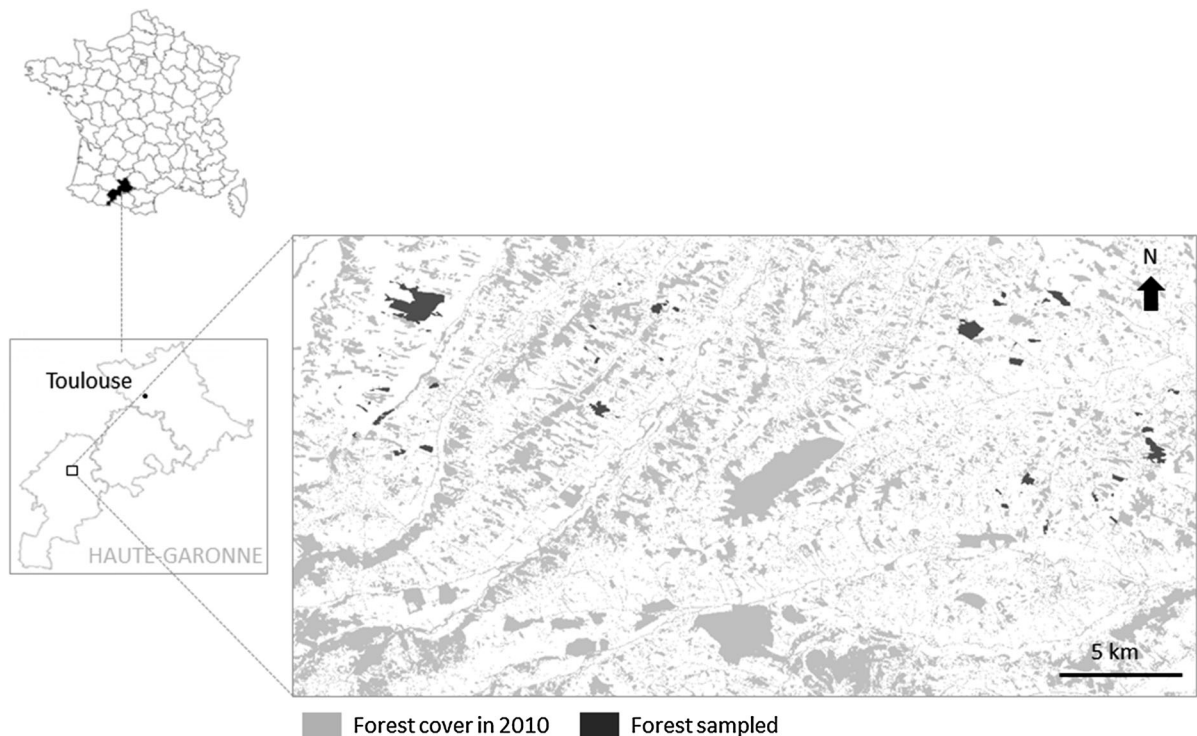
Fig. 1 Map showing the study site in southwest France, and inset showing the location of the 48 woodlands sampled

2000 (10 May–10 June, spring and 13 September–13 October, autumn), using Malaise traps. The collection bottles had been replaced every 2 weeks in spring and every month in autumn. We selected 48 woodlands from Ouin et al. (2006) according to a gradient of surface area, isolation, and type of management, to cover different types of forest structure and composition. The number of traps per woodland was adjusted to the patch area in order to obtain an equivalent trapping intensity for each woodland (Table 1). The majority of small

woodlands (<5 ha) contained only one trap. More traps were added in larger woodlands. A total of 99 Malaise traps were installed in the woodlands to be surveyed.

Hoverfly forest species were determined according to the Syrph the Net (StN) database (Speight et al. 2000). The focus was on forest species because they were shown by Ouin et al. (2006) to be more sensitive to forest patch area and isolation (Ouin et al. 2006). The names of all the 27 forest species sampled are listed in Appendix 1.

Table 1 For each class of woodland area: number of traps, number of woodlands in the class, average forest species richness per woodland

Class of surface area (A) (ha)	No. of traps	No. of woodlands	Average forest species richness per woodland
A < 5	1	29	2.48 ± 1.68
5 < A < 10	2	9	3.77 ± 1.74
10 < A < 15	3	3	2.45 ± 1.37
15 < A < 25	4	4	2.48 ± 2.10
45 < A < 60	7	2	3.6 ± 0.98
150 < A < 200	14	1	5.67

## Structural heterogeneity variables of woodlands

Structural variables were surveyed in summer 2011 using a rapid stand description protocol (Larrieu and Gonin 2008) in a 1-ha circular plot centred around each trap. In this way, a total of 99 ha was sampled. Eight forest structure and composition attributes were assumed to be relevant to hoverfly assemblages: (1) the number of indigenous tree species; (2) the number of large standing dead trees (diameter at breast height (dbh) >40 cm) including whole dead trees, snags or stumps more than 1.5 m tall; (3) the number of large lying deadwood (diameter >40 cm and length >1 m); (4) the number of very large living trees (dbh >70 cm); (5) the number of microhabitat-bearing trees (only living trees), a tree being counted once for each type of microhabitat it carried, i.e. empty cavities, cavities with mould, sporophores of saproxylic fungi, dendrothelms, missing bark, cracks, broken crowns, large amount (>20 %) of deadwood in the crown; (6) a diversity index equal to the sum of microhabitat-bearing trees considering a maximum of two trees bearing the same type of microhabitat per plot; (7) the proportion (%) of open area (clearings, edges, areas with a well-developed herb layer composed of flowering plants); and (8) the number of aquatic habitat types (using a reference list of ten types). Finally, the average value of each of these variables per trap in one woodland was calculated to test the effect of structural heterogeneity on the species richness of hoverflies. Because Malaise traps catch adults looking for flower resources (mainly in clearings) structural variables described adult habitats directly but larvae habitats only indirectly.

Area, connectivity and historical variables of woodlands

Aerial colour infrared orthophotos taken in 2010 (BDOrtho®, French mapping agency IGN) were used to estimate the current area and connectivity of each woodland. Connectivity was captured in terms of isolation, i.e. as the forest density in the surrounding landscape of one focal patch (Tischendorf et al. 2003; Magle et al. 2009). Forest density was measured as percentage forest cover excluding the focal patch. Starting from the boundaries of the focal patch, a buffer area was created with a 4.8 km radius (Fig. 2), which was assumed to be the appropriate scale for analysis of the effect of isolation on the hoverfly community (Ouin et al. 2006). The choice of such a large scale is explained by the high dispersal capacity of hoverflies (Sarthou and Speight 2005). The forest density index was correlated with other area-weighted distance-based metrics of connectivity such as, e.g. Hanski's index (Spearman correlation Rho = 0.75, p-value <0.001 with for the 2010 dataset; Hanski and Thomas 1994; Magle et al. 2009).

Fig. 2 A combination of factors including structural heterogeneity, area, connectivity and historical continuity was measured at local to landscape scale to explain the spatial patterns of forest hoverfly species richness
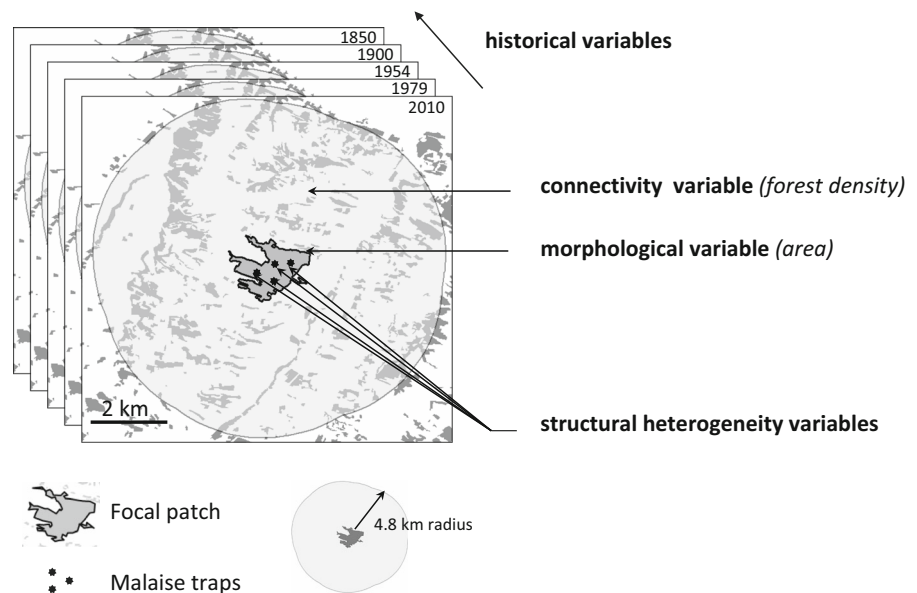
Historical spatial data were also used to quantify the effect of changes in woodland area and isolation on current species richness, expressed as forest continuity over time. In addition to old orthophotos dating from 1953–1954 to 1979 (Fig. 3), two historical maps were used. The first historical map is a French military 'Etat Major' colour map at a scale of 1:40,000, which dates from the middle of the 19th century (IGN 2011). The sheets in this map series we used are 241 NE, 241 NO, 229 SE, 229 SO. The second map is a revised version of the first one produced 1900 in black and white at a scale of 1:80,000 (Nadal 2011). These historical maps were geo-referenced with a third order polynomial transformation (70 ground control points, root mean square error—RMSE—was about 55 m). Woodlands were digitised at a 1.7-m resolution according to a rule base defined by cartographic experts to ensure the homogeneous representation of the objects (Favre et al. 2012). Old aerial black and white IGN photographs (flight missions on 24/07/1953 and 12/06/1954 at a scale of 1:25,000, and on 18/06/1979 at a scale of 1:29,000) were ortho-rectified using a 25-m resolution digital terrain model and applying a linear transformation (40 ground control points, RMSE about 30 m). Finally, datasets of woodlands produced for the fifth time period were manually matched in order to build the corresponding relations for related spatial entities and to estimate changes.

Changes in woodland area and connectivity were computed by retrospective analysis. For the current time period t, woodlands were always equal to one single spatial object. However, for past time periods, it was possible that the current woodland matched several older forest fragments because of disappearance or aggregation processes from a past period to the present. In this case, when one-to-many or many-to-many matching relationships appeared between time periods, the fragmented woodland was considered to be a complex object (or "meta-object") composed of simple objects. The area of the complex object was defined as the sum of all the areas of the simple objects. For connectivity, the convex hull containing all the simple objects was created to represent the extent of the meta-object. A buffer (radius 4.8 km) was created around this convex hull starting from its boundaries and the proportion of forest within this neighbouring area was calculated, excluding the convex hull area. Finally, relative changes (in %) in woodland area and connectivity between each consecutive time period and between 1850 and 2010 were estimated, along with the historical area and connectivity at each date. A semi-quantitative variable was defined to provide information on whether forest continuity had been maintained over time since the first historical map. To this end, four groups of woodlands were identified: the older ones present in all cartographic data since 1850 (continuity variable value = 1, patches >160 years old), since 1900 (continuity variable value = 2, patches about 110–160 years old), since 1954 (continuity variable value = 3, patches about 56–110 years old) and since 1979 (continuity variable value = 4, patches about 31–56 years old).

Statistical analyses

All statistical analyses were performed using R 2.3.0.1 software (R Development Core Team 2014) and the "vegan" R package (Oksanen et al. 2007).

Because differences in species richness may be due to difference in sampling effort, species rarefaction curves (Gotelli and Colwell 2001) were calculated for each woodland which had more than one trap (i.e. whose area >5 ha, n = 19) by randomly sampling traps with 100 permutations. Based on the rarefaction curves (Appendix 2), the expected average species richness for each woodland was estimated to be equivalent to the sampling effort of one single trap. In this way, we removed the potential bias related to the sampling effort before statistical analyses.

Relationships between species richness and explanatory variables were explored using generalised linear models (GLM). Poisson distribution was used to fit the species richness models. Variance inflation factors (VIF) were checked using the 'VIF' R package (Lin 2009) to prevent multicollinearity between covariates. No VIF values or correlation coefficients between explanatory variables exceeded the recommended thresholds of diagnostic indices (VIF < 10; correlation coefficients $|r| < 0.7$) (Dormann et al. 2013).

Two main analyses were explored and associated models were tested (Table 2). The contribution of each explanatory variable to the current hoverfly forest species richness per woodland was measured (Model 1). Current $\log_{10}$-transformed area, connectivity and structural heterogeneity variables were incorporated in addition to the historical woodland continuity
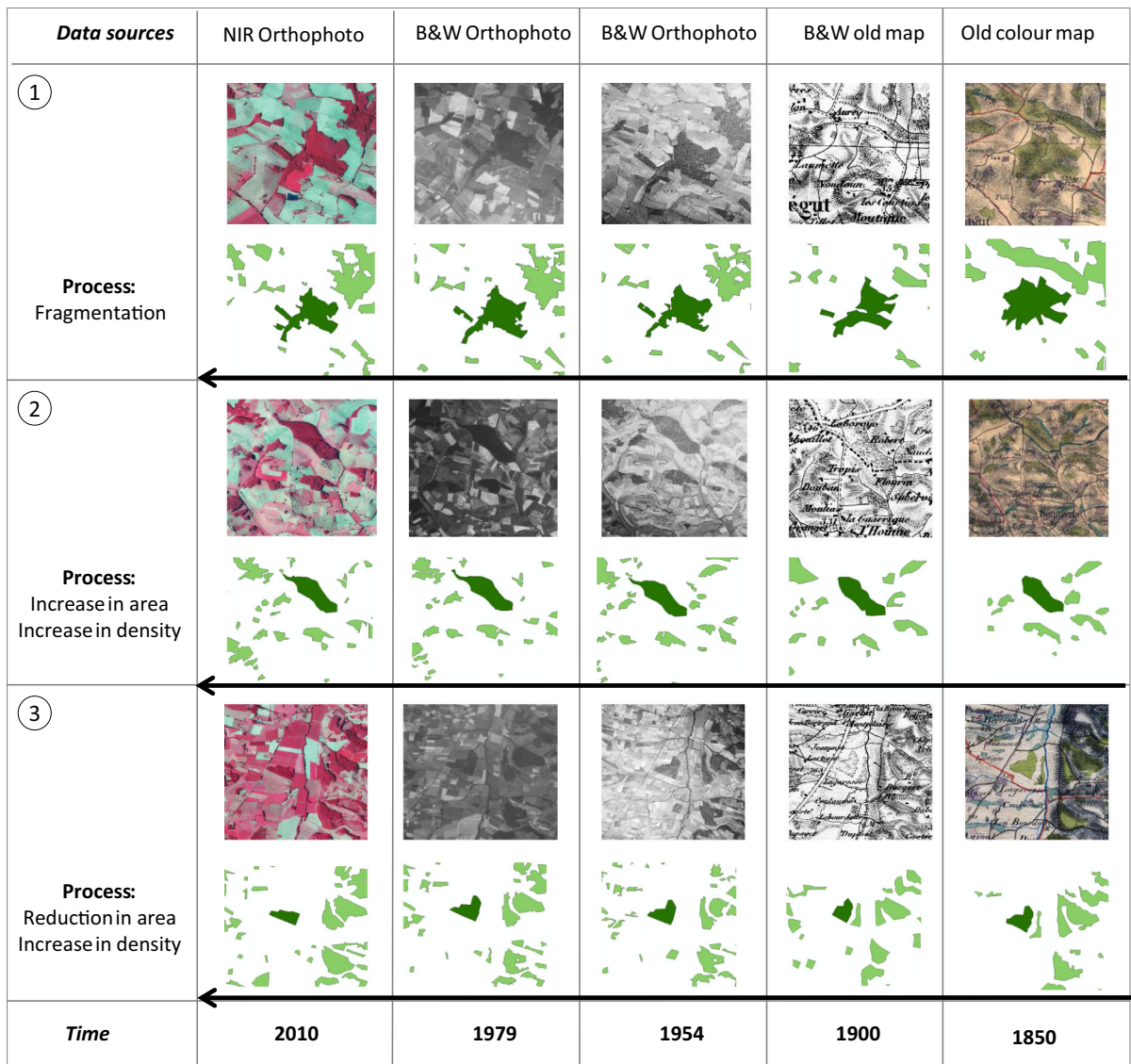
Data sources	NIR Orthophoto	B&W Orthophoto	B&W Orthophoto	B&W old map	Old colour map
① **Process:** Fragmentation					
② **Process:** Increase in area Increase in density					
③ **Process:** Reduction in area Increase in density					
Time	**2010**	**1979**	**1954**	**1900**	**1850**

Fig. 3 Excerpts from the spatial data sources with examples of forest evolution for some of the woodlands sampled (in *dark green*). (Color figure online)

(giving a total of 11 factors). Interaction terms between historical continuity and (i) current connectivity, (ii) the average number of microhabitats per woodland, and (iii) the average number of large standing deadwood per woodland, respectively, (3 additional factors) were also tested, under the hypothesis that forest historical continuity positively influences these three structural variables. For the two last additional factors, historical continuity does not necessarily imply maturity (Cateau et al. 2015), but a very recently established forest cannot be mature.

This first analysis included all the woodlands surveyed (n = 48).

The role of past changes in area and the connectivity of the woodlands were investigated to explain forest species richness. First, all types of changes in the woodlands (e.g. reduction in size, increase in isolation) since 1850 were incorporated into the model, in addition to current area and connectivity of the woodlands (Model 2a). The analysis was performed using the woodlands present at each date, i.e. showing historical continuity over time (n = 28).

Table 2 GLMs tested to explain species richness of hoverfly forest specialists

Explanatory variables		Description
Model (1) with current area, connectivity, structural heterogeneity and historical continuity		
Model form: $E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_3 + \beta_4 + \beta_5 + \beta_6 + \beta_7 + \beta_8 + \beta_9 + \beta_{10} + \beta_{11} + \beta_{12} + \beta_{13} + \beta_{14}$		
Log (Area 2010)	β_1	Current area of woodland (orthophoto 2010)
Connect 2010	β_2	Current forest density in a buffer zone with a 4.8 km radius (orthophoto 2010)
AvgNb_ATS	β_3	Current average number of indigenous tree species per woodland?
AvgNb_STW	β_4	Current average number of large standing deadwood per woodland
AvgNb_LDW	β_5	Current average number of large lying deadwood per woodland
AvgNb_VLLT	β_6	Current average number of very large living trees per woodland
AvgNb_MH	β_7	Current average number of microhabitats per woodland
AvgNb_TreeMH	β_8	Current average number of trees with microhabitats per woodland
AvgOpen_Area	β_9	Current average size of open areas per woodland
AvgNb_Aquatic	β_{10}	Current average number of aquatic habitats per woodland
Histo_continuity	β_{11}	Historical forest continuity over time (since 1850 = 1; since 1900 = 2; since 1954 = 3; since 1979 = 4)
Histo_continuity:Connect2010	β_{12}	Interaction term between historical forest continuity and current forest density
Histo_continuity:AvgNb_STW	β_{13}	Interaction term between historical forest continuity and large standing deadwood
Histo_continuity:AvgNb_MH	β_{14}	Interaction term between historical forest continuity and microhabitats
Model (2a) with current area and connectivity with their past dynamics since 1850		
Model form: $E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_{21} + \beta_{22} + \beta_{23} + \beta_{24} + \beta_{25} + \beta_{26} + \beta_{27} + \beta_{28} + \beta_{29} + \beta_{30}$		
Log (Area 2010)	β_1	Current area of woodland (orthophoto 2010)
Connect 2010	β_2	Current forest density in a buffer with a 4.8 km buffer radius (orthophoto 2010)
ΔArea 2010–1979	β_{21}	Change in area (%) between 2010 and 1979
ΔCon 2010–1979	β_{22}	Change in connectivity (%) between 2010 and 1979
ΔArea 1979–1954	β_{23}	Change in area (%) between 1979 and 1954
ΔCon 1974–1954	β_{24}	Change in connectivity (%) between 1979 and 1954
ΔArea 1954–1900	β_{25}	Change in area between (%) 1954 and 1900
ΔCon 1954–1900	β_{26}	Change in connectivity (%) between 1954 and 1900
ΔArea 1900–1850	β_{27}	Change in area between (%) 1900 and 1850
ΔCon 1900–1850	β_{28}	Change in connectivity (%) between 1900 and 1850
ΔArea 2010–1850	β_{29}	Change in area between (%) 2010 and 1850
ΔCon 2010–1850	β_{30}	Change in connectivity (%) between 2010 and 1850
Model (2b) with current area and the most recent dynamics since 1979		
Model form: $E(y) = \beta_0 + \beta_1 + \beta_2 + \beta_{21} + \beta_{22} + \beta_{31}$		
Log (Area 2010)	β_1	Current area of woodland (orthophoto 2010)
Connect 2010	β_2	Current forest density in buffer area with a 4.8 km radius (orthophoto 2010)
ΔArea 2010–1979	β_{21}	Change in % area between 2010 and 1979
ΔCon 2010–1979	β_{22}	Change in connectivity (%) between 2010 and 1979
ΔArea 2010–1979: Connect 2010	β_{31}	Interaction term between ΔArea 2010–1979 and Connect 2010
Models (2c) with current area or past area (1979) of isolated woodlands (Connect 2010 <15 %)		
Model form: $E(y) = \beta_0 + \beta_1$ or $E(y) = \beta_0 + \beta_{32}$		
Log (Area 2010)	β_1	Current area of woodland (orthophoto 2010)
Log (Area 1979)	β_{32}	Past area of woodland (orthophoto 1979)

Second, we focused the analysis on the most recent period (1979–2010), expecting a possible time-lag in the response of hoverflies to changes in the landscape (Bommarco et al. 2014). The role of the current area, of the change in area during the period 1979–2010, and the effect of interaction between the change in area and current connectivity were tested (Model 2b). This analysis included all the woodlands (n = 48). Finally, we compared the effect of the area in 1979 and the area in 2010 on the current species richness in isolated woodlands (current connectivity <15 %; n = 16) to identify a possible extinction debt or colonization credit (models 2c).

The most parsimonious models were also assessed using the Akaike information criterion (AIC) (Burnham and Anderson 2004). A stepwise backward selection of variables was carried out to select the "best" model with the lowest AIC. Variance partitioning was also calculated from the best model to measure the independent contribution of each variable to the explained variance of the response variable.

The goodness of fit of the models was quantified by examining the amount of the explained deviance (D^2) and of the adjusted explained deviance (adj-D^2), which takes the number of observations and the number of explanatory variables into account (Guisan and Zimmermann 2000). This adjusted measure makes it possible to compare models that include different combinations of variables.

Results

Changes in woodland spatial patterns

The current and historical spatial data showed that among the 48 woodlands surveyed, 28 showed historical continuity over time since 1850, four since 1900, 14 since 1954, and two since 1979. No woodland that had appeared after 1979 was identified. When all the woodlands were taken into consideration, the average woodland area was seen to have decreased between 1850 and 1954 (Fig. 4a), whereas connectivity increased with an increase in the number of woodlands (Fig. 4b). When old woodlands showing historical continuity since 1850 (n = 28) were taken into consideration, their connectivity increased from 11.2 % in 1850 to 16.5 % in 2010 (Fig. 4d), but not their area (Fig. 4c).

Response of hoverfly species richness to current area, connectivity, structural heterogeneity and historical continuity

A total of 3,044 individuals belonging to 27 hoverfly species were captured in the 99 Malaise traps set up in the 48 woodlands. The average number of species per woodland (±SD) estimated from species accumulation curves to an equivalent sampling effort of one single trap was 2.81 ± 1.73.

Five predictors of species richness were retained after the analysis of AIC: current woodland area, current connectivity, historical continuity over time, average number of microhabitats per woodland (AvgNb_MH, hereafter called "microhabitats") and the interaction term between historical continuity and microhabitats. These variables comprised the "best model" (i.e. the model with the lowest AIC) in the first analysis (Model 1; adj-D^2 = 27.90). A strong positive relationship (p-value <0.01) was found between woodland area and species richness along with a positive effect of the interaction between microhabitats and historical continuity (Table 3; Fig. 5a). Microhabitats were negatively related to species richness only in the oldest woodlands (Appendix 3). In addition, historical continuity showed a strong negative relationship with species richness, indicating that the number of species was higher in old woodlands (continuity = 1) than in recent ones (continuity >1; Fig. 5a). Microhabitat variables also showed a weak negative effect (p-value <0.05; Fig. 5a). Finally, a weak positive effect of current connectivity explained species richness of forest hoverflies (Fig. 5a).

Response of hoverfly species richness to current area, connectivity and spatial dynamics since 1850

The AIC-based stepwise selection showed that in the model with the lowest AIC, two variables explained species richness when past spatial dynamics were included (adj-D^2 = 29.24): the area in 2010 and a change in area between 1979 and 2010 (Table 3, Model 2a). Like in the previous model, there was a positive relationship between current area and species richness, as illustrated by the partial residual plots (Fig. 5b). In contrast, a negative effect (p-value <0.05) of change in area between 1979 and 2010 was observed (Fig. 5b). Because the average area of the woodlands increased between 1979 and 2010
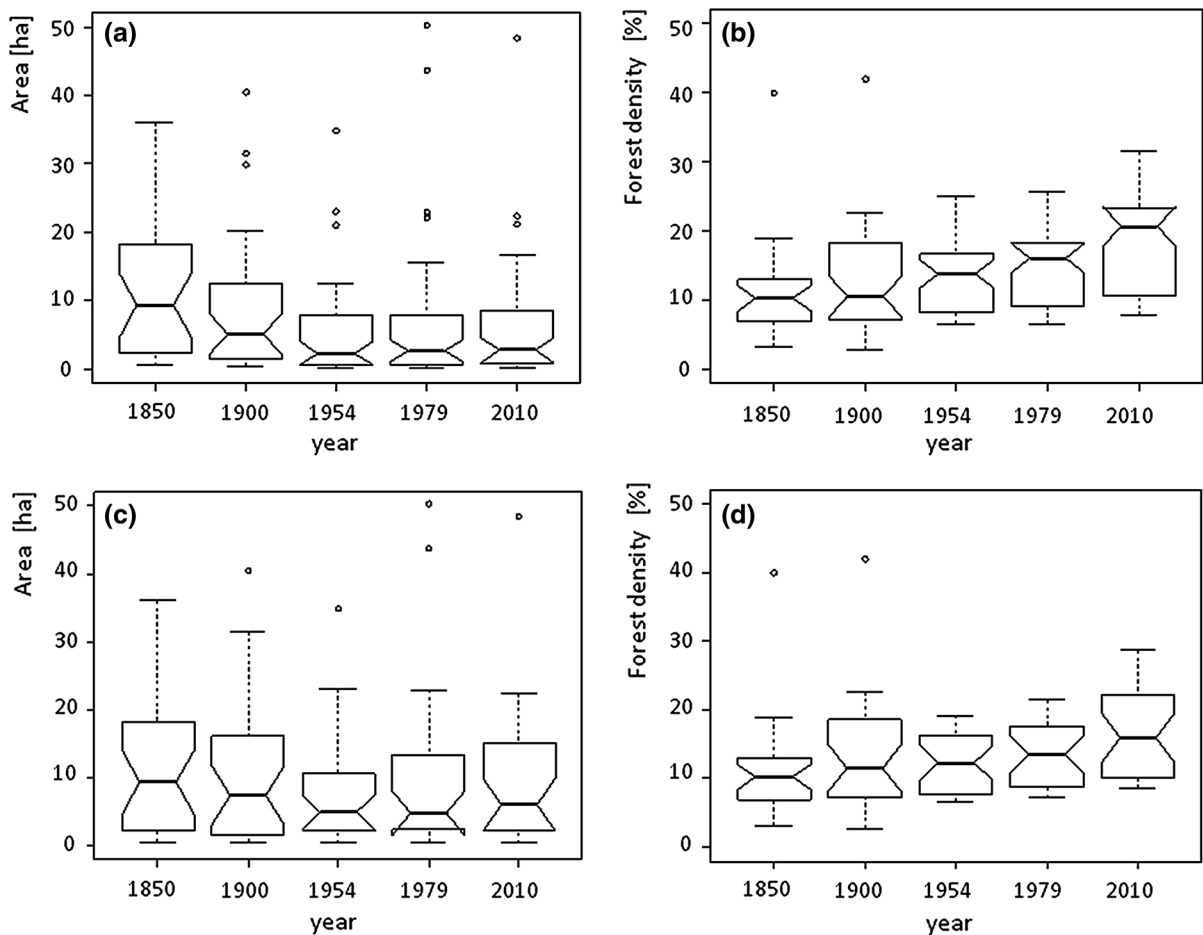
Fig. 4 Distribution of woodland area and forest density (i.e. connectivity) from 1850 to 2010 including all woodlands at each date (plots **a** and **b**) or only woodlands showing historical continuity over time after 1850 (plots **c** and **d**). The notched box whisker plots show medians (*line*) and the interquartile range (from 1st to 3rd quartiles; 50 % of data). The notch displays a confidence interval around the median. If two boxes notches do not overlap, there is strong evidence that their median differ significantly (95 % confidence). Notches are the non-parametric equivalent to the standard error of the mean and are calculated as $\pm 1.58 \times$ interquartile range/square root of sample size

(+6.48 %) (Fig. 4), we expected a positive effect of change in area during this period. The negative effect we observed suggested a time-lag in the response of hoverflies to a change in area. We consequently conducted an in-depth analysis with a third model (Model 2b, see below), focused on the most recent time period 1979–2010, and including all the woodlands present after 1979 (n = 48).

Response of hoverfly species richness to current area and the most recent dynamics since 1979

The most parsimonious model based on AIC selection identified three main predictors when only the most recent spatial dynamics were included in the model (Model 2b): current woodland area, change in area between 1979 and 2010, and interaction between the change in area in the period 1979–2010 and current connectivity (adj-D^2 = 18.49; Table 3). Positive and negative effects were observed with the first two predictors, respectively, in accordance with the previous model (Model 2a, Fig. 5c). A positive relationship was also found for the interaction between change in area in the period 1979–2010 and current connectivity, suggesting that the effect of change in woodland area must be interpreted in relation to their current connectivity. The histogram of current connectivity (Fig. 6a) revealed two distinct groups of woodlands with different connectivity:

Table 3 Results of GLMs explaining species richness of hoverfly forest specialists

Explanatory variables	Estimates	p-value	Sign. level	AIC	D^2 (%)	D^2 adjusted (%)	Relative contribution (%)
Model (1) with current area, connectivity, structural heterogeneity and historical continuity (n = 48)							
Null				186.55			
Log (Area 2010)	0.177	0.008	**	176.76	35.57	27.90	36.37
Connect 2010	0.024	0.097	(*)				21.84
Histo_continuity	−0.063	0.033	**				14.99
AvgNb_MH	−0.432	0.009	*				11.74
Histo_continuity:AvgNb_MH	0.031	0.003	**				15.04
Model (2a) with current area and connectivity with their past dynamics since 1850 (n = 28)							
Null				105.6			
Log(Area 2010)	0.210	0.008	**	100.63	34.48	29.24	56.52
ΔArea 1979–2010	−0.01	0.017	*				43.47
Model (2b) with current area and the most recent dynamics since 1979 (n = 48)							
Null				186.55			
Log(Area 2010)	0.160	0.002	**	179.37	23.69	18.49	58.95
ΔArea 1979–2010	−0.04	0.020	*				19.20
ΔArea 1979–2010: Connect 2010	0.001	0.017	*				21.83
Models (2c) with current area for isolated woodlands (Connect 2010 <15 %) (n = 16)							
Null				59.88			
Log (Area 2010)	0.209	0.063	(*)	55.37	21.50	15.89	100
With past area 1979 for isolated woodlands (Connect 2010 <15 %) (n = 16)							
Null				59.88			
Log (Area 1979)	0.228	0.049	*	54.93	24.18	18.77	100

Explanatory variables were selected using the Akaike information criterion (AIC). Due to the different sized samples used in the models (n = 48 in model (1) and model (2b); n = 28 in model (2a); n = 16 in models (2c)), AIC values are not directly comparable

Significance codes: *** p-value <0.001; ** p-value <0.01; * p-value <0.05; (*) p-value <0.1

one with less than 15 % current connectivity (n = 16), and the other with more than 15 % current connectivity (n = 32) (Fig. 6a). A negative relationship was observed between change in area in the period 1979–2010 and the species richness of forest hoverflies when only woodlands in the group whose current connectivity <15 % were considered (Fig. 6b). In contrast, a positive relationship was observed when only woodlands in the group whose current connectivity >15 % were considered (Fig. 6b). In other words, when woodlands are well connected, the increase in area during 1979–2010 had a positive effect on species richness, as expected. In isolated woodlands, the increase in area did not lead to an increase in species richness.

Finally, since current species richness of the set of woodlands with current connectivity <15 % (n = 16) was better explained by woodland area in 1979 than in 2010 (adj-D^2 = 18.77, p-value = 0.049 and adj-D^2 = 15.89, p-value = 0.06,

respectively; Model 2c in Table 3), we assumed the coexistence of extinction debt and colonization credit in these isolated woodlands. It depends on the direction (negative or positive) of the change in area from 1979 to 2010. In other words, observed species richness in these woodlands would be higher or lower than expected as regard to their spatial characteristics.

Discussion

Area, connectivity, historical continuity and microhabitat density mainly explain richness of forest specialists

Our results showed that the species richness of forest specialist hoverflies was mainly explained by a combination of four factors at different analytical
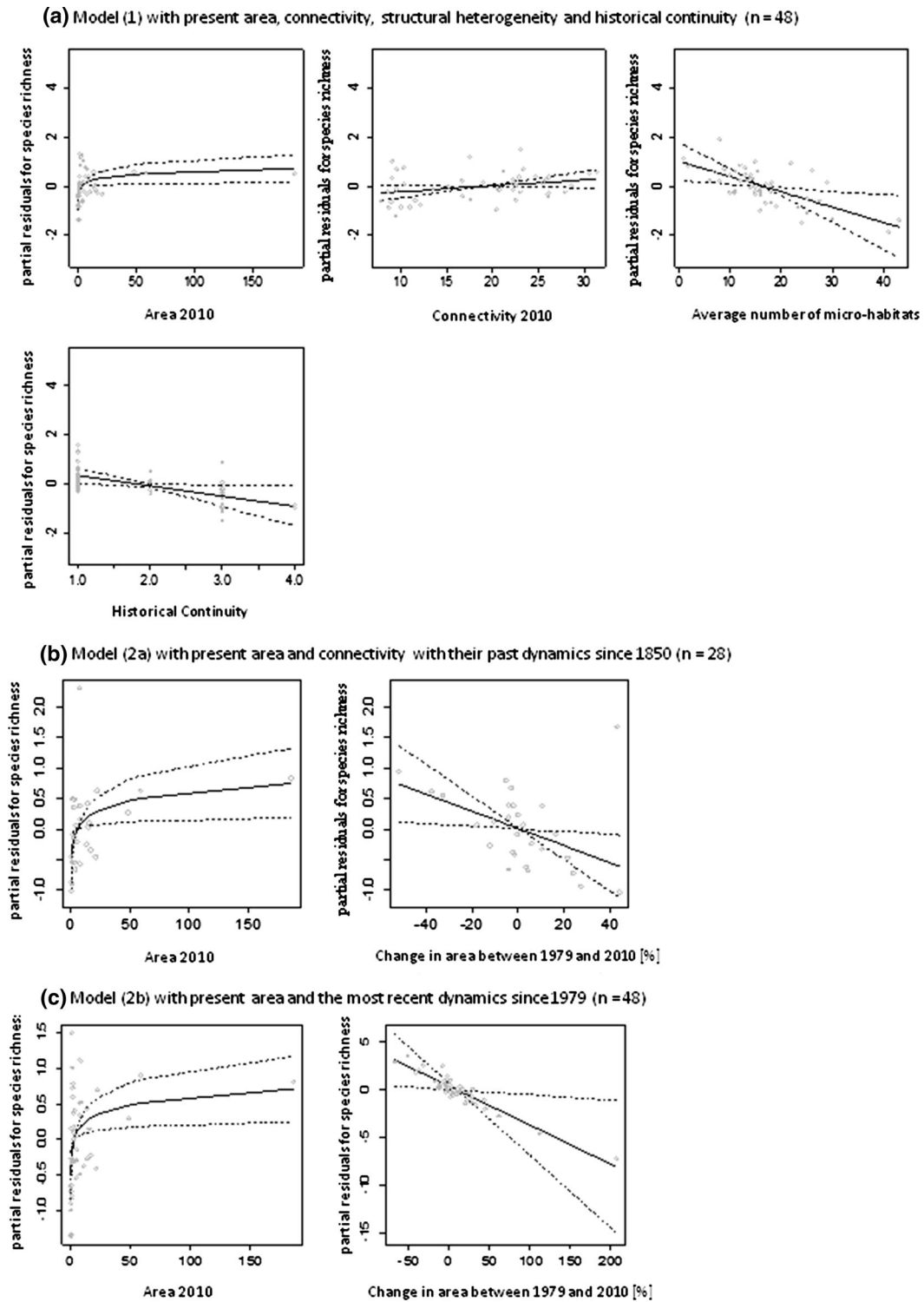
Fig. 5 Partial residual plots of the GLM models explaining species richness of hoverfly forest specialists
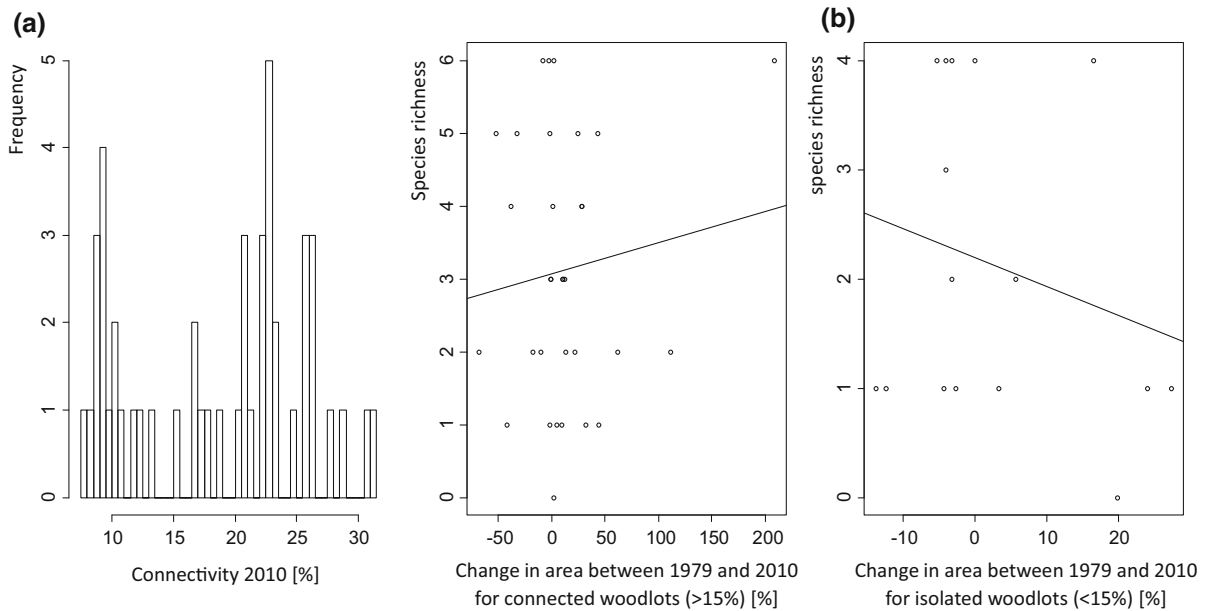
(a)

(b)

Fig. 6 Based on the frequency distribution of current forest density (**a**), two groups of woodlands were distinguished: isolated woodlands (density <15 %) and connected woodlands (density >15 %). Interaction plots (**b**) showing the relationship between species richness of forest hoverflies (*y axis*) and a change in area between 1979 and 2010 (*x axis*) combined with a change in woodland connectivity (i.e. forest density in the neighbourhood). For well-connected woodlands, the increase in area had a positive effect on species richness. In isolated woodlands, the increase in area had a negative effect, suggesting a time-lag in the response of hoverflies to a change in area

scales: the average density of microhabitats (local effect), the current area of the woodland (patch-scale effect), its connectivity (landscape-scale effect) and the historical continuity of woodland state (temporal effect).

The current woodland area was the main factor with a positive effect on species richness (36.37 % of total explained variation). The effect of area is well-known in the habitat patch framework (Connor and McCoy 1979; Andren 1994) and is consistent with result of previous studies on forest hoverfly specialists (e.g. Ouin et al. 2006) as well as grassland specialists and generalists (Meyer et al. 2009; Bommarco et al. 2014). The increase in species richness with an increase in patch area is predicted by the equilibrium theory of island biogeography (MacArthur 1967). The habitat diversity hypothesis (Root 1973; Huston 1994) is one of the hypotheses proposed to explain this positive relationship. Larger fragments of woodland are often more heterogeneous than small ones and therefore are more likely to provide critical resources for different species.

The current level of connectivity also played a positive role in the species richness of forest hoverflies, as observed in a previous study (Meyer et al. 2009). Generally, habitat connectivity has a positive effect on species diversity, in particular on specialist species with low dispersal ability (Hanski 2005).

Interestingly, in this study we showed that forest hoverflies may be sensitive to "habitat continuity", i.e. connectivity over time (Hanski 2005), while "habitat connectivity" represents connectivity in space. Although hoverflies are generally very skilful flying insects, their vagrancy varies with the species (Speight et al. 2013), and some adult specimens have been trapped after they have travelled several hundred metres from their emergence habitat (Sarthou and Sarthou 2007). We found that old woodlands hosted more species than the recent ones. The higher species richness in old woodland patches could be due to the presence of certain species, such as *Criorhina floccosa*, *Doros destillatorius* or *Brachylapoides lentus*, whose larvae only use microhabitats in the standing trees (Speight et al. 2013). These species are observed far more frequently in old woodlands than in recent ones, and only very rarely outside forests (Speight et al. 2013). They might be unwilling to cross an

unfavourable matrix such as large fields, in which case they would not easily be able to colonise favourable recently established woodlands.

Surprisingly, the density of microhabitats was found to be negatively correlated with species richness, especially in the oldest woodlands. Nevertheless, the larvae of saproxylic species, which composed the majority (72.4 % ± 21.6) of the forest specialist hoverflies, are strongly dependent on microhabitats associated with old and senescent trees (Speight 1989; Speight and Good 2003; Speight et al. 2013). In addition, no correlation was found between deadwood and hoverfly richness. These results may mean that the procedure used to count microhabitats and deadwood was not appropriate for hoverflies, although it was appropriate for saproxylic beetles (Bouget et al. 2013; Bouget et al. 2014a, b). On the other hand, these results might be linked to the fact that act sampling was carried out in only 1 year, as Fayt et al. (2006) reported a positive relationship between saproxylic hoverflies and the amount of deadwood, but also found significant variation in the species richness of saproxylic hoverflies between years, independently of the supply of deadwood. Our results also indicate that variables related to microhabitats and deadwood are probably not the only key factors explaining saproxylic hoverfly richness. Indeed, adults of all hoverfly species are floricolous (Speight et al. 2013) and Fayt et al. (2006) found higher species richness of saproxylic hoverflies in open stands, which provide the ecological conditions required for a species-rich herb layer as a source of pollen and nectar for adults.

Connectivity determines how historical changes in woodland area affect richness

Several studies have analysed the effects of history on plant or insect diversity in fragmented forests and grasslands, but they often estimate this effect by comparing diversity between patches with distinct dynamics (Piqueray et al. 2011; Guardiola et al. 2013). In the presence of complex dynamics (including an increase or decrease in area combined with an increase in connectivity and isolation), grouping patches according to their temporal trajectory may be challenging. In addition, it may lead to including several typologies of change, resulting in more extensive analyses (Piqueray et al. 2011). In our case, because several processes act together (an increase or decrease

in area and connectivity over time), changes in spatial patterns were directly incorporated into the models in addition to interaction terms between processes. Our results showed contrasted effects of changes in area during the most recent period (1979–2010) depending on the level of connectivity. In well-connected woodlands, a positive effect of changes in area on species richness was observed, indicating that both an increase and a decrease in area can be compensated for by colonization-extinction dynamics (MacArthur 1967). A negative effect was found in isolated woodlands, revealing a possible time lag in the response of the hoverfly community to landscape changes.

These findings reinforce the conclusions of previous studies stating that not only past or current spatial patch characteristics are important in explaining present biodiversity patterns, but also changes in patch area and potentially connectivity (Metzger et al. 2009). It also underlines the importance of analysing these spatial pattern dynamics jointly. Evidence for a potential interactive effect of area and connectivity has already been observed on the species richness of insect communities (Rösch et al. 2013).

A meta-analysis comparing bird response to forest fragments versus true islands concluded that forest fragments do not function as true islands (Brotons et al. 2003). The authors interpret this result as being a compensatory effect of the surrounding matrix in terms of availability of resources and enhanced connectivity. However, in our case, since only forest specialist hoverflies were considered, no resource was available in the matrix for larvae (although flower resources could be available for adults). Therefore, for adults, connectivity between forest patches may enable the persistence of the hoverfly community in the landscape through the dispersion of insects between ancient and recent patches (and vice versa).

Are hoverfly forest communities concerned by extinction debt or colonization credit?

Studies which examined potential extinction debt mainly focused on vascular plants, saproxylic cryptogams or birds, and rarely on short-lived animals (Kuussaari et al. 2009). Despite the potentially good dispersal capacity of hoverflies (Speight et al. 2013) and their high turnover rate, a delayed response to a change in habitat area was observed in a recent study on hoverfly generalists and specialists of semi-natural

grasslands (Bommarco et al. 2014). Moreover, specialist species strictly associated with the forest ecosystem and whose larvae have very specific microhabitat requirements, are assumed to be more sensitive to environmental changes than generalists and thus to become respectively more easily extinct, or to survive in an extinction debt, (Kuussaari et al. 2009). In a landscape with low connectivity, we highlighted both extinction debt for hoverflies in woodlands whose area decreased between 1979 and 2010 (ten woodlands with <15 % connectivity), and colonization credit in woodlands whose area increased during the same period (six woodlands with >15 % connectivity). Unfortunately, detecting extinction debt using past and current habitat characteristics did not allow us to estimate its magnitude (Kuussaari et al. 2009). Nevertheless, our results emphasise that even several decades are not sufficient for forest hoverfly assemblages to reach equilibrium with respect to their spatial patch characteristics.

Conclusion

This study demonstrated that the current species richness of forest hoverflies is influenced by a combination of factors from the plot to the landscape scale. Therefore, conservation of forest hoverflies should not only focus on local (i.e. stand) conditions. Our findings also reveal the interest of using a change-oriented approach to explain current species distribution patterns. When hoverflies are used as bio-indicators, the fact that there may be a time-lag in the response of this taxon to changes in environmental conditions needs to be taken into account.

Incorporating historical changes into landscape ecological studies can be a very promising way to advance our understanding of all the factors affecting current species diversity. However, this would require an extensive spatio-temporal database covering a wide range of sources of historical data, whose creation would be a challenge in itself. In many cases, historical maps are not available and the reconstruction of patch history can take a long time. However, recent advances in automatic processing of digital historical maps and aerial photographs (Leyk et al. 2006; Baily et al. 2011; Herrault et al. 2013) should make it possible to take the effects of history into consideration more

systematically in the future. With this in mind, closer collaboration between landscape historians, geo-information scientists, and ecologists is very promising and should be encouraged.

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