Edge contrast does not modulate edge effect on plants and pollinators

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Edge contrast does not modulate edge effect on plants and pollinators

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Abstract

Edge contrast, is one of the main determinants of edge effects. This study examines the response of plant and pollinator diversity (bees and butterflies) to forest edge contrast, i.e. the difference between forests and adjacent open habitats with different disturbance regimes. We also investigated a potential cascading effect from plants to pollinators and whether edge structure and landscape composition mediate the relationship between edge contrast and beta diversity of pollinators. We sampled 51 low-contrast edges where forests were adjacent to habitats showing low levels of disturbance (i.e. grey dunes, mowed fire-breaks, orchards, grasslands) and 29 high-contrast edges where forests were adjacent to more intensively disturbed habitats (i.e. tilled firebreaks, oilseed rape) in three regions of France. We showed that plant diversities were higher in edges than in adjacent open habitat, whatever the edge contrast. However, plant beta diversity did not differ significantly between low and high-contrast edges. While we observed higher pollinator diversities in adjacent habitats than in low-

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contrast edges, there were no significant differences in pollinator beta diversity depending on edge contrast. We did not observe a cascading effect from plants to pollinators. Plant and bee beta diversities were mainly explained by local factors (edge structure and flower cover) while butterfly beta diversity was explained by surrounding landscape characteristics (proportion of land cover in grassland).

Keywords: Forest edges, butterflies, wild bees, beta diversity, landscape composition, France.

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Introduction

Most of Europe's forest cover is made up of fragmented forests (Larsson, 2001) resulting mainly from land-use changes, like habitat conversion for agriculture but also reforestation of agricultural land over historical time (Andrieu, Ladet, Heintz & Deconchat, 2011; Dupouey, Dambrine, Laffite & Moares, 2002; Tilman et al., 2001), and road network (Ibisch et al., 2016). These small forests are characterized by their small area, their isolation from other forests and their high edge/core-area ratio. Forest edges are defined as the transition zone between open habitats and forests (Matlack & Latvaitis, 1999). They can present a great variability in their three-dimensional structure such as their width, their shape or tree stem density (Essen, Ringvall, Harper, Christensen & Svensson, 2016), and the quantity and quality of available habitats in edges depend in part on their structure (Didham & Lawton, 1999; Ries et al., 2004a). Forest edge characteristics are also under human control: they are mainly managed by woodlot owners and farmers to prevent tree growth from encroaching on the field or shading the crop and to specific cutting operations for firewood (Du Bus de Warnaffe, Deconchat, Ladet & Balent, 2006), and they are also subject to disturbance from forestry and adjacent farming practices such as tillage, pesticide drift or mowing (Kleijn & Verbeek, 2000).

Several local factors can influence the magnitude of edge effects: edge orientation and structure, the quality and quantity of resources and/or refugia found in edges and their adjacent habitats and edge contrast (Ries, Fletcher, Battin & Sisk, 2004a).

Edge contrast expresses the differences in quality and/or vegetation structure (height, density) between the two adjacent habitats forming the edge (Angelstam, 1986). Several studies investigated how edge contrast could mitigate edge effect (Ries, Fletcher, Battin & Sisk, 2004a), based on the hypothesis that when edge contrast is low, i.e. when the two adjacent habitats have few qualitative or structural differences, then their associated communities are more similar than in high-contrast edges. This similarity can be expressed in terms of total specific diversity and abundance, or within functional groups. Reino et al. (2009) showed a tendency for stronger responses to high-contrast edges (old and tall eucalyptus plantations vs. fallow fields) than to low-contrast edges (young and short oak plantations vs. fallow fields). The same trend was found for forest dung beetles sampled in tropical

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wood edges, which showed a neutral response for low-contrast edges (mature plantations) but edge avoidance for high-contrast edges (recent plantations) (Peyras, Vespa, Bellocq & Zurita, 2013). More rarely, similarity between animal or plant communities between forest edges and adjacent open habitat have been estimated with beta diversity indices. Yekwayo, Pryke, Roets and Samways (2016) showed lower beta diversity and lower species replacement of ground-living arthropods in low contrast edges (natural forests vs. pine plantations) than in high-contrast edges (natural forest vs. grasslands), and Eldegard, Totland and Moe (2015) showed an increased turnover of species with edge contrast.

In addition to local factors, there is a growing number of studies showing that edge effects also depend on the landscape context. Reino et al. (2009) showed that positive edge responses of bird abundances tended to be strongest in less fragmented landscapes, except for steppe birds. In their synthesis, Porensky and Young (2013) conclude that studies from a variety of ecosytems show that edge-effect interactions can have significant consequences for ecosystems and conservation. Moreover a negative effect of management intensity of the surrounding agricultural landscape was demonstrated on plant diversity in wood edges (Chabrerie, Jamoneau, Gallet-Moron & Decoq, 2013).

In this study, we investigated the response of plant and pollinator (bees and butterflies) diversity to forest edge contrast. In agricultural landscapes, semi-natural habitats, including forest edges, are an essential source of feeding (flowers and host plants), nesting resources (below-ground and above-group bee nesters) for pollinators (Steffan-Dewenter et al., 2006; Morandin & Kremen, 2013) and overwintering sites (Sarthou et al., 2005). In the adjacent habitat, the availability of these resources can depend on habitat persistence. As a consequence, we defined edge contrast level depending on soil disturbance: we considered a forest edge to be low-contrast when it was adjacent to open habitat with permanent vegetation cover and low levels of soil disturbance (i.e. grey dunes, mowed fire-breaks, orchards, grasslands), and high-contrast when the adjacent open habitat showed higher disturbance rates (vegetation removal and ploughing for tilled firebreaks, oilseed rape crops). We tested whether plant and pollinator communities between forest edge and adjacent habitats are more similar in low-contrast edges than in high-contrast edges. We also investigated whether similarity of bee and butterfly communities between forest edge and open habitat depends on edge structure (height and width) and on landscape context: grassland and forest cover, and woody edge

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length (forest edges plus hedges). Finally, studies investigating edge effects on different biological models that are functionally linked showed cascading effects between various compartments of the ecosystems. Wimp, Murphy, Lewis and Ries (2011) showed that the decline in specialist herbivores and in their associated predators was driven by an increase in generalist predators near edges. Similarly, Montgomery, Kelly, Robertson and Ladley (2003) showed that higher fruit set of the mistletoe *Peraxilla tetrapetala* (Loranthaceae) in edges was due to higher visitation rates of pollinators on edges rather than greater nutrient resource availability. We thus discussed whether the response of plants to edge contrast cascades up to pollinators.

Materials and methods

Study sites

Forest edges and their adjacent habitats were sampled in three regions of France: Aquitaine (A), Centre (C) and Midi-Pyrénées (MP). These regions have different forest types (intensive forest management / farm forests, conifers / oak species, large / small forests) (Fig. 1 and see Appendix A).

The Aquitaine region, on the Atlantic coast in south-western France, has the largest planted pine forest in Europe - the "Landes de Gascogne" forest – dedicated to wood production. According to the landscape surrounding the studied edges, 67% of the land is covered by maritime pine plantations (*Pinus pinaster* Aiton) (average size: 5.2 ha), (see van Halder, Barbaro & Jactel, (2010) for details). The remaining part of the land is covered by herbaceous firebreaks running through. At the Atlantic coast the pine forest is bordered by grey dunes (10% of the studied landscapes). Firebreaks are either mowed or tilled and grey dunes are not managed. The climate is thermo-atlantic (mean annual temperature, 12 ◦C; mean annual precipitation, 700 mm) and the elevation is low (c. 50 m a.s. l.).

The Centre region, south of Paris, is mostly dedicated to intensive crop production (mostly cereals, OSR – oilseed rape – and corn), which covers 47% of the studied landscapes, whereas grassland covers 15%. Forests cover nearly 20% of the the studied landscapes. Most forests are small (average size: 2.2 ha) and are dominated by oak (*Quercus petraea* and *Q. robur*) and hornbeam

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(*Carpinus betulus*) coppice-with-standards used for timber and firewood production. The climate is oceanic with slight continental influences (mean annual temperature, 10.6 ∘C; mean annual precipitation, 640 mm).

The Midi-Pyrénées region is situated in the south-west of France. This study was conducted in the Long Term Ecological Research Network Vallées et Coteaux de Gascogne (LTER_EU_FR_003) (43°17'N, 0°54'E). This hilly region (250–400 m a.s.l.) is characterized by mixed crop-livestock farming system with a mosaic of small forests (26%, average size: 1.5 ha), grasslands (28%) and crop fields (39%, mainly winter cereals, rapeseed, maize and sunflower) (Choisis et al., 2010). The dominant tree species in the forests are pedunculate oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* Lieblein). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5 ∘C; mean annual precipitation, 750 mm).

Site selection

We selected 70 sites with a forest edge bordering open habitat (see Appendix A). Within each region, we selected low-contrast edges where forests were adjacent to habitat showing low levels of anthropogenic disturbance (51 in total) and high-contrast edges where forests were adjacent to more intensively disturbed habitats (29 in total). Depending on the region, adjacent habitats of low-contrast edges were grey dunes, mowed fire-breaks (region A), orchards (C) or grasslands (MP), and those of high-contrast edges were tilled firebreaks (A) or oilseed rape crops (C and MP). Thirty three sites were selected in region A, 21 in region C and 26 in region MP (Table 1). In each region, forests were selected to be, as far as possible, of the same type (size, tree composition, management). Forest edges were selected to be as straight as possible and at least 100 m long. Only sites with direct contact between forest and open adjacent habitat were considered (no stream, no road or lane). Forest boundaries were defined as the line formed by trees with a diameter of at least 5 cm at breast height (Fig. 2). Edge habitat was defined as the transition zone between wood boundary and the adjacent habitat (Fig. 2). We defined as high-contrast edges, those having adjacent habitats with regular soil disturbance causing a temporary removal of vegetation (tillage in half of the firebreak, tillage and crop

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harvesting in the rapeseed). The open habitat of low-contrast edges had permanent vegetation cover (no disturbance in dunes, mowing in grasslands, in half of the firebreaks and in orchards) (Table 1).

Biodiversity sampling

Sampling of bees (Apoidea) and butterflies (Rhopalocera) was conducted in 2011, vascular plant species were recorded in 2011 (region C and partly in region A) and in 2012 (region A, region MP and partly in region A) in the edge and in the adjacent habitats (Table 1, Fig. 2). Plant surveys comprised abundance-dominance records of all vascular plant species according to the Braun-Blanquet scale (Braun-Blanquet 1956). Data from each vegetation layer (herbaceous: 0-0.3 m, shrub: 0.3-7 m and tree: >7 m) were recorded in May-June 2011 or 2012. Surveys were conducted in five 2 x 2 m quadrats regularly arranged along two 100-m-long transects parallel to the border (Fig. 2). The first transect was located at the edge and the second, 20 m into the adjacent open habitat (Alignier, Alard, Chevalier & Corcket, 2014).

Bees were trapped using pan traps (exposed for 15 days in June 2011). Pan traps consisted of two plastic bowls (a yellow and a white one) sprayed with a UV-reflection paint (S.P.R.L. Spray-color 18 133UK, Brussels, Belgium) and mounted on wooden poles at vegetation height in the open habitat (Westphal et al., 2008). Pan traps were filled with a liquid composed of approximately 2.4 L of water, 0.6 L of monopropylene glycol for conservation and a few drops of liquid soap to lower surface tension. To limit inconvenience to the farmers, pan traps were not placed in grazed grasslands and were located at the edge and 10 m away into the other adjacent habitats. Bees were trapped in all regions, except in grasslands in region MP (because of grazing) and in tilled firebreaks in region A (Table 1). All collected bee specimens were stored in a freezer, dried, mounted and identified by the same persons to species level where possible.

Butterflies (Lepidoptera: Rhopalocera) were monitored four times a year (in May, June, July and August 2011) along two 100-m-long transects (Pollard & Yates, 1993) placed at the edge and within the adjacent field, 20 m away from the edge. Transect walks (4 minutes) were undertaken between 10:00 am and 5:00 pm, when weather conditions were suitable for butterfly activity: dry conditions, low wind speed (<5 on the Beaufort scale), warm temperature (>15 °C) and bright

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weather. Butterflies were recorded in a fixed width band of 2.5 m on either side of the transect and 5 m ahead. Individuals were determined at the species level, visually or after net-trapping (and release). The total number of individuals per species for the four surveys was scored.

Edge variables

On each site, we measured a set of variables to characterise the edge and the adjacent open habitat. Edge structure was described by four variables: h1 (canopy height), h2 (height of the bottom of tree crown), h3 (height between the top of the shrub layer in the understory and the bottom of tree crown) and edge width (length between wood boundary and the border of the adjacent habitat) (Table 2, Fig. 2). The border of the adjacent habitat was defined as the limit of the farming management (for crops: the last seeding line, for grassland: electric fence for grazed grassland or last traces of the mowing for hay meadows). Concomitantly to butterfly surveys, flower cover was visually estimated using the Braun-Blanquet scale along the butterfly transects in the edge and in the adjacent habitat (including rape seed when flowering in region C). We selected the highest cover value of the four visits for each edge and its adjacent habitat, and calculated the difference in nectar resource between them (Diff_Nect).

Landscape variables

Landscape potential to sustain plants and pollinators was evaluated by quantifying semi-natural elements in a 500 m buffer area, centred on the middle of the edge transect. Landscape variables were: the percentage of buffer area covered by grasslands (%grass) and forests (%wood), and the cumulative length of forest edges and twice the length of hedgerows (to take into account both sides of the hedges) (Woody edge, in m) (Table 2).

Data analysis

The uneven design result from the availability of the suitable sites which varied between region, but also from further practical constraints, among which (i) we were not allowed by owners to leave pan traps in grazed grassland (actually all grasslands in MP), (ii) some firebreaks were mowed and other

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tilled (region A), (iii) a grassland was converted to wheat between the two years of the study (region MP). This prevent us from testing our hypothesis on all the studied biological models, statistical analyses were done per site and per taxa, with statistical methods robust to uneven sampling size. All statistical analyses were performed with R 3.2.3 (R Development Core Team 2015). We did not detect any autocorrelation of model residuals (R package ncf, function plot.spine.correlog).

Gamma-like diversity

Two gamma-like diversities were calculated for a given type of edge contrast per region: one pooling all the individuals recorded in the edge habitat, and one in the adjacent habitat (e.g. all the butterflies encountered in forest/grassland edges vs. in grasslands of region MP). We compared gamma-like diversity between edge and adjacent habitat for each taxon (plants, bees, butterflies) for each type of edge contrast and within each study region using diversity profiles. Diversity profiles provide a faithful graphical representation of the shape of a community; they show how the perceived diversity changes as the emphasis shifts from rare to common species (Leinster and Cobbold, 2012). We used Hill (1973) diversity profiles such as:

$$^qD = \left(\sum_{i=1}^{R} p_i^q\right)^{1/(1-q)}$$

where q is the order of diversity and $p_i = n_i/N$ (n_i: number of individuals of species i and N: the total number of individuals).

In this study, we used a range of order for diversity from 0 to 2 according to the literature (Marcon, Scotti, Hérault, Rossi & Lang, 2014): ^0D being species richness (SR), ^1D the exponential of the Shannon Diversity Index (e^H) and ^2D Simpson's Reciprocal Index (1/D). According to the theory of diversity ordering, one community can be regarded as more diverse than another only if its Rényi diversities are higher all along the curve (no intersection) (Tothmeresz, 1995). The order of diversity for edge and adjacent habitat communities were calculated using the R packages Entropart (Marcon &

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Hérault, 2015). A potential sampling bias of existing species was taken into account in the DivProfile function of the Entropart package.

Beta diversity

Beta diversities of plants and pollinators between the edge and the paired adjacent habitat were calculated using the Bray-Curtis dissimilarity index upon abundance data. Low values of the Bray-Curtis index indicate that communities have similar species composition and abundance, while high values indicate that they are different. The significance of the difference between beta diversity according to edge contrast was tested using t-test on simple linear modelling between the Bray-Curtis dissimilarity index and the adjacent habitat type.

Finally, we tested whether plant beta diversity between wood edge and the adjacent open habitat was related to edge structure (h1, h2, h3, Width) and landscape variables (%grass, %wood, Woody_edge). The same analysis was conducted for pollinator beta diversity with an additional variable: the contrast in flora between both habitats. This contrast was estimated using two variables: (i) the plant beta diversity (for all plant species) between the edge and the paired adjacent habitat (Beta_Flora) and (ii) the difference in the flower cover between edge and adjacent habitat (Diff_Nect). Linear mixed effect models (LMMs) for plant and pollinator beta diversities were fitted with the above variables as fixed factors, and adjacent habitat nested in the region as a random factor. The quality of fit of each LMM was assessed by examining the normality and randomness of the standardized residuals. We then performed a multi-model inference procedure based upon the bias-corrected Akaike's information criterion (AICc) using the "MuMIn" R package (Barton, 2016). The overall best model and all competing models were ranked in relation to the difference in their AICc scores. Only models with ΔAICc < 10 (from the model with the lowest AICc) were considered in the multi-model inference procedure. Significance of fixed effects in the averaged model was tested using the Wald test. We did not detect any auto-correlation of model residuals (R package ncf, function plot.spine.correlog). We made a partitioning of the turnover (linked with species replacement) and nestedness (linked with species loss) components of Jaccard beta diversity (Baselga, 2010) (function

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beta.pair, package betapart). Within each region and each taxa, we did not observe any significant difference of turnover component between high and low-contrast edges (data not shown).

Results

Comparisons of gamma-like diversity between low and high-contrast edges

In total, 462 plant species, 111 Apoidea species (6417 individuals) and 66 butterfly species (2850 individuals) were recorded (see Appendix A). Gamma-like diversity of plants was higher in edges than in adjacent open habitat in all regions, for low as well as for high-contrast edges, except for both types of firebreaks in Aquitaine (Fig. 3). Gamma-like diversity of bees did not show any consistent pattern depending on edge contrast. In low-contrast edges, the diversity profile was higher in edges than in adjacent habitats in region C, but lower in region A. In high-contrast edges, the diversity profile was lower in edges than in the adjacent habitats in region C, while they showed more diverse bee communities in edges than the adjacent habitats in region MP (Fig. 3). In low-contrast edges, butterfly communities were more diverse in adjacent habitats than in edges in all regions except in region MP where the grassland/forest low-contrast edges had intersecting diversity profiles (Fig. 3). For high-contrast edges, only one of the three cases showed non-intersecting curves: butterfly communities were more diverse in edges than in adjacent habitats in oilseed rape/forest edges in region C.

Beta diversity

Beta diversity for plants was not significantly different between low and high-contrast edges, except in region A where beta diversity in mowed firebreaks (low-contrast edges) was lower than in dunes (low-contrast edges) and tilled firebreaks (high-contrast edges) (Fig. 4). For bees, the only region where bees were sampled in high and low-contrast edges showed no significant differences in Bray-Curtis indices (Fig. 4). Butterfly communities in region MP were more similar between edge and adjacent open habitat in low-contrast edges than in high-contrast edges. In region C, low-contrast

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edges and high-contrast edges showed no significant difference. In region A, butterfly beta-diversity showed a similar pattern than plant beta-diversity: their communities in mowed firebreaks (low-contrast edges) were more similar between edge and adjacent habitat than in dunes (low-contrast edges) and tilled firebreaks (high-contrast edges) (Fig. 4). Proportion of species found only in edge, in adjacent habitat or shared differed among region, edge type and taxa (Fig. 5). It varied from almost 70% of shared species between forest edges and adjacent habitat (in region C and MP) to 30% for plants and butterflies in high contrast edges in oil seed rape in region C.

Beta diversity relationships with edge structure and landscape context

Plant beta diversity was significantly and positively affected by the total height of the edges (h1) and the height between the top of the shrub layer in the understory and the bottom of tree crown (h3) (Table 3a). Plant communities were thus more similar where edge heights were comparatively low.

Multi-model inference for bees revealed that beta diversity was significantly and positively affected by the difference in nectar resources between the edge and the adjacent habitat, i.e. bee communities differed more between edge and adjacent habitat when edge contrast in blooming plant cover was higher (Table 3b). For butterflies, beta diversity was significantly and negatively affected by the amount of grassland in the landscape and the height of the bottom of tree crown (h2) (Table 3c, Fig. 6), indicating that butterfly communities were more similar between edges and adjacent habitats in landscapes with higher grassland cover and for edges showing a higher bottom of tree crown.

Discussion

Gamma-like diversity of plants is higher in edges

Our results indicate that whatever the contrast, gamma-like diversity for plants was higher in edges than in open adjacent habitats in two regions (MP and C). These results are consistent with studies of edge effect on plants, suggesting that species richness and diversity are generally higher in edges than

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in adjacent habitats (Matlack et al., 1999). The higher order of diversity observed in edges could be due to the addition of both woody and open habitat species, but also to the presence of edge specific species (Duelli, Studer, Marchand & Jakob, 1990). Additionally, edges can act as barriers to seed dispersal and provide shelter for numerous species (Cadenasso, Pickett, Weathers & Jones, 2003). However, our results did not indicate any common pattern of gamma-like plant diversity in low versus high contrast edges. An explanation could be our definition of the disturbance regimes we considered, based on vegetation removal and soil disturbance. First, it did not take into account chemical spraying (herbicide, insecticide) in OSR and particularly in orchards, which could also influence pollinators. Further studies may thus consider these chemical disturbances as well as structural complexity and perennial vegetation to identify the type contrast. However the availability of the data about chemical application may be an obstacle to go beyond structural differences. Second, the similarity of gamma-like diversity in edges and in adjacent habitats in the Aquitaine region, with numerous shared species, suggests that other factors structure plant biodiversity there and lead to community homogenisation, possibly particular ecological conditions (low moisture and nutrient-holding capacity of sandy soil). Another factor can be forest management (forests in Aquitaine region are plantations that are more intensively managed than forests in the two other regions, with succession of planting and clear cuts temporarily similar to open adjacent habitat), as forest characteristics have been shown to influence edge effect (Zurita, Pe'er, Bellocq & Hansbauer, 2012).

Higher gamma-like diversity of pollinators in open habitats adjacent to low-contrast edges

For both pollinator groups, when there was a difference of gamma-like diversity profiles in low-contrast edges, in most cases the adjacent habitat hosted the highest diversity (4 cases out of 6). However, these differences were in general weak. Bees and butterflies are known to be more abundant and diverse in habitats providing resources (nectar and pollen) (Carvell, 2002; Kwaiser & Hendrix, 2007; van Halder et al. 2010; Villemey et al. 2015). Our study suggests that habitats adjacent to low-contrast edges may thus have offered more resources than forest edges (flowers for both pollinators, and/or host plants for butterflies, nest site for ground nesting bees).

In high-contrast edges, we did not detect any common pattern: in two cases out of five the diversity profiles did not differ significantly between adjacent habitats and edges. In two out of the three significant cases, pollinator gamma-like diversity was higher in edges than in adjacent habitats (bees in OSR/wood edges in region MP and butterflies in OSR/wood edges in region C). Edges may have provided more plant resources (flower and butterfly host plants) than adjacent habitats. These findings are in accordance with one of the predicted changes of population abundance near habitat edges of the resource-based model proposed by Ries and Sisk (2004b): when resources are concentrated along the edges, a positive response of abundance is expected.

The gamma-like diversity profile of bees showed contrasting patterns even for similar adjacent habitats. Bee diversity profile was higher in OSR crops than in the edge in the region C while it was the contrary in the region MP (lower diversity profile in OSR than in the edge). In region C, bees may have been attracted by resources provided by the crop itself and by the weeds in the field (Bretagnolle & Gaba, 2015) but not in region MP as the trapping occurred after the flowering period of the OSR. The higher species richness of plants in region C than in region MP (respectively: 25.7 vs 7.5, $W = 305$, $p < 0.01$) may have offered more resources in region C's OSR fields than those of region MP.

Plant and pollinator beta diversity responded more to edge structure and landscape factors than to edge contrast

Overall, our results do not support the hypothesis that beta diversity differs according to edge contrast. These results could indicate that exchanges, through seed dispersal for plants, between the edge and adjacent habitat have homogenized both communities irrespective of the edge contrast. This hypothesis is supported by the relatively high number of species shared between edge and adjacent habitat whatever the region (except for OSR for plants and butterflies in region C and MP). Similarly, we demonstrated that beta diversity of pollinators was unaffected by edge contrast. In our case, the absence of response of plant diversity to edge contrast may have induced a similar pattern at a higher trophic level. The only exception was observed in butterfly communities in regions MP and A. In MP they were more similar in low-contrast edges (with grassland or mowed firebreaks, respectively, in

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regions MP and A) than in high-contrast edges (with OSR in MP and tilled firebreaks in region A). Similar results were found in arid contexts for butterfly communities (Pe'er, van Maanen, Turbé, Matsinos & Kark, 2011). However, butterfly communities in dunes presented high dissimilarity following beta diversity plant response. Dunes ecosystems are highly dynamic, with plant communities dominated by annual species, which contrasts with the relative stability of forest edges. As for gamma-like diversity, the absence of a beta diversity response to edge contrast could be due in part to our definition of the disturbance regimes, based on soil and vegetation removal, without considering other anthropogenic disturbances like for example chemical disturbance in orchards, or natural disturbances in dunes. The lack of consistency in edge contrast effects in the literature could be due to the multiple ways to consider a contrast in a forest edge: difference in structure, in disturbance, in habitat availability.

Beta diversity of plants responded mainly to edge structure. Plant communities were more dissimilar between edges and open adjacent habitat when edges were tall. Tall edges offer moisture and climatic conditions closest to the forest, so they may host more woody plant species and fewer open habitat species. Forest edge structure has already been shown to change micro-climatic conditions in tropical forest (Didham et al., 1999).

Our study indicates that edge and landscape characteristics are key factors in explaining variation in beta diversity for pollinators: high contrast in blooming cover between edges and their adjacent habitats was related to less similar bee communities. As bee beta diversity patterns were not linked to plant beta diversity observed in the same sites, we confirmed that differences in blooming cover instead of overall plant diversity is the main driver of bee beta diversity, in accordance with other studies (Dramstad & Fry, 1994; Mandelik, Winfree, Neeson & Kremen, 2012; Potts, Vulliamy, Dafni, Ne'eman & Willmer, 2003). In addition, in our study, similarity between butterfly communities at edges and adjacent habitats were higher in landscape showing a higher cover of grassland. A high proportion of grassland in landscapes may homogenize the butterfly communities in edges and adjacent habitats by reducing the distance from the nearest grassland, especially for the less mobile species (Ockinger & Smith, 2007; Steffan-Dewenter & Tscharntke, 2000). Bee beta diversity as well as plant beta diversity responded to local factors, while butterflies responded to the landscape factor

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even though bees and butterflies are mobile organisms. Indeed, bees are central place foragers bringing food back to a nest to benefit their offspring (Westrich, 1996) whereas butterflies look for nectar- and host-plants, or a mating partner, with no compulsory return to a given site (Vane Wright & Ackery, 1981). According to the optimal foraging theory (Schoener, 1989), bees are more sensitive to the quality of the habitat and distance to the flower resources than butterflies, and thus may react to more local factors than butterflies.

Conclusion

Our results fail to support the hypothesis that low-contrast edges have more similar communities than high-contrast edges, with the exception of one case. We did not demonstrate any direct cascading effect between beta diversity of plants and pollinators in edges but we confirmed the importance of flower cover at the local scale and grassland amount at the landscape scale to drive pollinator beta diversity at wood-open habitat edges. Our results highlight the importance of considering landscape context to understand edge effect on non-central place foragers such as butterflies.

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References

Alignier, A., Alard, D., Chevalier, R., & Corcket, E. (2014). Can contrast between forest and adjacent open habitat explain the edge effects on plant diversity? *Acta Botanica Gallica,* 161, 253-259.

Alignier, A., & Deconchat, M. (2013). Patterns of forest vegetation responses to edge effect as revealed by a continuous approach. *Annals of Forest Science,* 70, 601-609.

Andrieu, E., Ladet, S., Heintz, W., & Deconchat, A. (2011). History and spatial complexity of deforestation and logging in small private forests. *Landscape and Urban Planning,* 103, 109-117.

Angelstam, P. (1986). Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos, 47, 365-373.

Balent, G., & Courtiade, B. (1992). Modelling bird communities/landscape patterns relationships in a rural area of South-Western France. *Landscape Ecology,* 6, 195-211.

Barton, K. (2016). Multi-Model Inference. R package 'MuMIn'. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134-143.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A., Ran, T.A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture Ecosystems & Environment,* 146, 34–43.

Bouvier, J.C., Toubon, J.F., Boivin, T., & Sauphanor, B. (2005). Effects of apple orchard management strategies on the great tit (*Parus major*) in southeastern France. *Environmental Toxicology and Chemistry,* 24, 2846–2852.

Braun-Blanquet, J. (1956). Plant sociology: the study of plant communities. In: H.J. Oosting, & W.H. Freemannand (Eds.), *The study of plant communities*. San Francisco.

Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agron. Sustain. Dev.,* 35, 891-909.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., & Jones, C.G. (2003). A framework for a theory of ecological boundaries. *Biosicence,* 53, 750-758.

Carvell, C. (2002). Habitat use and conservation of bumblebees (*Bombus spp.*) under different grassland management regimes. *Biological conservation,* 103, 33-49.

Chabrerie, O., Jamoneau, A., Gallet-Moron, E., & Decoq, G. (2013). Maturation of forest edges is constrained by neighbouring agricultural land management. *Journal of Vegetation Science,* 24, 58-69.

Chen, J.Q., Franklin, J.F., & Spies, T.A. (1993). Contrasting microclimates among clear-cut, edge, and interior of old-growth douglas-fir forest. *Agricultural and Forest Meteorolog,* 63, 219–237.

17

Cross, J., Fountain, M., Marko, V., & Nagy, C. (2015). Arthropod ecosystem services in apple orchards and their economic benefits. *Ecological Entomology, 40 (Supplt 1)*, 82-96.

Didham, R.K., & Lawton, J.H. (1999). Edge structure determine the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica, 31*, 17-30.

Dramstad, W., & Fry, G. (1995). Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agriculture, Ecosystems & Environment*, 53, 2, 123-135.

Du Bus de Warnaffe, G., Deconchat, M., Ladet, S., & Balent, G. (2006). Variability of cutting regimes in small private woodlots of south-western France. *Annals of Forest Science*, 63, 915–927.

Duelli, P., Studer, M., Marchand, I., & Jakob, S. (1990). Population movements of arthropods between natural and cultivated areas. *Biological conservation,* 54, 193-207.

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

Eldegard, K., Totland, Ø., & Moe, S.R. (2015). Edge effects on plant communities along power line clearings. *Journal of Applied Ecology*, 52, 871-880.

Essen, P.A., Ringvall, A.H., Harper, K.A., Christensen, P., & Svensson, J. (2016). Factors driving structure of natural and anthropogenic forest edges from temperate to boreal ecosystems. *Journal of Vegetation Science,* 27, 482-492.

Fletcher, R.J. (2005). Multiple edge effects and their implications in fragmented landscapes. *Journal of Animal Ecology, 74*, 342-352.

Hill, M.O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54, 427-432.

Ibisch, P.L., Hoffman, M.T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., DellaSala, D.A., Vale, M.M., Hobson, P.R., & Selva, N. (2016). A global map of roadless areas and their conservation status. *Science*, 354, 1423-1427.

Kleijn, D., & Verbeek, M. (2000). Factors affecting the species composition of arable field boundary vegetation. *Journal of Applied Ecology 37*, 256–266.

Kwaiser, K.S., & Hendrix, S.D. (2007). Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agriculture Ecosystems and Environment,* 124, 3-4, 200-204.

Larsson, T.B. (2001). Biodiversity evaluation tools for European forests. *Ecological Bulletins, 50*, 1-237.

Mandelik, Y., Winfree, R., Neeson, T., & Kremen, C. (2012). Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications, 22*, 1535-1546.

Marcon, E., & Héraultt, B. (2015). An R package to measure and partition diversity. *Journal of Statistical Software, 67* 1-26.

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Marcon, E., Scotti, I., Hérault, B., Rossi, V., & Lang, G. (2014). Generalization of the partitioning of Shannon diversity. *PLoS One,* 9, 3, e90289.

Matlack, G.R., & Latvaitis, J.A. (1999). Forest edges. In: H.M. Jr (Ed.), *Maintaining biodiversity in forest ecosystems* (pp. 210-233). Cambridge: University press.

Michel, V.T., Jiménez‑Franco, M.V., Naef‑Daenzer, B., & Grüebler, M.U. (2016). Intraguild predator drives forest edge avoidance of a mesopredator. *Ecosphere,* 7, 3, e01229.

Montgomery, B.R., Kelly, D., Robertson, A.W., & Ladley, J.J. (2003). Pollinator behaviour, not increased resources, boosts seed set on forest edges in a New Zealand Loranthaceous mistletoe. *New Zealand Journal of Botany, 41*, 277-286

Ockinger, E., & Smith, H.G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology, 44*, 50-59.

Pe'er, G., van Maanen, C., Turbé, A., Matsinos, Y.G., & Kark, S. (2011). Butterfly diversity at the ecotone between agricultural and semi-natural habitats across a climatic gradient. *Diversity and Distributions*, 17, 6, 1186-1197.

Peyras, M., Vespa, N.I., Bellocq, M.I., & Zurita, G.A. (2013). Quantifying edge effects: the role of habitat contrast and species specialization. *Journal of Insect Conservation, 17*, 807-820.

Pollard, E., & Yates, T.J. (Eds.). (1993). *Monitoring butterflies for ecology and conservation.* London: Chapman et Hall.

Porensky, L.M., & Young, T.P. (2013). Edge-effect interactions in fragmented and patchy landscapes. *Conservation Biology*, 27, 509-519.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology, 84*, 2628-2642.

Reino, L., Beja, P., Osborne, P.E., Morgado, R., Fabião, A., & Rotenberry, J.T. (2009). Distance to edges, edge contrast and landscape fragmentation: Interactions affecting farmland birds around forest plantations. *Biological conservation, 142*, 824-838.

Ries, L., Debinski, D.M., & Wieland, M.L. (2001). Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology, 15*, 401-411.

Ries, L., Fletcher, R.J., Battin, J., & Sisk, T. (2004a). Ecological responses to habitat edges: mechanisms, models and variability explained. *Annual Review of Ecology, Evolution and Systematics, 35*, 491-522.

Ries, L., & Sisk, T.D. (2004b). A predictive model of edge effects. *Ecology, 85*, 2917-2926.

Ries, L., & Sisk, T.D. (2010). What is an edge species ? The implications of sensitivity to habitat edges. *Oikos, 119*, 1636-1642.

Schoener, T.W. (1989). Food webs from the small to the large. *Ecology, 70*, 1559-1589.

Steffan-Dewenter, I., & Tscharntke, T. (2000). Butterfly community structure in fragmented habitats. *Ecology Letters, 3*, 449-456.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., & Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science, 292*, 281-284.

Tothmeresz, B. (1995). Comparison of methods for diversity ordering. *Journal of Vegetation Science, 6*, 283-290.

van Halder, I., Barbaro, L., & Jactel, H. (2010). Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important? *Journal of Insect Conservation, 15*, 591-601.

Vane Wright, R.I., & Ackery, P.R. (1981). The biology of butterflies. In: R.I. Vane Wright, & P.R. Ackery (Eds.), *The biology of butterflies*. British museum: Academic Press.

Villemey, A., Van Halder, I., Ouin, A., Barbaro, L., Chenot, J., Tessier, P., Calatayud, F., Martin, H., Roche, P., & Archaux, F. (2015). Mosaic of grasslands and woodlands is more effective than habitat connectivity to conserve butterflies in French farmland. *Biological conservation, 191*, 206-205.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, J., Vaissière, B., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., & Steffan-Dewanter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs, 78*, 653-671.

Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In: A. Matheson, S.L. Buchmann, W.P. O'Tool, & I.L. Williams (Eds.), *The conservation of bees.* Academic Press.

Wimp, G.M., Murphy, S.M., Lewis, D., & Ries, L. (2011). Do edges responses cascade up or down a multiptrophic food web? *Ecology Letters, 14*, 863-870.

Yekwayo, I., Pryke, J.S., Roets, F., & Samways, M.J. (2016). Responses of ground living arthropods to landscape contrast and context in a forest-grassland mosaic. *Biodiversity and Conservation*, 26, 631-651.

Zurita, G., Pe'er, G., Bellocq, M.I., & Hansbauer, M. (2012). Edge effects and their influence on habitat suitability calculations: a continuous approach applied to birds of the Atlantic forest. *Journal of Applied Ecology*, 49, 503-512.

List of figures
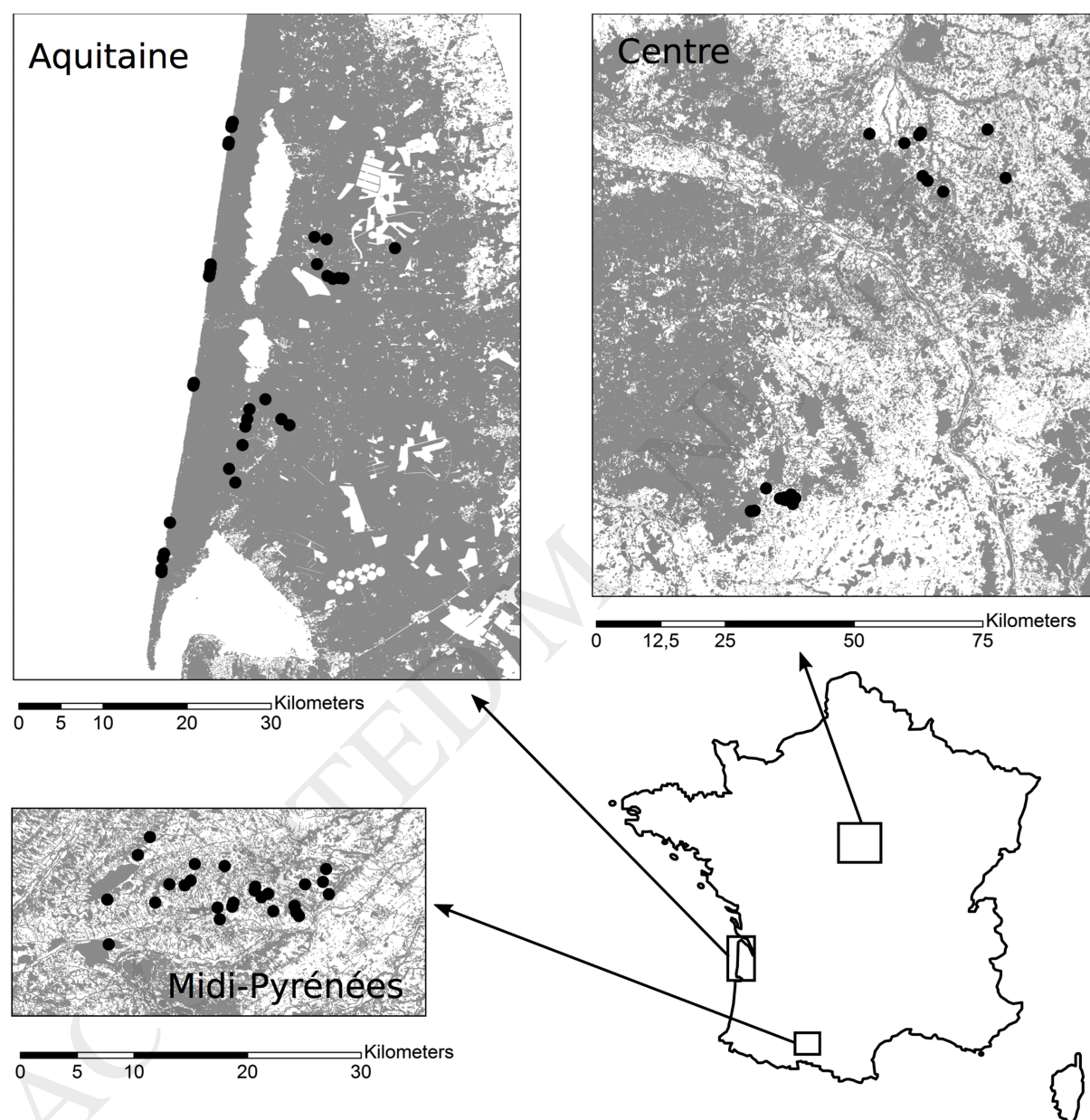
**Fig. 2.** Edge is defined as the transition zone between the wood boundary and the managed adjacent open habitat. It is characterized by the height of the canopy (h1), height of the bottom of tree crown (h2), and the height between the shrub layer and the bottom of the tree crown (h3). Plants (grey squares), butterflies (rectangular) and bees (circles) were sampled in the edges and in the adjacent open habitat.

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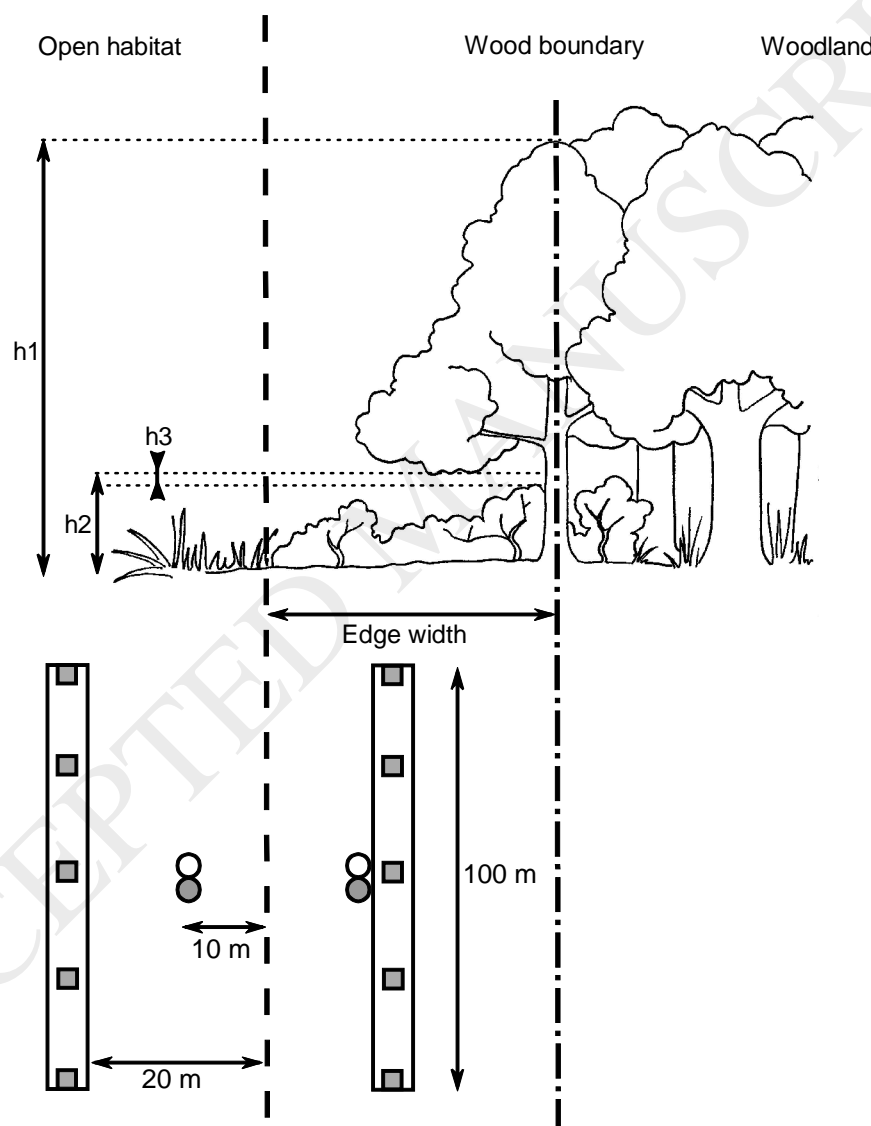
Fig. 3. Alpha diversity profiles for plants, bees and butterflies in each region (A: Aquitaine, C: Centre, MP: Midi-Pyrénées), according to the order of diversity, q. When q = 0 alpha diversity = species richness; when q = 1 alpha diversity = exponential of Shannon Index (e^H) and when q = 2 alpha diversity = Simpson's Reciprocal Index. Alpha diversity profiles were shown for edge (dotted line) and adjacent habitat (solid line) in each edge contrast type. OSR = oilseed rape.

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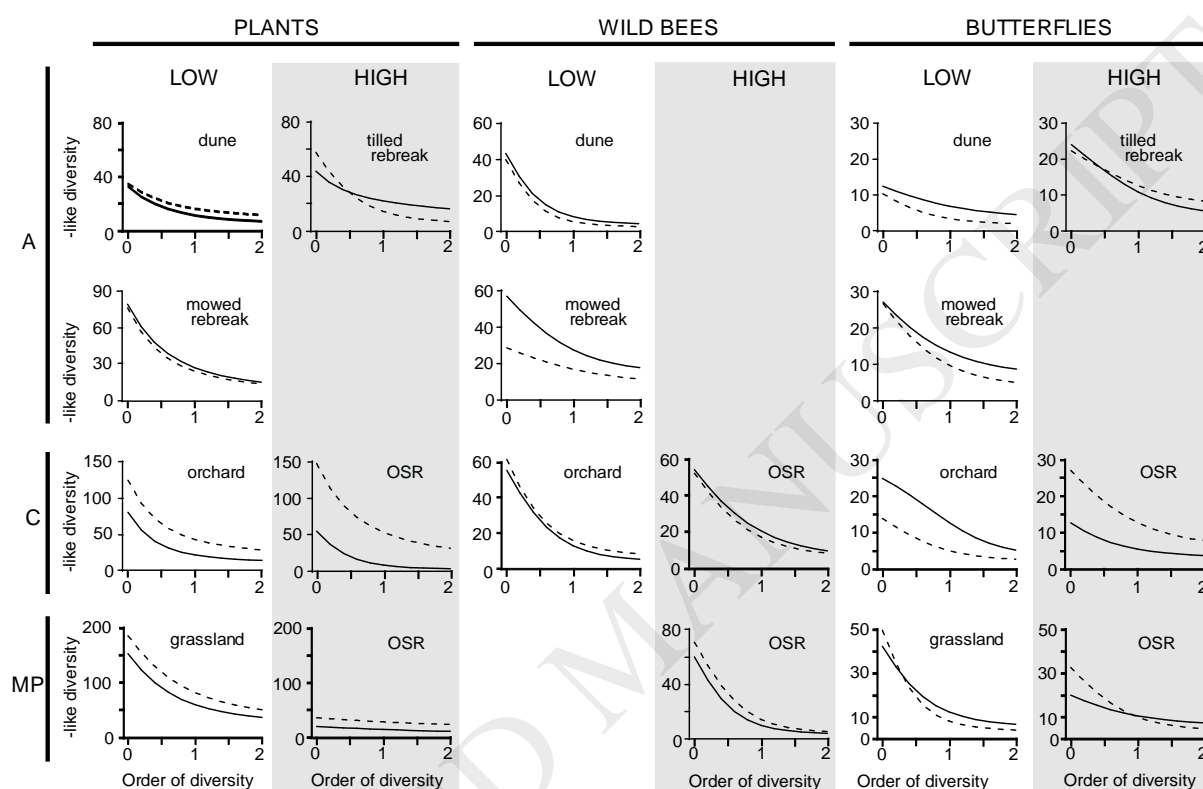
Fig. 4. Barplots of the coefficients of linear models between the Bray-Curtis dissimilarity index and the adjacent habitat type (dunes, mowed firebreak, tilled firebreak, orchard, oilseed rape crops - OSR - , and grassland) for (A) plants, (B) bees and (C) butterflies in each region (Aquitaine, Centre, Midi-Pyrénées). Empty bars correspond with low-contrast edges, and hatched bars with high-contrast edges. The significance of the differences between Bray-Curtis indices were calculated for each region and taxa independently, different letters indicate significant differences at $p < 0.05$.
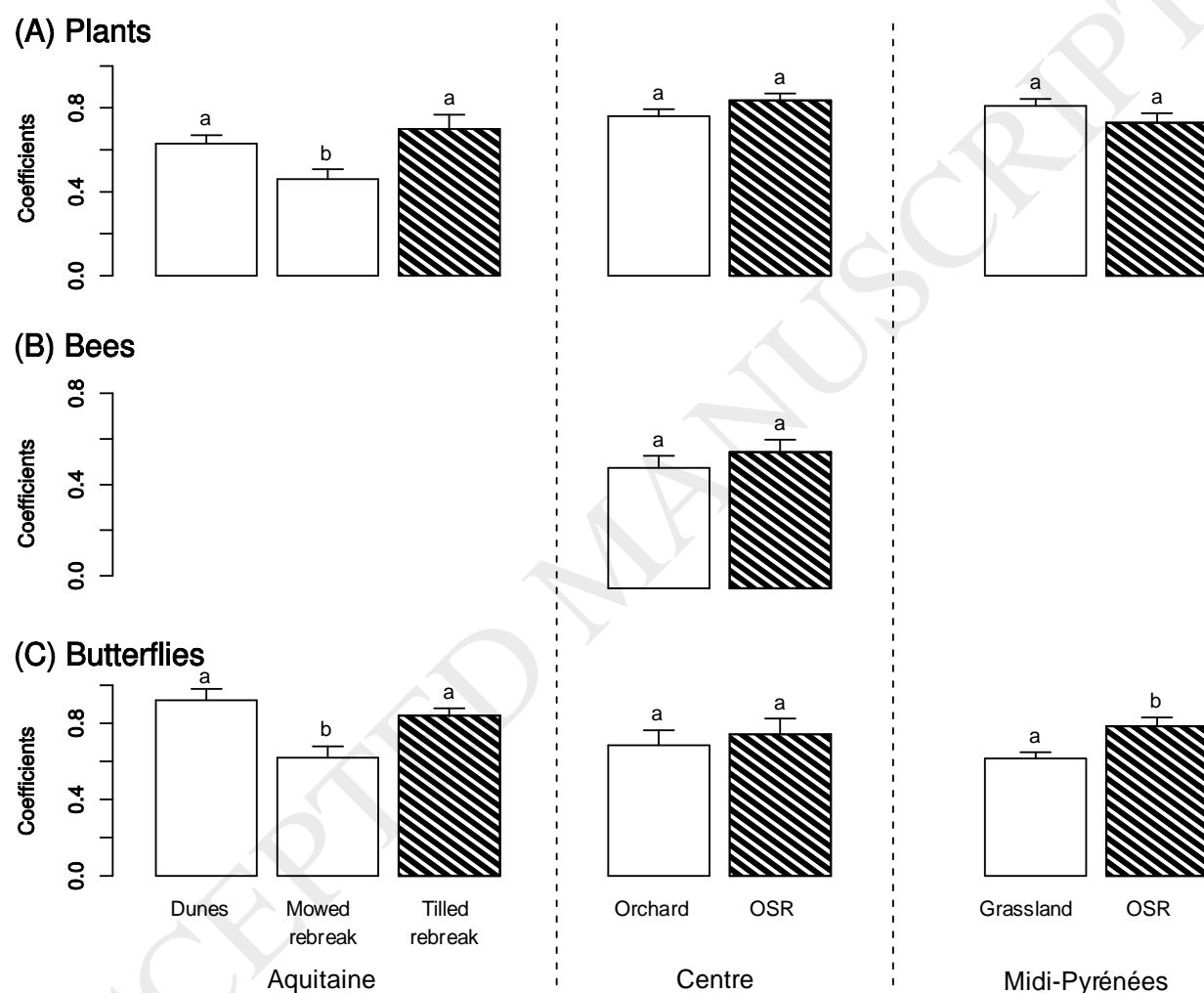
Fig. 5. Proportion of species found uniquely in edge (black bars), in adjacent habitat (empty bars) or shared between edge and adjacent habitat (hatched bars), for (A) plants, (B) bees and (C) butterflies in each region (A: Aquitaine, C: Centre, MP: Midi-Pyrénées).

(A) Plants

(B) Bees

(C) Butter ies

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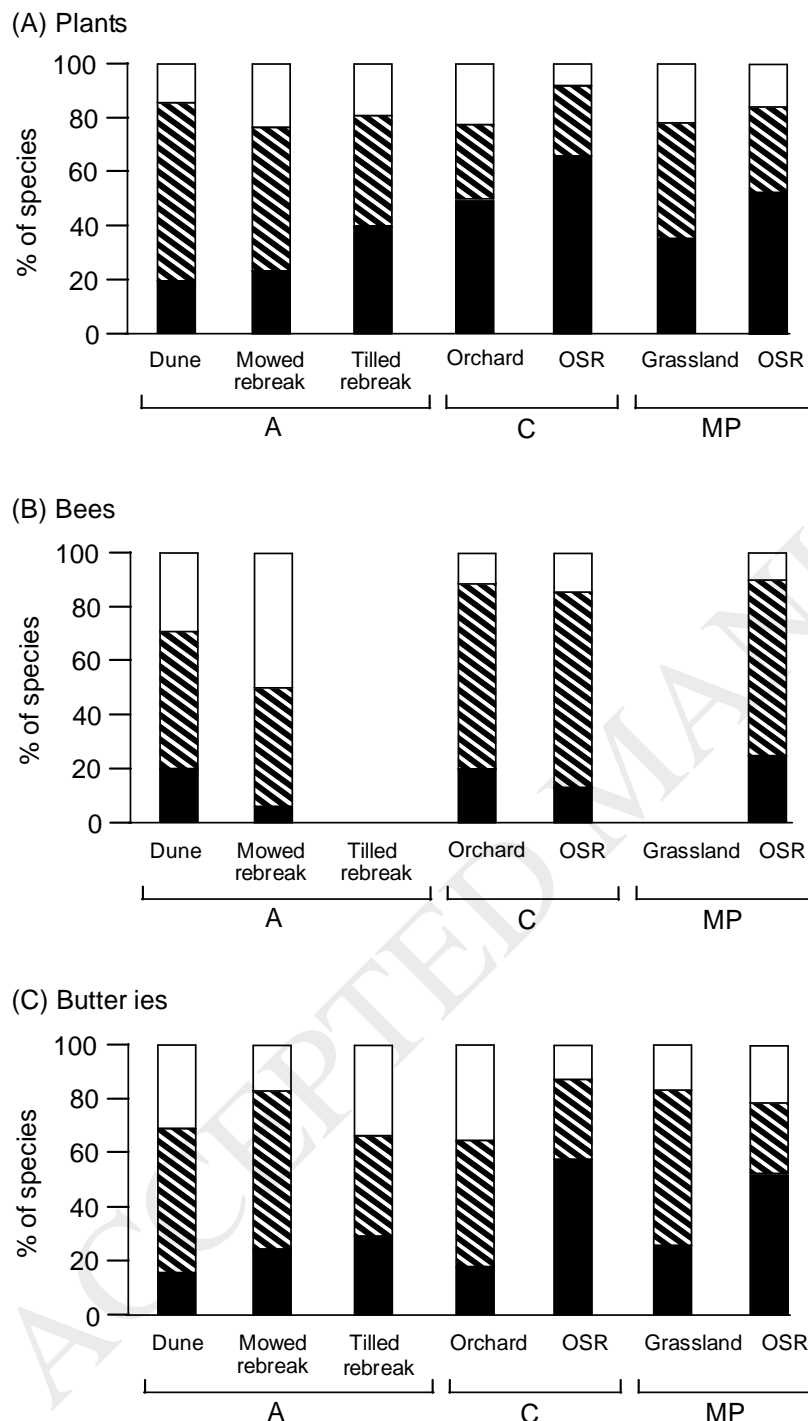
Fig. 6. Plots of significant effects in linear mixed models for (A) bees and (B) butterflies. Solid line represents the linear fitting, dotted curve is a smoothing curve, and grey zone is the confidence interval of the linear fitting (A: Aquitaine, C: Centre, MP: Midi-Pyrénées).

(A) Bees

(B) Butterflies

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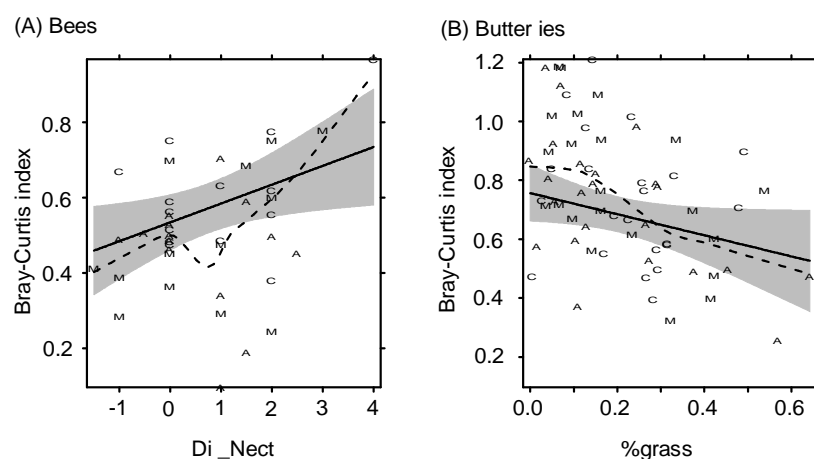
Table 1. Description of selected forest edges and sample size for each taxonomic group and region (A: Aquitaine, C: Centre, MP: Midi-Pyrénées).

Region	Forest type	Adjacent habitat	Contrast	Anthropic disturbance	Edge sample size		
					Plants	Bees	Butterflies
A	Conifer plantation	Dunes	Low	No disturbance	16	6	15
		Mowed firebreaks	Low	Mowing	4	6	8
		Tilled firebreaks	High	Tillage	8	0	9
C	Deciduous forests, coppiced	Orchards	Low	Perennial crop with pesticide	11	11	11
		Oilseed rape crops	High	Conventional farming with tillage, chemical fertilizers and pesticide	10	10	10
MP	Deciduous forests, coppiced	Grasslands	Low	Permanent grasslands with mowing and/or grazing	15	0	16
		Oilseed rape crops	High	Conventional farming with tillage, chemical fertilizers and pesticide	8	10	8

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Table 2. Mean and standard error of explanatory variables used in the multi-inference models to explain plant, bee and butterfly beta diversities. % of grassland, % of woods and Woody linear edge were calculated on a buffer of 500m radius centered on the butterfly and plant transects. The other variables characterized the edge (h1, h2, h3 and width, see Fig. 2) and the difference in plant communities between the edge and adjacent open habitat (Beta_Flora: plant beta diversity for all plant species between the edge and the paired adjacent habita , Diff_Nect: difference in the flower cover between edge and adjacent habitat).

	Aquitaine		Centre		Midi-Pyrénées		All landscapes	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
% grass	17.9	2.7	15.1	2.5	29.9	2.7	20.6	1.7
% wood	57.4	3.2	36.0	4.2	28.2	2.5	42.0	2.4
Woody edges (m)	4959	297	6034	549	8055	411	6227	267
h1 (m)	12.2	0.53	18.2	0.70	17.5	0.90	15.6	0.50
h2 (m)	6.0	0.31	6.2	0.92	3.2	0.27	5.3	0.33
h3 (m)	3.13	0.37	0.81	0.32	1.06	0.25	1.9	0.24
Width (m)	20.6	4.4	7.62	0.61	5.04	0.54	12.1	1.99
Diff_Nect	1.20	0.24	1.24	0.28	0.33	0.13	0.94	0.14
Beta_Flora	0.49	0.03	0.80	0.02	0.73	0.07	0.70	0.03

Table 3. Model-averaged coefficients for beta diversity: a) plants, b) bees and c) butterflies. In bold, significant values at p < 0.05.

	Estimate	SE	t-value	p-value
a) Plants				
Intercept	0.81	0.03	32.40	
Woody edge	-0.03	0.02	-1.77	0.077
%forest	0.04	0.02	1.82	0.069
%grass	0.01	0.02	0.25	0.805
h1	0.04	0.02	2.03	**0.043**
h2	-0.00	0.02	-0.01	0.985
h3	0.05	0.02	2.05	**0.040**
Width	0.01	0.02	0.30	0.766
b) Bees				
Intercept	0.57	0.03	17.81	
Woody edge	0.01	0.03	0.21	0.835
%forest	0.05	0.03	1.77	0.076
%grass	-0.01	0.03	-0.36	0.719
h1	-0.04	0.03	-1.09	0.274
h2	0.01	0.03	0.38	0.704
h3	0.04	0.03	1.25	0.213
Width	-0.04	0.03	-1.26	0.208
Diff_nect	**0.06**	**0.02**	**2.37**	**0.017**
Beta_flora	-0.01	0.03	-0.47	0.624
c) Butterflies				
Intercept	0.68	0.03	22.79	
Woody edge	0.02	0.02	0.65	0.512
%forest	-0.01	0.02	-0.67	0.503
%grass	**-0.05**	**0.03**	**-1.96**	**0.049**
h1	0.05	0.03	0.67	0.095
h2	-0.05	0.03	-1.95	**0.050**
h3	0.05	0.03	1.83	0.066
Width	-0.04	0.03	-1.34	0.179
Diff_nect	0.02	0.02	0.70	0.481
Beta_flora	0.00	0.03	0.13	0.896

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