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Woodland habitat quality prevails over fragmentation for shaping butterfly diversity in deciduous forest remnants

Inge van Halder [a,b,*], Jean-Yves Barnagaud [a,b,c,d], Hervé Jactel [a,b], Luc Barbaro [a,b]

[a] INRA, BIOGECO, UMR 1202, F-33610 Cestas, France
[b] Univ. Bordeaux, BIOGECO, UMR 1202, F-33600 Pessac, France
[c] Ecoinformatics and Biodiversity, Department of Biosciences, Aarhus University, 8000 Aarhus, Denmark
[d] CEFE UMR 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, Vertebrate Ecology and Biogeography, 1919 route de Mende, 34293 Montpellier, France

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ABSTRACT

The effects of forest fragmentation on biodiversity can be partitioned into habitat loss and increased isolation of habitat fragments. Habitat quality may however prevail over the effects of fragment area and isolation, especially for mobile animals such as butterflies. To test this hypothesis we surveyed butterfly communities in 36 deciduous forest fragments embedded in a conifer plantation matrix, along two orthogonal gradients of fragment area and isolation. We also sampled eight deciduous riparian forests to compare the complete pool of forest butterflies, expected to be found in riparian forests, to the composition of deciduous fragments. We quantified the effects of deciduous woodland area, isolation and quality on total and forest butterfly richness, community composition and several Community-Weighted Mean traits known to mediate butterfly responses to habitat fragmentation. For the 36 fragments, forest butterfly richness and community composition were not affected by fragment area or isolation but by habitat quality, especially host-plant composition. Riparian forests had higher forest butterfly richness and hosted more habitat specialists, with higher sensitivity to temperature extremes, than deciduous forest remnants. We thus provide new evidence that habitat quality can prevail over fragment area and isolation in shaping the composition of butterfly communities in mosaic landscapes.

1. Introduction

Habitat loss and isolation have been identified among the main drivers of biodiversity decline in a wide array of ecosystems worldwide. The landmark theoretical frameworks of island biogeography (MacArthur and Wilson, 1967) and metapopulation ecology (Hanski, 1999) accordingly predict lower species richness in small, isolated fragments of habitat than in large, connected ones. Population sizes in small habitat fragments are lower compared to large fragments, and are therefore subject to higher extinction risks due to demographic, environmental and genetic stochasticity (Hanski, 1998). Furthermore, isolated and small fragments receive few immigrants from the surrounding landscape, thereby decreasing the rescue of small populations or the colonization of empty fragments.

Recent reviews summarized the relative influence of habitat area and isolation as determinants of species richness and occurrence patterns (Ewers and Didham, 2006; Öckinger et al., 2010; Prugh et al., 2008). In general, increasing fragment area and connectivity have a positive effect on species richness, but the relationship is not as straightforward as expected (Ewers and Didham, 2006). For instance, a meta-analysis showed that fragment area and isolation explained only 25% of the deviance in 785 animal species occupancy patterns (Prugh et al., 2008). In addition to fragment area and isolation, patch-level factors such as edge length, habitat quality and heterogeneity, as well as surrounding matrix attributes are known to have a significant effect on species occurrence and population size (Börschig et al., 2013; Jonsson et al., 2009; Perović et al., 2015; Prevedello and Vieira, 2010; Prugh et al., 2008; Tscharntke et al., 2002).

Responses to habitat loss and isolation are species-specific, depending on species ecological niches and life-history traits (Ewers and Didham, 2006; Steffan-Dewenter and Tscharntke, 2000). Dispersal capacity, niche breadth and reproductive potential are key determinants of species persistence in fragmented landscapes (Ewers and Didham, 2006). High dispersal capacity favors movements between distant habitat fragments, and is therefore

* Corresponding author at: INRA, BIOGECO, UMR 1202, F-33610 Cestas, France.
E-mail address: Inge.VanHalder@pierroton.inra.fr (I. van Halder).

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critical for the persistence of small or sink populations. Mobile species are thus expected to be less sensitive to habitat fragmentation, although species with intermediate or high dispersal capacities are sometimes more vulnerable than sedentary species (Ewers and Didham, 2006; Samways and Lu, 2007; Thomas, 2000). Species with broad ecological niches (generalists) usually perform better within fragmented landscapes than specialists, due to their capacity to cope with more diverse trophic resources (Steffan-Dewenter and Tscharntke, 2000) and less stringent habitat requirements. High reproductive potential also allows species recovering more quickly from low population levels and enhances colonization through higher number of emigrants and rapid population growth (Fahrig, 2001; Vance et al., 2003). Larger-bodied species may experience higher extinction risk in fragmented landscapes than smaller-bodied species due to the indirect effects of population size, growth rate, competitive exclusion and greater resource and area requirements (Brown, 2007; Henle et al., 2004; Pe'er et al., 2014). Baguette and Stevens (2013) showed that butterfly wing size, a proxy for body size, is positively related to minimum area requirements for butterflies. Wing size is also positively, although weakly, correlated with mobility (Stevens et al., 2013) and the positive relationship between body size and fragmentation sensitivity is not universal (Barbaro and van Halder, 2009; Henle et al., 2004). Because of these trait-related species-specific responses to habitat fragmentation, small isolated habitat fragments will not only contain less species but also a functionally different community than large, connected ones (Öckinger et al., 2010; Perović et al., 2015).

Loss of natural and semi-natural forests represents a major cause of biodiversity decline worldwide (Brockerhoff et al., 2008). Forests harbor between 50% and 90% of Earth's terrestrial species (World Resources Institute et al., 1992) and deforestation and changes in forest management are significant drivers of species loss (Baillie et al., 2004; van Swaay et al., 2006). The extent of forest biodiversity decline does not only depend on the area and quality of the remaining forest fragments but also on the landscape context. Plantation forests often harbor less biodiversity than semi-natural forests but more than agricultural crops and they represent a higher-quality matrix than croplands for forest species able to use them as a compensatory habitat. Afforestation of agricultural land with forest plantations can therefore provide complementary resources and improve connectivity between semi-natural forests (Brockerhoff et al., 2008).

Here, we focused on butterfly diversity in deciduous forest fragments within a matrix of conifer plantations. Although butterflies are iconic species for nature conservation they are rarely studied in temperate forest ecosystems and we are lacking information on the effect of forest management and landscape planning on the dynamics of forest butterfly communities. We also used butterflies as a model because they are known to be sensitive to habitat fragmentation (Öckinger et al., 2010), their life-history traits are consistently documented (Bink, 1992) and they form distinct assemblages in conifer plantation vs. deciduous forests in the study area (van Halder et al., 2008).

We investigated the effects of fragment area, isolation and habitat quality on the taxonomic and functional composition of butterfly communities in native deciduous forest fragments embedded within a pine plantation matrix. We further sampled within the same region butterfly communities in eight deciduous riparian forests in which we expected to find the complete forest species pool of the study area, as we hypothesized that even the largest fragments may not contain all local forest species. We specifically tested the following predictions:

(i) The diversity of forest butterflies increases with deciduous forest fragment area, connectivity and quality.
(ii) Butterfly communities of small, isolated forest fragments are characterized by mobile species with generalist habitat and dietary requirements, small wing size and high reproduction rates.
(iii) Riparian forests harbor a higher species richness than fragments, and their taxonomic and functional community composition differ from fragments, with more habitat- and dietary-specialized, sedentary species, with large wing size and low reproduction rates.

2. Material and methods

2.1. Study sites

The study sites were located in the Landes de Gascogne forest in south-western France, an area of 10,000 km^2 dominated by plantations of native maritime pine (*Pinus pinaster*). The region is covered by nutrient poor, acid podzol soils with a pH of 3.5–5.5, has a thermo-atlantic climate and low elevation (c. 50 m a.s.l.). The landscape is dominated by even-aged pure maritime pine stands with a rotation cycle of 40–50 years forming a mosaic of herbaceous and shrubby clearcuts and firebreaks, and young, mid-class and older pine stands. These pine stands are interspersed by sandy tracks bordered by a herbaceous vegetation (see van Halder et al. (2008) for details). Within this pine plantation matrix, deciduous forest remnants occur as scattered fragments or as continuous riparian forests. These deciduous woodlands are dominated by *Quercus robur*, which coexists with *Q. pyrenaica* in drier sites and with *Alnus glutinosa* in more humid sites.

We selected 36 deciduous woodland fragments along two orthogonal gradients of fragment area (14 fragments of 0.3–2 ha, 12 fragments of 2–5 ha and 10 fragments of 5–12 ha) and deciduous woodland cover around each sampled fragment (varying from 0 to 6 ha in a buffer of 500 m around each fragment and from 0 to 23 ha in a buffer of 1000 m). Sampling a larger range of forest fragment sizes was impeded by the absence of deciduous fragments larger than 12 ha in the study area. For many butterfly species minimum area requirements for populations are in a range of 0.5–20 ha, but some species require larger areas (Bink, 1992; Warren, 1992). Sites were selected to ensure that the area of the sampled fragment and the quantity of deciduous woodlands in the landscape buffer were not correlated (Pearson's $r = -0.04$, $P = 0.80$ and $r = -0.10$, $P = 0.55$ for buffers of 500 m and 1000 m respectively). We additionally sampled eight deciduous riparian forests located in the same area as the fragments and used them as the reference habitat where we expected to find the entire species pool of woodland-butterflies of the study area. Riparian forests not only have a larger area than fragments, but also differ in some extent in vegetation composition, and therefore in habitat quality.

2.2. Butterfly sampling

Butterflies were sampled along transects of 50 m long and 5 m wide, following Pollard and Yates's method (1995). The number of transects was adjusted to account for the fact that larger fragments and riparian forests are more heterogeneous than small fragments in terms of habitat composition. Hence, we set up from 5 transects for the smallest fragment of 0.3 ha to 25 transects for the fragment of 12 ha and the riparian forests. We captured intra-site habitat heterogeneity by spreading transects across the diversity of local vegetation structures encountered at each site, including closed canopy cover, gaps, small tracks and forest edges. Butterflies were counted in each transect by a single trained observer (IVH), four times between May 11th and August 18th 2005 (Loos et al., 2015). For analyses, the number of individuals per species were