



# **Insect herbivory and avian insectivory in novel native oak forests: Divergent effects of stand size and connectivity**

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1 **Insect herbivory and avian insectivory in novel native oak forests:**  
2 **divergent effects of stand size and connectivity**

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## 16 Abstract

17 The value of novel native broadleaf woodlands for biodiversity conservation is important to  
18 consider for adequate forest management in rural landscapes. Passive reforestation has been  
19 proposed as a cost-efficient tool for creating networks of novel native forest stands that would help  
20 restoring biodiversity and associated ecosystem services. Yet to date the ecological functioning of  
21 such stands remains strongly understudied compared to forest remnants resulting from longer-term  
22 fragmentation. We assessed how the size and connectivity of newly established Pedunculate oak  
23 (*Quercus robur* L.) stands in rural landscapes of SW France affect rates of herbivory by different  
24 insect guilds as well as rates of avian insectivory and the abundance and richness of insectivorous  
25 birds. Comparing 18 novel forest stands along a gradient of size (0.04-1.15 ha) and cover of  
26 broadleaf forests in the surroundings (0-30% within a 500m radius), we found that even the smallest  
27 stands are colonised by leaf miners and chewers/skeletonizers, and that rates of herbivory are  
28 globally comparable to those reported from older and larger oak forests. The size of stands had a  
29 relatively minor effect on herbivory, whereas it increased the abundance of insectivorous bird. It  
30 also determined rates of avian insectivory as estimated by an experiment with plasticine  
31 caterpillars. These rates were however rather low and unrelated with the extent of herbivory in the  
32 stand. Overall, our study indicates that insect herbivores tend to react more rapidly to the  
33 establishment of novel native forests than their avian predators as the latter may depend on the  
34 development of larger patches of suitable habitat in the surrounding landscape. To favour a rapid  
35 build-up of diverse, and hence stable, trophic networks involving insect herbivores and their  
36 predators, woodland creation schemes should therefore primarily focus on habitat size and quality.

## 37 Keywords

38 Herbivory, Avian predation, Bird communities, Native oak forest, Connectivity, Afforestation

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## 41 **Introduction**

42 Forest fragmentation is well-known to alter patterns of species distribution and abundance, relationships  
43 between organisms and resulting ecosystem processes (Ewers and Didham, 2006; Fahrig, 2017; Haddad et  
44 al., 2015; Lindenmayer and Fisher, 2013). Among others, it exerts strong effects on trophic cascades such  
45 as plant-herbivore-predator interactions, eventually affecting rates of tree damage and health (Bagchi et al.,  
46 2018; Chávez-Pesqueira et al., 2015; Rossetti et al., 2017). While forest fragmentation continues to occur  
47 in many regions of the world, forest cover is increasing in many others as a consequence of active planting  
48 and passive afforestation following rural abandonment (Fuchs et al., 2015; Hansen et al., 2013). For  
49 instance, Europe has experienced a steady increase of forested surfaces by 0.8 million ha per year since  
50 1990 (Forest Europe, 2015), a trend that is expected to continue in the coming decades (Fuchs et al., 2015;  
51 Schröter et al., 2005). Habitat defragmentation through passive afforestation has been proposed as an  
52 effective tool to reinforce biodiversity and ecosystem functioning in rural and urban landscapes where forest  
53 stands were formerly sparse and isolated (Fischer et al., 2006; Rey Benayas et al., 2008; Rey Benayas and  
54 Bullock, 2012). Yet little ecological research has to date focused on newly established native forest stands  
55 and we largely ignore whether trophic interactions in such stands underlie similar mechanisms as in  
56 remnants of similar sizes but resulting from forest fragmentation.

57 Novel native forest stands establish from a few founder trees that colonize an available habitat patch within  
58 an unsuitable matrix through long-distance dispersal and fill their neighbourhood with their offsprings  
59 (Gerzabek et al., 2017; Sezen et al., 2005). Such stands share certain characteristics that set them apart from  
60 those created by fragmentation: (i) they typically are quite small-sized – even smaller than the smallest  
61 fragments of remnant forest; (ii) they are dominated by young trees, resulting in a reduced amount and range  
62 of habitats available to forest-dwelling species (Franklin, 1988; Fuller et al., 2018); and (iii) all their species  
63 necessarily originate from colonization events over a limited period of time, implying that these systems are  
64 triggered by immigration credit instead of extinction debt (Jackson and Sax, 2010). Recent studies on insect  
65 and bird species richness along chronosequences of novel native forest development have shown that these  
66 are rapidly colonized by woodland generalists whereas specialists can still remain absent even 150 years  
67 after forest establishment (Fuentes-Montemayor et al., 2015; Fuller et al., 2018; Whytock et al., 2018).  
68 These studies also revealed that local stand characteristics are relatively more important than landscape  
69 characteristics for successful colonization by insects and birds. Similar findings have been reported for  
70 planted forests (reviewed in Burton et al., 2018). However, their consequences for trophic relationships  
71 between plants, insect herbivores and insectivores remain unknown.

72 Despite the differences between novel native forest stands and remnant forest fragments, the ecological  
73 mechanisms underlying trophic cascades involving trees, insect herbivores and birds can to some extent be

74 inferred from fragmentation studies. These have documented that the size and connectivity of forest stands  
75 can shape trophic cascades very differently depending on the relative importance of the bottom-up and top-  
76 down effects involved (De La Vega et al., 2012; Rossetti et al., 2014). Thus, small and isolated forest stands  
77 provide less and possibly lower-quality resources to herbivores (Chávez-Pesqueira et al., 2015) and their  
78 colonization requires longer-distance movements that increase energetic and fitness costs (O'Rourke and  
79 Petersen, 2017), eventually resulting in lower herbivore abundance (De La Vega et al., 2012; Simonetti et  
80 al., 2007). However, small stands also experience greater edge effects which typically go along with  
81 increased herbivory (Bagchi et al., 2018; De Carvalho Guimarães et al., 2014). On the other hand, insect  
82 herbivores are more likely to colonize small but closer novel forest stands while their predatory vertebrates  
83 are more likely to colonize more distant but larger ones (Barbaro et al., 2014; Bereczki et al., 2014; Cooper  
84 et al., 2012; Maguire et al., 2015).

85 There is broad consensus that, generally, predators can notably reduce insect herbivory by regulating  
86 herbivore populations (Böhm et al., 2011; Letourneau et al., 2009; Maguire et al., 2015; Rosenheim, 1998).  
87 However, their actual relevance in novel native forest stands depends strongly on how both prey and  
88 predators respond to stand size and connectivity (Gripenberg and Roslin, 2007). This study investigated  
89 how levels of insect herbivory, avian predation and the abundance and diversity of insectivorous birds in  
90 recently established native Pedunculate oak (*Quercus robur*) forest stands are influenced by their size and  
91 the cover of broadleaf forest in the surrounding landscape. Specifically, we addressed the following  
92 questions: (i) Does herbivory increase or decrease along gradients of increasing stand size and connectivity?  
93 (ii) Does avian predation increase or decrease along the same gradients? (iii) Are the observed trends related  
94 with the local abundance and diversity of insectivorous birds? We contrast our findings with those reported  
95 from studies of forest fragmentation and discuss implications in a context of increasing forest connectivity  
96 following ongoing changes in landscape use and management (Burton et al., 2018; Rey Benayas and  
97 Bullock, 2012).

## 98 **Material and methods**

### 99 **Study area and selection of study sites**

100 The study was carried out in the Landes de Gascogne region (south-western France) about 40 km southwest  
101 of Bordeaux (44°41'N, 00°51'W). The region is characterized by an oceanic climate with mean annual  
102 temperature of 12.8°C and annual precipitation of 873 mm over the last 20 years. The area is covered by  
103 extensive plantations of maritime pine (*Pinus pinaster* Ait.) interspersed with small stands of broadleaved  
104 forests that are dominated by Pedunculate oak (*Quercus robur* L.) and contain Pyrenean oak (*Quercus*

105 *pyrenaica* Willd.), birch (*Betula pendula* L.) and other tree species in minor abundance. Such stands are  
106 largely exempt from forest management. Many are actively expanding (Gerzabek et al., 2017), favoured by  
107 a recent change in silvicultural management that tends to conserve broadleaved trees recruiting within  
108 adjacent pine plantations as a mean of conservation biological control (Castagneyrol et al., 2014; Dulaurent  
109 et al., 2011).

110 We carefully selected a total of 18 novel oak forest stands along gradients of stand size and connectivity  
111 (Fig. A1). To ensure that forest stands were of recent origin, we confirmed on aerial photographs from the  
112 1950s that only very few trees were present at that time. We measured the stand area (henceforth referred to  
113 as stand size) as the minimum polygon including all oak trees with a stem diameter at breast height of  $\geq 3$  cm  
114 (range: 0.04-1.15 ha; Table A1). The basal area of the stand was also measured and was highly correlated  
115 with stand size so we decided to include only stand size in the analysis (Pearson  $r = 0.92$ ,  $P < 0.05$ ). We  
116 quantified the spatial connectivity of stands to more ancient forests by calculating the cover of broadleaf  
117 forests in a circular buffer of 500 m radius around each stand (range: 0-30%). The size of the buffer (78.5  
118 ha) has previously been shown to be well-suited for studying plant-herbivore-predator interactions (Barbaro  
119 et al., 2014; Chaplin-Kramer et al., 2011). Preliminary analyses revealed that the results were qualitatively  
120 the same with buffers of 250, 750 and 1000 m radius. Habitat mapping was based on aerial photos using  
121 QGIS version 2.18.13 (Quantum GIS Development Team, 2017). Stand size and connectivity were not  
122 correlated (Fig. A1; Pearson  $r = 0.39$ ,  $P = 0.11$ ).

## 123 Leaf insect herbivory

124 In early June 2017, we haphazardly selected four adult oak trees in each forest stand for assessing herbivory  
125 and avian predation. On each tree, we haphazardly cut two south facing and two north facing branches,  
126 respectively, at 4 and 8 m height and haphazardly sampled 20 fully developed leaves from each branch  
127 (summing 80 leaves per tree and 320 per stand). Leaves were taken to the laboratory for counting the number  
128 of leaf mines and galls per leaf and for estimating the percentage of leaf surface consumed or scratched by  
129 chewing and skeletonizing herbivores. A previous study (Giffard et al., 2012) had shown that the most  
130 common chewers and skeletonizers in the study area are Lepidoptera and Hymenoptera (sawfly) larvae. We  
131 distinguished eight levels of surface damage (0%, 1-5%, 6-10%, 11-15%, 16-25%, 26-50%, 51-75%,  
132 and >76%). The gall records were finally discarded from the study because they were too infrequent for  
133 independent analyses. In the following, we will refer to 'herbivory' as the tree level average leaf area  
134 removed by chewing or skeletonizing invertebrates, and to 'number of mines' as the average number of  
135 mines per leaf. We used the number of mines instead of the proportion of leaves with mines as 9 % of leaves  
136 had more than one mine.

## 137 **Avian predation**

138 We used dummy caterpillars made of plasticine (Staedler, Noris Club 8421, green[5]) to estimate predation  
139 on insect herbivores. Although not representative of absolute predation rates in the wild, this method allows  
140 to compare relative avian predation across stands (González-Gómez et al., 2006; Gunnarsson et al., 2018;  
141 Lövei and Ferrante, 2017). Plasticine caterpillars were 30 × 3 mm and light green to mimic late-instar larvae  
142 of caterpillars commonly found on oak in the field (Barbaro et al., 2014). We secured 10 plasticine  
143 caterpillars at 1.5-2 m height in the canopy of each of our four experimental trees per stand using 0.5 mm  
144 metal wires. Predation on plasticine caterpillars was surveyed every six to eight days from 15th May to 15th  
145 June (Low et al., 2014). Previous studies have shown that this time period matches the peak activity of  
146 insectivorous birds in the study area and is therefore relevant to quantify variation in avian predation  
147 (Barbaro et al., 2014; Bereczki et al., 2014; Castagneyrol et al., 2017). All caterpillars with beak marks left  
148 by insectivorous birds were recorded and replaced with undamaged ones during each survey. We decided to  
149 discard marks putatively left by insectivorous arthropods because we did not assess insectivorous arthropod  
150 communities of the stands (see below for birds). Previous to statistical analysis, we standardized our  
151 observation by calculating the mean daily predator activity per tree.

## 152 **Bird communities**

153 We surveyed the insectivorous bird community in each forest stand using 10-min point counts. Censuses  
154 were performed by a trained observer between 6:00 and 9:00 a.m. from the centre of the stand. Each stand  
155 was censused twice, once between 26th May and 2nd June and a second time between 21th and 29th June  
156 during the exposure period of plasticine caterpillars. All birds within the stand were recorded. Further  
157 analysis considered only those species that have a predominantly insectivorous diet during the breeding  
158 season. We used the highest count of a given species during any of the censuses as estimate of its abundance  
159 within the stand.

## 160 **Data analysis**

161 We built three types of models for our different response variables. First, we used linear mixed-effect models  
162 (LMM) to model either insect herbivory or the number of mines as a function of stand size ('Size'), stand  
163 connectivity in the surrounding landscape ('Connectivity') and their interaction ('Size × Connectivity').  
164 Size, Connectivity and Size × Connectivity were included as fixed effects and the identity of the stand as a  
165 random factor. With these predictors three different models were built, each with one further fixed effect, to  
166 assess the influence of insectivorous birds on herbivory. These additional fixed effects were either predation

on plasticine caterpillars (measured experimentally) or the abundance or species richness of insectivorous birds in the stand (recorded during point counts). We analysed these effects separately because of their non-independence. Second, we modelled predation on plasticine caterpillars as a function of stand size, stand connectivity and their interaction. All were included as fixed effects and stand identity as random effect. Adopting the same approach as for herbivory and the number of mines, we built three models with either herbivory or the abundance or species richness of insectivorous birds per stand as additional fixed effect. Third, we built a generalised linear model (GLM) with stands as replicates to assess the effect of stand size, connectivity and their interaction on the abundance and richness of insectivorous birds. We used Quasi-poisson and Poisson error distributions to model bird abundance and bird species richness, respectively.

All continuous predictor variables were scaled and centred prior to modelling to make their coefficients comparable (Schielzeth, 2010). We first built a full model including all fixed effects, interactions and random factors. Then we applied model simplification by sequentially removing non-significant fixed effects, starting with the least significant interaction. We stopped model simplification with the minimum adequate model when all non-significant terms were taken out. Hereafter, we only report statistics for the simplified models. We estimated and compared model fit by calculating marginal and conditional  $R^2$  (respectively  $R_m^2$  and  $R_c^2$ ) in order to estimate the proportion of variance explained by fixed ( $R_m^2$ ) and fixed plus random factors ( $R_c^2$ ) (Nakagawa and Schielzeth, 2013).

All analyses were done in R version 3.4.1 (2018), using the following packages: *car*, *doBy*, *forecast*, *lmerTest*, *MuMIn* and *vegan* (Barton, 2018; Fox and Weisberg, 2011; Højsgaard and Halekoh, 2018; Hyndman et al., 2018; Kuznetsova et al., 2017; Oksanen et al., 2018).

## Results

Insect herbivory was on average ( $\pm$  se,  $n = 72$ )  $8.02 \pm 4.51$  % (Table A1). The effect of stand size on herbivory depended on the connectivity of the stand (significant Size  $\times$  Connectivity interaction, Table 1): herbivory tended to increase with stand size in landscapes with a low stand connectivity whereas it decreased in landscape where broadleaf forests were more abundant (Fig. 1). Neither avian predation on plasticine caterpillars nor bird abundance or richness had a significant effect on herbivory. The number of mines per leaf was on average  $0.07 \pm 0.05$  (Table A1) and decreased in stands that were more connected. Leaf miners were not affected by stand size (Table 1).



195 A total of 18 caterpillars out of the 720 exposed (2.5 %) presented marks of bird attacks. Avian predation  
196 slightly increased with stand size while it did not vary with stand connectivity or the abundance or richness  
197 of insectivorous birds in the stand (Table 1).

198 We detected a total of 17 bird species within the studied oak stands. The mean ( $\pm$  se,  $n = 18$ ) abundance  
199 was  $4.22 \pm 2.59$  individuals (range: 1 - 9) and the mean species richness was  $3.22 \pm 1.66$  (range: 1 - 6). The  
200 most abundant bird species were blue tit (*Cyanistes caeruleus*), common chaffinch (*Fringilla coelebs*) and  
201 chiffchaff (*Phylloscopus collybita*) (Fig. A2). These three species accounted for 38.2 % of all records. Total  
202 bird abundance increased with stand size (Fig. 2a, Table 2) and decreased with stand connectivity (Fig. 2b,  
203 Table 2). The strength of stand size and connectivity effects was comparable although their effects were  
204 opposite. Species richness did not vary with stand size nor with stand connectivity.

## 205 Discussion

206 Our study revealed that the size and connectivity of novel native forest stands affect herbivorous insects and  
207 insectivorous birds in different ways. While the abundance of leaf miners depended on stand connectivity  
208 alone, herbivory by chewers and skeletonizers was influenced by an interplay between stand size and  
209 connectivity, and bird abundance (but not species richness) showed consistent independent and opposite  
210 responses to stand size and connectivity. This divergence of relationships is likely to arise from differences  
211 in the spatial grain of habitat perception and use by the different trophic guilds. It illustrates the complex  
212 nature of trophic cascades involving trees, insect herbivores and insectivorous birds in novel native forest  
213 stands (Gripenberg and Roslin, 2007).

## 214 Insect herbivores

215 The observed decrease in the abundance of leaf mining insects with increasing stand connectivity contrasts  
216 with previous detailed studies of leaf miners on *Quercus robur* (Gripenberg et al., 2008; Tack et al., 2010)  
217 that reported the opposite trend. Importantly, however, these studies focused on a finer spatial grain since  
218 they compared individual oak trees with different small-scale ecological neighbourhoods, not with entire  
219 forest stands. While the context of their study implies limited movement ranges of leaf mining insects, our  
220 results suggest that low abundance of source populations in the surroundings does not limit the ability of  
221 this guild to colonise and persist in small novel forest stands. The observed trend could instead be triggered  
222 by a resource dilution effect (Otway et al., 2005) whereby herbivore concentrate on the fewer available host  
223 individuals (Bañuelos and Kollmann, 2011). Dietary specialists such as many leaf miners should be  
224 particularly concerned by resource dilution (Elzinga et al., 2005).

Herbivory by chewing and skeletonizing insects was triggered by stand size in areas where oaks were generally sparse. Positive relationships between stand size and herbivory have also been reported by several studies conducted in considerably larger forest fragments (De La Vega et al., 2012; Simonetti et al., 2007 but see Maguire et al., 2015; Silva and Simonetti, 2009). They could arise from a higher density and/or diversity of insect herbivores in larger stands (Chávez-Pesqueira et al., 2015), as predicted by the resource concentration hypothesis (Hambäck and Englund, 2005; Root, 1973). This hypothesis states that the intensity of physical and chemical cues makes these stands more likely to be found and colonised and less likely to be left by herbivores. The resource concentration hypothesis should be particularly relevant in small habitat patches, such as those of our study system. However, we found that leaf herbivory ceased to increase with stand size and started instead to decline when broadleaf forest became more abundant in the surroundings. We have two possible, non-exclusive explanations for this phenomenon: (i) colonization rates of chewers and skeletonizers could generally be so high in our study system that even the smallest forest stands will be effectively reached (and, if necessary, re-colonized) when a certain threshold abundance of suitable habitats and associated herbivore source populations exist in the landscape (Fahrig, 2013). This hypothesis is supported by the fact that novel established forest stands are very rapidly colonised by woodland generalist species (Fuentes-Montemayor et al., 2015; Fuller et al., 2018). Second, (ii) insect herbivory tends to be favoured by edge effects (De Carvalho Guimarães et al., 2014), especially when it involves generalist species (Bagchi et al., 2018). Edge effects decrease in larger stands, which would counteract other positive effects of stand size on herbivory. Both explanations together suggest that the patterns of leaf herbivory that we observed are likely to be primarily driven by a relatively limited set of mobile generalist species. These species generated however leaf consumption rates that were low but comparable to those recorded in many older and larger oak forests (Gunnarsson et al., 2018; Moreira et al., 2018; Sanz, 2001), and they enabled a quick build-up of trophic cascades even in the smallest and youngest stands of our study system (Hagen et al., 2012).

## Avian insectivores and insectivory

Overall bird abundance and species richness were rather low as well as the size of the stands compared to previous works conducted in the same area (Barbaro et al., 2005; Giffard et al. 2012), and so was also the rate of avian predation (Castagneyrol et al., 2017). Previous studies by Genua et al. (2017), Peter et al. (2015) and Ruiz-Guerra et al. (2012) also found an increase in bird abundance with an increase in continuous forest in the landscape. These forests were however larger than the stands of our study, supporting the idea that avian predation rate and bird abundance (but not species richness) increased with stand size. Overall, these findings suggest that the activity of insectivorous birds in our study system is constrained by the carrying capacity of their wooded habitats. Typical breeding season territories of the most frequently

recorded bird species actually exceed the size of our smallest stands (Hinsley et al., 1995) and only the largest stands could regularly sustain more than one territory of the same species. These large stands should also provide the broadest range of tree ages and vegetation structures to different species, although it certainly is still inferior to that of mature forests (Fuentes-Montemayor et al., 2015). Habitat diversity and quality might then also be behind our rather surprising finding that bird abundance (although not species richness) tended to decrease with increasing stand connectivity (Fig. 2). Around the least connected stands, the broadleaf forest cover typically consisted of small, early-successional woodland patches, whereas several of the most connected stands were close to more continuous, older forests, expected to host a large functional diversity of insectivorous birds. The habitat quality of our focal stands should hence equal or exceed that of their surroundings in the former case but be inferior in the latter. The lower use of stands located near larger forests could then be interpreted as a resource dilution effect (see also Berg, 1997; Brotons et al., 2003). That we failed to see this landscape-scale effect reflected in our predation experiment could then simply be due to the low overall number of caterpillar attacks that we recorded and/or other potential limitations of the experimental approach (Muchula et al., 2019). It is however consistent with previous studies that fail to correlate herbivory with predation on plasticine caterpillars (Bereczki et al., 2014; Castagneyrol et al., 2017; but see Gunnarsson et al. 2018).

## **Tree-herbivore-insectivore interactions and the management of novel native forests**

To date most studies on the ecological impacts of active or passive afforestation in fragmented landscapes have focused on patterns of biodiversity (reviewed in Burton et al., 2018), whereas functional ecological aspects have received far less attention (but see Rey Benayas and Bullock, 2012). Our study on bird-insect relationships in novel established native forest stands adds a novel perspective to this field. Taken together, our results indicate that novel forest stands can be very effectively colonised by different guilds of insect herbivores. Although this process is likely to involve primarily a subset of mobile generalist species, these alone can generate levels of herbivory that are quite comparable to those at later stages of forest succession and in areas with higher forest cover. In turn, the build-up of insectivorous bird communities tends to occur more slowly because these depend more than their prey on the development of suitable habitat patches of a certain minimum size (Genua et al., 2017). Birds, as long-lived mobile vertebrate insectivores, typically need to find enough substitutable or non-substitutable resources in the surrounding habitat patches to fulfil entirely their life cycles, namely landscape supplementation and complementation processes (Brotons et al., 2005; Dunning et al., 1992; Fahrig, 2017; Tubelis et al., 2004). Globally, we failed to detect any evidence of top-down control of herbivory by predators. As a consequence, trophic networks in our study system are

likely to underlie strong stochasticity, resulting in extensive among-stand heterogeneity and variation through time, which is also typical of forest ecosystems having experienced long-term fragmentation processes (Hagen et al., 2012; Bregman et al., 2015; Fahrig, 2017).

The value of native broadleaf woodlands for biodiversity conservation is important to consider for sustainable forest management in rural landscapes. Landscape defragmentation through networks of novel native forest stands represents a cost-efficient tool for restoring biodiversity and numerous associated ecosystem services (Rey Benayas and Bullock, 2012). Yet the dynamics and ecological functioning of novel native forest stands remain much less well understood than those of forest remnants resulting from fragmentation. Our study underpins that different trophic guilds respond very differently to these novel habitats depending on the spatial grain at which they perceive and exploit them (Gripengberg and Roslin, 2007). To favour a rapid build-up of diverse, and hence stable, trophic networks involving insect herbivores and their predators, woodland creation schemes should focus on habitat size and quality rather than connectivity, including a management that facilitates a diverse tree and understorey vegetation structure (see also Burton et al., 2018; Fuller et al., 2018).

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## Author contributions

E.V.C., B.C., A.H and I.V.H conceived the study and acquired the data. E.V.C and B.C analysed the data. E.V.C., B.C and A.H drafted the first version of the manuscript. All authors wrote the final version of the manuscript.

## References

Bagchi, R., Brown, L.M., Elphick, C.S., Wagner, D.L., Singer, M.S., 2018. Anthropogenic fragmentation of landscapes: mechanisms for eroding the specificity of plant–herbivore interactions. *Oecologia* 187, 521–533. <https://doi.org/10.1007/s00442-018-4115-5>

316 Bañuelos, M.J., Kollmann, J., 2011. Effects of host-plant population size and plant sex on a  
 317 specialist leaf-miner. *Acta Oecologica* 37, 58–64.  
 318 <https://doi.org/10.1016/j.actao.2010.11.007>

319 Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I., Brockerhoff, E.G., 2014. Bird functional  
 320 diversity enhances insectivory at forest edges: A transcontinental experiment. *Divers.*  
 321 *Distrib.* 20, 149–159. <https://doi.org/10.1111/ddi.12132>

322 Barthelemy, H., Stark, S., Olofsson, J., 2015. Strong responses of subarctic plant communities to  
 323 long-term reindeer feces manipulation. *Ecosystems* 18, 740–751.

324 Barton, K., 2018. MuMIn: Multi-Model Inference.

325 Bereczki, K., Ódor, P., Csóka, G., Mag, Z., Báldi, A., 2014. Effects of forest heterogeneity on the  
 326 efficiency of caterpillar control service provided by birds in temperate oak forests. *For. Ecol.*  
 327 *Manage.* 327, 96–105. <https://doi.org/10.1016/j.foreco.2014.05.001>

328 Berg, Å., 1997. Diversity and abundance of birds in relation to forest fragmentation, habitat  
 329 quality and heterogeneity. *Bird Study* 44, 355–366.  
 330 <https://doi.org/10.1080/00063659709461071>

331 Böhm, S.M., Wells, K., Kalko, E.K. V, 2011. Top-down control of herbivory by birds and bats in  
 332 the canopy of temperate broad-leaved oaks (*Quercus robur*). *PLoS One* 6.  
 333 <https://doi.org/10.1371/journal.pone.0017857>

334 Brotons, L., Herrando, S., Martin, J.-L., 2005. Bird assemblages in forest fragments within  
 335 Mediterranean mosaics created by wild fires. *Landsc. Ecol.* 19, 663–675.  
 336 <https://doi.org/10.1007/s10980-005-0165-2>

337 Brotons, L., Mönkkönen, M., Martin, J.L., 2003. Are Fragments Islands? Landscape Context and  
 338 Density-Area Relationships in Boreal Forest Birds. *Am. Nat.* 162, 343–357.  
 339 <https://doi.org/10.1086/376887>

340 Burton, V., Moseley, D., Brown, C., Metzger, M.J., Bellamy, P., 2018. Reviewing the evidence  
 341 base for the effects of woodland expansion on biodiversity and ecosystem services in the

342 United Kingdom. *For. Ecol. Manage.* 430, 366–379.  
 343 <https://doi.org/10.1016/j.foreco.2018.08.003>

344 Castagneyrol, B., Bonal, D., Damien, M., Jactel, H., Meredieu, C., Muiruri, E.W., Barbaro, L.,  
 345 2017. Bottom-up and top-down effects of tree species diversity on leaf insect herbivory.  
 346 *Ecol. Evol.* 7, 3520–3531. <https://doi.org/10.1002/ece3.2950>

347 Castagneyrol, B., Jactel, H., Charbonnier, Y., Barbaro, L., Dulaurent-Mercadal, A.M., 2014. Egg  
 348 mortality in the pine processionary moth: Habitat diversity, microclimate and predation  
 349 effects. *Agric. For. Entomol.* 16, 284–292. <https://doi.org/10.1111/afe.12056>

350 Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop  
 351 pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932.  
 352 <https://doi.org/10.1111/j.1461-0248.2011.01642.x>

353 Chávez-Pesqueira, M., Carmona, D., Suárez-Montes, P., Núñez-Farfán, J., Aguilar, R., 2015.  
 354 Synthesizing habitat fragmentation effects on plant-antagonist interactions in a phylogenetic  
 355 context. *Biol. Conserv.* 192, 304–314. <https://doi.org/10.1016/j.biocon.2015.10.002>

356 Cooper, J.K., Li, J., Montagnes, D.J.S., 2012. Intermediate fragmentation per se provides stable  
 357 predator-prey metapopulation dynamics. *Ecol. Lett.* 15, 856–863.  
 358 <https://doi.org/10.1111/j.1461-0248.2012.01808.x>

359 De Carvalho Guimarães, C.D., Viana, J.P.R., Cornelissen, T., 2014. A Meta-Analysis of the  
 360 Effects of Fragmentation on Herbivorous Insects. *Environ. Entomol.* 43, 537–545.  
 361 <https://doi.org/10.1016/j.apcata.2015.08.006>

362 De La Vega, X., Grez, A.A., Simonetti, J.A., 2012. Is top-down control by predators driving  
 363 insect abundance and herbivory rates in fragmented forests? *Austral Ecol.* 37, 836–844.  
 364 <https://doi.org/10.1111/j.1442-9993.2011.02345.x>

365 Dulaurent, A.M., Rossi, J.P., Deborde, C., Moing, A., Menassieu, P., Jactel, H., 2011. Honeydew  
 366 feeding increased the longevity of two egg parasitoids of the pine processionary moth. *J.*  
 367 *Appl. Entomol.* 135, 184–194. <https://doi.org/10.1111/j.1439-0418.2010.01547.x>

368 Dunning, J.B., Danielson, B.J., Pulliam, H.R., Ecology, I., 1992. Ecological Processes That  
 369 Affect Populations in Complex Landscapes. *Nord. Soc. Oikos* 65, 169–175.

370 Elzinga, J.A., Turin, H., Van Damme, J.M.M., Biere, A., 2005. Plant population size and isolation  
 371 affect herbivory of *Silene latifolia* by the specialist herbivore *Hadena bicruris* and parasitism  
 372 of the herbivore by parasitoids. *Oecologia* 144, 416–426. [https://doi.org/10.1007/s00442-](https://doi.org/10.1007/s00442-005-0096-2)  
 373 005-0096-2

374 Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to  
 375 habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* 81, 117–142.  
 376 <https://doi.org/10.1017/S1464793105006949>

377 Fahrig, L., 2017. Ecological Responses to Habitat Fragmentation Per Se. *Annu. Rev. Ecol. Evol.*  
 378 *Syst.* 48, annurev-ecolsys-110316-022612. [https://doi.org/10.1146/annurev-ecolsys-110316-](https://doi.org/10.1146/annurev-ecolsys-110316-022612)  
 379 022612

380 Fahrig, L., 2013. Rethinking patch size and isolation effects: The habitat amount hypothesis. *J.*  
 381 *Biogeogr.* 40, 1649–1663. <https://doi.org/10.1111/jbi.12130>

382 Fischer, J., Lindenmayer, D.B., Manning, A.D., Fischer, J., Lindenmayer, D.B., Manning, A.D.,  
 383 2006. Biodiversity, ecosystem function resilience : ten guiding principle commodity  
 384 production landsca. *Front. Earth Sci.* 4, 80–86.

385 Forest Europe, 2015. Forest Europe (2015) State of Europe’s forests 2015. Ministerial  
 386 Conference on the Protection of Forests in Europe.: Forest Europe, UNECE and FAO. State  
 387 of Europe’s Forests 2015. Status and Trends in Sustainable Forest Management in Europe,  
 388 2015. [WWW Document]. Minist. Conf. Prot. For. Eur. For. Eur. UNECE FAO. URL  
 389 <http://www.foresteurope.org/docs/fullsoef2015.pdf>

390 Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression, Second. ed. Sage,  
 391 Thousand Oaks {CA}.

392 Franklin, J.F., 1988. Structural and functional diversity in temperate forests, In Wilson,. ed.  
 393 Washington.

394 Fuchs, R., Herold, M., Verburg, P.H., Clevers, J.G.P.W., Eberle, J., 2015. Gross changes in  
 395 reconstructions of historic land cover/use for Europe between 1900 and 2010. *Glob. Chang.*  
 396 *Biol.* 21, 299–313. <https://doi.org/10.1111/gcb.12714>

397 Fuentes-Montemayor, E., Peredo-Alvarez, V.M., Watts, K., Park, K.J., 2015. Are woodland  
 398 creation schemes providing suitable resources for biodiversity? Woodland moths as a case  
 399 study. *Biodivers. Conserv.* 24, 3049–3070. <https://doi.org/10.1007/s10531-015-0997-2>

400 Fuller, L., Fuentes-Montemayor, E., Watts, K., Macgregor, N.A., Bitenc, K., Park, K.J., 2018.  
 401 Local-scale attributes determine the suitability of woodland creation sites for Diptera. *J.*  
 402 *Appl. Ecol.* 55, 1173–1184. <https://doi.org/10.1111/1365-2664.13035>

403 Genua, L., Start, D., Gilbert, B., 2017. Fragment size affects plant herbivory via predator loss  
 404 Lucy. *Oikos* 126, 1357–1365. <https://doi.org/10.1111/oik.04223>

405 Gerzabek, G., Oddou-Muratorio, S., Hampe, A., 2017. Temporal change and determinants of  
 406 maternal reproductive success in an expanding oak forest stand. *J. Ecol.* 105, 39–48.  
 407 <https://doi.org/10.1111/1365-2745.12677>

408 Giffard, B., Corcket, E., Barbaro, L., Jactel, H., 2012. Bird predation enhances tree seedling  
 409 resistance to insect herbivores in contrasting forest habitats. *Oecologia* 168, 415–424.  
 410 <https://doi.org/10.1007/s00442-011-2089-7>

411 González-Gómez, P.L., Estades, C.F., Simonetti, J.A., 2006. Strengthened insectivory in a  
 412 temperate fragmented forest. *Oecologia* 148, 137–143. [https://doi.org/10.1007/s00442-005-](https://doi.org/10.1007/s00442-005-0338-3)  
 413 0338-3

414 Gripenberg, S., Ovaskainen, O., Morriën, E., Roslin, T., 2008. Spatial population structure of a  
 415 specialist leaf-mining moth. *J. Anim. Ecol.* 77, 757–767.

416 Gripenberg, S., Roslin, T., 2007. Nordic Society *Oikos* Up or down in Space? Uniting the  
 417 Bottom-up versus Top-down Paradigm and Spatial Ecology. *Oikos* 116, 181–188.

418 Gunnarsson, B., Wallin, J., Klingberg, J., 2018. Predation by avian insectivores on caterpillars is  
 419 linked to leaf damage on oak (*Quercus robur*). *Oecologia* 188, 733–741.  
 420 <https://doi.org/10.1007/s00442-018-4234-z>



421 Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E.,  
 422 Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster,  
 423 B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne,  
 424 B.A., Nicholls, A.O., Orrock, J.L., Song, D., Townshend, J.R., 2015. Habitat fragmentation  
 425 and its lasting impact on Earth's ecosystems. *Appl. Ecol.* 1, 1–9.  
 426 <https://doi.org/10.1126/sciadv.1500052>

427 Hagen, M., Kissling, W.D., Rasmussen, C., Cartensen, D., Dupont, Y., Kaiser-Bunbury, C.,  
 428 O’Gorman, E., Olesen, J., De Aguiar, M.A.M., Al., E., 2012. Biodiversity, species  
 429 interactions and ecological networks in a fragmented world, *Advances in ecological*  
 430 *research*. <https://doi.org/10.1016/j.pain.2008.02.025>

431 Hambäck, P.A., Englund, G., 2005. Patch area, population density and the scaling of migration  
 432 rates: The resource concentration hypothesis revisited. *Ecol. Lett.* 8, 1057–1065.  
 433 <https://doi.org/10.1111/j.1461-0248.2005.00811.x>

434 Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau,  
 435 D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L.,  
 436 Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest  
 437 cover change. *Science* (80-. ). 342, 850–853. <https://doi.org/10.1126/science.1244693>

438 Hinsley, A.S.A., Bellamy, P.E., Newton, I., Sparks, T.H., 1995. *Nordic Society Oikos Habitat and*  
 439 *Landscape Factors Influencing the Presence of Individual Breeding Bird Species in*  
 440 *Woodland Fragments* Published by: Wiley on behalf of Nordic Society Oikos Stable URL :  
 441 <http://www.jstor.org/stable/3677057> *Habitat and lands. J. Avian Biol.* 26, 94–104.

442 Højsgaard, S., Halekoh, U., 2018. *doBy: Groupwise Statistics, LSmeans, Linear Contrasts,*  
 443 *Utilities.*

444 Hyndman, R., Athanasopoulos, G., Bergmeir, C., Caceres, G., Chhay, L., O’Hara-Wild, M.,  
 445 Petropoulos, F., Razbash, S., Wang, E., Yasmeeen, F., 2018. *{forecast}: Forecasting functions*  
 446 *for time series and linear models.*

447 Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction  
 448 debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25, 153–160.  
 449 <https://doi.org/10.1016/j.tree.2009.10.001>

450 Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. {lmerTest} Package: Tests in Linear  
 451 Mixed Effects Models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>

452 Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G., Moreno, C.R., 2009. Effects of Natural Enemy  
 453 Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. *Annu.*  
 454 *Rev. Ecol. Evol. Syst.* 40, 573–592. <https://doi.org/10.1146/annurev.ecolsys.110308.120320>

455 Lindenmayer, D.B., Fisher, J., 2013. Habitat fragmentation and landscape change: an ecological  
 456 and conservation synthesis.

457 Lövei, G.L., Ferrante, M., 2017. A review of the sentinel prey method as a way of quantifying  
 458 invertebrate predation under field conditions. *Insect Sci.* 24, 528–542.  
 459 <https://doi.org/10.1111/1744-7917.12405>

460 Low, P.A., Sam, K., McArthur, C., Posa, M.R.C., Hochuli, D.F., 2014. Determining predator  
 461 identity from attack marks left in model caterpillars: Guidelines for best practice. *Entomol.*  
 462 *Exp. Appl.* 152, 120–126. <https://doi.org/10.1111/eea.12207>

463 Maguire, D.Y., Nicole, T., Buddle, C.M., Bennett, E.M., 2015. Effect of fragmentation on  
 464 predation pressure of insect herbivores in a north temperate deciduous forest ecosystem.  
 465 *Ecol. Entomol.* 40, 182–186. <https://doi.org/10.1111/een.12166>

466 Moreira, X., Abdala-Roberts, L., Berny Mier y Teran, J.C., Covelo, F., de la Mata, R., Francisco,  
 467 M., Hardwick, B., Pires, R.M., Roslin, T., Schigel, D.S., ten Hoopen, J.P.J.G., Timmermans,  
 468 B.G.H., van Dijk, L.J.A., Castagneyrol, B., Tack, A.J.M., 2018. Impacts of urbanization on  
 469 insect herbivory and plant defences in oak trees. *Oikos* 113–123.  
 470 <https://doi.org/10.1111/oik.05497>

471 Muchula, K., Xie, G., Gurr, G.M., 2019. Ambient temperature affects the utility of plasticine  
 472 caterpillar models as a tool to measure activity of predators across latitudinal and elevational  
 473 gradients. *Biol. Control* 129, 12–17. <https://doi.org/10.1016/j.biocontrol.2018.11.006>

474 Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining  $R^2$  from  
 475 generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.  
 476 <https://doi.org/10.1111/j.2041-210x.2012.00261.x>

477 O'Rourke, M.E., Petersen, M.J., 2017. Extending the 'resource concentration hypothesis' to the  
 478 landscape-scale by considering dispersal mortality and fitness costs. *Agric. Ecosyst.*  
 479 *Environ.* 249, 1–3. <https://doi.org/10.1016/j.agee.2017.07.022>

480 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R.,  
 481 O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018.  
 482 *vegan: Community Ecology Package*.

483 Otway, S.J., Hector, A., Lawton, J.H., 2005. Resource dilution effects on specialist insect  
 484 herbivores in a grassland biodiversity experiment. *J. Anim. Ecol.* 74, 234–240.  
 485 <https://doi.org/10.1111/j.1365-2656.2004.00913.x>

486 Peter, F., Berens, D.G., Grieve, G.R., Farwig, N., 2015. Forest Fragmentation Drives the Loss of  
 487 Insectivorous Birds and an Associated Increase in Herbivory. *Biotropica* 47, 626–635.  
 488 <https://doi.org/10.1111/btp.12239>

489 Quantum GIS Development Team, 2017 [WWW Document], n.d. URL <http://qgis.org> (accessed  
 490 1.4.17).

491 R Core Team, 2018. *R: A Language and Environment for Statistical Computing*.

492 Rey Benayas, J.M., Bullock, J.M., 2012. Restoration of Biodiversity and Ecosystem Services on  
 493 Agricultural Land. *Ecosystems* 15, 883–899. <https://doi.org/10.1007/s10021-012-9552-0>

494 Rey Benayas, J.M., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile  
 495 ecological restoration, conservation, and agricultural land use. *Front. Ecol. Environ.* 6, 329–  
 496 336. <https://doi.org/10.1890/070057>

497 Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats:  
 498 the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43, 95–124.

499 Rosenheim, J.A., 1998. Higher-Order Predators and the Regulation of Insect Herbivore  
 500 Populations. *Annu. Rev. Entomol.* 43, 421–447.  
 501 <https://doi.org/10.1146/annurev.ento.43.1.421>

502 Rossetti, M.R., González, E., Salvo, A., Valladares, G., 2014. Not all in the same boat: trends and  
 503 mechanisms in herbivory responses to forest fragmentation differ among insect guilds.  
 504 *Arthropod. Plant. Interact.* 8, 593–603. <https://doi.org/10.1007/s11829-014-9342-z>

505 Rossetti, M.R., Tschardt, T., Aguilar, R., Batáry, P., 2017. Responses of insect herbivores and  
 506 herbivory to habitat fragmentation: a hierarchical meta-analysis. *Ecol. Lett.* 20, 264–272.  
 507 <https://doi.org/10.1111/ele.12723>

508 Ruiz-Guerra, B., Renton, K., Dirzo, R., 2012. Consequences of Fragmentation of Tropical Moist  
 509 Forest for Birds and Their Role in Predation of Herbivorous Insects. *Biotropica* 44, 228–  
 510 236. <https://doi.org/10.1111/j.1744-7429.2011.00795.x>

511 Sanz, J.J., 2001. Experimentally increased insectivorous bird density results in a reduction of  
 512 caterpillar density and leaf damage to Pyrenean oak. *Ecol. Res.* 16, 387–394.  
 513 <https://doi.org/10.1046/j.1440-1703.2001.00403.x>

514 Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients.  
 515 *Methods Ecol. Evol.* 1, 103–113. <https://doi.org/10.1111/j.2041-210x.2010.00012.x>

516 Schröter, D., Cramer, W., Leeman, R., Prentice, I.C., Araujo, M., Arnell, N.W., Bondeau, A.,  
 517 Bugmann, H., Al., E., 2005. Ecosystem Service Supply and Vulnerability to Global Change  
 518 in Europe. *Science* (80-. ). 5752, 1333–1338. <https://doi.org/10.1126/science.1115233>

519 Sezen, U.U., Chazdon, R.L., Holsinger, K.E., Rica, C., 2005. Genetic Consequences of Tropical.  
 520 *Science* (80-. ). 2005. <https://doi.org/10.1126/science.1105034>

521 Silva, C.A., Simonetti, J.A., 2009. Inquiring into the causes of depressed folivory in a fragmented  
 522 temperate forest. *Acta Oecologica* 35, 458–461. <https://doi.org/10.1016/j.actao.2009.01.001>

523 Simonetti, J.A., Grez, A.A., Celis-Diez, J.L., Bustamante, R.O., 2007. Herbivory and seedling  
 524 performance in a fragmented temperate forest of Chile. *Acta Oecologica* 32, 312–318.  
 525 <https://doi.org/10.1016/j.actao.2007.06.001>

526 Storch, D., 1998. Densities and territory sizes of birds in two different lowland communities in  
527 eastern Bohemia. *Folia Zool.* 47, 181–188.

528 Tack, A.J.M., Ovaskainen, O., Pulkkinen, P., Roslin, T., 2010. Spatial location dominates over  
529 host plant genotype in structuring an herbivore community Published by : Ecological  
530 Society of America Linked references are available on JSTOR for this article : Your use of  
531 the JSTOR archive indicates your acceptance of t 91, 2660–2672.  
532 <https://doi.org/10.1890/09-1027.1>

533 Tubelis, D.P., Cowling, A., Donnelly, C., 2004. Landscape supplementation in adjacent savannas  
534 and its implications for the design of corridors for forest birds in the central Cerrado, Brazil.  
535 *Biol. Conserv.* 118, 353–364. <https://doi.org/10.1016/j.biocon.2003.09.014>

536 Van Dorp, D. Van, Opdam, P.F.M., 1987. Effects of patch size, isolation and regional abundance  
537 on forest bird communities 1, 59–73.

538 Whytock, R.C., Fuentes-Montemayor, E., Watts, K., Barbosa De Andrade, P., Whytock, R.T.,  
539 French, P., Macgregor, N.A., Park, K.J., 2018. Bird-community responses to habitat creation  
540 in a long-term, large-scale natural experiment. *Conserv. Biol.* 32, 345–354.  
541 <https://doi.org/10.1111/cobi.12983>

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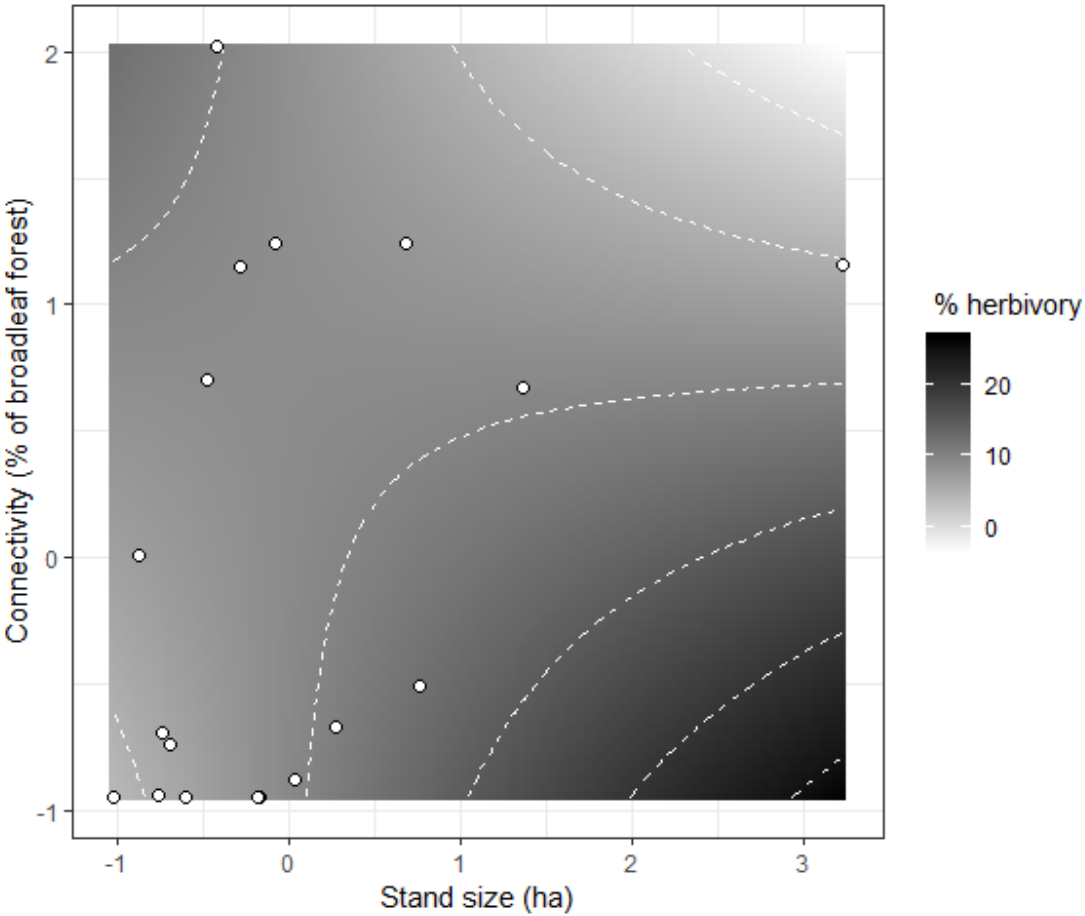
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**Figure captions**

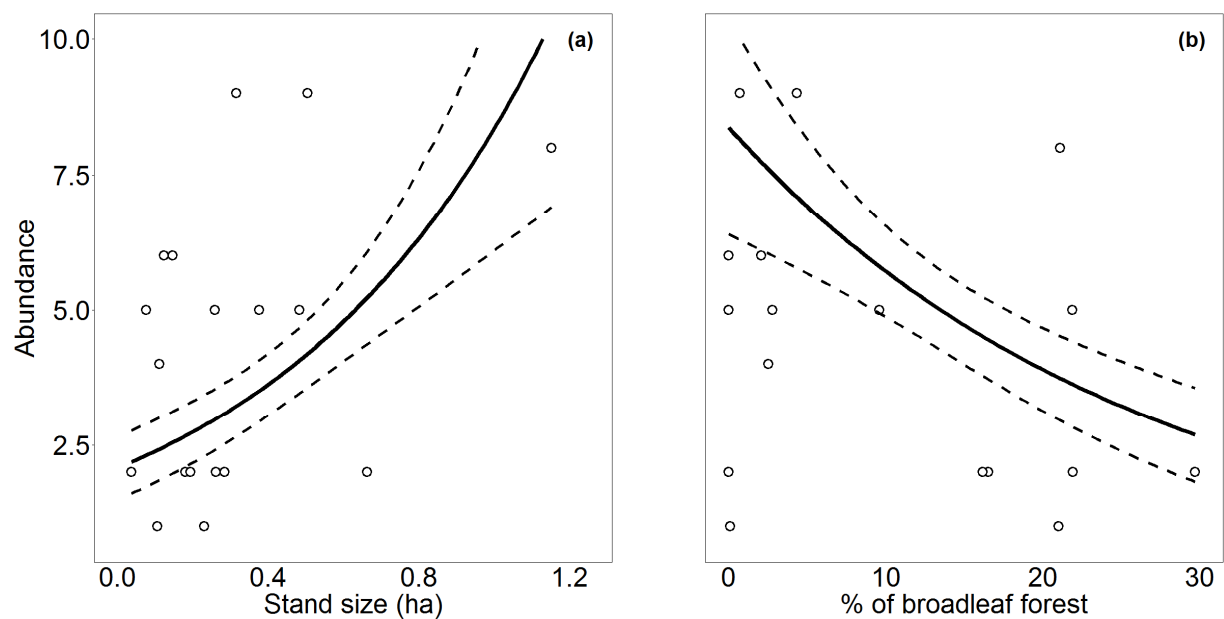
Fig. 1. Interactive effect of stand size and connectivity on herbivory. White to black colour scale and isolines show the predicted percentage of herbivory along standardized gradients of stand size (measured as the stand area) and stand connectivity (measured as the cover of broadleaf forest within a buffer of 500 m radius). White dots show the distribution of the original data.

Fig. 2: Effects of stand size and connectivity on bird abundance (a, b). Dots represent the individual stands. Solid lines and dashed lines represent model predictions and corresponding standard errors, respectively.

574 **Fig. 1**



585 **Fig. 2**





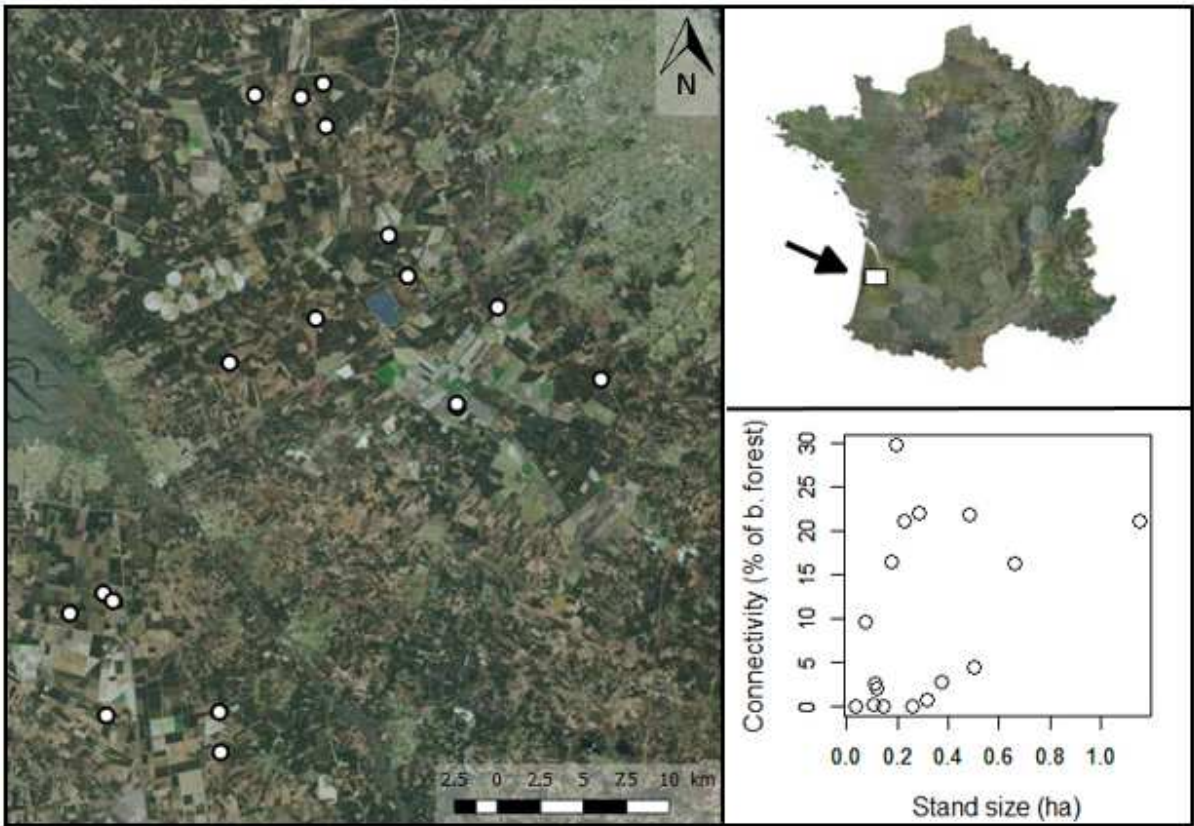
**Table 1.** Summary of LMM testing the effect of stand size, connectivity, their interaction and either Avian predation, abundance or richness on insect herbivory. For avian predation the effect of stand size, connectivity, their interaction and either herbivory, bird abundance or richness were tested. Significant variables are indicated in bold. Only predictors retained after model simplification are shown. Predictors were scaled and centred.  $R^2_m$  and  $R^2_c$  correspond to the variance explained by fixed and fixed plus random factors, respectively.

Response	Predictors	$\chi^2$	Df	Coef. $\pm$ SE	<i>P</i>	$R^2_m$ ( $R^2_c$ )
Herbivory	Size	0.06	1	2.010 $\pm$ 1.061	0.807	0.20 (0.43)
	Connectivity	0.87	1	-0.041 $\pm$ 0.784	0.351	
	Size $\times$ Connectivity	8.35	1	-2.933 $\pm$ 1.015	<b>0.004</b>	
No. of mines	Connectivity	4.53	1	-0.016 $\pm$ 0.007	<b>0.033</b>	0.10 (0.31)
Avian predation	Size	3.94	1	0.135 $\pm$ 0.068	<b>0.047</b>	0.06 (0.13)

**Table 2.** Summary of the GLM on insectivorous bird abundance and species richness as a function of stand size and connectivity. Only predictors remaining after model simplification are shown. Stand size and connectivity were previously standardized. LR: Likelihood Ratio.

Response	Predictors	$\chi^2$	Df	Coef. $\pm$ SE	<i>P</i>	$R^2_m$ ( $R^2_c$ )
Bird abundance	Size	8.569	1	0.373 $\pm$ 0.124	<b>0.003</b>	0.42 (0.43)
	Connectivity	6.554	1	-0.391 $\pm$ 0.164	<b>0.010</b>	

612 **Appendix A**



615 **Fig. A1.** Location map of the study area in the Aquitaine region, south-western France, showing  
616 the 18 oak stands at the top right and left of the figure, and figure showing stand size (ha) and  
617 connectivity of each stand at the bottom right of the figure.

**Table A1.** Information about the location and size of the oak stands included in the study and summary of the results of herbivory (% leaf damage and Number of mines), predation on plasticine caterpillars and bird abundance and species richness within each stand.

Stand	Latitude	Longitude	Stand size (ha)	No. of Oaks	Herbivory	No. of mines / leaf	Avian predation on caterpillars	Bird abundance	Bird species richness
1	44.743	-0.800	0.375	110	13.88	0.147	0.589	5	4
2	44.729	-0.733	0.123	28	4.68	0.078	0.089	6	4
3	44.764	-0.816	0.179	35	13.72	0.056	0.000	2	1
4	44.568	-1.011	0.315	50	4.41	0.069	0.268	9	6
5	44.564	-1.004	0.111	32	6.58	0.050	0.000	4	3
6	44.556	-0.035	0.106	30	6.50	0.059	0.268	1	1
7	44.834	-0.919	0.504	33	13.77	0.025	0.324	9	6
8	44.834	-0.885	0.229	71	5.81	0.044	0.893	1	1
9	44.842	-0.869	0.663	132	6.54	0.034	0.491	2	2
10	44.819	-0.865	0.483	150	4.92	0.056	0.000	5	4
11	44.677	-0.760	0.261	55	7.31	0.141	0.263	2	2
12	44.675	-0.759	0.036	17	5.58	0.103	0.781	2	2
13	44.693	-0.655	0.146	64	3.97	0.072	0.179	6	4
14	44.504	-0.004	0.193	43	10.55	0.022	0.179	2	2
15	44.692	-0.928	1.151	156	6.35	0.088	0.964	8	6
16	44.719	-0.869	0.283	29	11.65	0.066	0.536	2	2
17	44.509	-0.922	0.075	16	8.78	0.072	0.089	5	4
18	44.487	-0.920	0.258	38	9.40	0.075	0.655	5	4

634 **Fig. A2.** Proportion of the total abundance of each insectivorous bird species recorded during the  
 635 study. The total number of individuals per species is indicated on each bar.

