Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests

P. Janssen, Eugénie Cateau, M. Fuhr, B. Nusillard, Hervé Brustel, Christophe Bouget

To cite this version:

P. Janssen, Eugénie Cateau, M. Fuhr, B. Nusillard, Hervé Brustel, et al.. Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. Biodiversity and Conservation, 2016, 25 (6), pp.1167-1185. 10.1007/s10531-016-1116-8 . hal-02603471

Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests

Philippe Janssen, Eugénie Cateau, Marc Fuhr, Benoit Nusillard, Hervé Brustel, Christophe Bouget

P. Janssen and M. Fuhr
Université Grenoble Alpes, National Research Institute of Science and Technology for Environment and Agriculture (Irstea), UR EMGR, 2 rue de la Papeterie BP 76, F-38402 Saint-Martin-d'Hères, France

C. Bouget and B. Nusillard
National Research Institute of Science and Technology for Environment and Agriculture (Irstea), UR EFNO, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France

E. Cateau and H. Brustel
Université de Toulouse, Ecole d'Ingénieurs de Purpan, UMR 1201 Dynafor, F-31076 Toulouse Cedex 3, France

Corresponding author: P. Janssen (philippe.janssen@irstea.fr), phone +33 476762879, National Research Institute of Science and Technology for Environment and Agriculture (Irstea), UR EMGR, 2 rue de la Papeterie BP 76, F-38402 Saint-Martin-d'Hères, France

Abstract

Understanding the processes that shape biodiversity patterns is essential for ecosystem management and conservation. Local environmental conditions are often good predictors of species distribution and variations in habitat quality usually positively correlate to species richness. However, beside habitat limitation, species presence-absence may be constrained by dispersal limitation. We tested the relative importance of both limitations on saproxylic beetle diversity, using forest continuity as a surrogate for dispersal limitation and stand maturity as a surrogate for habitat limitation. Forest continuity relies on the maintenance of a forest cover over time, while stand maturity results in the presence of old-growth habitat features. Forty montane beech-fir forests in the French pre-Alps were sampled, under a balanced sampling design in which forest continuity and stand maturity were crossed. A total of 307 saproxylic beetle species were captured using flight-interception traps and Winkler-Berlese extractors. We explored the response of low- versus high-dispersal species groups to forest continuity and stand maturity. Saproxylic beetle diversity increased significantly with stand maturity and was mostly influenced by variables related to deadwood diversity at the stand scale and suitable habitat availability at the landscape scale. Surprisingly, no evidence of dispersal limitation was found, as diversity patterns were not influenced by forest continuity and associated variables, even for low-dispersal species. Our study demonstrates that in an unfragmented forest landscape, saproxylic beetles are able to colonize recent forests, as long as local deadwood resources are sufficiently diversified (e.g. tree species, position, diameter and/or decay stage).

Keywords: biodiversity patterns, forest continuity, stand maturity, saproxylic beetles.

Introduction

Understanding the processes that shape local species composition and diversity is a fundamental question in ecology (Sutherland et al. 2013). Variability in local species diversity is usually assumed to reflect differences in environmental conditions. This assumption relies both on the island biogeography theory (MacArthur and Wilson 1967) and the ecological niche theory (Hutchinson 1957), where species-rich sites result from species coexistence through habitat availability and heterogeneity, two complementary qualities usually correlated. However, beside habitat limitation, variability in local species diversity may result from dispersal limitations that constrain species movements toward suitable habitats (Pulliam 2000). Understanding the relative influence of dispersal versus habitat limitations has implications for biodiversity conservation and the management of ecosystems (Hodgson et al. 2011).

Species dispersal plays several fundamental roles in communities dynamics through the colonization of newly available habitats and genetic flow (Clobert et al. 2012). Dispersal is closely related to spatio-temporal variations in resource availability, given that species tend to move from poor-quality to high-quality habitats (Lowe 2009). However, dispersal abilities vary within and among species groups, which can be defined according to species traits such as flight ability for animals. Depending on dispersal abilities and distance to habitat source, colonization of newly available habitats may take more or less time and explain the absence of species from suitable habitats (Pulliam 2000).

Even for high-dispersal species, the ability to successfully establish a population in new habitat patches remains dependent on species-specific requirements. Species niche breadth shows the ability of a given individual species to perform as a function of resource availability (Devictor et al. 2010). Furthermore, habitat quality may contribute to species presence-absence patterns (Pulliam 2000). Indeed, habitats that include both a large amount and a diversity of resources may support a greater diversity of species, including specialists which are able to perform thanks to very specific resources. Variations in habitat quality therefore provide a practical framework in which to study patterns of species diversity.

In forest ecosystems, forest continuity and stand maturity have contrasting effects on biodiversity. Forest continuity is related to the maintenance of forest cover over time, regardless of stand maturity and management type. Ancient forests have been in continuous existence for at least 200 years while recent forests are mainly agricultural areas afforested during the last 200 years (Hermy and Verheyen 2007). Experimental studies testing the role of forest continuity in shaping community structure have largely focused on plants (Hermy and Verheyen 2007). Results have shown that plant species closely related to ancient forests were usually more adapted to forest interior conditions (e.g. shade tolerant) and have short-distance dispersal abilities (e.g. myrmecochory) (Verheyen et al. 2003; Sciama et al. 2009). However, the influence of forest continuity on other taxa remained unclear since very few studies have been conducted to date (e.g. Assmann 1999; Gossner et al. 2008; Buse 2012). Stand maturity is usually related to old-growth habitat features. Compared to mature stands, overmature stands are characterized by a greater proportion of very large trees (e.g. Whitman and Hagan 2007), and a larger abundance and diversity of deadwood (e.g. Meyer and Schmidt 2011) and tree-related microhabitats (e.g. Winter and Möller 2008). By enhancing habitat quality, overmature stands may improve species coexistence, especially for saproxylic species depending on specific deadwood resources (e.g. Stenbacka et al. 2010; Lassauce et al. 2012). Finally, overmature stands may highlight the effect of habitat limitation on biodiversity patterns.

Using forest continuity as a surrogate for dispersal limitation and stand maturity as a surrogate for habitat limitation, we evaluated the relative importance of both limitations on saproxylic beetle diversity patterns. Saproxylic beetles are a rich group of specialized species that depend on deadwood for at least a part of their lifecycle (Speight 1989). They are among the first organisms to colonize dying trees and, consequently, play a fundamental role in wood decomposition and nutrient recycling (Speight 1989; Siitonen 2001). Previous works have shown that saproxylic beetle diversity is closely linked to deadwood quantity (Lassauce et al. 2011; Lachat et al. 2012; Bouget et al. 2014) and that many species are more closely linked to specific deadwood qualities such as tree species, diameter, stage of decay and microhabitat presence (Jonsell et al. 2007; Brin et al. 2011; Bouget et al. 2013). Saproxylic beetle diversity may therefore respond to stand maturity. Moreover, dispersal abilities vary greatly among saproxylic species, i.e. between flightless and flying beetles. Since probability of colonization is a function of patch isolation in space and time (Clobert et al. 2012), response of saproxylic beetles to forest continuity may depend on their dispersal abilities.This suggests that low- and high-dispersal species may have different response patterns to both environmental conditions (Lassau et al. 2005; Janssen et al. 2009) and distance to sources (Irmler et al. 2010; Bouget et al. 2015).

Based upon a sampling design crossing forest continuity and stand maturity, we quantified the relative contribution of dispersal and habitat limitation on saproxylic beetle richness and abundance. We used information on flight ability to build species groups, i.e. flightless beetles (brachypterous and apterous) were considered as low-dispersal species and flying beetles (macropterous) were considered as high-dispersal species. We then studied the response of (i) total species, (ii) low-dispersal species and (iii) high-dispersal species to forest continuity and stand maturity. Specifically, we explored the following two hypotheses:

(1) Forest continuity induces dispersal limitation from habitat sources, i.e. ancient forests, to newly available habitats, i.e. recent forests. This limitation should influence low-dispersal species more than high-dispersal species, and may be a function of isolation from habitat sources. Regardless of stand maturity, we hypothesized that the richness and abundance of low-dispersal saproxylic beetle species would increase from recent to ancient forests, and that the proportion of ancient forests in the surrounding landscape and the distance at which they are found would be key parameters explaining diversity patterns.

(2) Stand maturity induces habitat limitation between structurally homogeneous habitats, i.e. mature stands, and structurally heterogeneous habitats, i.e. overmature stands. This limitation may influence specialized species, such as saproxylic beetles, and may be driven above all by resource availability. Regardless of forest continuity, we hypothesized that the richness and abundance of low- and high-dispersal saproxylic beetle species would increase from mature to overmature stands. We further hypothesized that deadwood quantity and quality would be key parameters explaining diversity patterns.

Materials and methods

Study area and sampling design

The study was carried out in the French pre-Alps, west of the Northern Alps Mountains (Fig. 1). The area encompasses the Vercors, Chartreuse and Bauges ranges (three Regional Natural Parks) characterized by a limestone substratum and a temperate climate. Landscapes are mainly covered by forests (63%) among which beech-fir stands are the most widespread. Owing to topographic and social constraints, forest management has been quite extensive and certain forest stands have not been managed for decades.

In 2014, we sampled 40 sites located in montane beech-fir forests at an altitude of 800 – 1500 m. The dominant tree species are European beech *Fagus sylvatica*, silver fir *Abies alba* and Norway spruce *Picea abies*. Our stratified and balanced sampling design crossed forest continuity and stand maturity. Forest continuity was characterized using 1:40 000 État-Major maps of France (Cateau et al. 2015), charted in the middle of the 19th century, and 1:10 000 up-to-date vegetation maps. Forest cover overlapping in both maps was considered to indicate ancient forests (AF, n=20), while current forest cover overlapping with crops or meadows in the État-Major maps was considered to indicate recent forests (RF, n=20). Stand maturity was *a priori* approached by forest prospections and confirmed after stand attribute measurements were taken. Among a larger sampling design of 70 stands, we selected 20 mature (AF=10, RF=10) and 20 overmature stands (AF=10, RF=10). To improve the independence of our observations and avoid edge influence, all sampling sites were established >1.2 km away from any other site, were located in ancient or recent forest stands >5 ha in area, and were >68 m from the nearest stand edge.

Insect sampling

Insects were collected using two sampling methods: flight-interception traps efficient at capturing flying beetles and Winkler-Berlese extractors of litter samples efficient at capturing flightless soil-dwelling beetles. From May to August 2014, three replicates of flight-interception traps were installed in each stand approximately 30 m apart and 1.5 m above the ground, for a total of 120 traps. Each trap consisted of two perpendicularly intercepting transparent plastic panes (40–60 cm), for a cumulative panel area of 1 m^2, with a funnel below leading to collecting vials filled with a mixture of 50% propylene glycol, 50% water and detergent to kill and preserve the insects. Flight-interception traps were emptied monthly. Flightless soil-dwelling beetles were sampled by sifting litter through 0.5 cm-mesh Winkler bags. In each stand, a total of six liters of litter samples was collected at the base of the six largest living trees: two beech, two fir and two spruce trees. Litter sifting was conducted in October 2014 and insects were extracted at the laboratory with Berlese funnels for one month (Cateau et al. 2016). Except for Staphylinidae beetles (excl. Pselaphinae and Dasycerinae), most saproxylic beetles were identified to the species or genus level, depending on the information available in the literature, by the authors and independent experts. Staphylinidae is one of the most diversified beetle families, and its identification is quite difficult and time-consuming. Moreover, saproxylic species richness and composition, with or without staphylinidea, respond similarly to stand and landscape gradients (Parmain et al. 2015).

Characterization of sampling sites

At the stand scale, each plot was characterized using a 10-m-radius and a 20-m-radius subplot. Within the 10-m-radius subplot (area: 314 m^2), we recorded all standing trees with a diameter at breast height (DBH) ≥

7.5 cm and all lying trunks with a diameter ≥ 7.5 cm at the base and ≥ 1 m in length. Within the 20-m-radius subplot (area: 1 256 m²), we recorded all standing trees with a DBH ≥ 30 cm and all lying trunks with a diameter ≥ 30 cm at the base and ≥ 1 m in length. For each standing tree and lying trunk, tree species, decay stage and tree microhabitats (cavities, sporophores of saproxylic fungi, ivy, sap runs, missing bark, cracks and shelter bark) were recorded whenever possible. For lying trunk, the diameter at both ends and in the middle section as well as length was recorded (only the portion located inside the plots was considered). Five decay stages were estimated based on resistance to tree caliper penetration: (I) hard wood, (II) caliper penetration < 1/4 of the tree diameter, (III) caliper penetration < 1/2 but > 1/4 of the tree diameter, (IV) caliper penetration < 3/4 but > 1/2 of the tree diameter, (V) caliper penetration > 3/4 of the tree diameter.

At the landscape scale, a Geographic Information System managed with ArcGIS 10.1 (Environmental Systems Research Inst., Redlands, CA, USA) was used to characterize the geographic context within a 500-m-radius around each sampling site. We used local scale vegetation maps provided by Regional Natural Parks to describe forest stand types and landscape composition around each plot.

Environmental variables

At the stand scale, latitude, longitude, altitude, exposure and slope were recorded at the center of the plots. The number of diameter classes was calculated using 2-cm-diameter classes. Deadwood diversity was estimated as the number of combinations formed by position (snags versus logs), species, decay class and 2-cm-diameter classes (Table 1).

At the landscape scale, variables based on spatial composition and configuration were computed. Landscape composition refers to the relative proportion of forests, beech-fir stands and ancient forests within a 500-m-radius around each sampling site, while landscape configuration refers to the spatial arrangement of patches within the landscape, i.e. perimeter-area ratio, distance to the nearest forest edge and distance to the nearest ancient/recent forest edge.

Statistical analysis

All statistical analyses were performed with R version 3.1.2 (R Core Team 2014).

Based upon data exploration (Zuur et al. 2010), independent variables with a skewness >1 were log or log+1 transformed to approximate normal distribution (see also correlation matrix, Online Resource Fig. 1 & 2).

We then test the significance of each environmental variable to forest continuity, stand maturity and the interaction term using two-ways ANOVA with Tukey's post-hoc tests (Table 1).

At regional scale (γ diversity), we estimated the performance of our sampling design by comparing the total number of species collected with the extrapolated species richness using incidence-based Chao estimator (vegan package). We then used rarefaction curves to compare accumulated species richness between ancient and recent forests, mature and overmature stands, ancient mature and ancient overmature stands, recent mature and recent overmature stands (BiodiversityR package).

At local scale (α diversity), we used two-ways ANOVA with Tukey's post-hoc tests to determine whether diversity patterns were influenced by forest continuity, stand maturity and their interaction. We then investigated whether saproxylic beetle richness and abundance were predicted by habitat and landscape features, using 30 *a priori* biologically plausible candidate linear models (Online Resource Table 2). Because, richness and abundance may not be independent, we furthermore assessed models performance with standardized richness as dependent variable, by including abundance as a covariate. To avoid biasing estimates toward forest continuity or stand maturity, ten models included variables describing forest continuity only, ten models included variables describing stand maturity only, and ten models included both types of variables. We used either Poisson or negative binomial regressions depending on the overdispersion of the count data and controlled for multicolinearity among explanatory variables with variance inflation factors (car package), *i.e*. only models with VIF <3 were considered (Zuur et al. 2010). To assess spatial autocorrelation, we used Moran's correlogram in the model residuals among sampling sites (ncf package). The significance of Moran's *I* coefficient at each distance class was evaluated with 999 permutations while the overall significance of the correlogram was tested with Bonferroni's correction (Legendre and Legendre 1998). To identify the most parsimonious regression model, we used Akaike's information criterion corrected for small sample sizes (Burnham and Anderson 2002). Moreover, as recommended by Burnham and Anderson (2002), we used model averaging to estimate parameter and associated unconditional standard errors based on the subset of top ranking models for which the sum of AIC_c weights reached ≥ 0.95 (MuMIn package). To determine the relative importance of forest continuity versus stand maturity for saproxylic beetles, we compared the sum of AIC_c weights for the three categories of models: forest continuity variables only, stand maturity variables only, and both types of variables (Burnham and Anderson 2002).

Results

Forest continuity and stand maturity

Compared to recent forest sites, ancient forest sites were included in a matrix that contained more forests ($p = 0.028$), more beech-fir stands ($p = 0.025$) and more ancient forests ($p < 0.001$) (Table 1). Ancient forest sites were also located at a greater distance from the forest edge ($p = 0.021$) and in patches with less complex shapes ($p = 0.005$) than recent forest sites.

Compared to mature stands, overmature stands were poorer in beech ($p = 0.033$) but richer in fir ($p < 0.001$) (Table 1). Overmature stands were also more heterogeneous ($p = 0.002$), with a greater number of very large trees ($p < 0.001$), a smaller number of stems ($p < 0.001$) and a higher diversity of tree microhabitats ($p < 0.001$). The deadwood compartment was more diversified ($p < 0.001$) and more abundant (volume of large logs, $p < 0.001$; number of large snags, $p < 0.001$) in overmature than in mature stands.

Finally, except for the perimeter-area ratio of forest cover ($p = 0.043$) and the volume of large logs ($p = 0.049$), all of the environmental variables were not influenced by the interaction term. Tukey HSD tests showed that the perimeter-area ratio of forest cover was more important in recent-mature stands than in ancient-mature stands ($p = 0.005$) and ancient-overmature stands ($p = 0.011$), and that the volume of large logs was more important in ancient-overmature stands than in ancient-mature stands ($p < 0.001$) and recent-mature stands ($p = 0.001$).

Diversity patterns of saproxylic beetles

A total of 307 saproxylic beetle species (18 729 individuals) belonging to 53 families were captured at the 40 sites (flight-intercept traps: 284 species, 16 884 individuals; Winkler-Berlese extractors: 52 species, 1 845 individuals). High-dispersal beetles encompassed 275 species (17 032) form 48 families, while low-dispersal beetles encompassed 27 species (1 666 individuals) from 5 families (Online Resource Table 1). Extrapolated species richness (Chao) indicated that species pool may encompass 385 (SD ±149) species, meaning that 80% of the saproxylic beetle diversity in the area was sampled.

The species pool of saproxylic beetles was much more influenced by stand maturity than by forest continuity (Online Resource Fig. 3). From sample-based rarefaction curves, overmature stands encompassed a pool of 281 (SD±5.56) species versus 239 (SD±5.04) species in mature stands, while ancient forests encompassed a pool of 267 (SD±5.34) versus 249 (SD±5.06) species in recent forests. Interaction between forest continuity and stand maturity confirmed previous patterns: ancient overmature stands were more diversified than ancient mature stands, with 235 (SD±5.37) and 196 (SD±5.03) species respectively. Recent overmature stands were also more diversified than recent mature stands, with 216 (SD±5.02) and 192 (SD±4.96) species respectively.

At local scale, diversity patterns were influenced by stand maturity but not by forest continuity or interaction term (Table 2). Total richness ($p = 0.012$) and abundance ($p = 0.003$), and high-dispersal richness ($p = 0.014$) and abundance ($p = 0.004$) all increased from mature to overmature stands.

Key parameters driving saproxylic beetle richness and abundance

Observed Moran's *I* in model residuals were non-significant for all of the dependent variables, indicating that spatial patterns were accounted for by forest continuity and stand maturity variables (Online Resource Fig. 4).

Model ranking

Overall, stand maturity models were far more powerful than forest continuity models in explaining diversity patterns (Table 3). Total and high-dispersal richness were best predicted by stand maturity model #1 (pseudo-R^2 range from 37% to 38%), while total and high-dispersal abundance were best predicted by forest continuity and stand maturity model #21 (pseudo-R^2 = 29%). Low-dispersal richness and abundance were best explained by the null model. When accounting for abundance in models, standardized richness was best predicted by the same best model as total richness (i.e. model # 1) but model performance increased substantially (pseudo-R^2 = 68%). Although some of these models show quite a strong support to explain diversity patterns, model selection uncertainty remains since associated AIC_c weight and evidence ratio were relatively low. We therefore used model averaging, ranging from the 5 to the 20 best models, to draw inferences about the variables influencing saproxylic beetles.

Model parameters

Forest continuity-associated variables mostly influenced abundance patterns (Table 4 & 5). Total and high-dispersal abundance increased with the proportion of beech-fir stands in the surrounding landscape but decreased with increasing distance to forest edge. Stand maturity-associated variables positively influenced both saproxylic beetle abundance and richness (Table 4 & 5). Standardized richness, total and high-dispersal richness and abundance increased with the diversity of deadwood types. Moreover, high-dispersal richness increased with the number of large snags, while standardized richness increased with the total abundance of saproxylic beetles but decreased with the number of very large trees. The other forest continuity- and stand maturity-associated variables we tested had little influence and none of them significantly influenced low-dispersal saproxylic beetles (Table 4 & 5).

Relative influence of forest continuity and stand maturity on saproxylic beetles

Judging from the sum of AIC_c weights for the models, richness patterns were mostly influenced by stand maturity (Fig. 2). For Total, standardized richness and high-dispersal richness, the cumulative AIC_c weight of stand maturity models was > 0.80. Indeed, six of the top ten models included only stand maturity variables. Remaining top ten models included both stand maturity and forest continuity variables. In contrast to richness patterns, abundance patterns were more heterogeneous. For total and high-dispersal abundance, the relative influence of stand maturity was lower (from 0.49 to 0.51) and models combining both stand maturity and forest continuity variables gained in importance (from 0.41 to 0.43). For these dependent variables, the cumulative AIC_c weight of forest continuity models was < 0.07. Finally, because low-dispersal richness and abundance were best explained by the null model, none of the models and associated metrics (i.e. AIC_c weight) is of any inferential value.

Discussion

Our results clearly show that saproxylic beetle diversity patterns were shaped by habitat limitation. No evidence of dispersal limitation was found. As indicators of habitat limitation, stand maturity models and associated variables performed much better than did forest continuity models and associated variables in explaining richness and abundance patterns of saproxylic beetles. In unfragmented montane forests, key parameters related to deadwood diversity at the stand scale and suitable habitat availability at the landscape scale appeared to be major drivers of saproxylic beetle diversity.

Dispersal limitation

Contrary to our first hypothesis, no evidence of dispersal limitation was found, i.e. diversity patterns were not influenced by forest continuity. This indicates that saproxylic beetles, even low-dispersal species, were able to successfully disperse and colonize newly available habitats. Previous studies have reported a significant effect of forest continuity on plants (e.g. Sciama et al. 2009), epiphytic bryophytes and lichens (e.g. Fritz and Brunet 2010), and carabids (e.g. Assmann 1999). For saproxylic beetles, the few existing studies have reported that recent forests were species poor sites (Gossner et al. 2008; Irmler et al. 2010; Buse 2012). In our study, forest continuity had no significant effect on saproxylic beetles richness and abundance; species accumulation curves simply indicated that ancient forests encompassed a larger species pool than recent forests. Given that most previous studies were conducted in fragmented landscapes, these apparently contradictory results may indicate confounding effects between forest continuity and fragmentation, as previously showed for plants (Jamoneau et al. 2012). In the Northern Alps, landscapes are dominated by unfragmented forests and recent forests have colonized agricultural areas next to ancient forest areas. Afforestation adjacent to ancient forests reduces the distance to habitat source and limits dispersal barriers within the habitat matrix (Honnay et al. 2002). This may have facilitated the colonization of recent forests by saproxylic beetles. Moreover, the assumption that flightless saproxylic beetles are dispersal-limited species is questionable. In our study, four of the six flightless saproxylic weevils (Curculionidae) presented as ancient forest relict species (Buse 2012) were recorded – *Acalles lemur*, *Kyklioacalles navieresi*, *Echinodera hypocrita*, *Trachodes hispidus* – and all of them were evenly present in both ancient and recent forests. In accordance with Horák et al. (2013), we believe that the dispersal ability of these flightless saproxylic species has probably been underestimated.

Beside dispersal limitation, it has been argued that forest continuity influences biodiversity patterns through habitat limitation (Hermy and Verheyen 2007). Even for highly connected patches, differences in habitat characteristics between ancient and recent forests may persist for centuries, especially for soil properties (Dupouey et al. 2002). These differences in habitat quality can limit species establishment in newly available forests by recruitment limitation (Honnay et al. 2002). Such long-lasting effects act directly on plant communities (Baeten et al. 2009) and indirectly on plant consumers (Gossner et al. 2008). Saproxylic beetles, however, should be more influenced by stand structural attributes than by understory vegetation and soil properties. If stand maturity parameters are not controlled for between ancient and recent forests (e.g. Irmler et al. 2010; Buse 2012), it may be hazardous to infer that the differences observed in biodiversity patterns are related to dispersal limitation (Nordén et al. 2014). Our sampling design was designed to disentangle the relative effect of dispersal limitation from habitat limitation and our results show that stand maturity was indeed independent from forest continuity. Habitat quality can therefore be regarded as homogeneous between ancient and recent forests. Although forest continuity may have acted on soil proprieties and associated plant communities, no effects were observed for saproxylic beetles. This indicates that, in unfragmented montane forests, dispersal limitation is not a major driver in shaping saproxylic beetle diversity patterns.

Habitat limitation

Habitat limitation was powerful to explain variation in species diversity. In accordance with our second hypothesis, the richness and abundance of saproxylic beetles increased with stand maturity, in both ancient and recent forests, from the regional species pool scale to the local diversity scale. This indicates that species requirements were best supported in overmature stands and that stand maturity allowed greater species coexistence regardless of forest continuity. This pattern may be related to a diversification in resource availability, given that habitat heterogeneity usually positively correlates to stand maturity (McElhinny et al. 2005). In our sampling design, structural attributes such as the number of diameter classes of standing trees, the number of very large living trees or the diversity of deadwood types, strongly increased with stand maturity. Stand maturity may therefore be viewed as a surrogate for habitat heterogeneity, which is known to have significant effects on biodiversity patterns, e.g. for wood-inhabiting fungi (Junninen et al. 2006), epiphytic bryophytes (Dittrich et al. 2013) and birds (Poulsen 2002). For saproxylic beetles, numerous studies have also reported a positive relationship between stand maturity and diversity patterns (e.g. Martikainen et al. 2000; Stenbacka et al. 2010; Lassauce et al. 2012). Our results are therefore consistent with knowledge related to the ecological niche theory and highlight the significance of habitat limitation as a major driver in shaping biodiversity patterns. However, low-dispersal saproxylic beetles were not influenced by stand maturity. This finding may indicate that, in our study, the variation in habitat quality between mature and overmature stands was not strong enough. Indeed, flightless saproxylic weevils depend on twigs for their development (Heijerman 2004), which are not a limiting resource in mountain forests (Barbati et al. 2014). Flightless saproxylic beetles, on the other hand, may be more dependent on environmental factors related to litter depth, soil moisture (Sroka and Finch 2006), altitude (Horák et al. 2013), climate and topography (Buse 2012).

Key parameters at stand scale

At the stand scale, parameters related to stand maturity, especially those linked to deadwood quality, provided relevant explanatory variables for species richness and abundance variation patterns. Although stand structural attributes have been pointed out as key parameters for saproxylic beetles (Ranius and Jansson 2000; Grove 2002), in our study, the diversity of deadwood types was by far the most powerful explanatory variable for diversity patterns. Deadwood diversity is related to habitat diversity and allows a larger range of species, including specialists, to coexist through an increase in the heterogeneity of the resource supply. The importance of deadwood diversity for saproxylic beetles has already been pointed out in boreal (Økland et al. 1996; Similä et al. 2003) and temperate forests (Brin et al. 2011; Bouget et al. 2013). However, contrary to our expectations, deadwood quantity was not as powerful as deadwood diversity in explaining diversity patterns. While richness of high-dispersal species was significantly influenced by large snag density, large log volume had no significant effect on saproxylic beetles. Large log volume has been pointed out as a key parameter for saproxylic species (e.g. Økland et al. 1996; Lachat et al. 2012; Bouget et al. 2014) and is a commonly used indicator for sustainable forest management (Forest Europe, UNECE and FAO 2011). Müller and Bütler (2010) stated that the amount and diversity of deadwood are usually correlated and, consequently, that it may be difficult to disentangle their relative influence. In our montane mixed forests, as in others forests (Grove 2002; Similä et al. 2003; Bouget et al. 2013), the total amount and diversity of deadwood were correlated (R = 0.75). Nevertheless, our deadwood diversity models consistently performed better than our deadwood amount models in explaining richness patterns of saproxylic beetles, even when controlling for species abundance. In line with Lassauce et al.'s meta-analysis (2011), our results confirm that deadwood diversity is of more importance than deadwood amount in shaping saproxylic diversity patterns in forest ecosystems.

Key parameters at landscape scale

At the landscape scale, parameters related to forest continuity had contrasting effects on saproxylic beetles but were found to be relevant in explaining abundance patterns. The proportion of beech-fir stands in the surrounding landscape increased the abundance of all dependent variables, except for low-dispersal species, while the proportion of forests and ancient forests had no effect. As previously demonstrated for plant species recovery in recent forests (De Frenne et al. 2011), our results underlines the importance for saproxylic beetles of suitable habitat availability at a larger scale. The abundance of many saproxylic species has been shown to increase with the proportion of suitable habitat at landscape scale in boreal forests (Gibb et al. 2006;

Laaksonen et al. 2008). These findings may indicate that larger source populations are available for colonization in stands surrounded by a larger proportion of suitable habitat (Gibb et al. 2006). This may be viewed as an additive effect of habitat limitation versus dispersal limitation at the landscape scale. However, total and high-dispersal species abundance decreased with distance to forest edge. This may be related to the attractiveness of the sunny conditions found along forest edges (Vodka and Cizek 2013). Moreover, several adult forms of saproxylic beetles are floricolous. The likelihood of them being captured increases with the availability of flowering plants, i.e. with the proximity to forest edge. This response pattern may be linked to edge effect, rather than to a negative effect of forest continuity. Our overall results highlight the relevance of considering multiple spatial scales to better characterize diversity patterns, in accordance with previous studies (e.g. Økland et al. 1996; Janssen et al. 2009).

Conclusion

We found that habitat limitation was the main ecological mechanism explaining saproxylic beetle diversity patterns in unfragmented montane forests. Habitat limitation was primarily driven by variations in deadwood diversity at the stand scale and by availability of suitable habitat at the landscape scale. In the ecological context of the Northern Alps, i.e. unfragmented forests, our results clearly show that dispersal limitation was not a causative factor for saproxylic beetle diversity. This suggests that biodiversity responses to forest continuity may depend on species groups and/or on the regional setting. Indeed, caution must be used in studies based on a limited group of taxa when generalizing the ecological mechanisms resulting from complex ecosystem modifications such as land use change. Saproxylic beetle conservation would benefit from forestry practices that maintain a diversity of deadwood types within stands, e.g. snags and logs of various diameters and in different stages of decay, and a high availability of overmature stands in the surrounding landscape.

Acknowledgements

We thank Gilles Favier, Sophie Labonne, Fanny Lebagousse, Carl Moliard and Pascal Tardif from IRSTEA for help on the field. We are grateful to Thierry Noblecourt (Scolytinae) and Olivier Rose (Ciidae) from ONF, Olivier Courtin, Julien Haran (Curculionidae) and Julien Delnatte (Elateridae) for taxonomic assistance. We also thank George Kunstler for his comments on the paper and Vicki Moore for correcting the English manuscript. The Vercors, Chartreuse and Bauges Natural Regional Parks as well as public (ONF) and private forest managers facilitated our work in the study area. Financial support was provided by IRSTEA and local contributors (Conseil Général de l’Isère and Bauges Natural Regional Park).

References

Assmann T (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). Biodivers Conserv 8:1499–1517.

Baeten L, Hermy M, Verheyen K (2009) Environmental limitation contributes to the differential colonization capacity of two forest herbs. J Veg Sci 20:209–223.

Barbati A, Marchetti M, Chirici G, Corona P (2014) European forest types and forest Europe SFM indicators: tools for monitoring progress on forest biodiversity conservation. For Ecol Manag 321:145–157.

Bouget C, Brin A, Tellez D, Archaux F (2015) Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches. Oecologia 177:911–920.

Bouget C, Larrieu L, Brin A (2014) Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecol Indic 36:656–664.

Bouget C, Larrieu L, Nusillard B, Parmain G (2013) In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers Conserv 22:2111–2130.

Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. J Insect Conserv 15:653–669.

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York

Buse J (2012) “‘Ghosts of the past’”: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. J Insect Conserv 16:93–102.

Cateau E, Courtin O, Brustel H (2016) How and when should flightless, saproxylic, litter-dwelling coleoptera be surveyed? Insect Conserv Divers Early View (Online Version)

Cateau E, Larrieu L, Vallauri D, et al (2015) Ancienneté et maturité : deux qualités complémentaires d’un écosystème forestier. C R Biol 338:58–73.

Clobert J, Baguette M, Benton TG, Bullock (eds) JM (2012) Dispersal ecology and evolution. Oxford University Press, New York

De Frenne P, Baeten L, Graae BJ, et al (2011) Interregional variation in the floristic recovery of post-agricultural forests: Recovery of post-agricultural forest. J Ecol 99:600–609.

Devictor V, Clavel J, Julliard R, et al (2010) Defining and measuring ecological specialization. J Appl Ecol 47:15–25.

Dittrich S, Hauck M, Jacob M, et al (2013) Response of ground vegetation and epiphyte diversity to natural age dynamics in a Central European mountain spruce forest. J Veg Sci 24:675–687.

Dupouey J-L, Dambrine E, Laffite JD, Moares C (2002) Irreversible impact of past land use on forest soils and biodiversity. Ecology 83:2978–2984.

Forest Europe, UNECE and FAO (2011) State of Europe’s forests 2011: status and trends in sustainable forest management in Europe. Ministerial Conference on the Protection of Forests in Europe, Oslo

Fritz Ö, Brunet J (2010) Epiphytic bryophytes and lichens in Swedish beech forests – effects of forest history and habitat quality. Ecol Bull 53:95–107.

Gibb H, Hjältén J, Ball JP, et al (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. Ecography 29:191–204.

Gossner MM, Engel K, Jessel B (2008) Plant and arthropod communities in young oak stands: are they determined by site history? Biodivers Conserv 17:3165–3180.

Grove SJ (2002) Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. Ecol Indic 1:171–188.

Heijerman T (2004) The weevil genera Acalles, Ruteria and Kyklioacalles in the Netherlands (Coleoptera: Curculionidae). Ned Faun Meded 21:61–78.

Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecol Res 22:361–371.

Hodgson JA, Moilanen A, Wintle BA, Thomas CD (2011) Habitat area, quality and connectivity: striking the balance for efficient conservation. J Appl Ecol 48:148–152.

Honnay O, Bossuyt B, Verheyen K, et al (2002) Ecological perspectives for the restoration of plant communities in European temperate forests. Biodivers Conserv 11:213–242.

Horák J, Vodka Š, Pavlíček J, Boža P (2013) Unexpected visitors: flightless beetles in window traps. J Insect Conserv 17:441–449.

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Symp Quant Biol 22:415–427.

Irmler U, Arp H, Nötzold R (2010) Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. J Insect Conserv 14:227–235.

Jamoneau A, Chabrerie O, Closset-Kopp D, Decocq G (2012) Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. Ecography 35:124–133.

Janssen P, Fortin D, Hébert C (2009) Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales. Ecography 32:423–432.

Jonsell M, Hansson J, Wedmo L (2007) Diversity of saproxylic beetle species in logging residues in Sweden – Comparisons between tree species and diameters. Biol Conserv 138:89–99.

Junninen K, Similä M, Kouki J, Kotiranta H (2006) Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29:75–83.

Laaksonen M, Peuhu E, Várkonyi G, Siitonen J (2008) Effects of habitat quality and landscape structure on saproxylic species dwelling in boreal spruce-swamp forests. Oikos 117:1098–1110.

Lachat T, Wermelinger B, Gossner MM, et al (2012) Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. Ecol Indic 23:323–331.

Lassauce A, Anselle P, Lieutier F, Bouget C (2012) Coppice-with-standards with an overmature coppice component enhance saproxylic beetle biodiversity: A case study in French deciduous forests. For Ecol Manag 266:273–285.

Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Indic 11:1027–1039.

Lassau SA, Hochuli DF, Cassis G, Reid CA (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? Divers Distrib 11:73–82.

Legendre P, Legendre L (1998) Numerical ecology, 2nd English edition. Elsevier Science BV, Amsterdam

Lowe WH (2009) What drives long-distance dispersal? A test of theoretical predictions. Ecology 90:1456–1462.

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton Univ Press, Princeton

Martikainen P, Siitonen J, Punttila P, et al (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol Conserv 94:199–209.

McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: Its definition and measurement. For Ecol Manag 218:1–24.

Meyer P, Schmidt M (2011) Accumulation of dead wood in abandoned beech (Fagus sylvatica L.) forests in northwestern Germany. For Ecol Manag 261:342–352.

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur J For Res 122:981–992.

Nordén B, Dahlberg A, Brandrud TE, et al (2014) Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Ecoscience 21:34–45.

Økland B, Bakke A, Hagvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodivers Conserv 5:75–100.

Parmain G, Bouget C, Müller J, et al (2015) Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests? Bull Entomol Res 105:101–109.

Poulsen BO (2002) Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. Biodivers Conserv 11:1551–1566.

Pulliam HR (2000) On the relationship between niche and distribution. Ecol Lett 3:349–361.

Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol Conserv 95:85–94.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Sciama D, Augusto L, Dupouey J-L, et al (2009) Floristic and ecological differences between recent and ancient forests growing on non-acidic soils. For Ecol Manag 258:600–608.

Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49:11–41.

Similä M, Kouki J, Martikainen P (2003) Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. For Ecol Manag 174:365–381.

Speight MCD (1989) Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg

Sroka K, Finch O-D (2006) Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). J Insect Conserv 10:335–350.

Stenbacka F, Hjälten J, Hilszczanski J, Dynesius M (2010) Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. Ecol Appl 20:2310–2321.

Sutherland WJ, Freckleton RP, Godfray HCJ, et al (2013) Identification of 100 fundamental ecological questions. J Ecol 101:58–67.

Verheyen K, Guntenspergen GR, Biesbrouck B, Hermy M (2003) An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. J Ecol 91:731–742.

Vodka š., Cizek L (2013) The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. For Ecol Manag 304:33–41.

Whitman AA, Hagan JM (2007) An index to identify late-successional forest in temperate and boreal zones. For Ecol Manag 246:144–154.

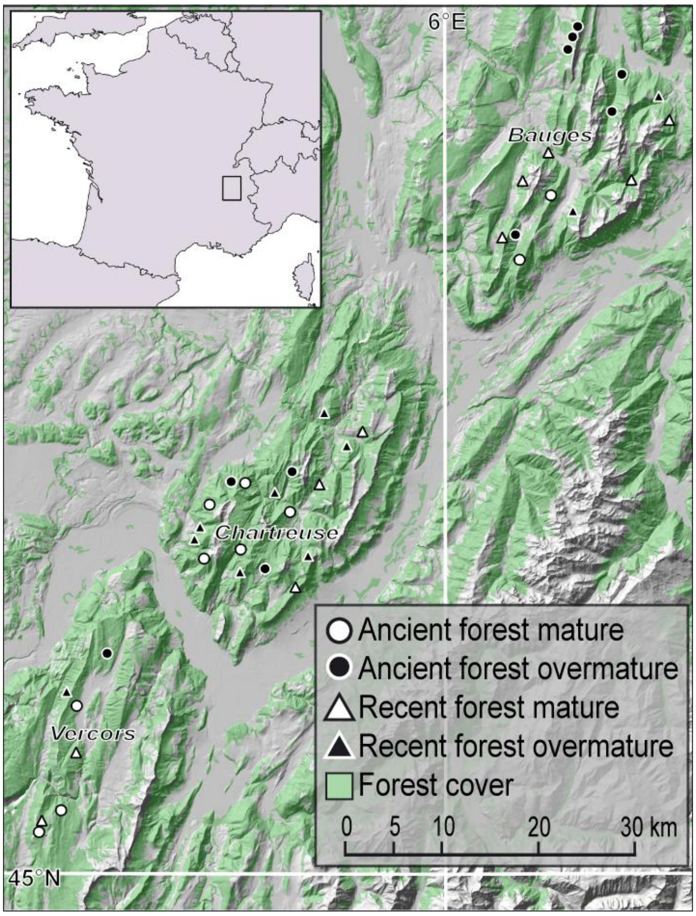
Winter S, Möller GC (2008) Microhabitats in lowland beech forests as monitoring tool for nature conservation. For Ecol Manag 255:1251–1261.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems: Data exploration. Methods Ecol Evol 1:3–14.

Figure captions

Fig. 1 Study area and distribution of sampling sites among ancient and recent forests and mature and overmature stands in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France

Fig. 2 Influence of parameters related to forest continuity and/or stand maturity on saproxylic beetle richness and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France. Sums of AIC_c weights are provided for models based exclusively on forest continuity variables (10 models), on stand maturity variables (10 models) or on both types of variables (10 models) plus the null model; Low-disp. = Low-dispersal, High-disp. = High-dispersal


6°E
Bauges
Chartreuse
Vercors
45°N
Ancient forest mature
Ancient forest overmature
Recent forest mature
Recent forest overmature
Forest cover
0 5 10 20 30 km

543 **Fig. 1**

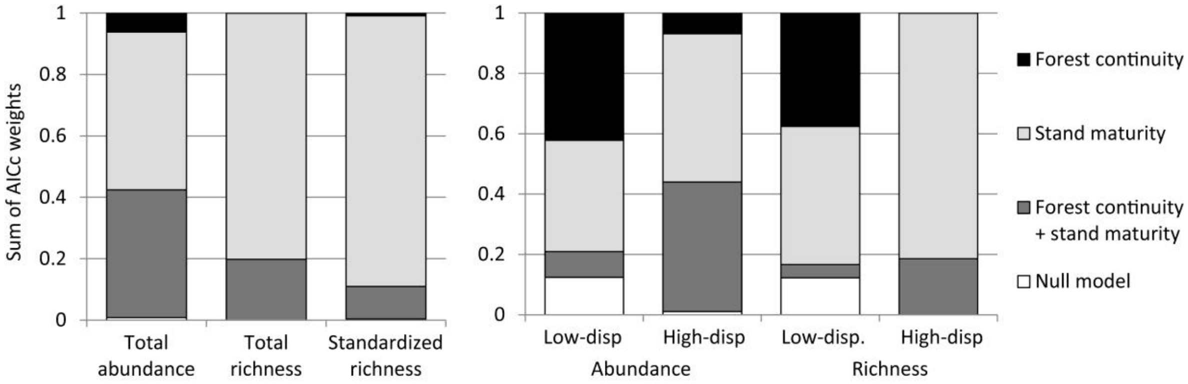

Sum of AICc weights
1
0.8
0.6
0.4
0.2
0
Total abundance
Total richness
Standardized richness
Low-disp
High-disp
Low-disp.
High-disp
Abundance
Richness
■ Forest continuity
☐ Stand maturity
■ Forest continuity + stand maturity
☐ Null model

Fig. 2

Table 1 Variation in forest continuity and stand maturity variables used to model saproxylic beetle richness and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France (BD = basal diameter, DBH = diameter at breast height, p-value based on two-ways ANOVA)

Variables	Description	Ancient Mean (±SD)	Recent Mean (±SD)	p-value	Mature Mean (±SD)	Overmature Mean (±SD)	p-value
lati	Latitude in decimal degrees	45.44 (±0.25)	45.42 (±0.21)	0.7777	45.38 (±0.23)	45.48 (±0.22)	0.1551
long	Longitude in decimal degrees	5.86 (±0.27)	5.88 (±0.26)	0.8203	5.84 (±0.27)	5.91 (±0.25)	0.3856
alti	Altitude in meters	1172 (±156.1)	1137 (±159.5)	0.5008	1171 (±160.0)	1137 (±155.7)	0.5070
slope	Slope in percentage	22.20 (±7.22)	25.63 (±7.21)	0.1409	24.02 (±7.76)	23.82 (±7.08)	0.9323
expo	Exposure in degrees	216.3 (±103.7)	226.0 (±113.7)	0.7841	206.1 (±108.1)	236.2 (±107.5)	0.3941
Stand maturity variables measured at stand scale							
G_beech	Beech basal area in m^2	1.42 (±0.85)	1.53 (±1.07)	0.7123	1.80 (±0.80)	1.15 (±1.01)	0.0334
G_fir	Fir basal area in m^2	3.30 (±2.28)	2.97 (±2.21)	0.5594	1.79 (±1.15)	4.48 (±2.24)	0.0000
G_spruce	Spruce basal area in m^2	1.07 (±1.04)	1.49 (±1.27)	0.3093	1.50 (±1.28)	1.05 (±1.01)	0.3345
N_trees_classes	Number of diameter classes of standing trees	21.55 (±3.05)	21.60 (±3.10)	0.9542	20.15 (±2.35)	23.00 (±3.03)	0.0022
N_trees	Number of living trees per hectare	93.8 (±40.66)	108.1 (±48.32)	0.2476	124.5 (±46.94)	77.4 (±26.92)	0.0004
N_large_trees	Number of very large living trees (DBH > 62.5 cm)	3.35 (±4.15)	3.45 (±3.36)	0.9001	0.60 (±0.88)	6.20 (±3.35)	0.0000
Vol_large_cwd	Volume of large logs (BD > 30 cm) in m^3	2.47 (±3.65)	1.20 (±1.82)	0.0986	0.31 (±0.61)	3.36 (±3.49)	0.0002

N_large_snags	Number of large snags (DBH > 30 cm)	1.95 (±2.39)	1.25 (±1.89)	0.2090	0.35 (±0.59)	2.85 (±2.43)	0.0000
Alpha_cwd	Diversity of deadwood types	13.30 (±9.70)	10.05 (±5.33)	0.1174	7.30 (±4.46)	16.05 (±8.23)	0.0001
Alpha_mh	Diversity of tree microhabitats	2.20 (±2.07)	2.60 (±1.76)	0.4211	1.25 (±1.02)	3.55 (±1.90)	0.0000
Forest continuity variables measured at landscape scale							
Prop_Forest	Forest proportion within a 500-m-radius (%)	93.72 (±7.85)	86.73 (±11.62)	0.0289	88.06 (±12.90)	92.39 (±6.78)	0.1666
Prop_BF	Beech-fir proportion within a 500-m-radius (%)	84.99 (±16.18)	72.61 (±17.04)	0.0252	77.13 (±17.32)	80.48 (±18.08)	0.5311
Prop_Ancient	Ancient forest proportion within a 500-m-radius (%)	86.06 (±10.71)	39.35 (±25.65)	1.1158	62.90 (±32.09)	62.51 (±29.86)	0.9507
Complex_Forest	Perimeter-area ratio of forest cover	0.005 (±0.001)	0.008 (±0.004)	0.0054	0.007 (±0.004)	0.006 (±0.002)	0.1011
Dist_Forest	Distance to the nearest forest edge in meters	367.3 (±243.4)	216.8 (±125.2)	0.0212	312.5 (±234.8)	271.6 (±175.5)	0.5165
Dist_Past_Edge	Distance to the nearest ancient/recent edge in meters	386.1 (±320.7)	249.7 (±320.3)	0.1940	335.2 (±329.8)	300.5 (±325.3)	0.7382

Table 2 Mean (±SD) of dependent variables in relation to forest continuity and stand maturity in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France (p-value based on two-ways ANOVA)

Dependent variable	Forest continuity			Stand maturity		
	Ancient	Recent	p-value	Mature	Overmature	p-value
Total richness	75.1 (±19.95)	72.8 (±17.44)	0.6887	66.6 (±15.44)	81.3 (±18.79)	0.0125
Total abundance	457.8 (±207.05)	478.6 (±182.94)	0.7128	379.8 (±152.23)	556.6 (±192.18)	0.0033
Low-dispersal richness	8.3 (±1.90)	9.0 (±2.44)	0.3103	8.3 (±2.16)	9.0 (±2.21)	0.3103
Low-dispersal abundance	38.4 (±16.75)	44.9 (±16.41)	0.2282	39.6 (±16.22)	43.6 (±17.33)	0.4555
High-dispersal richness	66.4 (±19.81)	63.0 (±16.04)	0.5372	57.8 (±14.77)	71.6 (±18.38)	0.0149
High-dispersal abundance	419.1 (±209.29)	432.5 (±177.96)	0.8114	339.6 (±156.13)	512.0 (±188.55)	0.0040

Table 3 Top-ranking models among 31 models predicting saproxylic beetle richness and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France, as assessed with Akaike's information criterion corrected for small sample size (AIC_c). Dependent variable, model number, related group model (continuity, maturity or both), number of estimated parameters including the intercept (k), AIC_c, AIC_c weight (W), adjusted R^2 and evidence ratio (ER), i.e. Akaike weight of best model/Akaike weight of second best model, are provided

Dependent variable	Top-ranking	Type	k	AIC_c	W	R^2	ER
Total richness	1	Maturity	2	332.7	0.546	0.38	3.4
Total abundance	21	Continuity + Maturity	4	534.2	0.211	0.29	1.4
Standardized richness	1	Maturity	3	311.5	0.380	0.65	1.3
Low-dispersal richness	31	Null	1	184.1	0.122	0.00	1.0
Low-dispersal abundance	31	Null	1	339.3	0.124	0.00	1.3
High-dispersal richness	1	Maturity	2	329.5	0.525	0.37	3.4
High-dispersal abundance	21	Continuity + Maturity	4	534.9	0.239	0.29	1.4

Table 4 Average coefficients (AC) and confidence intervals (CI) for each variable of the top ranking models (i.e. sum of AIC_c weights ≥0.95) predicting total saproxylic beetles richness and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France. The 95% confidence interval of coefficients in bold excluded 0, NA = not available

Parameter	Total abundance		Total richness		Standardized richness	
	AC	CI	AC	CI	AC	CI
(Intercept)	**6.000**	**(4.012; 7.988)**	**3.821**	**(3.408; 4.234)**	**3.620**	**(3.319; 3.923)**
Abundance	NA	NA	NA	NA	**0.001**	**(0.001; 0.001)**
N_tree_classes	0.041	(-0.007; 0.089)	0.001	(-0.022; 0.024)	-0.009	(-0.026; 0.008)
N_large_trees	0.160	(-0.015; 0.336)	-0.029	(-0.114; 0.056)	**-0.069**	**(-0.133; -0.007)**
Vol_large_cwd	0.110	(-0.103; 0.323)				
N_large_snags	0.193	(-0.010; 0.397)				
Alpha_cwd	**0.281**	**(0.082; 0.480)**	**0.225**	**(0.130; 0.319)**	**0.148**	**(0.066; 0.230)**
Alpha_mh	-0.016	(-0.098; 0.066)	0.012	(-0.026; 0.050)	0.012	(-0.014; 0.039)
Prop_Forest	0.003	(-0.013; 0.020)	-0.003	(-0.011; 0.006)	-0.004	(-0.010; 0.002)
Prop_BF	**0.010**	**(0.002; 0.019)**				
Prop_Ancient	-0.001	(-0.005; 0.003)	0.000	(-0.002; 0.002)	-0.0001	(-0.002; 0.002)
Complex_Forest	0.160	(-0.282; 0.602)				
Dist_Forest	**-0.282**	**(-0.556; -0.007)**	-0.010	(-0.148; 0.128)	0.073	(-0.034; 0.180)
Dist_Past_Edge	-0.130	(-0.276; 0.015)	-0.051	(-0.121; 0.019)	-0.008	(-0.065; 0.049)

Table 5 Average coefficients (AC) and confidence intervals (CI) for each variable of the top ranking models (i.e. sum of AIC$_c$ weights ≥0.95) predicting low-dispersal (Low-disp.) and high-dispersal (High-disp) saproxylic beetles richness and abundance in the Vercors, Chartreuse and Bauges ranges, Northern Alps, France. The 95% confidence interval of coefficients in bold excluded 0, NA = not available

Parameter	Low-disp. abundance		Low-disp. richness		High-disp. abundance		High-disp. richness	
	AC	CI	AC	CI	AC	CI	AC	CI
(Intercept)	**3.761**	**(2.644; 4.878)**	**2.175**	**(1.090; 3.259)**	**5.932**	**(3.800; 8.065)**	**3.669**	**(3.210; 4.128)**
Abundance	NA	NA	NA	NA	NA	NA	NA	NA
N_tree_classes	0.030	(-0.014; 0.074)	0.027	(-0.011; 0.065)	0.043	(-0.012; 0.097)	-0.001	(-0.026; 0.024)
N_large_trees	0.057	(-0.089; 0.202)	0.007	(-0.115; 0.130)	0.169	(-0.035; 0.372)	-0.027	(-0.121; 0.067)
Vol_large_cwd	-0.013	(-0.178; 0.152)	-0.092	(-0.259; 0.076)	0.126	(-0.113; 0.366)		
N_large_snags	-0.028	(-0.206; 0.151)	0.018	(-0.154; 0.190)	0.222	(-0.010; 0.453)	**0.205**	**(0.105; 0.306)**
Alpha_cwd	-0.044	(-0.240; 0.152)	0.039	(-0.130; 0.208)	**0.325**	**(0.104; 0.547)**	**0.245**	**(0.141; 0.349)**
Alpha_mh	0.033	(-0.036; 0.102)	0.023	(-0.034; 0.080)	-0.026	(-0.117; 0.065)	0.010	(-0.031; 0.052)
Prop_Forest	-0.011	(-0.028; 0.006)	-0.003	(-0.015; 0.009)	0.005	(-0.014; 0.024)	-0.003	(-0.012; 0.007)
Prop_BF	-0.001	(-0.008; 0.007)	0.003	(-0.005; 0.011)	**0.011**	**(0.001; 0.021)**		
Prop_Ancient	-0.003	(-0.007; 0.001)	-0.001	(-0.004; 0.003)	-0.001	(-0.006; 0.004)	0.000	(-0.002; 0.002)
Complex_Forest	0.165	(-0.145; 0.475)	0.179	(-0.125; 0.482)	0.134	(-0.377; 0.645)		
Dist_Forest	0.126	(-0.185; 0.436)	-0.048	(-0.261; 0.165)	**-0.333**	**(-0.645; -0.021)**	-0.004	(-0.157; 0.148)
Dist_Past_Edge	0.015	(-0.129; 0.158)	-0.011	(-0.134; 0.111)	-0.150	(-0.317; 0.016)	-0.056	(-0.133; 0.022)