



# The scale of saproxylic beetles response to landscape structure depends on their habitat stability

Gwendoline Percel · Fabien Laroche · Christophe Bouget

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## Abstract

**Context** Forest management and disturbances cause habitat fragmentation for saproxylic species living on old-growth attributes. The degree of habitat spatiotemporal continuity required by these species is a key question for designing biodiversity-friendly forestry, and it strongly depends on species' dispersal. The “stability–dispersal” model predicts that species using stable habitats should have lower dispersal abilities than species associated with ephemeral habitat and thus respond to habitat availability at smaller scales.

**Objectives** We aimed at testing the stability–dispersal model by comparing the spatial scales at which saproxylic beetle guilds using substrates with contrasted stability (from stable to ephemeral: cavicolous, fungicolous, saproxylophagous and xylophagous

guilds) are affected by landscape structure (i.e. habitat amount and aggregation).

**Methods** We sampled saproxylic beetles using a spatially nested design (plots within landscape windows). We quantified habitat availability (tree cavities, polypores and deadwood) in 1-ha plots, 26-ha buffers around plots and 506-ha windows, and analyzed their effect on the abundance and diversity of associated guilds.

**Results** The habitat amount within plots and buffers positively affected the abundance of the cavicolous and the fungicolous guilds whereas saproxylophagous and xylophagous did not respond at these scales. The habitat aggregation within windows only positively affected the saproxylophagous species richness within plots and also on the similarity in species composition among plots.

**Conclusions** Beetle guilds specialized on more stable habitat were affected by landscape structure at smaller spatial scales, which corroborated the stability–dispersal model. In managed forests, the spatial grain of conservation efforts should therefore be adapted to the target habitat lifetime.

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G. Percel (✉) · F. Laroche · C. Bouget  
UR EFNO, Irstea, Domaine des barres,  
F-45290 Nogent-sur-Vernisson, France  
e-mail: g.percel@hotmail.fr

G. Percel  
Département recherche, développement et innovation,  
Office National des Forêts, Boulevard de Constance,  
F-77300 Fontainebleau, France

**Keywords** Fragmentation · Habitat amount · Habitat aggregation · Scale of effect · Species dispersal · Forest management

## Introduction

Anthropogenic fragmentation, induced by the expansion of human activities, leads to a modification of the landscape structure (i.e. amount and spatial arrangement of habitats) which is currently considered a major threat to biodiversity (Haddad et al. 2015). It has long been recognized that the scale at which analyses are conducted can influence the detection of environmental effects on biodiversity (Wiens 1989; Levin 1992). However, the scales at which landscape variables have the strongest effect on biodiversity (i.e. “scale of effect”) are not always clear and their determinants are currently poorly known (Miguet et al. 2016).

Among several factors, dispersal ability is considered to be one of the most important mechanisms explaining response to landscape structure at species (Hanski 1999) and community levels (Cadotte 2006). Indeed, highly-dispersive organisms should be able to move more freely across the landscape, hence colonize habitats over larger distances than poorly-dispersive species. Thus, contrasted species dispersal ability, underlying different landscape perception, should lead to response at various spatial scales (D'Eon et al. 2002). In that sense, a theoretical study showed that dispersal distance strongly and positively influences the scale of effect of habitat amount on population abundance (Jackson and Fahrig 2012). More particular, by using an individual based simulation model, these authors suggested that landscape structure should be measured at a radius equal to 4–9 times the median dispersal distance of the target species. Nevertheless, few studies have empirically tested the relationship between dispersal abilities and scale of effect—especially for invertebrates (Jackson and Fahrig 2015). Besides, the relationship between landscape structure and dispersal ability may be mediated by habitat stability, including habitat-related characteristics such as year-to-year resource persistence and habitat predictability, through the “stability–dispersal” conceptual model (Southwood 1977; Travis and Dytham 1999). According to this model, species associated with ephemeral habitat (e.g. early-successional habitats) are expected to harbor better dispersal abilities and therefore should respond to landscape structure at larger spatial scale than species living on more persistent substrates (about insects, see e.g. Harrison 1980; Barbosa et al. 1989).

Spatial patterns of old-growth attributes in managed forest provide an ideal semi-natural case study for testing the stability–dispersal conceptual model. In managed forests, the distribution of old-growth attributes such as deadwood (DW) and tree-related microhabitats (TreMs) is altered due to intensive harvesting. Compared with subnatural forest ecosystems—where old-growth attributes are continuously created at fine grain through natural disturbances (Larrieu et al. 2014b), ensuring a spatiotemporal continuity of habitats for associated saproxylic species (McMullin and Wiersma 2019)—managed forest areas consist in a mosaic of simplified stands, relatively uniform in size and shape (Boutin and Hebert 2002), and characterized by reduced DW and TreM density and diversity (Lombardi et al. 2008; Larrieu et al. 2012, 2014a; Bouget et al. 2014).

Little information is currently available concerning the dispersal ability of many saproxylic taxa (e.g. flying beetles), mainly due to methodological challenges combined with the high cost to obtain dispersal estimates at the species level (review in Feldhaar and Schauer 2018; Komonen and Müller 2018). Indirect cues about dispersal are thus crucial for overcoming this empirical limitation. Studies about processes driving the response of saproxylic species to fragmentation have frequently used body size (e.g. Brin et al. 2016; Janssen et al. 2017) or wing size (e.g. Gibb et al. 2006a; Bouget et al. 2015) as proxies for flight performance and dispersal. However these phenotypic surrogates could lead to misinterpretation (see Davies et al. 2000; Ewers and Didham 2006 for body size). Using the habitat-stability conceptual framework to ordinate dispersal abilities may be a relevant alternative, especially when it comes to saproxylic species, which live on a range of habitats with contrasted stability in time. For example, hollow trees are generally considered to be stable habitats, with a persistence way above the typical harvesting rotation length of managed forests (Ranius et al. 2009), while the fruiting bodies of wood-decaying fungi are more short-lived habitats with a lifetime estimated at only a few decades or less for perennial species such as *Fomes* spp. (Stokland et al. 2012).

To date, only partial evidence of the relationship between saproxylic habitat stability and the scale of effect of landscape structure has been provided by previous studies. Jacobsen et al. (2015) highlighted a smaller scale of response for generalist beetles using

deadwood stems from many tree species occurring throughout the forest cycle than for specialist beetles associated to aspen deadwood, which occurs only during the pioneer forest stages and thus considered as a more ephemeral habitat. Conversely, in a multi-scale study about the effect of forest amount on 31 longhorned beetles, Holland et al. (2005) did not find any support that species using more stable habitat (i.e. fresh deadwood) responded at smaller scales than species developing in more ephemeral conditions (i.e. decayed deadwood). In addition, these studies only focused on few species within taxonomical or ecological groups based on host tree preferences, restricting the generalization of results to the whole of saproxylic beetles community.

In light of the stability–dispersal conceptual framework, our objective was to compare the spatial scales at which the composition of distinct saproxylic beetle guilds using substrates with contrasted stability (from stable to ephemeral: cavicolous, fungicolous, saproxylophagous and xylophagous guilds) is affected by the availability of their habitat within a managed temperate forest in France. Using a spatially nested sampling design, we addressed the following two questions. Firstly, at what scale does the amount of surrounding habitat have an effect on the abundance and species richness of each saproxylic beetle guild within plots? We hypothesized that saproxylic beetles developing in stable habitats (e.g. the cavicolous guild) would respond to the habitat amount at smaller spatial scales than those using more ephemeral habitats (e.g. the xylophagous guild). Secondly, how does habitat aggregation within landscape windows affect the  $\gamma$ -diversity (species richness within a given window) and the  $\beta$ -diversity (dissimilarity of species composition among plots within a given windows) of each guild? We hypothesized that, for some beetle guilds (whose dispersal abilities is limited at window scale), habitat aggregation would positively affect the  $\gamma$ -diversity because it should generally provide species with an easier access to the totality of the habitat within windows. We expected a negative effect of habitat aggregation upon  $\beta$ -diversity (i.e. a greater homogenization of species composition among plots within windows where habitats are well-aggregated), because species can move more easily or “percolate” across the entire landscape and therefore occupy more plots (i.e. increase of the plot occupancy rate within windows).

## Materials and methods

### General description of the studied forest

The study was carried out in the French lowland temperate forest of Compiègne, 14,382 ha in area dominated by deciduous tree species (91%), particularly *Fagus sylvatica* (41%), *Quercus robur* (20%), and *Q. petraea* (7%) often mixed with *Carpinus betulus*. Most of the forest is managed under an even-aged silvicultural regime, with “mature” (i.e.  $50 \leq \text{DBH} < 70$  cm) and “overmature” (i.e.  $\text{DBH} \geq 70$  cm) stands representing respectively 30% and 5% of its area. The spatial heterogeneity of saproxylic habitat has been increased by conservation schemes (set-aside some forest stands) and recent catastrophic events (storms, drought-induced decline), making the Compiègne forest a relevant area for study the effects of landscape structure on saproxylic beetle diversity.

### Spatial distribution of saproxylic beetle habitats at forest scale

We built a distribution map of the habitats used by saproxylic beetles (i.e. TreMs and DW) over the entire forest, at the highest spatial resolution possible. For this purpose, we computed a statistical model (GLM) calibrated on field surveys (687 plots of 0.28 ha) to predict the availability of nine elementary saproxylic habitat within 30 m-pixels. The pixel represents an arbitrary spatial unit of discretization to describe and predict the distribution of habitats within forest. The pixel size (0.09 ha) was chosen to preserve the complex shape and boundaries of stands. Eight forest stand variables (five silvicultural and three ecological factors), known to affect the occurrence of saproxylic habitats, were used as predictors. We restricted the mapping to stands dominated by deciduous species. Therefore, we did not model coniferous stands where the availability of habitats was considered null. Finally, we obtained raster distribution maps over the entire forest of predicted occurrence probability per pixel for each elementary saproxylic habitat (see online supplementary material, Appendix 1 for an extensive description of saproxylic habitats, predictors, selected models, and distribution maps).

Because analyzing each elementary habitat independently would have been too complex both in terms of sampling design and in terms of data analysis, we

grouped them into two broad categories: (i) cavities and (ii) deadwood plus polypores (see online supplementary material, Appendix 2 for further justification of these categories). Within a category, all the distribution maps were summed to generate a single map where pixel scores ( $a$ ) correspond to the expected number of distinct elementary habitats in the pixel, which may be interpreted as a “potential habitat” value (i.e. reflects the ability of each pixel to provide saproxylic habitats). For example, for cavities, we summed the occurrence probability of trunk-base rot-hole, trunk rot-hole and woodpecker breeding cavities (see online Appendix 2 for details).

### Windows selection procedure

We selected windows contrasted in terms of habitat aggregation but homogeneous in terms of habitat amount, which was fixed at an intermediate level within the existing range in the Compiègne forest. We controlled the habitat amount at window scale to intermediate values because we expected this setting to maximize the effects of habitat aggregation (Villard and Metzger 2014), which are otherwise hard to evidence. We considered windows of 506 ha ( $2.25 \times 2.25$  km). The habitat amount within windows (AMOUNT) was calculated by summing the score ( $a$ ) of each pixel included in the window. The AMOUNT index for a category of habitats therefore quantified the sum of potential habitat areas over each elementary habitat included in the category. Second, an index of habitat aggregation within windows (AGGREG) was calculated based on the connectivity probability index (PC, Saura and Pascual-Hortal 2007) derived from graph theory:

$$AGGREG = \frac{\sum_{i=1}^n a_i \times \sum_{j \neq i} a_j \times p_{ij}}{AMOUNT^2} \quad (1)$$

where  $p_{ij}$  is the probability that an individual in pixel  $i$  can successfully disperse to pixel  $j$  and is modelled using a decreasing function of distance including a scale parameter  $\alpha$ :

$$p_{ij} = \frac{1}{1 + \left(\frac{d_{ij}}{\alpha}\right)} \quad (2)$$

*AGGREG* corresponds to the probability that two elementary habitats randomly drawn from the window get connected by a dispersal process with typical distance  $\alpha$ .

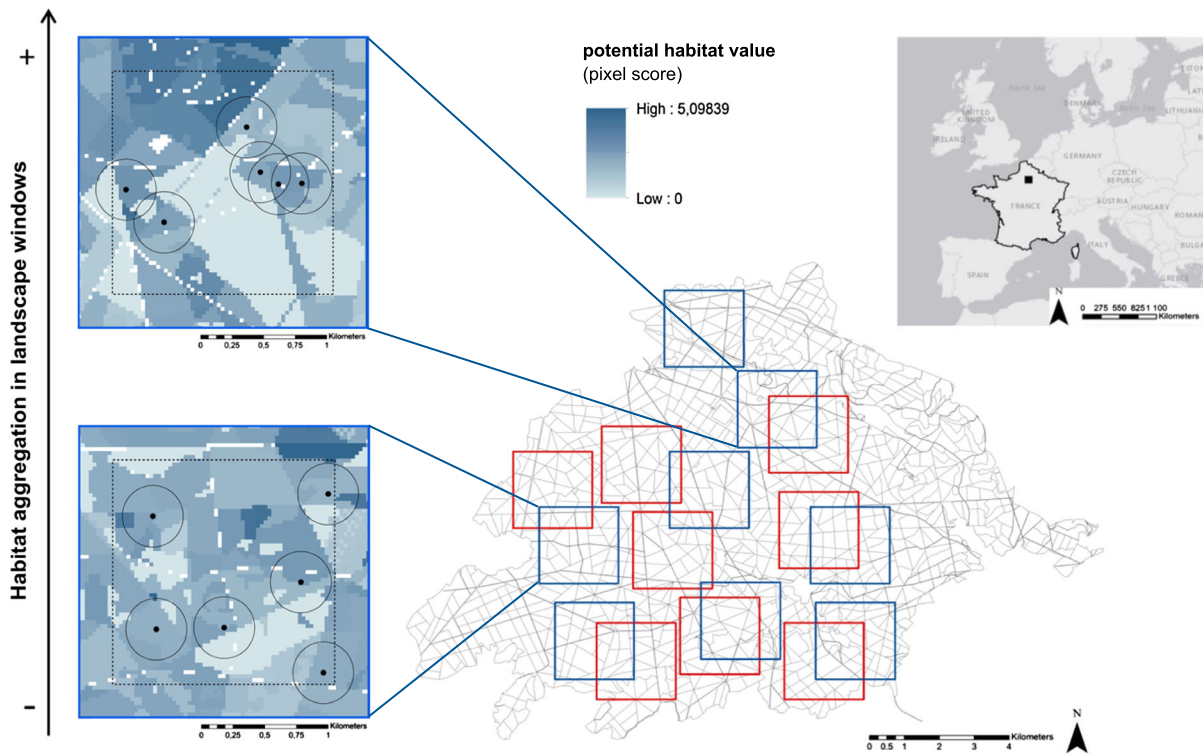
Overall, 16 windows were selected—eight for the cavity category and eight for the deadwood-polypore category (Fig. 1). We ensured that the selected windows within each category were distributed over the entire forest. Since analyses for the two habitat categories were conducted independently, window overlap between them was allowed (see online Appendix 2 for a detailed description of the selected windows).

### Saproxylic beetle sampling design

Inside the  $1.75 \times 1.75$  km (306 ha) central area of the 16 selected windows, six sampling plots were set up in oak or beech mature high forest stands (i.e. dominant trees with  $DBH \geq 50$  cm). Within each plot, two unbaited transparent flight-interception traps (Poly-trap<sup>TM</sup>, E.I.P., Toulouse, France) were installed, one with and one without the central part colored in black (Bouget et al. 2008a). The traps were set approximately 1.5 m above the ground and 20–40 m from each other. Four monthly samples were collected from April to August 2016, and all the samples from each plot were pooled before analysis. Thus, 48 sampling plots were set up in each habitat category; however, since some plots were used for both habitat categories due to window overlap, the sampling design comprised 160 traps on 80 plots in total.

### Identifying saproxylic beetles and defining ecological groups

Except for a few hard-to-identify families, which were excluded from the dataset, flying saproxylic beetles were identified to the species or genus level (see online supplementary material, Appendix 3 for a complete taxonomic list). Based on ecological traits available from the FRISBEE database (Bouget et al. 2008b), we first identified three groups according to “habitat preference”—i.e. cavicolous, fungicolous and lignicolous species, associated with cavities, wood-decaying fungi and deadwood, respectively. Then, we used “trophic regime” to distinguished lignicolous saproxylophagous species developing in decayed deadwood



**Fig. 1** Location of the Compiègne forest in France and description of the nested study design. Eight 506-ha landscape windows representing a habitat aggregation gradient, independently of amount, have been selected for each saproxylic habitat category—cavity (red squares) and deadwood-polypore (blue squares). Each window included six 1-ha sampling plots with a

26-ha buffer centered on plots. Grey polygons correspond to forest stands and the blue color gradient represents the potential habitat value for each pixel (maximum values are reached when the pixel is likely to have a high occurrence probability for all elementary saproxylic habitats included in the category). (Color figure online)

from xylophagous species developing in fresh deadwood. Finally, we defined four guilds along a continuum from stable to ephemeral habitat: (i) cavicolous species dwelling in stable and slowly maturing tree cavities, which we considered as “perennial stayer species” sensu Nordén and Appelqvist (2001) because we believe that such species are typically sedentary, (ii) fungicolous species associated with fruiting bodies of wood-decaying fungi (polypores) and (iii) lignicolous saproxylophagous species associated with decayed deadwood, both considered as “shuttle species” sensu Nordén and Appelqvist (2001), and (iv) lignicolous xylophagous species associated with ephemeral fresh deadwood, considered as “tracking-colonist species”.

Landscape structure metrics for biodiversity analysis at three spatial scales

At the window scale, we recorded the aggregation index (AGGREG; Eq. 1) with a scale parameter  $\alpha = 5$  (typical dispersal distance equal to  $5 \times 30 \text{ m} = 150 \text{ m}$ ). Within windows, we defined an intermediate spatial scale materialized by 26-ha square buffers ( $510 \text{ m} \times 510 \text{ m}$ ) centered on each sampling plots. We computed a habitat amount index within each buffer (AMOUNT.BUF) by summing the potential habitat value of each pixel included in the buffer. At the 1-ha plot scale, we used a density index (DENSITY) directly obtained from field record of saproxylic habitats, following the same protocol as for the calibration of the predictive model of elementary saproxylic habitats distribution at the forest scale.

## Statistical analyses of saproxylic beetle diversity at plot and window scale

First, we ran generalized linear mixed models (GLMMs; *lme4* R-package; Bates et al. 2017) to test the response of saproxylic beetle diversity within plots to landscape structure. The dependent variables were the abundance of individuals (AB) and the species richness (SR) for each stability–dispersal guild—i.e. cavicolous, fungicolous, saproxylophagous, and xylophagous. The independent variables were AGRREG index measured at 506-ha windows scale, AMOUNT.BUF index measured at 26-ha buffer scale and DENSITY index measured at 1-ha plot scale. These three landscape structure metrics were computed for each habitat associated with beetle guilds—i.e. cavities, polypores and deadwood (Table 1). All the independent variables were standardized to a mean of 0 and a standard deviation of 1. Species richness was fitted with a Poisson distribution and abundance with a negative binomial distribution to control for over-dispersion. In the models, we have considered “windows” as spatially implicit random effects on the intercept. We analyzed the contribution of the independent variables through model averaging (“*dredge*” function in the *MuMIn* R-package; Barton 2018). Only models with  $\Delta AIC < 2$  compared to the best model were included in the estimation of coefficients. We calculated the relative importance of each independent variable by summing the Akaike weights of all plausible models where the target variable was included (“*importance*” function in the *MuMIn* R-package; Barton 2018).

**Table 1** Values of landscape structure metrics (min; max; mean  $\pm$  standard deviation) measured at different spatial scales—habitat aggregation at windows scale (AGRREG),

Landscape structure metrics	Spatial scales	Values	Saproxylic habitats		
			Cavities	Polypores	Deadwood
AGGREG	506-ha windows	Min; max	1.48e <sup>-1</sup> ; 1.62e <sup>-1</sup>	1.44e <sup>-1</sup> ; 1.56e <sup>-1</sup>	1.44e <sup>-1</sup> ; 1.56e <sup>-1</sup>
		Mean $\pm$ SD	1.53e <sup>-1</sup> $\pm$ 3.82e <sup>-3</sup>	1.49e <sup>-1</sup> $\pm$ 3.93e <sup>-3</sup>	1.49e <sup>-1</sup> $\pm$ 3.76e <sup>-3</sup>
AMOUNT.BUF	26-ha buffer	Min; max	5.89e <sup>+1</sup> ; 4.09e <sup>+2</sup>	7.62e <sup>+1</sup> ; 1.67e <sup>+2</sup>	2.19e <sup>+2</sup> ; 4.92e <sup>+2</sup>
		Mean $\pm$ SD	2.66e <sup>+2</sup> $\pm$ 8.67e <sup>+1</sup>	1.16e <sup>+2</sup> $\pm$ 1.96e <sup>+1</sup>	3.59e <sup>+2</sup> $\pm$ 5.72e <sup>+1</sup>
DENSITY	1-ha plot	Min; max	0; 53	0; 25	0; 16
		Mean $\pm$ SD	8.60 $\pm$ 9.58	3.73 $\pm$ 5.69	5.15 $\pm$ 3.83

Standard deviation (SD)

Second, for each of four stability–dispersal guilds, we evaluated the effect of habitat aggregation at the window scale on the  $\beta$ -diversity—i.e. species composition dissimilarity between the six sampled plots within windows. A dissimilarity index was computed for each window (based on the Sorensen index) with the “*beta.multi*” function in the *betapart* R-package (Baselga et al. 2013). As a complementary analysis, we also evaluated the effect of habitat aggregation at the window scale on the average plot occupancy rate—i.e. proportion of plots in the window occupied by each species, averaged across all the species of the focal guild (high values meant that all species tended to occupy all the plots in the window, while low values meant that species tended to occur in a small number of plots in the window). At last, we evaluated whether habitat aggregation at the window scale affected the  $\gamma$ -diversity—i.e. species number pooled from the six sampled plots within each window. For these three analyses (plot occupancy rate,  $\beta$ - and  $\gamma$ -diversity), the significance of habitat aggregation at the window scale on the response variables was assessed with Spearman correlation tests. All statistical analyses were performed with the R software (version 3.4.1).

## Results

### Beetle data overview

Overall, 308 saproxylic beetle species associated to deciduous tree species were trapped, corresponding to 13,007 individuals. The numbers of species and

habitat amount at buffer scale (AMOUNT.BUF), and habitat density at plot scale (DENSITY)—for each of the three saproxylic habitats (cavities, polypores, deadwood)

individuals trapped in windows set for cavity habitat category were similar to those trapped in windows set for deadwood-polypore habitat category, with 272 species (8225 individuals) and 265 species (7527 individuals), respectively. In cavity category windows, we analyzed the response of the 13 cavicolous beetle species (159 individuals), whereas in deadwood-polypore category windows, we included the 44 fungicolous beetle species (1105 individuals), the 54 saproxylophagous beetle species (1928 individuals) and the 66 xylophagous beetle species (2095 individuals) (see online supplementary material, Appendix 3 for taxonomic list).

Multi-scale effects of landscape structure on  $\alpha$ -diversity

The four stability–dispersal guilds of saproxylic beetles did not respond to the same landscape structure metrics at the same spatial scales (Table 2).

Cavicolous guild abundance showed a significant positive response to the amount of cavities only at small spatial scales—i.e. 1-ha plot ( $\beta = 0.28$ ,  $p = 0.03$ ) and 26-ha buffer ( $\beta = 0.36$ ,  $p = 0.02$ ). Similarly, fungicolous guild abundance increased with the amount of polypores only at the 26-ha buffer scale ( $\beta = 0.21$ ,  $p = 0.003$ ). The saproxylophagous guild was rather sensitive to habitat aggregation at window scale. The saproxylophagous species richness in plots responded positively and significantly to an increase in deadwood aggregation within windows ( $\beta = 0.10$ ,  $p = 0.03$ ), and no significant effect was demonstrated at smaller spatial scales. Finally, regarding xylophagous beetles, no significant effect of landscape structure metrics at any spatial scale was found, either in terms of abundance or species richness.

**Table 2** Multi-model averaged estimates of standardized coefficients ( $\pm$  standard error) and p-values of landscape structure metrics at three spatial scale on abundance and

species richness of the four stability–dispersal guilds (cavicolous, fungicolous, saproxylophagous, xylophagous)

Stability–dispersal guilds		Landscape structure metrics						
		INTERCEPT Std. coef $\pm$ SE	506-ha window AGGREG Std. coef $\pm$ SE	Imp	26-ha buffer AMOUNT.BUF Std. coef $\pm$ SE	Imp	1-ha plot DENSITY Std. coef $\pm$ SE	Imp
Cavicolous	AB	1.00 $\pm$ 0.18 ( $< 2e-16$ )			<b>0.36 <math>\pm</math> 0.15</b> <b>(0.02)</b>	1.00	<b>0.28 <math>\pm</math> 0.13</b> <b>(0.03)</b>	1.00
	SR	0.37 $\pm$ 0.15 (0.01)	0.08 $\pm$ 0.14 (0.57)	0.15			0.15 $\pm$ 0.13 (0.25)	0.26
Fungicolous	AB	3.13 $\pm$ 0.07 ( $< 2e-16$ )	0.06 $\pm$ 0.07 (0.43)	0.22	<b>0.21 <math>\pm</math> 0.07</b> <b>(0.003)</b>	1.00	- 0.05 $\pm$ 0.07 (0.42)	0.22
	SR	2.05 $\pm$ 0.09 ( $< 2e-16$ )			0.05 $\pm$ 0.06 (0.45)	0.23		
Saproxylophagous	AB	3.66 $\pm$ 0.08 ( $< 2e-16$ )	0.12 $\pm$ 0.08 (0.14)	0.43	- 0.13 $\pm$ 0.09 (0.13)	0.46	0.07 $\pm$ 0.09 (0.43)	0.11
	SR	2.43 $\pm$ 0.05 ( $< 2e-16$ )	<b>0.10 <math>\pm</math> 0.05</b> <b>(0.03)</b>	0.80			0.05 $\pm$ 0.05 (0.31)	0.25
Xylophagous	AB	3.55 $\pm$ 0.25 ( $< 2e-16$ )						
	SR	2.40 $\pm$ 0.07 ( $< 2e-16$ )			0.04 $\pm$ 0.05 (0.42)	0.31		

Habitat aggregation at windows scale (AGGREG); habitat amount at buffer scale (AMOUNT.BUF); habitat density at plot scale (DENSITY); abundance (AB); species richness (SR), Standardized coefficient (std. coef); standard error (SE); relative importance of landscape structure metrics (imp). P-values in brackets and significant results in bold

## Effect of habitat aggregation within windows on $\beta$ -diversity and occupancy rate

For saproxylophagous beetles, the  $\beta$ -diversity analysis (i.e. species composition dissimilarity between the six sampled plots within a given windows) revealed a significant negative correlation (Spearman rank correlation coefficient  $r_{SXY} = -0.83$ ,  $p = 0.02$ ; Fig. 2) with habitat aggregation measured within each landscape window. No significant effect was detected for the other three guilds. Multi-site  $\beta$ -diversity appeared to be higher for cavicolous beetles, despite a considerable variation ( $\text{mean}_{CAV} = 0.80$ ,  $\text{sd}_{CAV} = 0.14$ ), than for fungicolous, saproxylophagous and xylophagous beetles (respectively,  $\text{mean}_{FUN} = 0.69$ ,  $\text{sd}_{FUN} = 0.05$ ;  $\text{mean}_{SXY} = 0.67$ ,  $\text{sd}_{SXY} = 0.04$ ;  $\text{mean}_{XYL} = 0.70$ ,  $\text{sd}_{XYL} = 0.05$ ; Fig. 2).

The analysis of the average plot occupancy rate for each guild also only showed a significant effect of habitat aggregation on saproxylophagous beetles—i.e. the average number of occupied plots within windows was higher for this guild as deadwood aggregation increased ( $r_{SXY} = 0.83$ ,  $p = 0.02$ ; Fig. 3). Contrary to  $\beta$ -diversity, the average plot occupancy rate was lower for cavicolous beetles than for the other three guilds, independently of habitat aggregation ( $\text{mean}_{CAV} = 0.30$ ,  $\text{sd}_{CAV} = 0.11$ ;  $\text{mean}_{FUN} = 0.40$ ,  $\text{sd}_{FUN} = 0.05$ ;

$\text{mean}_{SXY} = 0.41$ ,  $\text{sd}_{SXY} = 0.04$ ;  $\text{mean}_{XYL} = 0.38$ ,  $\text{sd}_{XYL} = 0.05$ ; Fig. 3).

## Effect of habitat aggregation within windows on $\gamma$ -diversity

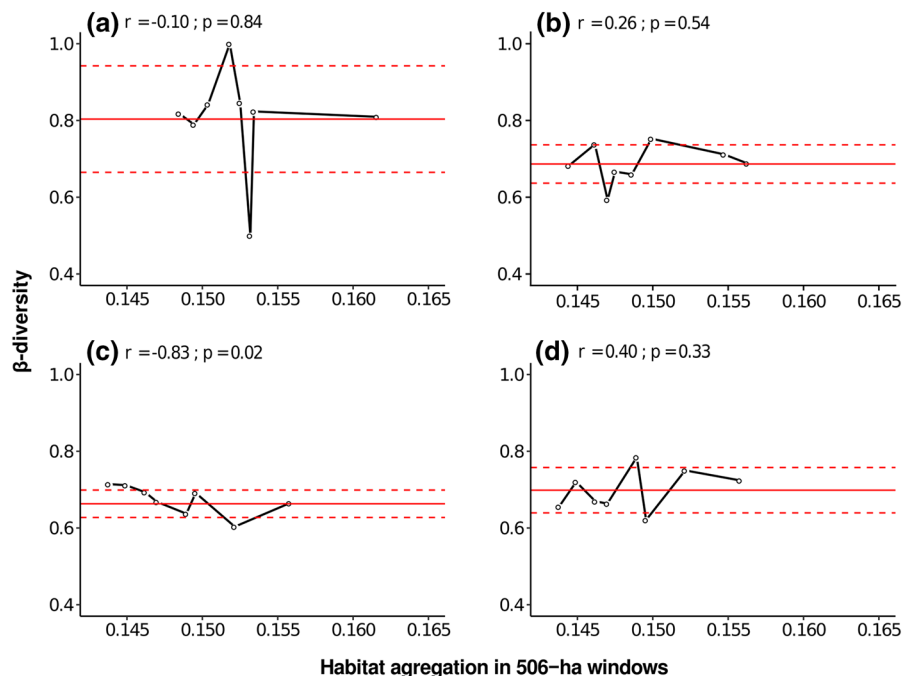
We did not observe any significant effects of habitat aggregation on  $\gamma$ -diversity (species richness) at the window scale for the four stability–dispersal guilds (Spearman  $r_{CAV} = -0.14$ ,  $p = 0.73$ ;  $r_{FUN} = 0.02$ ,  $p = 0.95$ ;  $r_{SXY} = 0.34$ ,  $p = 0.41$ ;  $r_{XYL} = 0.52$ ,  $p = 0.19$ ; Fig. 4). This is probably partly due to the low number of windows available to test correlations ( $n = 8$  windows).

## Discussion

### Saproxylic beetles respond to landscape structure at different spatial scales due to contrasting habitat stability

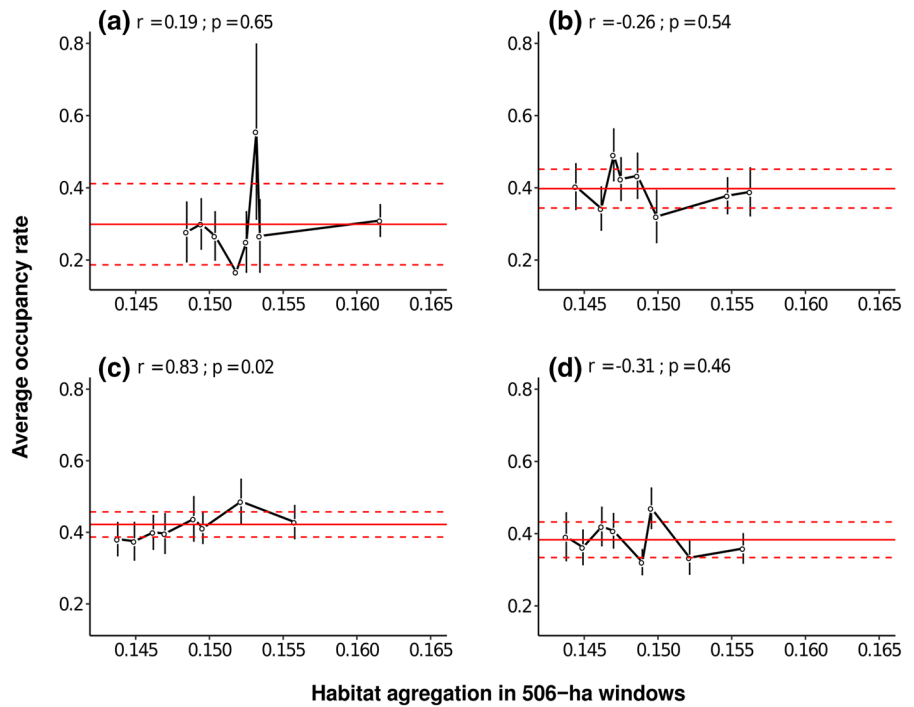
One of our most important findings is that the scale of response of the four saproxylic beetle guilds (i.e. cavicolous, fungicolous, saproxylophagous and xylophagous) increases with decreased stability of their habitat. This results is consistent with the stability–

**Fig. 2** Effects of habitat aggregation at window scale on the  $\beta$ -diversity for each of the four stability–dispersal guilds. Each point represents the value of species dissimilarity index between the six sampled plots within given window. Significance was tested with a Spearman correlation test. The solid horizontal red line represents the mean and the dashed horizontal red line represents the standard deviation of  $\beta$ -diversity over the eight landscape windows.  
**a** Cavicolous,  
**b** Fungicolous,  
**c** Saproxylophagous,  
**d** Xylophagous beetles.  
 (Color figure online)

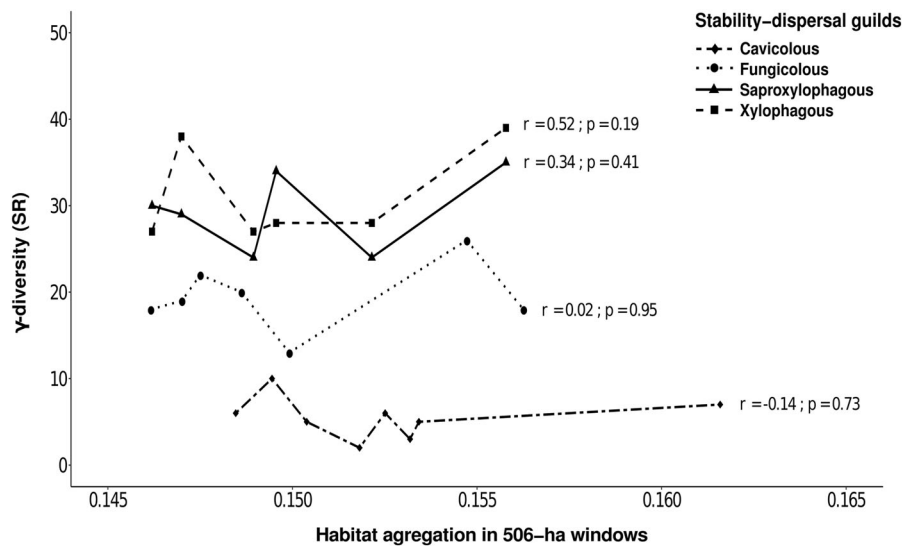




**Fig. 3** Effects of habitat aggregation at window scale on the average plot occupancy rate for each of the four stability–dispersal guilds. Each point represents the average number ( $\pm$  standard error) of plots occupied by all species present in the window. Significance was tested with a Spearman correlation test. The solid horizontal red line represents the mean and the horizontal dashed red line the standard deviation of the average plot occupancy rate over the eight landscape windows. **a** Cavicolous, **b** Fungicolous, **c** Saproxylophagous, **d** Xylophagous beetles. (Color figure online)



**Fig. 4** Effects of habitat aggregation at window scale on the  $\gamma$ -diversity for each of the four stability–dispersal guilds. Each point represents the species richness (species number within each window pooled from the six sampled plots). Significance was tested with a Spearman correlation test



dispersal conceptual framework which predict that species using ephemeral habitat should have higher dispersal abilities than species developing in more stable habitat (Southwood 1977). Particularly, with our multi-scale nested design, we showed that the cavicolous guild, which we considered as “perennial stayer species” according to the classification proposed by Nordén and Appelqvist (2001), was the only

group positively affected (in terms of abundance) by habitat density within 1-ha plots. At the 26-ha buffer scale, both cavicolous and fungicolous beetles responded to habitat amount. By contrast, at window scale, only the saproxylophagous species richness showed a positive significant response to habitat aggregation whereas the others stability–dispersal guilds did not respond. Finally, we did not find any

significant response of xylophagous species considered as “tracking-colonist species” to landscape structure at the three spatial scales (Table 2).

Furthermore, we found that an increase in habitat aggregation at the window scale significantly increased the similarity among plots (i.e. lower  $\beta$ -diversity and higher species occupancy rate) only for the saproxylophagous guild. This means that increased aggregation of deadwood facilitates the colonization of more plots by these species and contributes to the homogenization of species communities within windows. The fact that changes in habitat aggregation at the window scale affects the saproxylophagous guild species distribution and that the habitat amount at buffer scale does not affect abundance or species richness in plots tends to suggest that dispersal limitation of this group occurs somewhere between 250 m (the half of buffer side length), which seems to be an distance easy to overcome, and 2.25 km (the side length of the window) where limited dispersal seems to happen. This range is congruent with the distance of 1 km already highlighted for saproxylophagous beetles associated with oak deadwood in temperate (Franc et al. 2007) and boreal forest (Gibb et al. 2006b). By contrast, habitat aggregation did not have a significant effect on the  $\beta$ -diversity of the three others guilds. We suggest distinct explanations for the cavicolous guild on the one hand, and fungicolous and xylophagous guilds on the other hand. The average plot occupancy rate across cavicolous species remained at a relatively low level compared to fungicolous and xylophagous species. This suggests that increasing cavities aggregation within a 506-ha landscape did not allow cavicolous species to occupy more plots. Therefore, cavicolous species tended to stay near their habitat plots and did not seem to percolate in the window, even when habitat are well-aggregated, suggesting strong dispersal limitation. This result is congruent with previously published data about the low dispersal ability of some cavicolous beetles (Ranius 2006; Hedin et al. 2008). Conversely, for fungicolous and xylophagous species, the number of occupied plots (resp.  $\beta$ -diversity) remained at high level (resp. low level) even when habitat aggregation was low within windows, which suggests that they can spread in windows without distance limitation. For xylophagous beetles, this finding is consistent with the fact that we found no effect of habitat amount at smaller scales, and it globally suggests that these species are able to

move quite freely within windows. These beetles are therefore likely to be sensitive to landscape structure at larger scales ( $> 500$  ha) due to their high average dispersal ability, which clocks in at several tens of kilometers for some species (e.g. Jactel and Gaillard 1991). It is more surprising to find no effect of habitat aggregation at windows scale for fungicolous guild which was affected by habitat amount at buffer scale (in terms of abundance) but not at plot scale. Windows could thus a priori seem in the ideal range of scale of effect (sensu Jackson and Fahrig 2012) to show some sensitivity to habitat aggregation. Of course, we cannot discard the explanation that aggregation effects are studied only on eight windows, resulting in low power, and that the effect could have remained undetected. In addition, the scales of effect need not be the same for community composition (species richness, occupancy rates, Sorensen  $\beta$ -diversity indices), which rely on presence-absence of species, and community abundance, which rely on species abundance (Miguet et al. 2016).

Overall, our results are consistent with the predictions of the stability–dispersal conceptual model: (i) cavicolous has sufficiently low dispersal abilities to show sensitivity to the plot scale (in abundance), while other groups associated to less stable habitat do not; (ii) cavicolous and fungicolous species have sufficiently low dispersal ability to show sensitivity to the buffer scale (in terms of abundance), while other groups associated to less stable habitats do not; (iii) only saproxylophagous guild show sensitivity to habitat aggregation at window scale (in terms of species richness) while cavicolous and fungicolous guilds associated with more stable habitat do not because changes occur at too large a scale for their dispersal abilities, and the xylophagous species do not either because any configuration at window scale is equivalent for them given their strong dispersal abilities. Importantly, we emphasize that our results revealed no inconsistency such as a “gap” in the guild responses along the stability gradient that is guilds associated to very stable and very ephemeral habitats responding to some scale but guilds associated to habitat with intermediate stability not doing so.

Even if the stability–dispersal conceptual model represents an interesting theoretical framework to compare scales of response between different species guilds, it may not be systematically successful in any context and should be applied cautiously. In particular

the homogeneity of species within guilds in terms of dispersal ability can be questioned. The variation in scale of response had already been observed for fungicolous beetles (Komonen 2008), even among species with similar habitat requirements (Jonsson 2003; Jonsson et al. 2003). This finding was also raised for others beetle guilds—i.e. for cavicolous beetles (from 192 to 2760 m; Ranius et al. 2011a); for saproxylous longhorn beetles (from 800 to 2000 m; Saint-Germain and Drapeau 2011) and for xylophagous species associated with fresh aspen deadwood (scale ranging from 10 to 1000 m; Ranius et al. 2011b).

Implications for forest management:  
towards a spatialized conservation strategy

Understanding species response mechanisms to landscape structure and identifying the scales of effect in relation to species dispersal ability are critical for implementing efficient biodiversity conservation strategies. In our study, we found that habitat aggregation in a logged forest matrix, with controlled intermediate habitat amount, had a positive influence on the saproxylous species by facilitating access to habitats. Consequently, although the amount of habitat in the landscape could be the dominant driver for saproxylous beetles (e.g. Seibold et al. 2017), our results suggests that habitat spatial arrangement should also be considered, which is congruent with a recent study on saproxylous beetles inhabiting hollow oaks (Mestre et al. 2018). As already suggested by Kouki et al. (2001) in Fennoscandian fragmented forests, aggregation of saproxylous habitat (DW, TreMs) could be improved by simultaneously setting aside forest areas (i.e. forest reserves; Bouget et al. 2014; Paillet et al. 2015; Larrieu et al. 2017) and increasing saproxylous habitat availability in the managed forest matrix (Franklin and Lindenmayer 2009).

One of the greatest challenges for taking spatial arrangement into account in conservation strategies comes from the fact that species respond to habitat aggregation at different spatial scales. According to our results, for stable habitat species (with probably low dispersal abilities), such as cavicolous beetles, it seems more relevant to concentrate protection efforts within sites where the species are already present than to scatter sites across the landscape—i.e. increase the amount of habitat in the surrounding area (Ranius et al.

2011a). By contrast, ephemeral habitat species (with probably higher dispersal abilities), such as (sapro-) xylophagous beetles, could benefit from a greater spread of stand with high quality habitat at much larger scales (Ranius and Kindvall 2006).

A second challenge for managers stems from the high species turnover among landscape windows: different landscapes harbor different species (see partitioning diversity in online supplementary material, Appendix 4). This is probably due to unmeasured environmental gradients (e.g. a sub-canopy temperature gradient in the Compiègne forest; Lenoir et al. 2017), which are the main drivers of community composition at the forest scale (i.e. inter-window scale) through a “species sorting” process (Leibold et al. 2004). As a result, landscape features present at the window scale, such as habitat aggregation, had no predictable effect on  $\gamma$ -diversity for our studied guilds, even for saproxylous species for which the window scale seemed an appropriate spatial extent (Fig. 4). Environmental gradients commonly gain in importance as the scale of analysis increases in studies of species diversity patterns (e.g. Thuiller et al. 2015). Our findings regarding high species turnover are consistent with other studies in forest contexts, which found significant  $\beta$ -diversity even at relatively small scales—e.g. between stands within a forest area of more than 500 ha (Müller and Goßner 2010), or between sites within a landscape of ca. 10 km<sup>2</sup> (Rubene et al. 2015). In terms of conservation, fine-scale species sorting indicates that forest biodiversity could benefit from dispersing conservation sites spatially over the entire forest.

## Conclusion

Our study highlighted that four guilds of saproxylous beetles respond to landscape structure (i.e. habitat amount and aggregation) at different spatial scales in compliance with a gradient of habitat lifetime. Therefore, the stability–dispersal model seems to be an adequate framework to analyze saproxylous beetles spatial distribution within managed forests. From an applied conservation perspective, the stability of habitats may contribute to determine the spatial scale at which conservation efforts should be aggregated for targeted guilds. For each saproxylous guild, our study suggests that an ideal network of habitat should be

aggregated at the appropriate scale and cover the various environmental conditions present in the forest. Such a strategy would then achieve two objectives simultaneously: (i) improving species persistence at the fine scale by facilitating the movement of individuals among habitat units, and (ii) maximizing species diversity at larger scale (i.e. over the whole forested area). The next challenging question is now to determine whether it is possible to meet the requirements of habitat continuity for several guilds and taxa in a single conservation design. In that respect, fractal theory (Mandelbrot 1983; With 1997) offers stimulating perspectives towards creating networks of areas with high densities old-growth attributes that efficiently conciliate contrasted scales within a single design.

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