Conservation of butterfly communities in mosaic forest landscapes : effects of habitat quality, diversity and fragmentation

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Par Inge VAN HALDER

Conservation des communautés de papillons de jour dans les paysages forestiers hétérogènes :

effets de la qualité, de la diversité et de la fragmentation des habitats

Sous la direction de : Hervé JACTEL
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Soutenue le 6 janvier 2017

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Contenu

1. Introduction

Lycaena tityrus

1.1. Global biodiversity loss

There is a general awareness that we are facing an important, unseen worldwide loss of biodiversity. The current rates of species' extinctions are estimated to be 1000 times the likely background rate of extinctions and are projected to continue or to accelerate (Millennium Ecosystem Assessment, 2005). The International Union for Conservation of Nature (IUCN) has assessed to date the status of 71.576, mostly terrestrial and freshwater species in its Red Lists of Threatened Species. Among them 860 are extinct and 21.286 are threatened, with 4.286 considered critically endangered (Pimm et al., 2014). However, the number of assessed species represents for many groups only a few percent of the total number of described species. For vertebrates 62% of described species have currently been evaluated, but for flowering plants only 7% and for insects only 0.6% (IUCN, 2015). Furthermore, these figures concern only global extinctions and threat status and not the local decrease in species abundances. It is estimated that more than 50% of species are declining due to human activities (McKinney and Lockwood, 1999). For example, 70% of birds are thought to be declining in range or abundance worldwide, while in the UK 70% of bees, wasps and ants and 74% of butterflies are declining (McKinney and Lockwood, 1999).

These species declines affect also community composition and may cause important impacts on many ecosystem functions and services (Newbold et al., 2015). Indeed, beside moral, aesthetic and cultural arguments, the maintenance of ecosystem functioning is a major justification to limit biodiversity loss. Biodiversity affects, through the associated **ecosystem services,** human well-being directly and indirectly. These services include provisioning services (e.g. food, water, timber and fiber); regulating services (e.g. regulation of climate, floods, diseases, wastes and water quality); cultural services (e.g. recreation, aesthetic enjoyment) and supporting services (e.g. soil formation, photosynthesis and nutrient cycling) (Millennium Ecosystem Assessment, 2005). The loss of biodiversity is thus very likely to affect one or more of these ecosystem services.

Species most vulnerable to extinctions are rare species, i.e. species with few individuals and a limited distribution. It has been assumed that these species, because of their low numbers, play a limited role for ecosystem services. However, they often have unique combinations of functional traits and thus increase disproportionately the functional diversity of communities and the potential associated services (Mouillot et al., 2013a). Another consequence of species loss is the worldwide decline of specialist species leading to a large-scale biotic homogenization (Clavel et al., 2010; McKinney and Lockwood, 1999). Biotic homogenization often replaces unique endemic species by widespread species. Winners are species that not only do not decline, but also expand their ranges, such as invasive species. Winners and losers can also be characterized by certain trait combinations; winners have traits associated with rapid range expansion, like small size, high fecundity, rapid dispersal and are generalists (McKinney and Lockwood, 1999). Biotic homogenization does therefore not only lead to a taxonomic homogenization, but also to a functional homogenization with a decrease in functional diversity of communities (Devictor et al., 2008).

The most important **drivers of biodiversity loss** are habitat loss, degradation and fragmentation, climate change, invasive exotic species and overexploitation (Didham et al., 2012; Millennium Ecosystem Assessment, 2005; Newbold et al., 2015; Pimm et al., 2014). In this manuscript we focus on the effects of land-use changes including habitat loss, degradation and isolation on biodiversity patterns, because these are likely the main causes of present biodiversity losses in terrestrial ecosystems of Europe and are main drivers of species occurrence patterns.

Land-use type and land-use intensity have a strong effect on local species richness and abundance as demonstrated by Newbold et al. (2015) in a recent, worldwide meta-analysis. The authors estimated a global, average reduction in local species richness of 13.6% compared to richness in primary vegetation, but with strong differences between land-uses and land-use intensities (Figure 1).

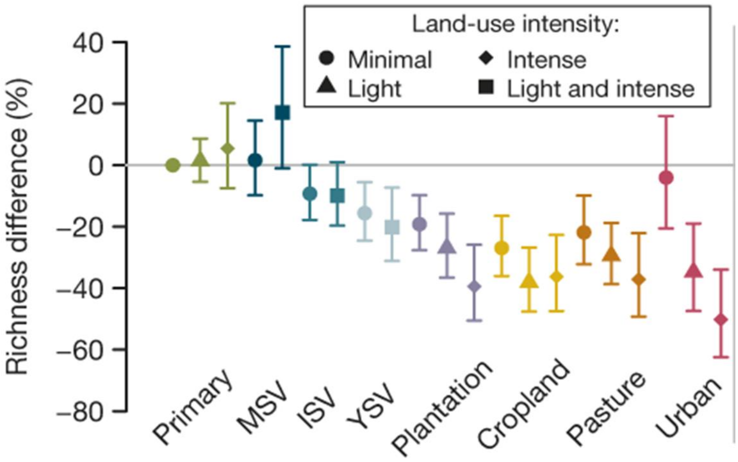

Figure 1. Differences in richness (%) for land uses and land-use intensities based on an analysis of data from 284 publications including 26.953 species. Primary – primary vegetation; MSV - mature secondary vegetation; ISV - intermediate secondary vegetation; YSV - young secondary vegetation; Plantation - plantation forest; Land-use intensity is categorized as minimal (circle), light (triangle), intense (diamond) or combined light and intense (square), error bars show 95% confidence intervals (Newbold et al., 2015).

Most actions that have been undertaken to conserve biodiversity have been partly successful. These actions include activities with a primary objective of conservation, such as the set aside of protected areas, species protection measures, ecosystem restoration or actions based on the sustainable use of ecosystems, including the payment for biodiversity-based ecosystem services and management practices considering biodiversity conservation (Millennium Ecosystem Assessment, 2005). However, many of these actions are not sufficient and other important indirect and direct drivers of biodiversity change have to be addressed. For example the conservation of biodiversity in protected areas is threatened by climate change and demands global actions to limit its negative effect. Similarly, the management of ecosystem services cannot be sustainable globally if the growth in consumption continues at the same rate (Millennium Ecosystem Assessment, 2005).

To maintain or restore biodiversity at a more local scale, we first have to identify the key mechanisms that drive species diversity and community composition at this scale and propose adequate conservation measures.

1.2. From the patch to the landscape level

Each species needs specific abiotic and biotic conditions and resources. Hutchinson (1957) defined this combination of *n* environmental requirements as the **fundamental niche** of a species, that can be seen as an "*n*-dimensional hypervolume". Every point within this hypervolume allows species existence. In reality, species will only occupy a part of this niche, the **realized niche**, because of direct and indirect interactions with other species at the same or different trophic levels (Hutchinson, 1957; Lortie et al., 2004). The species niche can be separated in the Grinnelian and Eltonian niche. The Grinnellian niche describes the response of a species to resources, while the Eltonian niche focuses on the impact of the species on its environment (functional niche) (Devictor et al., 2010). Ecological specialization (specialist vs. generalist species) is closely linked to the niche concept, as specialization can be defined as a restricted ecological niche breath (Devictor et al., 2010).

The species' niche can thus be seen as a summary of its requirements and tolerances, whereas the **habitat** refers the place where it lives (Begon et al., 2009). There are many definitions of habitat (Dennis et al., 2003; Hall et al., 1997). Hall et al. (1997) defined habitat "*as the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism. Habitat is thus organism specific*". Dennis and Shreeve (1996) included a spatial element in their definition by incorporating species movement: "*habitat is a zone (area) comprising a set of resources, consumables and utilities, for the maintenance of an organism. The resources occur in union and/or intersect and may also be equivalent; links between resource outlets are established by individual searching movements of the organism*". The different resources needed by a species are thus not necessary found at the same place, which complicates the delimitation of the habitat. Dennis et al. (2003) further developed this habitat model based on resource distribution and individual movements, using butterflies as a model (see Figure 2). When resources are spatially distinct, this model shows similarities with the landscape complementation and supplementation model developed by Dunning (1992), corresponding to the use of patches with non-substitutable or substitutable resources, respectively and ultimately leads to the concept of multi-habitat species. These models indicate that the habitat scale should be extended beyond the patch scale.

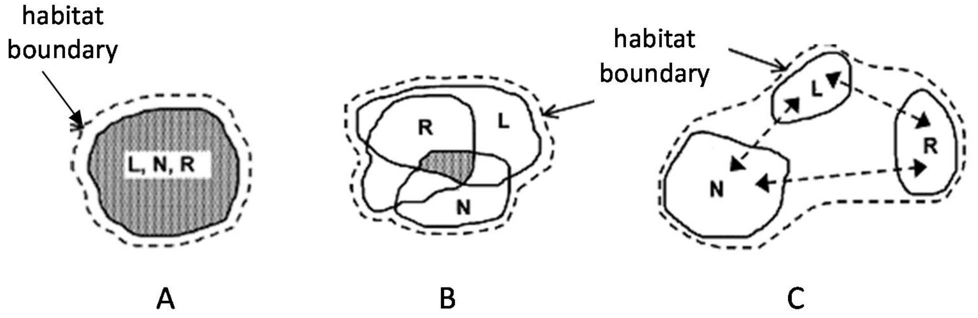

Figure 2. The habitat model based on resource distributions and individual movements. The combination of resources gives a habitat. For simplicity only three resouces are illustrated, using butterflies as a model: N - nectar, L - larval host-plants, R - roost sites. In A all resoucres are found within the same area; in B resoucres are partly seperated but overlapping in the centre, limited movements are necessary to acces different resources; in C resources appear in seperated patches necessitating movements between these patches. Habitat boundaries are easier to identify in A and B than in C (adapted from Dennis et al. (2003)).

The necessity to enlarge the spatial scale is also evident if local population dynamics are considered. Numbers of individuals in a population are governed by four processes: births, deaths, immigration and emigration and population growth or decline is the outcome of these four processes. This indicates that not only local processes count for population survival, but also landscape processes (immigration and emigration), as clearly demonstrated by metapopulation models (Hanski, 1999).

These different concepts highlight thus the necessity to enlarge the patch scale to a larger, landscape scale. Species' presence and abundance are affected by complex, interacting processes at different spatial scales and it is generally accepted that multi-scales approaches are necessary to understand species distribution patterns. Methods and concepts of community ecology should therefore be combined with those of landscape ecology to understand species distribution patterns and community composition.

1.3. Concepts in landscape ecology

A landscape can be defined as a portion of land. It is spatially heterogeneous in at least one factor of interest, and has a spatial extent from several square meters to kilometers (Turner et al., 2001). Landscapes can be characterized by their organization, heterogeneity, diversity and dynamics (Burel and Baudry, 1999). Landscape size to be studied depends on the species or communities of interest and will occupy a spatial extent between an organisms home range and its regional distribution (Dunning et al., 1992; Jackson and Fahrig, 2012).

Landscape ecology focuses on the interactions between spatial patterns and ecological processes, that is, the causes and consequences of spatial heterogeneity across a range of scales. Landscape ecology thus explicitly addresses the importance of spatial configuration for ecological processes, i.e. the effects of spatial arrangement of landscape components. The study of landscape level patterns and processes forms thus a bridge between within patch studies in population and community ecology and continent wide, macro-ecology studies (Dunning et al., 1992; Tscharntke et al., 2012).

1.3.1. Starting point: the Island Biogeography Theory

The basis of several landscape ecological theories is formed by MacArthur and Wilson's (1967) **Island Biogeography Theory** (IBT). In IBT the number of species on an island is determined by the balance between the colonization rate of species from a species pool on the mainland and the local extinction rate of species on the island. Colonization and extinction rates vary with island size and isolation, leading to higher species richness on large islands close to the mainland.

IBT shows similarities with **metapopulation models** (Hanski, 1999; Levins, 1969), by highlighting the importance of colonizations and extinctions for species survival. IBT leaded also to many studies on **Species-Area-Relationships (SARSs)**, based at first on real islands but rapidly transposed to terrestrial ecosystems with islands represented as **habitat fragments in a hostile matrix**, leading to different SAR-approaches and to a huge number of studies on the effects of **habitat fragmentation** on species richness (Haila, 2002).

These concepts differ in their objectives and focus. IBT and SARs deal with species richness, many fragmentation studies analyze species richness or species occurrences, while metapopulation models focus on individual species by analyzing their presence or population dynamics. These concepts also differ in their vision of the landscape: only habitat patches may be considered while the surrounding landscape composition is ignored (IBT, SAR, metapopulation models). Alternatively, the complex structure of the landscape can be taken into account, as for example in more recent fragmentation studies and in the **landscape mosaic concept** (Duelli, 1992).

In **IBT** all species are equal, habitat islands only differ in size and isolation and are separated by an inhospitable ocean. Since the 1980's on, these ideas were questioned for terrestrial systems and the effects of a heterogeneous matrix, of non-uniform habitat fragments and of species traits were gradually included in different concepts, for example in fragmentation studies (Haila, 2002). Likewise metapopulation models became more realistic by including local population dynamics, habitat size and quality and functional connectivity (Baguette and Mennechez, 2004).

1.3.2. Metapopulation models

Levins described in his **classical metapopulation** concept (1970), a metapopulation as a 'population' consisting of many local populations. All local populations have a substantial probability of extinction and a species can only persist at the regional i.e. metapopulation level (Hanski, 1999). Like IBT, Levins' model is based on extinctions and recolonizations and has simplified assumptions: all patches are identical in area and quality and have no explicit spatial location; patches are either occupied or empty (Hanski, 1999). Later on, in **structured metapoplulation models**, local population dynamics were included in spatially explicit habitat patches differing in habitat quality. These models differ however from concepts of landscape ecology in that they do not consider the different effects of surrounding landscape composition and configuration.

Despite the simplicity of the first, classical metapopulation model, it had a high importance for our conceptual perception of the landscape by highlighting the importance of movement of individuals between local populations, and by underlining that the landscape scale matters for population dynamics (Baguette, 2004). Metapopulation theory emphasized the importance of landscape connectivity for species conservation and stimulated the implementation of corridors and stepping stones in landscape management. Metapopulation models have also advanced our understanding of population dynamics at the landscape scale, for example by calculating the metapopulation capacity of a landscape, which determines the survival probability of a species in a landscape. A species is predicted to survive if the metapopulation capacity of the landscape is greater than a species-specific threshold value (Hanski and Ovaskainen, 2000). Metapopulation models differ in their concepts and complexity, and in the way spatial configuration is taken into account. Figure 3 illustrates some types of metapopulation models.

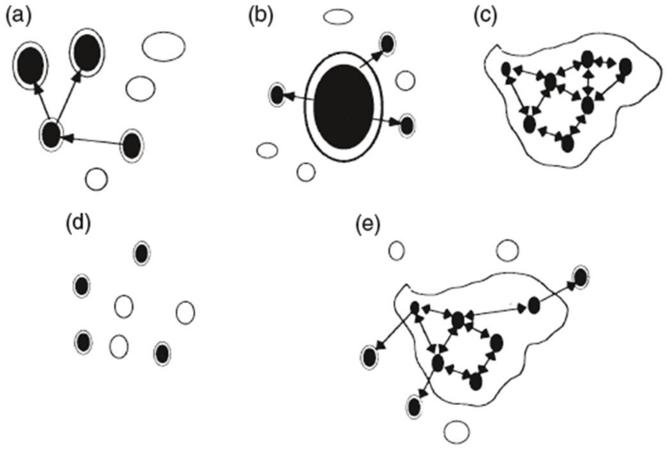

Figure 3. Different types of metapopulation models. Filled circles- occupied, unfilled – vacant sites. Lines indicates the boundary of a population. Arrows indicate migration. (a) Levins metapopulation model, (b) core-satelite metapopulation model, (c) patchy population model, (d) non-equilibrium metapopulation model, (e) a combination of c and b (Harrison, 1991).

1.3.3. Species-Area Relationships and the SLOSS-discussion

The IBT concept that species richness increases with island size led to many ecological and theoretical studies on **Species-Area Relationships (SARs)**. The two main ecological processes leading to SARs are higher population survival due to increasing population size with increasing 'island' area (the IBT idea) and increasing habitat heterogeneity in larger 'islands', providing more different niches (Ricklefs and Lovette, 1999; Rybicki and Hanski, 2013). The relative and combined effect of area and heterogeneity depend on the biological traits of the studied taxon. Habitat-diversity effects are likely stronger in taxa with high degrees of habitat specialization and with populations large enough to have a low probability of stochastic extinction (Ricklefs and Lovette, 1999). Different types of SAR models are actually distinguished, based on the way species are sampled and the spatial configuration of the habitat. Spatial configuration can be based on continuous vs. fragmented habitats and the latter can be true or habitat islands, with different aggregation possibilities of the fragments (Rybicki and Hanski, 2013).

Related to the SARs are the discussions on the best strategies to adopt for biodiversity conservation. Given a certain habitat amount, the question is if it is better to have a "Single Large Or Several Small" fragments, the so-called **SLOSS-discussion**. The rule of thumb adapted from the mid-1970s was that, based on IBT, one large reserve will conserve more species than several small (Ovaskainen, 2002; Tjorve, 2003). Despite a large number of theoretical and empirical studies the question is still unresolved (Tjørve, 2010). For the same habitat amount, smaller fragments can contain more species than one large fragment of the same total size (see Figure 4), and this effect can be attributed to the greater environmental heterogeneity covered by several small fragments than one large (Tscharntke et al., 2012). The majority of SLOSS-studies concluded that 'Several Small' is the best strategy, but exceptions exist and the results seem to depend on the form of the species-area curve, minimum area requirements, species' mobility and on the level of species nestedness (Tjørve, 2010). Species nestedness occurs when the species of sites with low species richness are subsets of species-rich sites (Wright and Reeves, 1992). A trade-off may exist for distances between patches: a larger distance will reduce species nestedness (thus in favor of SS), but will also diminish species dispersal and thus population survival (thus SL better). The optimal solution will also depend if we want to preserve as many species as possible, or threatened species with large minimum area requirements (Tjørve, 2010).

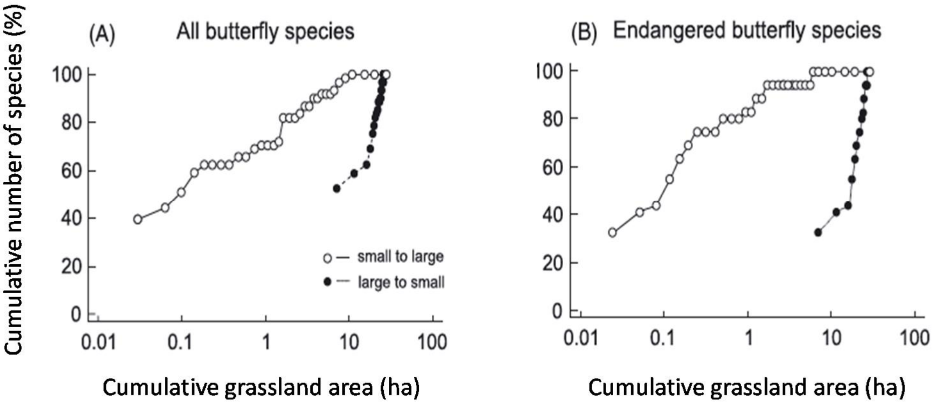

Figure 4. Cumulative number of butterfly species (% of all species) in relation to the cumulative area of calcareous grasslands. Area is cumulated starting from the smallest area and stepwise adding the next smallest (open points) or starting with the largest area stepwise adding the second largest (filled points) for (A) all butterfly species and (B) endangered (red data book) butterfly species (Tscharntke et al., 2002a). For the same total habitat amount, smaller fragments contain thus more species than one or several large fragment of the same total size

1.3.4. Habitat loss and fragmentation

Most authors define **habitat fragmentation** as a landscape-scale process by which habitat loss results in the division of large, continuous habitats into a greater number of smaller patches of lower total area, isolated from each other by a matrix of dissimilar habitats (Didham, 2010; Fahrig, 2003). In contrast with the early SAR concept, the spatial configuration of fragments is explicitly taken into account. Habitat fragmentation is considered one of the most important processes contributing to biodiversity loss and changes in community structure in human-managed landscapes (Didham, 2010). However the concept of habitat fragmentation is ambiguous because it includes both a reduction in area and a change in spatial pattern (Haila, 2002). The process of habitat fragmentation has several effects on habitat pattern: (1) reduction in habitat amount, (2) increase in number of habitat patches, (3) decrease in size of habitat patches, and (4) increase in isolation of patches. The process of habitat loss, however, can result in different, non-linear effects on fragmentation metrics (Figure 5). Moreover, each component of fragmentation may affect differently biodiversity (Fahrig, 2003). Because of these confounding effects between habitat amount and patch size and isolation, Fahrig (2003) recommended a separation between habitat loss and fragmentation *per se,* i.e. the breaking-apart of habitat. These effects can be separated by landscape selecting procedures, e.g. by selecting landscapes with the same habitat amount but with a different spatial pattern (Laurance, 2008), or by appropriate statistical methods. However when fragmentation *per se* is evaluated after the variance due to habitat loss is extracted from the data, the variance explained by both habitat loss and fragmentation is not taken into account, thereby underestimating the fragmentation effect (Didham et al., 2012).

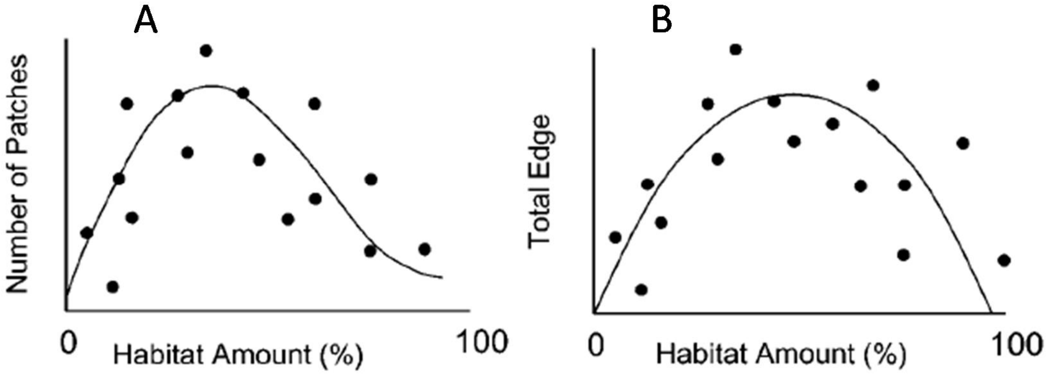

Figure 5. Non-linear relationships between habitat amount and two fragmentation metrics: (A) number of patches and (B) total edge (based on Fahrig (2003)).

In general, habitat loss has been shown to have a strong negative effect on biodiversity, while effects of fragmentation *per se* can be negative or positive and often of lower magnitude (Fahrig, 2003). The, somewhat unexpected, positive effect of habitat fragmentation *per se* may be caused by altered species interactions, asynchronous patch disturbances, positive edge effects, increased immigration, reduced isolation and increased landscape complementation (Dunning et al., 1992; Fahrig, 2003). The literature on habitat fragmentation is huge and several 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), with often a more important effect of area than isolation. In a recent paper Fahrig (2013) states that only landscape habitat amount matters for species richness and that spatial configuration has no or only a very weak effect, a point of view contested by Hanski (2015). He states that habitat fragmentation *per se* may have little effect when the landscape habitat amount is large, but when the remaining habitat cover is low, fragmentation certainly matters as demonstrated by empirical and modelling studies (Hanski, 2015).

The weak overall percentage of variance in species richness or presence explained by habitat loss and isolation in several meta-analyses and reviews may be due to the confounding effect of other factors. In particular, it seems that **habitat quality**, **edge effects** and landscape **matrix attributes** play an important role on species occurrences and population sizes in fragmented landscapes (Börschig et al., 2013; Jonsson et al., 2009; Laurance, 2008; Perović et al., 2015; Petit et al., 2004; Prevedello and Vieira, 2010; Prugh et al., 2008; Tscharntke et al., 2002b).

1.3.5. Habitat quality

Habitat quality can be defined as the ability of the environment to provide conditions appropriate for individual and population persistence (Mortelliti et al., 2010). The deterioration of habitat quality is, with habitat loss and fragmentation, one of the three main processes leading to biodiversity loss (Fischer and Lindenmayer, 2007). The process of habitat degradation can thus lead to a landscape pattern of patches with different quality. The same pattern can however also result from pre-existing differences in environmental heterogeneity (Mortelliti et al., 2010).

Habitat quality can play an important role for species occurrence patterns (Thomas et al., 2001). In low-quality habitats a species may decline, occur at lower densities or may be unable to breed (Fischer and Lindenmayer, 2007; Thomas et al., 2001). These low quality patches can act as an ecological trap or function as sink. An ecological trap is a behavioral phenomenon: it occurs when organisms prefer a habitat which turns out to be less suitable for its further development or that of its offspring than other available habitats (Robertson and Hutto, 2006). Pulliam (1988) considered habitat quality at the base of source-sink dynamics: in high-quality source habitats, births and immigration exceed death and emigration, while in low-quality sink habitats, the opposite applies. Source-sink dynamics thus clearly illustrate the link between local and landscape processes. The effect of habitat quality on population densities also implies that improving habitat quality, may compensate, to a certain level, for habitat loss.

Habitat quality should ideally be measured by its effect on population processes, like reproduction, survival and population growth rate (Mortelliti et al., 2010). However these measurements are complicated and habitat quality is often quantified by measurements of habitat structure or of limiting resources (Figure 6). The latter seem in many cases a good proxy for habitat quality (Mortelliti et al., 2010).

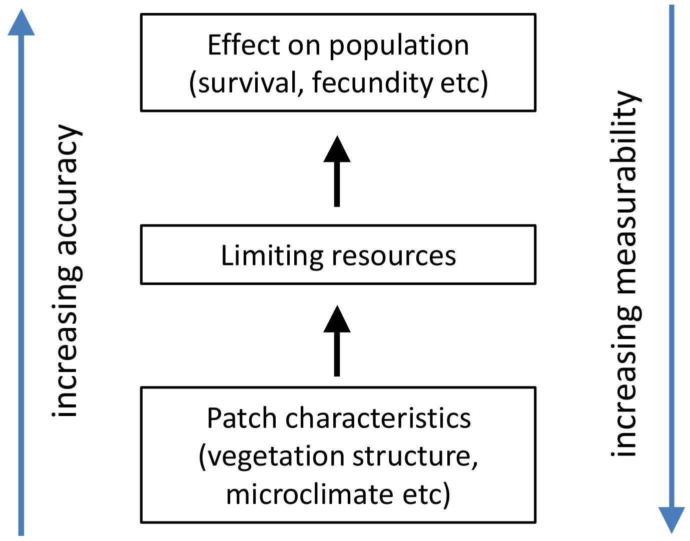

Figure 6. The hierarchical relationship among the different possible levels at which patch quality can be assessed (Mortelliti et al., 2010).

Intra-patch **heterogeneity** can also influence species richness and is considered as one of the possible drivers of the species-area-relationship. Larger patches are generally more heterogeneous than small patches and will thus contain more niches (Huston, 1994; Rybicki and Hanski, 2013), but will also diminish the area of available habitat for each species.

1.3.6. Edge effects

Habitat fragmentation and the consequent reduction of patch size leads to an increased length of edges in landscapes (Fletcher, 2005). As edge effects tend to increase with diminishing fragment size, area and edge effects are often confounded, and many area-related biodiversity losses may be caused by edge effects or by synergistic edge and area effects (Laurance, 2008). Edge effects alter many aspects of the structure, dynamics and species composition of fragmented ecosystems (Laurance, 2008). Species either avoid edges, are more abundant near edges, or show no edge preference (Ewers and Didham, 2006; Ries and Sisk, 2004). Species that specialize on resources found only in interior habitats will avoid edges where habitat quality, predation risk or micro-climate are less favourable (Fletcher, 2005; Lehtinen et al., 2003; Spector and Ayzama, 2003; Stevens and Husband, 1998). In small patches these ‘interior species’ may be negatively affected by the high edge to interior ratio and could, with ongoing fragmentation, become extinct as fragment size further decreases. In contrast, positive edge effects on abundance of individual species have also been reported (Downie et al., 1996; Duelli et al., 2002; Ries et al., 2004). Species richness is often highest at habitat edges and is thought to be caused by three mechanisms: (i) by spill-over of individuals as they disperse into the adjacent non-habitat, leading to an accumulation of species of both habitats near the edge, (ii) by the presence of essential resources at the edge that are rare or absent in adjacent patches, and (iii) by increased access to complementary resources that are located in two adjacent patches (Dunning et al., 1992; Ries and Sisk, 2004).

Species behaviour at edges is also an important factor affecting dispersal through the landscape. For example, edge avoidance behaviour may hinder dispersal between habitat fragments (Haynes and Cronin, 2006; Ries and Debinski, 2001; Schtickzelle and Baguette, 2003), but could improve dispersal along corridors bordered by ‘hostile’ edges (Haddad, 1999; Sutcliffe and Thomas, 1996).

1.3.7. Landscape matrix composition and configuration

Early habitat fragmentation studies were based on the far too simplistic hypothesis that the landscape between habitat fragments, the ‘matrix’, was uniform, non-habitat (Haila, 2002). The matrix is however not uniform, but contains patches of different types (land-uses). The matrix can be characterized by its composition (cover of different patch types) and the spatial configuration of patches. Recent studies have largely acknowledged that matrix composition and configuration can enhance or mitigate the effects of habitat fragmentation on species diversity (Driscoll et al., 2013). Matrix composition next to the patch will change **edge effects** and can also change the microclimate of the habitat patch with possible negative effects on patch-dependent species (Driscoll et al., 2013). Matrix composition and edge contrasts can also influence **dispersal** between habitat patches (Ewers and Didham, 2006; Eycott et al., 2012; Laurance, 2008; Ricketts, 2001). Dispersal is a complex process than can be divided into three distinct stages (emigration, displacement in the matrix and immigration) and each stage is influenced by matrix composition and configuration (Baguette and Van Dyck, 2007, see Figure 7). In general, movement is enhanced by a matrix similar in structure to the species' habitat (Eycott et al., 2012). However, a dissimilar matrix element can also stimulate species to move faster through it, although they are more reluctant to enter it (Kuefler et al., 2010). The degree to which the landscape facilitates or impedes movements among resource patches is defined as 'landscape connectivity'. Connectivity can be measured based on the behavior of dispersing individuals (functional connectivity) or on the structure of the landscape (structural connectivity) (Kindlmann and Burel, 2008).

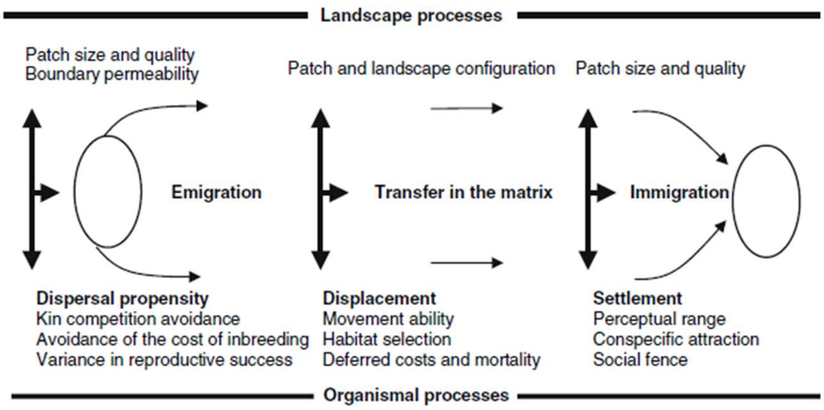

Figure 7. Schematic view of the three stages of dispersal and the interactions between biotic and landscape processes at each stage (Baguette and Van Dyck, 2007).

Species can also find **complementary or supplementary resources** (Figure 8) in the matrix (Dunning et al., 1992), and it is therefore not strictly correct to apply the term 'matrix', as it carries connotations of inhospitable environments (Ewers and Didham, 2006). Moreover, as the matrix is not 'empty', species living in the matrix can also enter habitat fragments and alter species-interactions in the remnant patch.

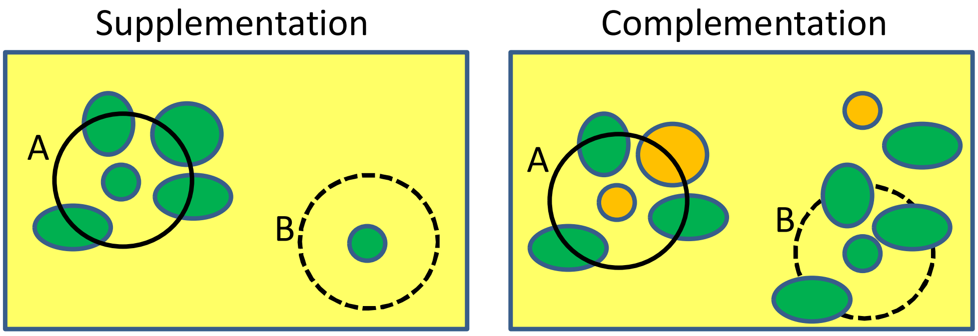

Figure 8. Landscape supplementation and complementation. Supplementation : a species needs resources found in green patches, but each patch is too small for population survival, so it can survive only if more patches are within the dispersal distance of the species. Complementation : a species that needs complementary resources found in different patches (green and orange) will survive when these resources are close to each other (A) not when one habitat is too rare (B), adapted from Dunning et al. (1992).

Driscoll et al. (2013) summarized these different matrix effects into three core effects influencing patch-dependent species: effects on dispersal, effects of resources in the matrix and effects on the abiotic environment in habitat patches. These core effects are in turn modified by five ’dimensions’: spatial variation and spatial scale of the matrix, temporal variation and temporal scale of the matrix, and species adaptation.

1.3.8. From the fragment-matrix concept to a landscape mosaic-concept

The conceptual model formulated by Driscoll et al. (2013) is still based on a patch-matrix model but with a more important and structured role of the matrix. A more holistic vision of the landscape is presented by the **mosaic concept** (Duelli, 1992)**,** where both the composition and configuration of different patches in a landscape are drivers of biodiversity patterns.

Duelli (1992) proposed with his ‘**mosaic concept**’ a landscape model that can predict biodiversity in cultivated landscapes. In this concept, that was presented as an alternative to IBT, biodiversity in a landscape increases with (1) the number of different habitat types, (2) the number of patches and ecotone length (Figure 9) and (3) the area of semi-natural habitats (Duelli, 1997). Landscape composition and configuration do not only have an effect on overall, landscape biodiversity but also on local richness and community composition. Since structurally complex landscapes support more species than simple landscapes, habitat patches in complex landscape will receive more colonists which leads to a higher species richness (Tscharntke et al., 2012). Landscape composition and configuration seem to play an important role in driving biodiversity patterns, through complementation and supplementation, edge effects, species dispersal, species spill-over, patch disturbance dynamics, source-sink dynamics and species interactions (Dunning et al., 1992; Tscharntke et al., 2012).

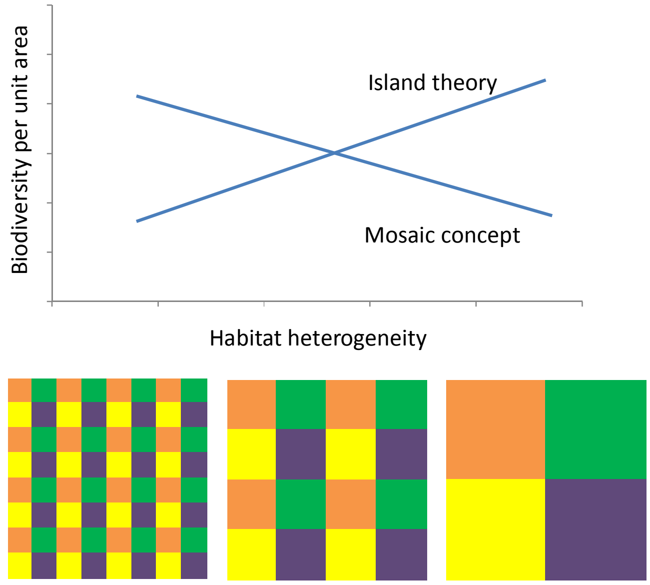

Figure 9. Biodiversity as a function of the number of habitat patches (with the same number of biotype types) and the length of ecotones (Duelli, 1997).

Landscape mosaics can be characterized by their composition and configuration and summarized by measures of heterogeneity or complexity. In his mosaic-concept, Duelli (1997) defined habitat heterogeneity as the number of patches and ecotone length. Since then, different definitions of landscape heterogeneity have been used in the literature. Fahrig et al. (2011) proposed more recently a framework to define landscape heterogeneity. They decomposed the heterogeneity of a landscape by its **compositional heterogeneity** (the number and proportions of different patch types) and its **configurational heterogeneity** (the spatial arrangement of patch types), see Figure 10. Landscapes with more patch types will contain more species because they will harbor the species of each patch type and the multi-habitat species that need several patch types (Fahrig et al., 2011). However with increasing number of patch types the area of each type will decrease, leading probably to a peak in species richness at intermediate levels of compositional heterogeneity. Increase in configurational heterogeneity will increase the edge length, will shorten distances between patches and favor supplementation or complementation and can change species interactions (Fahrig et al., 2011). Compositional and configurational heterogeneity can affect different aspects of biodiversity. For example, Perović et al. (2015) showed that grassland butterfly species richness increased with compositional landscape heterogeneity, whereas butterfly functional diversity increased with configurational heterogeneity, with more vulnerable species in landscapes with a high configurational heterogeneity. Higher landscape compositional heterogeneity can also increase richness stability, (defined as the temporal variation in species richness), as shown by Devictor and Jiguet (2007) for bird species.

Heterogeneity measures will depend on patch type classification used in landscape mapping. The classification is generally based on a human perception of the landscape (e.g. land cover or land-use types), that does not necessarily correspond to a species perception of the landscape. To create meaningful maps, **functional cover types** have to be distinguished that are based on the presence of resources needed by a particular species or species group (Fahrig et al., 2011; Perović et al., 2015).

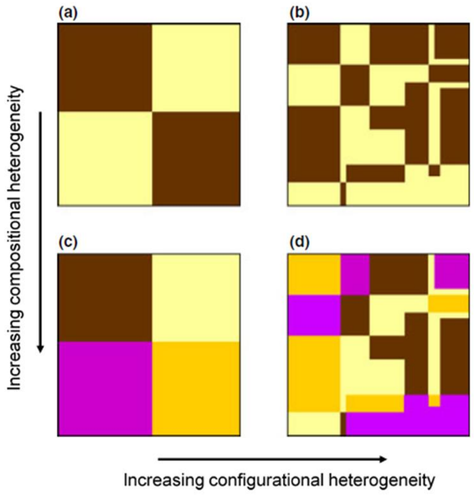

Figure 10. The two major axes of spatial heterogeneity: compositional and configurational heterogeneity. Each large square is a landscape and different colors represent different patch types (Fahrig et al., 2011).

1.3.9. The continuum model

The mosaic landscape concept is based on a landscape composed of different patches. However landscapes can also be seen as composed of gradual gradients as proposed in the '**continuum model**' (Fischer and Lindenmayer, 2006). Continuum theory is widely accepted in vegetation ecology but has received little attention in animal ecology. In the continuum model, conditions or resources needed by a specific species are mapped in a continuous way along environmental gradients (so not as patches), and give rise to habitat suitability maps by combination of different gradients (Figure 11). Furthermore, the continuum model enables integrating species with different requirements in complex ways. The continuum model does not suggest that fragmentation-related processes do not exist, but provides the possibility to add ecological complexity by incorporating other explanatory variables related to conditions and resources. Its focus is thus more on modelling species niches with single species or communities as response variables (Fischer and Lindenmayer, 2006). However it needs more accurate information on species requirements and spatial data and is thus more difficult to apply.

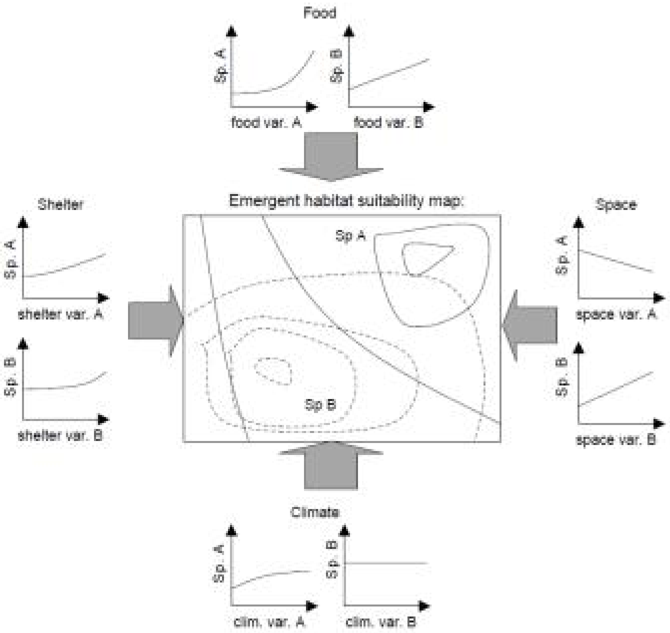

Figure 11. Schematic view of the continuum model for two hypothetic species A and B (Sp. A and Sp. B). Combination of availability of different resources and conditions (food, space, climate, shelter) leads to emergent habitat suitability maps per species, indicated as habitat contour maps (Fischer and Lindenmayer, 2006).

1.3.10. An integrated view of different landscape models

The different concepts existing in landscape ecology were recently summarized in one framework by Didham et al. (2012). They consider 1) the degree of interdependence of species responses to landscape characteristics and 2) the degree of interdependence of the various components of habitat fragmentation as structuring the differences between ecological concepts (see Figure 12). On the x-axis of this figure we can see at the left side a complete independence of habitat loss vs.

fragmentation *per se* (Fahrig, 2003), while on the right side they are dependent. The second axis represents the species interdependence. In IBT all species respond to spatial patterns of habitat in the same way, whereas in the continuum model (Fischer and Lindenmayer, 2006) each species responds individually to ecological gradients. Didham et al. (2012) advocate that these processes are not independent and should be integrated in a causal model, taking into account interactions among spatial components in order to evaluate their effect on biotic mechanisms that in turn can affect population and community responses (births, deaths, emigration and immigration).

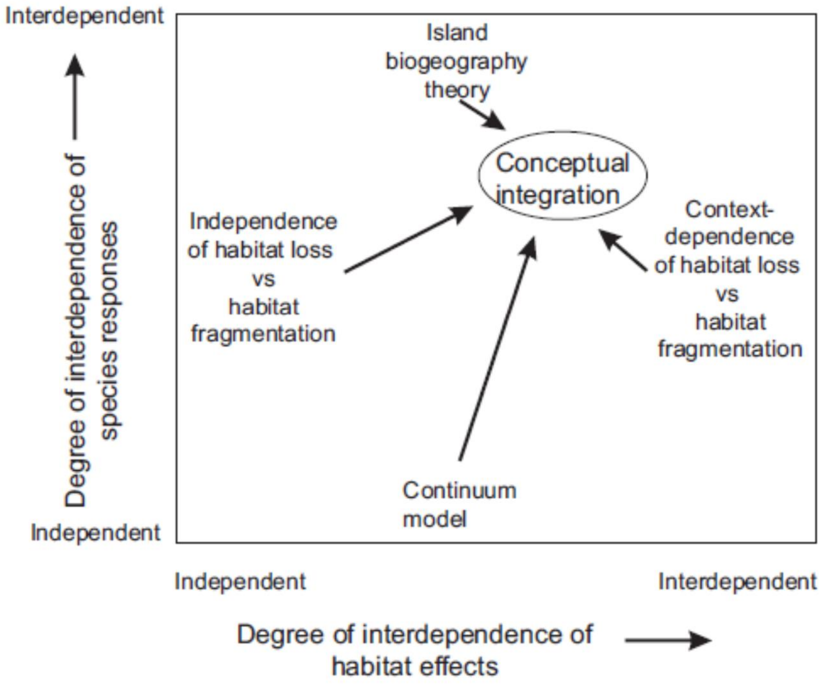

Figure 12. A conceptual representation of the main ideas in habitat fragmentation studies based on independence or interdependence of habitat effects and species responses, after Didham et al. 2012.

1.3.11. Which landscape scale to consider?

A recurrent question in landscape ecology is the spatial extent or size of the landscape that has to be considered in biodiversity studies. The extent will depend strongly on the taxa studied. Landscape extent will in general increase with trophic level, from plants via herbivores to parasitoids and predators, but will also depend on specialization and body size, with large, generalist species related to larger landscape extents than small, specialist species (Tscharntke et al., 2005). However, even within a taxonomic group large differences between species may exist. For example, Schmidt et al. (2008) showed that arable spider species presented very contrasting responses to the landscape context, both for the direction of effects and for the relevant spatial scale. Buffer size radii with the highest correlation between landscape variables and individual species densities varied from 95 to 3000 m and potentially reflected species' dispersal distances (Figure 13). Likewise, Deconchat et al. (2009) showed for abundance of New-Zealand bird species that the size of landscape buffers with the highest percentage of explained deviance varied between 200 and 3000 m among species. Moreover, the optimal buffer size was dependent on the landscape cover type used in analyses. Based on modelling studies, Jackson and Fahrig (2012) analyzed at which landscape scales total habitat amount best explained population responses in species that differed in dispersal distances, reproductive rates and movement behavior. Dispersal distance was the best predictor, leading to a general guideline that the radius of a landscape should be 4-9 times the median dispersal distance or 0.3-0.5 times the maximum dispersal distance. More precise movement behavior reduced scales, whereas reproductive rate had little effect.

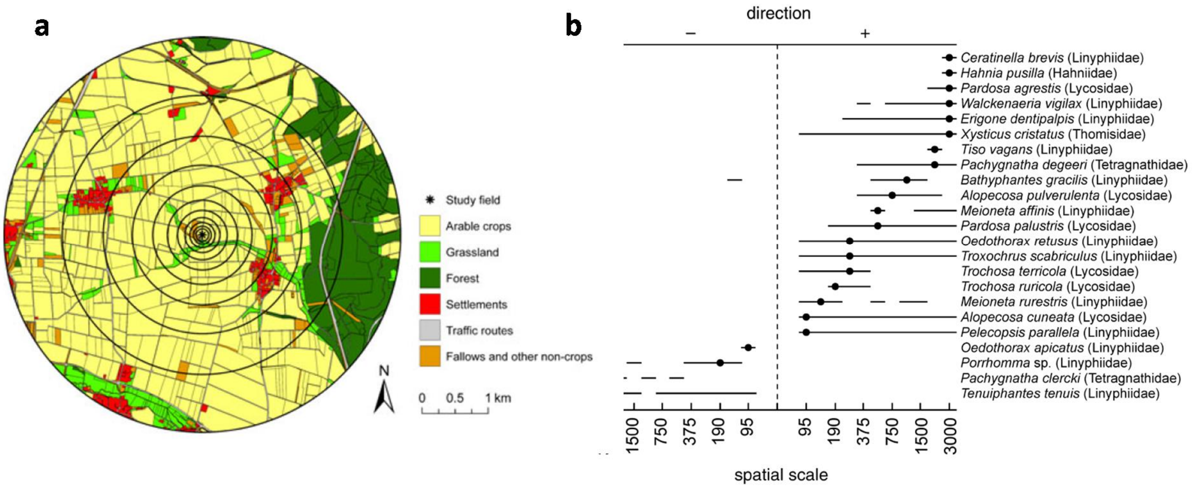

Figure 13. (a) Landscape map of a study site with the 11 landscape scales considered and (b) direction and spatial scale of correlations between landscape composition and local densities of spider species. Lines show the scales with significant correlations. The spatial scale with the strongest correlation is marked with a dot (source: Schmidt et al., 2008).

When analyzing not one but several landscape variables, each variable can have its strongest effect at a different scale, since different ecological processes may be involved (Deconchat et al., 2009). It is to be expected that models that select the best scale for each predictor perform better than single-scale models. However Martin and Fahrig (2012) showed for three mammal species that multi-scale models did not outperform single-scale models. They explained this result by the fact that species show either a similar response at several scales, that the response occurs at a common scale or are due to similarities in landscape structure at different scales.

1.4. Species traits and fragmentation

Responses to habitat quality and landscape structure are often species-specific and depend on species ecological niches and traits (Ewers and Didham, 2006; Steffan-Dewenter and Tscharntke, 2000). Traits can be defined as any morphological, physiological or phenological feature, usually measured at the individual level (Mouillot et al., 2013b). Investigating how species with different trait values respond to multi-scale modifications in environmental conditions, such as changes in land-use or management practices, will increase our understanding of mechanisms behind observed changes in community composition (Devictor et al., 2008; McGill et al., 2006; Mouillot et al., 2013b; Öckinger et al., 2010). The use of species traits also allows to compare communities sampled in different regions and can reveal general ecological responses irrespective of regional differences in species composition (Winqvist et al., 2014). It also allows comparing the trait mediated responses of different taxonomic groups to environmental conditions. Trait based studies are increasingly used to explain species sensitivity to landscape changes, but can also be used to explain or predict trend status of species (WallisDeVries, 2014).

Trophic level, dispersal capacity, niche breadth, reproductive potential and body size are considered important determinants of species persistence in fragmented landscapes (Ewers and Didham, 2006, Figure 14). For example, species at higher **trophic levels**, such as predators and parasitoids, are often more affected by landscape changes, especially when they are specialized in resources or habitats, than those of lower trophic levels (Tscharntke et al., 2012). High **dispersal capacity** favors movements between distant habitat patches. Mobile species are thus expected to be less sensitive to habitat isolation (Ewers and Didham, 2006). The relationship can however be more complex. For example, butterfly species with intermediate dispersal capacity have declined most, followed by sedentary and mobile species (Thomas, 2000). This might be explained by their higher sensitivity to habitat fragmentation, caused by higher minimum area requirements and higher mortality rates during dispersal between fragments.

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 to recover more quickly from low population numbers and enhances colonization through higher number of emigrants and rapid population growth (Vance et al., 2003). **Larger-bodied species** may experience higher extinction risk in fragmented landscapes than smaller-bodied species. The effect of body size is indirect and acts through correlations between body size and population size, growth rate, competitive exclusion and resource and area requirements (Brown, 2007; Henle et al., 2004; Pe’er et al., 2014). These relationships are however complex. Baguette and Stevens (2013) showed that butterfly wing size, a proxy for body size, is positively related to minimum area requirements, suggesting that large species need large, less fragmented habitats. Wing size is also positively, although weakly, correlated with mobility (Stevens et al., 2013) suggesting that large species can better cope with fragmentation *per se*. The positive relationship between body size and fragmentation sensitivity is thus not universal (Henle et al., 2004). This example also illustrates that life history traits cannot be regarded separately. Traits are connected by trade-offs and are co-adapted to maximize fitness under particular environmental conditions (Stevens et al., 2012). For example, species inhabiting varying environments are predicted to have a high dispersal capacity and *r*-selected traits such as high fecundity. It is therefore necessary to take into account the relationships between traits and to analyze the main trait associations of a species group (WallisDeVries, 2014).

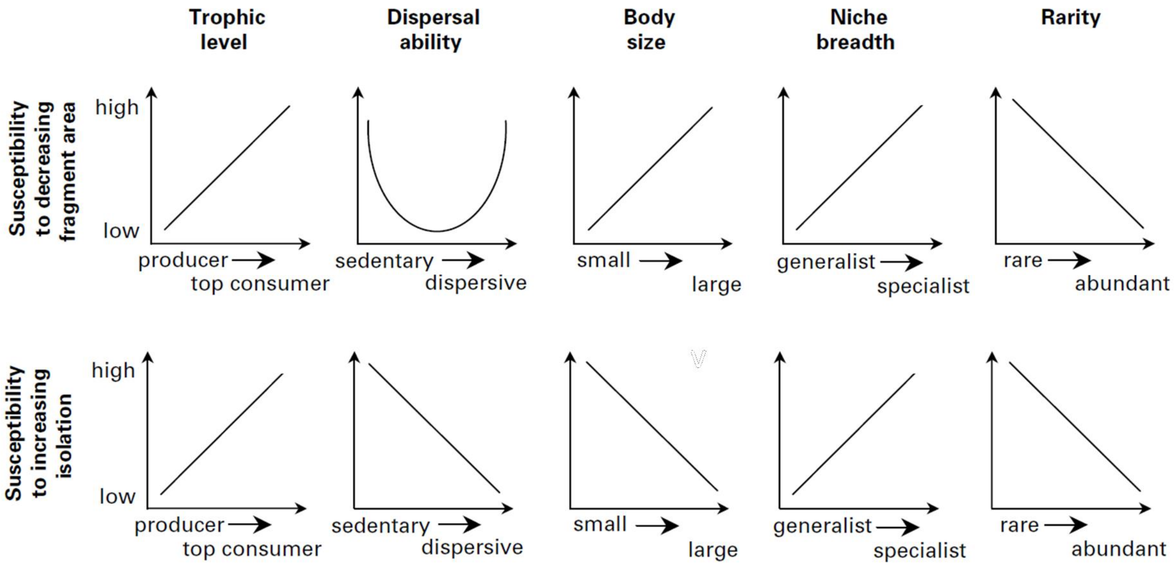

Figure 14. Predictions of trait-mediated responses of species to fragment area and isolation (Ewers and Didham, 2006).

1.5. Forests and biodiversity

Forests represent a critical habitat for a major part of the world's biodiversity. For example, WWF and IUCN have identified 234 priority centers of plant diversity worldwide. About 80 % these "hot spots" are found in forests. Likewise, 83 % of areas identified worldwide by BirdLife International as important for birds with restricted breeding ranges are located in forests (Matthews et al., 2000). These areas with high conservation value for plants and birds are mainly found in the tropics.

Forests are being lost at an alarming rate. The global deforestation rate in the period 1990–2005 was estimated at 13 million hectares per year (FAO, 2006). This important loss, fragmentation and degradation of forests have caused a serious decline of their associated biodiversity. The loss of forest area varies considerably between regions and continents and is recently most severe in some tropical and sub-tropical regions (Brockerhoff et al., 2013). Future loss (period 2010-2100) of natural forests is expected to be about 30% at a global scale (Brockerhoff et al., 2013).

Europe is the only major region with a net increase in forest area over the period 1990–2005 and almost half of this increase results from an increase in forest plantations (FAO, 2007). European forests have however experienced very important changes by human activities during the past millennia. Most of Europe has been deforested in the past, but many areas have been partly reforested in the last centuries, as illustrated in Figure 15 for France. As a result, only 4 % of Europe's forest area is classified as primary forest, compared with 27 % globally (FAO, 2007). In Europe, 10.5 % of the forest area is designated for conservation, which is very comparable with the global average of 10 % (FAO, 2007).

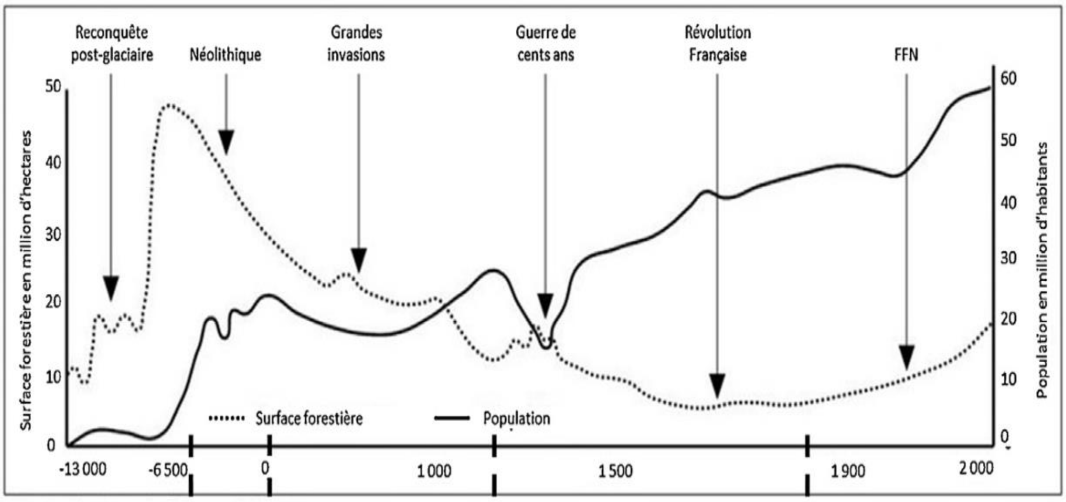

Figure 15. Forest area and human population In France from 13000 BC to today (Cateau et al., 2015).

1.5.1. Plantation forests

Planted forests are defined as forests predominantly composed of trees established through planting or deliberate seeding, where the planted/seeded trees are expected to constitute more than 50 % of the growing stock at maturity (FAO, 2012). In the period 1990-2015 the worldwide area of forest decreased from 4.28 billion hectares to 3.99 billion hectares. In the same period the area of planted forests increased from 167.5 to 277.9 million hectares, representing thereby nowadays almost 7 % of the total forest area (Payn et al., 2015). The highest increase in area of planted forests occurred in the temperate regions (Figure 16). An extrapolation of the current trends suggests that over 30% of the remaining natural forest area will be lost by the end of the century, with planted forests then representing more than 20% of the total forest area (Brockerhoff et al., 2013).

Planted forests are in the vast majority of cases tree monocultures, since only less than 0.1% of plantations worldwide are made of tree species mixtures (Nichols et al., 2006). They are also characterized by an intensive silvicultural management and a simplified structure (even-aged), compared to (semi-)natural forests. Plantation stands are composed of fast growing, exotic or native trees and are in general clear-cut at the end of their rotation cycle. Landscapes dominated by plantation forests are therefore composed of a mosaic of stands of similar composition, but of different size and age. Compared to semi-natural forests, plantation forests show high spatial and temporal dynamics (through clear-cuts) and a higher cover of early successional stages.

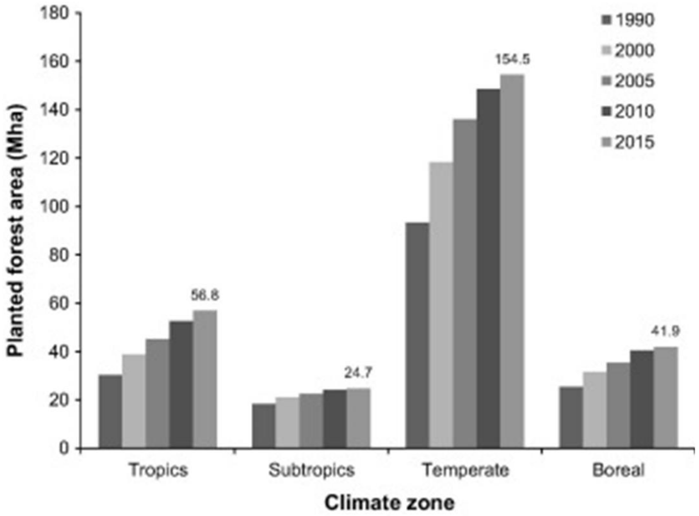

Figure 16. Changes in area of planted forests by climate zone (Payn et al., 2015).

Plantation forests are often considered less valuable for biodiversity conservation than natural forests. Many, but not all studies comparing plantations to more natural forests have indeed shown an impoverished flora and fauna in plantations (Carnus et al., 2006; Lindenmayer and Hobbs, 2004; Moore and Allen, 1999). However, when plantation forests are compared to other intensive land uses such as agricultural crops or degraded pastures the comparison changes in favor of plantation forests (Brockerhoff et al., 2008). Plantation forests are not always the ecological desert that they are sometimes supposed to be, but can be a surrogate habitat for native species (Barbaro et al., 2005; Brockerhoff et al., 2008; Jofré et al., 2016). They can also have beneficial effects as landscape matrix elements by offering supplementary and complementary resources, by increasing connectivity of natural forest remnants or by acting as a buffer to mitigate negative edge effects for forest interior species (Aune et al., 2005; Brockerhoff et al., 2008; Fischer et al., 2006, Figure 17). Their beneficial role as matrix elements does not only apply to forest species, but also to species of other habitat types such as grasslands. For example, Ockinger et al. (2012b) showed a positive effect of a forested matrix on grassland butterflies compared to an arable matrix and attributed this effect to resources present in the forest matrix. Biodiversity conservation in plantation landscapes will however also depend on the presence of more natural habitat elements, such as wetlands or late successional stages of remnant forest, within the plantation matrix (Fischer et al., 2006; Lindenmayer and Hobbs, 2004). The role of other landscape elements for biodiversity will also depend on landscape history and thus on habitat types present before plantations were installed (Lindenmayer and Hobbs, 2004).

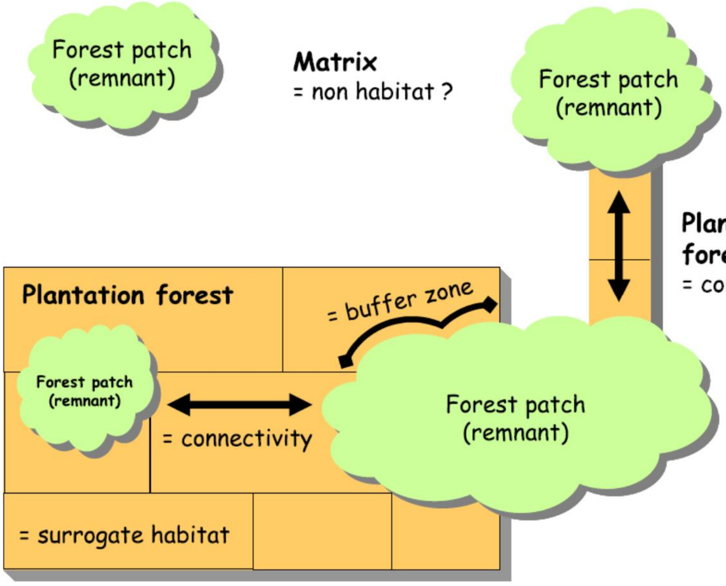

Figure 17.The role plantation forest can play at the local level (habitat or surrogate habitat) and at the landscape level (corridor, buffer zone), (Brockerhoff et al., 2008).

1.6. Butterflies as a model

Butterflies are used as model organisms in very different ecological disciplines such as evolutionary ecology, behavioral ecology and landscape ecology (Dennis, 1992; Hanski, 1999; Settele et al., 2009). Several characteristics of butterflies facilitate their use in ecological studies, such as their diurnality, conspicuousness, phytophagous life cycle, analyzable demography and a wealth of natural history knowledge (Watt and Boggs, 2003).

Butterflies are diurnal, attractive, colorful and relatively large insects that are relatively easy to identify. Their identification is also largely facilitated by a limited number of species compared to other insect groups. At least in northwestern Europe most species can be recognized directly in the field. Some have to be captured to verify certain details, but can be released directly, and only for a few groups genitalia examination is necessary (Lafranchis, 2000). Their beauty and ease of identification explain why butterflies have been studied by entomologists for centuries. More recently, with the awareness of biodiversity loss, butterflies have been largely adopted in citizen science programs. Most countries have nowadays national or regional butterfly atlases and in many European countries butterfly monitoring programs exists (van Swaay et al., 2008), based on the British Monitoring Scheme started in 1976 by Pollard (Pollard, 1977). These atlases and monitoring programs provide detailed information on species distribution and trends at different spatial and temporal scales.

The fact that butterflies are diurnal and relatively large also facilitates to observe, follow or capture them in the field and thus favors their use in behavioral and demographic studies. Numerous ecological studies on their life cycle and habitat use provided much knowledge on individual butterfly species. For most west-European butterfly species different life history traits are therefore available in the literature (Baguette and Stevens, 2013; Bink, 1992).

Butterflies can be observed in very different **habitat types**, with the exception of aquatic environments. Van Swaay et al. (2006) identified the main biotopes for 436 European butterfly species. Biotopes vary from cliffs, bogs, heathlands, different types of grasslands, scrub, to coniferous or deciduous woodlands. The most species-rich biotopes in Europe are dry grasslands, notably dry calcareous grasslands and steppes (274 species) and alpine and subalpine grasslands (261 species). Different types of woodlands also harbor a significant number of species, e.g. mixed woodlands (187 species), broadleaved deciduous forests (186 species) and coniferous woodlands (156 species).

Butterflies are phytophagous insects, their larvae often feed on specific host-plants and most adult butterflies need flowers for nectaring. Their degree of habitat and larval food plant specialization varies widely among species. Their dispersal capacity is also very variable, with species that migrate over Europe to sedentary species with a mean dispersal distance of a few tens of meters (Stevens et al., 2013). The mean dispersal distance of all northwesten European species was estimated to be 200 m (Stevens et al., 2013). Their scale of dispersion makes them adequate models for addressing habitat fragmentation issues, as shown by the many studies on this subject, and for studying meta-population dynamics (Hanski, 1999).

Most butterfly species have at least one generation a year and have high reproductive rates (Bink, 1992), which permits rapid population changes and measurable reaction to global changes. Butterflies are, as all insects, ectothermic species and depend for all aspects of their biology on weather and climatic conditions. They are therefore particularly **sensitive to climate change** and are used as biological models for measuring its effect. Climatic requirements of species (e.g. Species Temperature Indexes – STI) are described in literature (Schweiger et al., 2014) and used to analyze the effect of climate warming on butterfly species and communities (Devictor et al., 2012; Settele et al., 2008; Wallisdevries and Swaay, 2006). At the local scale, the **micro-climate** is known to affect strongly habitat use and survival of butterflies (Dennis and Sparks, 2006; Wallisdevries and Swaay, 2006). Their sensitivity to climatic conditions has however also the disadvantage that inventories can only be done under certain weather conditions and that annual fluctuations in numbers caused by weather conditions complicate reliable trend calculations in monitoring programs.

Conservation status and threats

European and national red lists clearly show that butterflies are declining across Europe. About 9% of European butterflies are classed as threatened on the European red list and 31% of European butterfly species experienced a decline in their populations over the last 10 years (van Swaay et al., 2010). The overall decline in distribution in Europe over a period of 25 years is estimated to be 11 %, with habitat generalists declining very slowly (-1%), compared to specialist species of grasslands (-19%), wetlands (-15%) and forests (-14%) (van Swaay et al., 2006).

The decline of butterflies is mainly caused by agricultural intensification, drainage, abandonment of agricultural land, climate change and changing biotope management (van Swaay et al., 2010, 2006, Figure 18).

The massive loss of biotopes has led to the subsequent isolation of remaining biotopes which is estimated to affect 87% of threatened species (van Swaay et al., 2010, 2006).

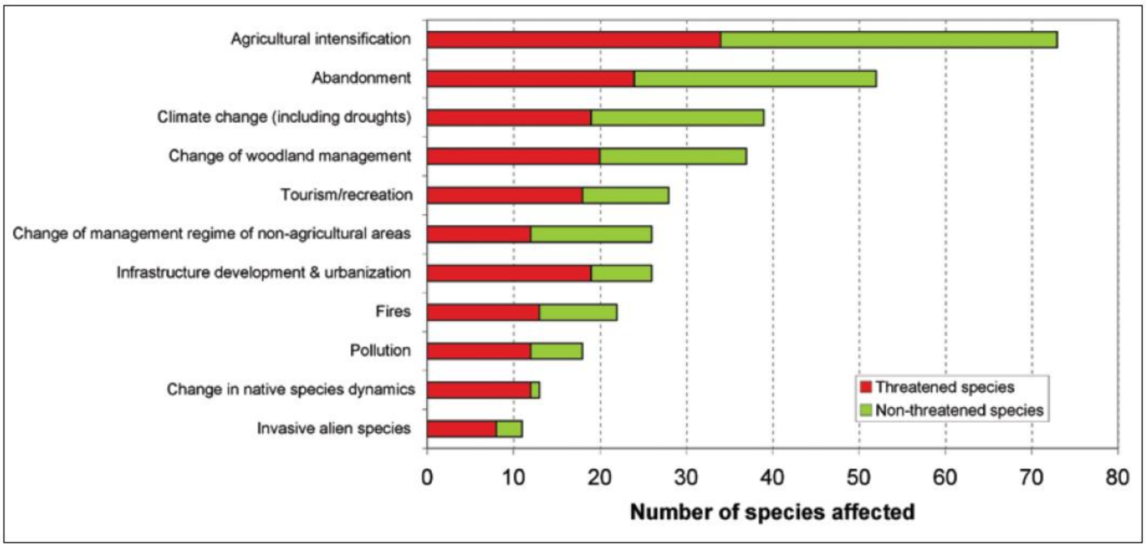

Figure 18. Major threats to European butterflies (van Swaay et al., 2010).

Changing management seems also to represent the major threat for **forest butterflies**. The loss of open woodland habitats following a shift from traditional management, such as short-rotation coppice systems, to high forest systems was already recognized as a problem in western European countries. It seems to be now a general problem across Europe (van Swaay et al., 2006). Figure 19 illustrates this effect of forest management changes on woodland butterflies differing in habitat preferences: species needing open areas have decreased most (Liley et al., 2004).

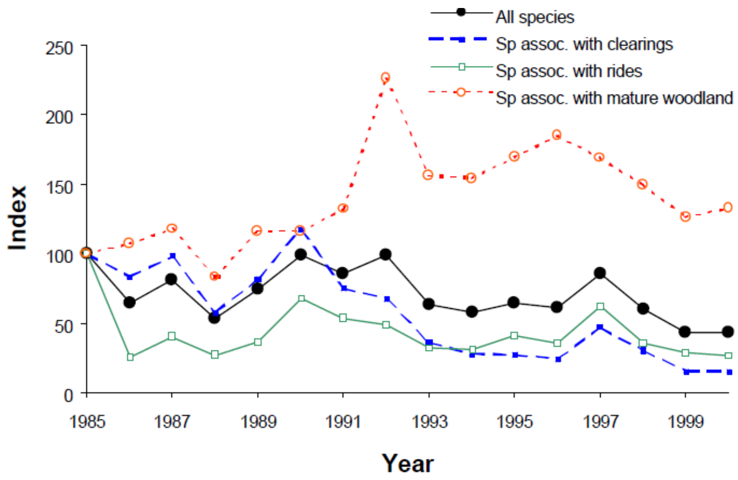

Figure 19. Monitoring data of woodland butterflies in the United Kingdom, for all species and for species associated with clearings, rides and mature woodland (Liley et al., 2004)

Butterflies are thus iconic species for nature conservation and for ecological studies but they are rarely studied in temperate forests and even less in plantation forests. Forest can harbor an important number of butterfly species, including forest specialist species and generalist butterflies. Forest specialists depend on a variety of forest structures, such as large deciduous woodland blocks, rides and glades, clearing, edges, and coppiced areas. Large deciduous woodlands with a complex structure can thus contain many butterfly species. Plantation forests are considered to be very poor in butterfly species, because of their dense tree canopy preventing the development of a herbaceous layer (Lafranchis, 2000). This might be a reason why butterflies are rarely studied in plantation forest landscapes. Forest butterflies are also more difficult to sample than grassland butterflies. Some species, such as the purple hairstreak (*Favonius quercus),* seldom visit flowers for nectaring and spend most of their time in the tree canopy. Other forest species, such as the white admiral (*Limenitis camilla*), occur in low numbers, complicating their assessment.

Butterflies and ecosystem services

Providing ecosystem services can be considered an additional value for a biological model as this provides a supplementary justification for model choice and a better reception to management recommendations. As all organisms, butterflies are integrated in food webs; they are used by predators (other insects, small mammals, birds,) and parasitoids as food sources, thereby fulfilling a role in ecosystem functioning. Most adult butterflies visit flowers for nectar, but their role as pollinators is less important than that of bees and bumblebees, although butterfly pollination seems essential for some plant species, such as *Dianthus deltoides* and *Viscaria vulgaris* (Jennersten, 1984). Butterflies are thus considered to provide only limited ecosystem services compared to other insect groups that may have a major role as pollinators or as natural enemies of pests. However, an important ecosystem service of butterflies is a cultural service: aesthetic enjoyment.

Possible negative effects associated with butterflies

Among native European butterflies only *Pieris brassicae* and *P. rapae* cause damage to crops (cabbages). A recently introduced butterfly species from the south of Africa, *Cacyreus marshalli,* has colonized a large part of Europe. The larval host plants are cultivated *Pelargoniums* and the species can cause damage on these ornamental plants. Caterpillars of butterflies do not cause urtications, as do those of some moth species (e.g. processionary moths).

Butterflies as biodiversity indicators

Butterflies are appreciated by the public and are therefore used as **flagship species** in biodiversity conservation programs. Flagship species can be defined as "*popular, charismatic species that serve as symbols and rallying points to stimulate conservation awareness and action*" (Barua, 2011). However the question is whether they are appropriate **indicator species** for biodiversity. The term 'indicator species' can be defined in different ways and is used here for species whose presence indicates the presence of a set of other species and whose absence indicates the lack of that entire set of species (Lindenmayer et al., 2000). The richness of different taxa may be correlated for several reasons: i) random coincidence, ii) interactions between taxa, iii) similar response to common factors and iv) response to different environmental factors that spatially covary (Eglington et al., 2015; Wolters et al., 2006).

Many studies have compared species richness, or other diversity metrics, between different taxa in order to find biodiversity indicators. A recent meta-analysis including 320 case studies of correlations between plant and animal species richness showed an overall positive correlation (Castagneyrol and Jactel, 2012). The correlation was stronger for herbivores and pollinators, including butterflies, that have a direct functional link with plant species, than for predators and detritivores. However, plant species richness accounted on average for only 20% of variation (R^2) of animal richness. Another meta-analysis, comparing 237 species richness correlations between 43 taxa showed a similar positive correlation, with species richness of one group explaining on average only 14% of the richness of another group (Wolters et al., 2006). Correlation coefficients differed much between studies, but the taxonomic distance between compared groups was not an important factor explaining this variation. The authors conclude that no taxon seems to be a universal predictor for all other groups.

Butterflies depend directly on vegetation composition for larval and adult feeding and their richness can be positively correlated with plant species richness (Grill et al., 2005; Steffan-Dewenter and Tscharntke, 2000; Su et al., 2004), but correlations may also be absent (Su et al., 2004; Vessby et al., 2002; Weibull et al., 2003) or not causal when larger spatial scales are considered (Hawkins et al., 2003). Butterfly richness may also be correlated with the richness of other pollinators such as bumblebees (Vessby et al., 2002).

However, the use of richness as biodiversity measure is questionable and may be better replaced by community composition measures (Su et al., 2004). For example, Eglinton et al. (2015) showed a positive correlation between bird and butterfly richness in the UK, but the correlation for community specialization became non-significant at smaller scales, i.e. when latitude was accounted for. This can be explained by the sensitivity of specialist butterfly species to local vegetation composition, whereas birds are more associated with particular habitat types rather than specific plant resources.

Thomas (2005) discussed the use of butterflies as indicator species for other insect groups and concluded that, apart from aquatic and saproxylic insects, butterflies seem adequate indicators of change for many other insect groups. However he also recommends that studies should be extended to other groups, which seems a cautious conclusion since taxonomic or functional correlations have shown to be very variable.

1.7. Objectives and hypotheses of this thesis

Many ecological studies tried to identify factors that drive patterns of biodiversity and to propose measures to maintain and restore biodiversity and associated processes. These studies concern all types of ecosystems, plantation forests included. Maintaining or restoring biodiversity is defined as one of the criteria for sustainable forest management. To take accurate measures to conserve or restore biodiversity in landscapes dominated by plantation forests we have to understand how local and landscape factors affect the diversity of different taxonomic groups. Butterflies, a group showing severe declines and sensitive to fragmentation, have rarely been studied in these kinds of landscapes, even though this landscape type is increasing in surface worldwide. This lack of information makes it difficult to propose management measures at the stand or landscape level to enhance butterfly diversity.

The **first objective** of this thesis is therefore to describe and understand how butterfly species occurrences and community composition vary in mosaic landscapes dominated by plantation forests.

The **second objective** is to identify the key factors at different spatial scales (local and landscape levels) that explain the observed patterns and can be used by forest managers and landscape planners to maintain or restore butterfly diversity in forest plantation landscapes.

To achieve these goals we first analysed butterfly community composition in all main habitat types present in our study area (chapter 2). Next we analysed differences in species composition between edges and patch interiors (chapter3) and we analysed fragmentation effects on one habitat type, deciduous woodlands, that occur as scattered patches in the landscape of pine plantations (chapter 4). In each chapter we analysed how local and landscape factors affect these occurence patterns and we discussed ecological mechanisms related to the observed patterns. Finally we integrated butterfly ecological traits in our analyses to better understand the relationships between species occurence patterns and local and landscape features (chapter 4 and 5).

More precisely we addressed the following questions:

Questions	**Chapters**
Do habitat types in a pine plantation landscape differ in butterfly species richness and community composition?	2 & 3
What is the contribution of pine stands to butterfly diversity in mosaic, pine plantation landscapes?	2 & 3
What is the contribution of semi-natural habitats to butterfly diversity?	2 & 3
What is the contribution of edge habitats to butterfly diversity?	3
What is the relative importance of vegetation composition, habitat-type and landscape composition and configuration on butterfly diversity?	2 & 3
What is the effect of deciduous forest fragment quality, size and connectivity on butterfly diversity in pine plantation landscapes?	4
Do species ecological traits explain butterfly community responses to local and landscape variables?	4 & 5
Which mechanisms at the local and landscape level are related to species occurence patterns (e.g. habitat complementation/supplementation, habitat area and isolation)?	2, 3, 4 & 5
Which landscape ecological models best describe species distribution patterns in mosaic, pine plantation landscapes (fragment-matrix model, mosaic concept, continuum model)?	2, 3, 4 & 5

1.8. Study region: the Landes of Gascony Forest

The Landes of Gascogne Forest, situated in the south-west of France (Figure 20), represents with almost one million hectares of native maritime pine (*Pinus pinaster*) stands the largest continuous plantation forest in Europe. The whole region is covered by nutrient poor, acidic podzolic soils with a pH of 3.5-5.5 (Trichet et al. 1999). The climate is Atlantic with between 800 and 1200 mm of annual rainfall and a mean annual temperature of 12° (Jolivet et al., 2007).

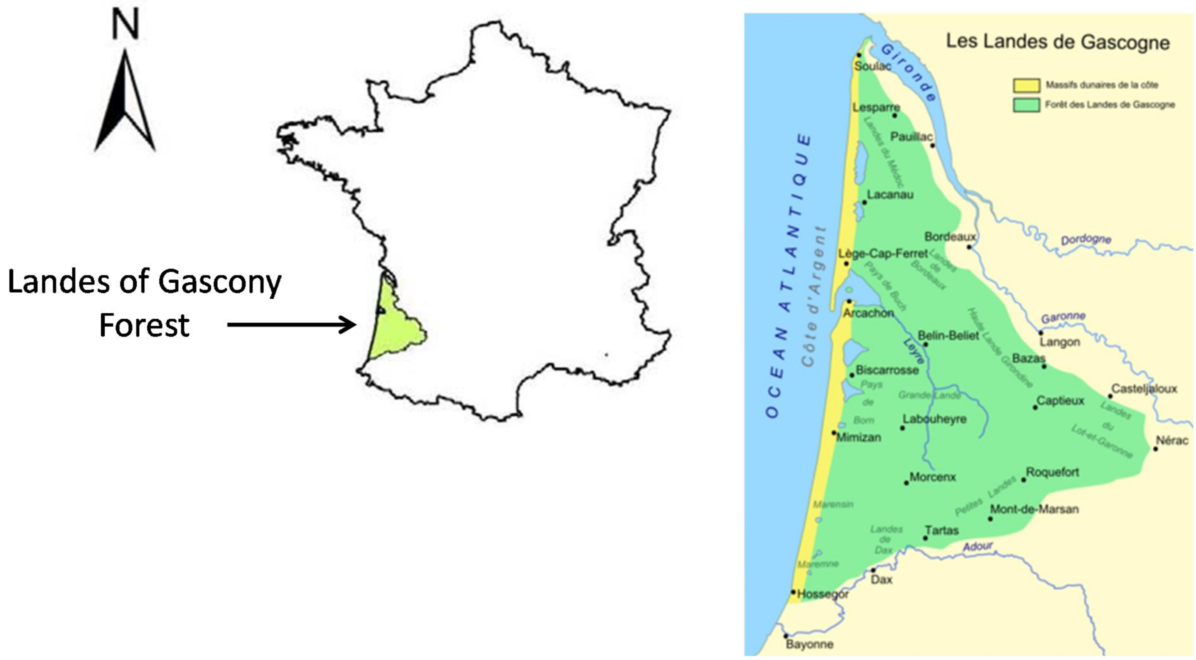

Figure 20. Map of France with the localization of the Landes of Gascony Forest and detail of the region.

1.8.1. Landscape changes from the postglacial period onwards

The landscape of the Landes of Gascony is nowadays dominated by a mosaic of even-aged maritime pine stands. In the past the landscape has however undergone huge changes: from a forested landscape it changed to a very open heathland landscape and 150 years ago it changed again to a forested landscape, but dominated by intensively managed, monospecific stands.

At the beginning of the postglacial period (*i.e.* Preboreal period, 10200 - 8800 BP) climate warming in the region favored the development of a forest cover dominated by *Pinus sylvestris* and a herbaceous layer with grasses and *Ericacea*e. In the following, boreal period (8800 - 7500 BP) more thermophilous tree species such as *Quercus robur, Q. pyrenaica, Alnus glutinosa, Fagus sylvatica* and *Pinaster pinaster* arrived in the region. *P. pinaster* increased its cover at the end of the Atlantic period (7500- 4500 BP) and mixed forests with *Q. robur, A. glutinosa* and *P. pinaster* covered probably large areas in that period (Jolivet et al., 2007).

The Landes of Gascony is a flat and poorly drained region. Mixed forests were therefore mainly present on drier sites along rivers and on (inland) dunes, while marches dominated the wetter parts. The first human settlements were concentrated on these drier, forested parts and leaded to the first human-induced deforestations. The Bronze age showed an increase in human activities leading to a more open landscape. During the Middle Ages the region changed markedly due to large deforestations leading to an open, heathland landscape (Faure and Galop, 2011). To cultivate their crops on the nutrient-poor soils, farmers were dependent on the manure of sheep. During the day, sheep grazed on the large heathlands and were gathered every evening in barns to collect their manure. About 15 to 30 ha of heathland were necessary for 1 hectare of crop (Jolivet et al., 2007). This agro-pastoral scheme leaded thus to a very open landscape. Pines and oaks were not absent from the landscape but appeared as small woodlands. The first texts of managed pine forest date from the 14th century, but their area was limited by a lack of drainage and roads (Sargos, 1997). In the 18th and 19th century the area planted with pines increased and the Landes department contained already 70.000 ha of pine stands in 1789 and 149.00 ha in 1852 (Sargos, 1997). In 1857 a law was adopted by Napoleon III, ordering the communes to drain their land and plant it with native pine trees, leading to a rapid change of the still very open, heathland landscape into a forested landscape (Figure 21). Until the 1940's pine stands were mainly used for resin and quality wood and had a rotation cycle of 80-90 years. After the Second World War the forest system changed fundamentally and is nowadays characterized by soil preparation, fertilization, trees planted in lines, use of fast growing tree varieties, intensive stand management and a rotation cycle of 35-50 years (Jolivet et al., 2007). Prospective plans foresee scenarios with a further reduction of the rotation cycle to 25 years with more wood production for bio-energy (Jolivet et al., 2007).

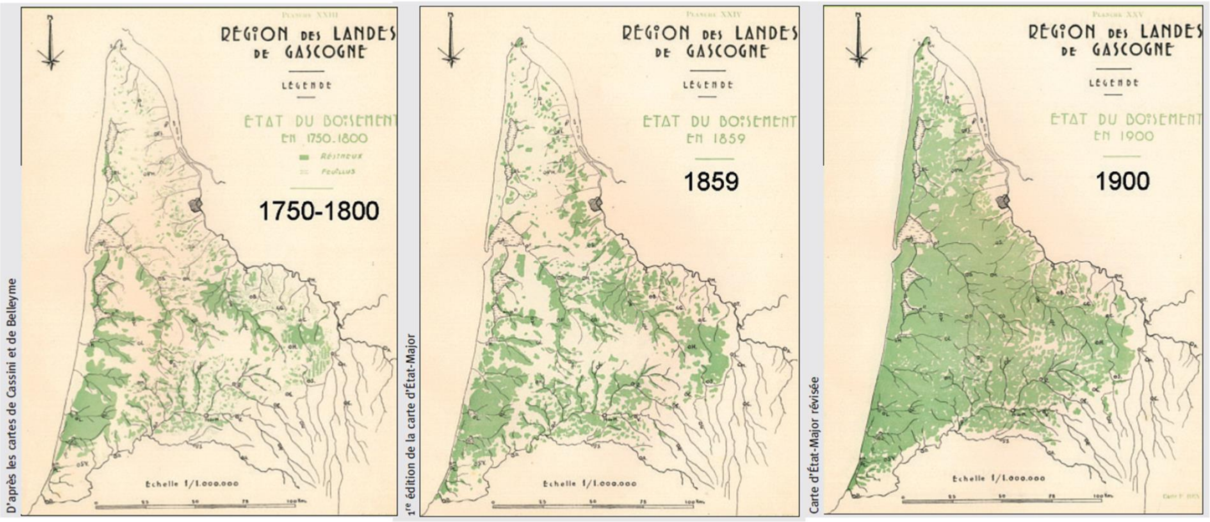

Figure 21. Changes in forest cover in the Landes of Gascony between 1750 and 1900 (Jolivet et al., 2007).

1.8.2. Today's landscape composition of the region

The landscape in the Landes of Gascony is nowadays dominated by a mosaic of even-aged stands of maritime pine trees (see Figure 22 as an example). Deciduous woodlands are rare and found along rivers or as scattered patches of a few hectares. Open areas in the landscape are mainly represented by pine clearcuts, firebreaks and powerlines and by agricultural fields. Agricultural fields occupy only 15% of the area and are constituted for 75% by large fields of irrigated corn or vegetables (Mora et al., 2012).

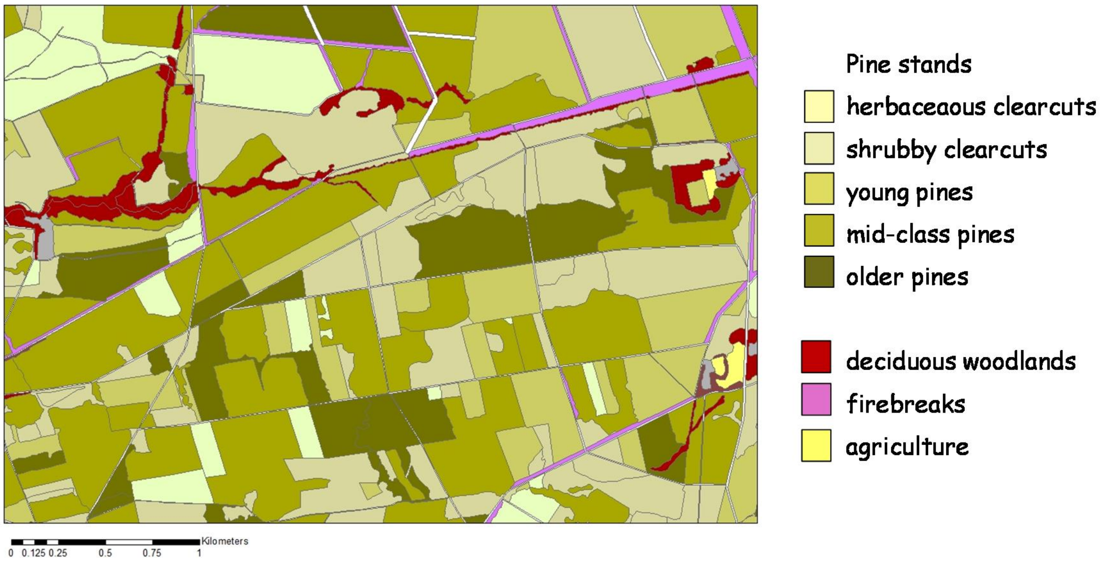

Figure 22. Example of the landscape in the Landes of Gascony forest showing the typical mosaic of even-aged pine stands, deciduous woodlands and firebreaks (commune of Biganos in Gironde).

Pine stands

The pine stands in the Landes of Gascony have a rotation cycle of 40 to 50 years. After soil preparation (ploughing) and fertilization (with phosphorus), pines are planted (70 % of stands), or sown, in lines 4 m apart (density of 1250 plants/ha). Stands undergo three to four thinning operations (final density of ca. 300 trees/ha) and understory is mechanically removed every 5 years with a heavy roller (Mora et al., 2012).

Differences in soil moisture have an important effect on tree growth and on the understory vegetation in pine stands. Three vegetation types are in general distinguished (Guillot, 2011; Timbal and Maizeret, 1998):

- Wet heathland vegetation: the groundwater level is close to 0.3 m in winter and the vegetation is dominated by *Molinia caerulea* with presence of *Erica tetralix* and *Erica ciliaris.*
- Mesophilous heathland vegetation: under intermediate moisture conditions with a groundwater level fluctuating between 1 and 2 m the vegetation is dominated by *Ulex europaeus* and *Pteridium aquilinum* with presence of *Erica scoparia* and *Erica cinerea.*
- Dry heathland vegetation: the groundwater level is always below 2 m and the vegetation is characterized by the presence of *Calluna vulgaris*, *Erica cinerea* and *Helianthemum alyssoides.*

Deciduous woodlands

Deciduous woodlands are found along rivers or as scattered patches of a few hectares. They are generally dominated by *Quercus robur*, on dry sites by *Q. pyrenaica* and along rivers by *Alnus glutinosa* and *Q. robur.* Their management is very extensive and they are mainly used for pigeon hunting, mushroom collecting or firewood. The riparian forests are characterized by their larger size and more heterogeneous soil moisture conditions. These forests can be considered partly as ancient forests as they are present on the maps of 1750-1800 (see Figure 21). However the area along the river was also the preferred area for settlements and was thus also used for agriculture (grasslands, crops) and silviculture (pines). The origin of the scattered woodlands seems more diverse, in some cases they can been localized on older maps, sometimes they correspond to ponds that are colonized by broadleaved trees due to drainage, or they correspond to isolated settlements.

Broadleaved trees are thus found in these deciduous woodlands, but also in mixed stands, in the undergrowth in pine stands or as hedges along some pine stands.

Linear elements

Different types of linear elements can be distinguished in the study area. The forested landscape is interspersed by a very dense network of sandy tracks that separate pine stands. Between the track and the pine stand a strip of several meters wide constitutes the 'forest edge' and is composed of a herbaceous vegetation and sometimes by a scrub zone. The herbaceous vegetation is in general mown once or twice a year.

Firebreaks and powerlines represent linear elements with a much larger width, varying between 15 to 100 m. They can have a heathland vegetation, as described above for the pine stands, or a grassland vegetation, dominated by for example *Holcus lanatus* or *Anthoxanthum odoratum*. Management of firebreaks and powerlines is very diverse. In the study region the usefulness of firebreaks in preventing forest fires is considered doubtful and only firebreaks that are classified in a fire prevention scheme are mown once a year in summer. Other, private firebreaks are mown less often (every 4-8 years) or are progressively transformed into pine plantations. Management of powerlines is in general extensive (every 4-8 years) and aims at suppressing the regrowth of woody species, but in some cases they are mown annually.

Figure 23. Examples of land cover types in the study area: a - young pine stand, b - old pine stand, c - firebreak, d – deciduous woodland.

1.9. Study sites

Within the Landes of Gascony region we selected two main study areas for butterfly sampling: Tagon (5000 ha), situated 35 km southwest of Bordeaux and Solferino (10500 ha), located 65 km to the south of Tagon (Figure 24). Both sites are dominated by maritime pine plantations, present similar types of soils, and include different degrees of landscape heterogeneity. The Tagon area was selected because birds, spiders and carabid beetles were already sampled in this area, thereby allowing a multi-taxa analysis of local and landscape effects. The Solferino area is situated within a larger area that was used for studies on indirect indicators of biodiversity, such as forest cover and tree species richness. Within these two areas we selected 83 sites that were used for the studies presented in the next chapters.

For the study on the effect of area and isolation of deciduous woodland fragments on butterfly communities (chapter 4), we selected deciduous woodlands within the Tagon and Solferino area, but also in nearby areas (Figure 25), to have a set of sites with uncorrelated gradients of deciduous woodland area and isolation. Since the study region is homogeneous, the local butterfly species pool does not change fundamentally between areas.

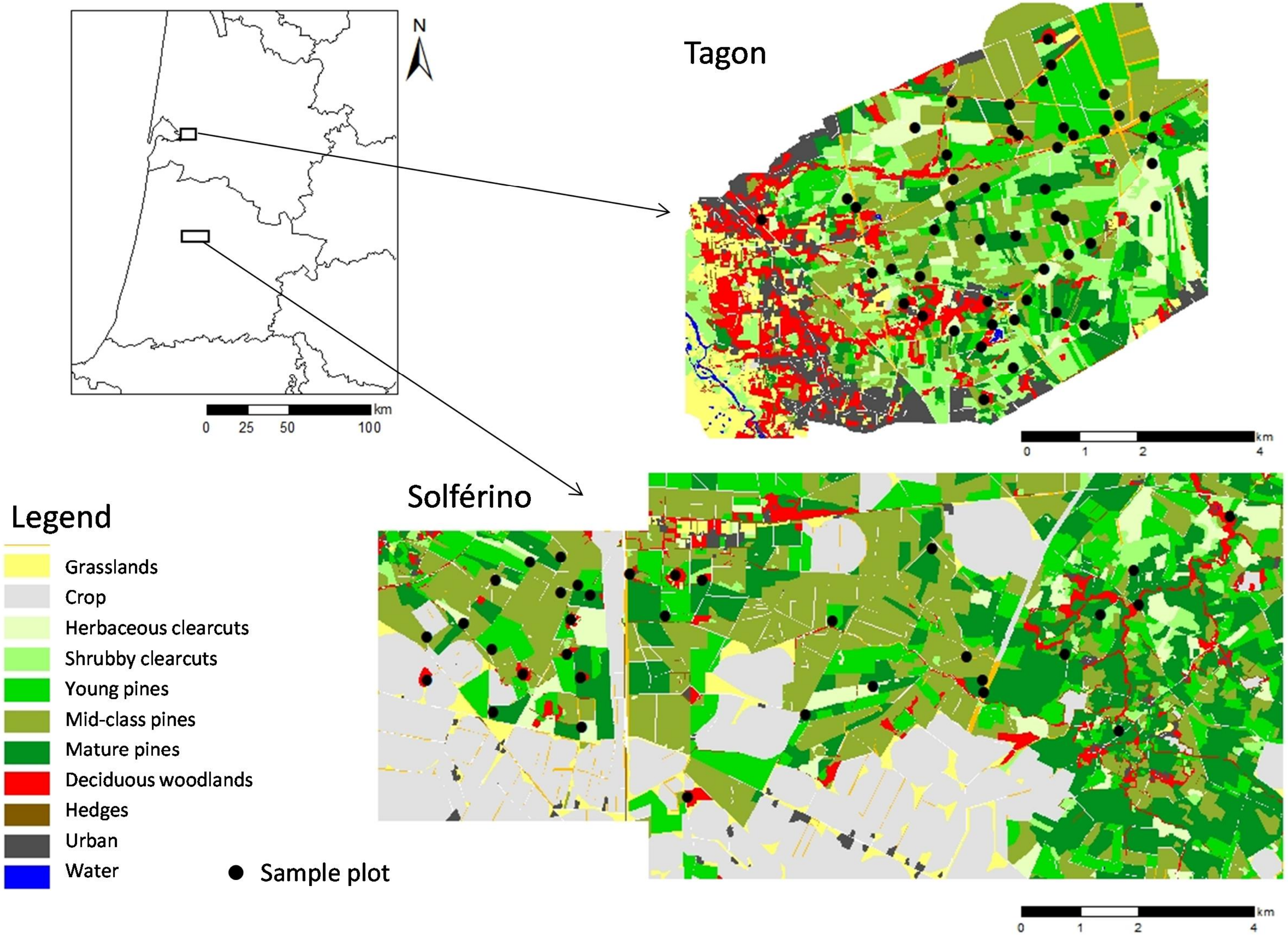

Figure 24. Map with the location of the two study areas in the south-west of France and location of the sampled plots within each site (chapter 2 and 3).

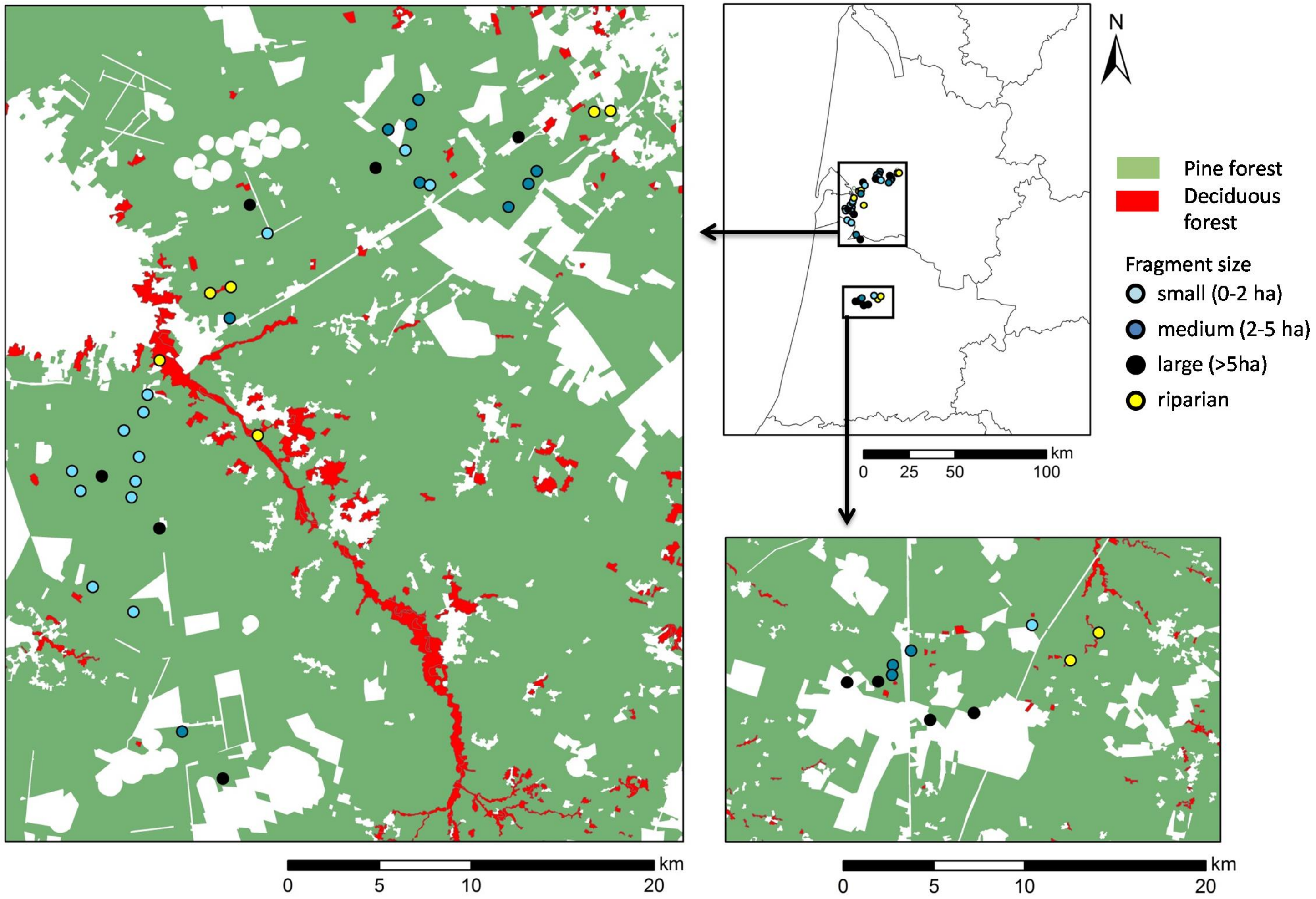

Figure 25. Map with the position of the 44 sampled deciduous woodlands (chapter 4), with size classes of the different fragments. The background indicates the presence of maritime pine forests (green) and of larger deciduous woodlands, including riparian forests (red). For the analyses the cover of deciduous woodlands was mapped in a buffer of 1000 m from the center of each woodland using aerial photos with a pixel size of 50 cm and thus corresponding to a much more detailed landscape mapping.

1.10. Butterfly sampling

Pollard developed in 1976 the 'transect-method' for sampling butterflies (Pollard, 1977; Pollard and Yates, 1993). The 'transect-method' has been validated by testing the observer-effect and by verifying the correlations with population estimates obtained by capture-mark-recapture methods in the same sites (Pollard, 1977; Thomas, 1983). This method, also referred to as 'Pollard walks', is nowadays widely accepted as the standard method for sampling butterflies in ecological studies and for monitoring schemes (van Swaay et al., 2008). The method consists of walking slowly a fixed transect and counting all butterflies at the species level within a fixed distance of the observer (generally 2.5 m on either side and 5 m ahead of the observer, Figure 26). A distance of 2.5 m may appear short, but it allows having a high species detectability, with a rather constant detectability for small and large species and for species in different habitat types.

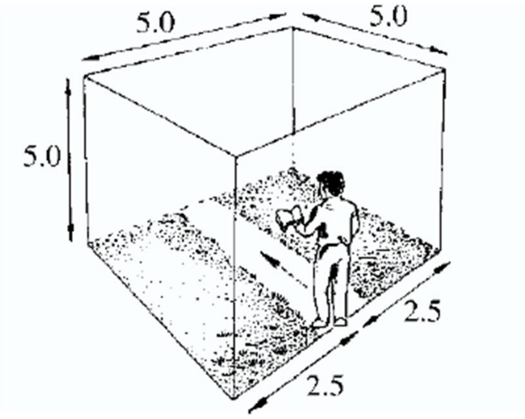

Figure 26. Transect method for butterfly monitoring. The observer notes, while walking slowly, all species in a virtual box of 5x5x5 m (Thomas, 2005).

1.10.1. Number of visits and transect length

Although the transect-method is largely accepted, the transect length and number of visits differs strongly between ecological studies. For example, Wettstein and Schmid (1999) visited their 540 m long transects twice, while Clausen et al. (2001) visited their transects of 30 m twelve times. As each butterfly species flies only in a limited period between spring and autumn, several visits are necessary to include most species in a survey (Roy et al., 2007). Limited resources of money, time and people oblige to make a compromise between the number of sampled sites, visits per site and transect length (Lang et al., 2016; Loos et al., 2015a). Reducing the number of visits appears to have less impact on the response variable than limiting the number of sites, as shown by Roy et al. (2007), using British monitoring data. They showed that for detecting a 25% reduction in abundance over 10 years, 220 sites are needed with a weekly visit method (i.e. 26 annual visits) and 430 sites with three annual visits. Likewise, Lang et al. (2016) showed that by reducing the number of visits from seven to four still 80-90% of species were recorded, as long as summer visits were included. However they also observed that species number strongly depended on transect length and concluded that transect lengths of 1-1.5 km are the most cost-effective to detect an effect on species richness (Figure 27). However, Loos et al. (2015a) showed that reducing the number of 50 m transects per site from 4 to 3 had only a limited effect on butterfly species richness estimates.

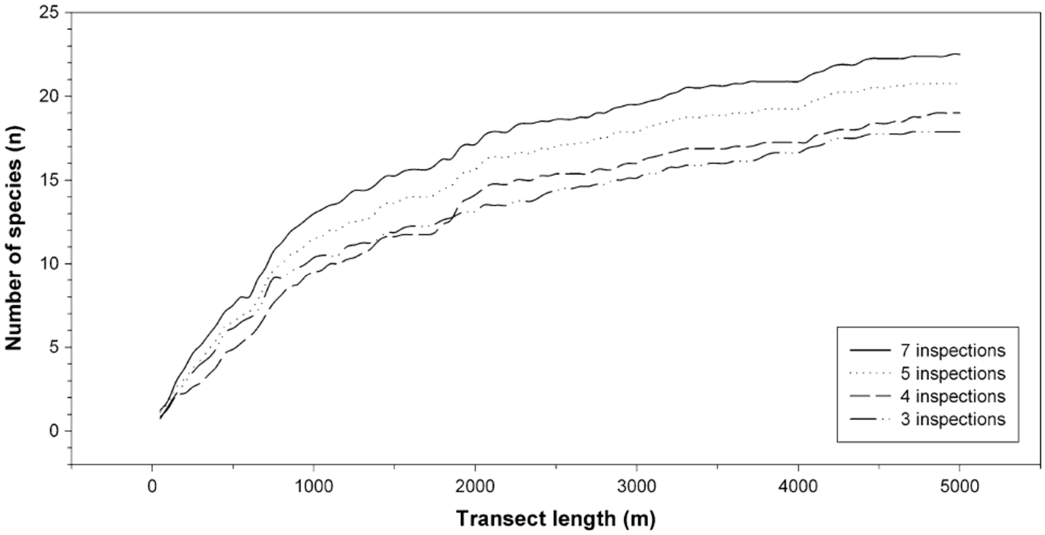

Figure 27. Effect of number of visits and transect length on observed number of species per transect (Lang et al., 2016).

In our studies we visited each site four times. The total transect length differed per study. For the study on butterfly communities within habitat patches we applied a transect length of 400 m (chapter 2). In the study on edge effects (chapter 3) transect length was 200 m, since we were limited by the edge length of habitat patches (pine stands, deciduous woodlands and firebreaks). Finally, for the study on deciduous woodlands (chapter 4) we applied a transect length increasing with woodland area in order to incorporate the habitat heterogeneity, but calculated a rarefied species richness based on the minimum transect length in the smallest woodlands (250 m).

1.10.2. Butterfly diversity measures

Biodiversity can be quantified in many ways and at different levels, for example by species richness and evenness measures or by indices of taxonomical, phylogenetic or functional diversity within or between sites (Heino et al., 2008; Mouchet et al., 2010; Purvis and Hector, 2000). Species richness represents the most often used measure of biodiversity. However, richness provides only limited information as sites with the same number of species can contain very different species or can have very different abundances per species. Analyzing abundance or presence of individual species may permit to identify variables affecting each species and to detect variables important to several species or with opposite effects on species. Nevertheless, if many species are analyzed, it may be difficult to adequately summarize the information. Analyzing community composition by multivariate ordination methods allows keeping species identities while relating communities to environmental variables. The use of species traits may further increase our understanding of ecological processes involved. For example the use of richness of particular species groups (e.g. number of sedentary species, of specialist species) can be much more informative than using total species richness (Öckinger et al., 2010; Villemey et al., 2015).

We used a large set of measures for the analyses of butterfly data: abundance or presence of individual species, species richness, composition of species communities and measures based on species traits or characteristics (community weighted mean (CWM) trait values, RLQ analyses linking traits to environmental variables via the species x sites matrix, richness of forest species and threatened species). For the analyses of the effects of habitat area and isolation on butterflies (chapter 4), we selected six traits considered to affect species sensitivity to habitat fragmentation: wing size, mobility, reproductive capacity, habitat range, thermal tolerance and larval host plant range. In chapter 5 we related 12 traits characterizing rarity, biogeographical distribution, body size, trophic guild, dispersal power, reproductive potential and phenology of three taxonomic groups (birds, carabid beetles and butterflies) to the same set of variables describing landscape composition and configuration.

1.11. Choice of local and landscape variables

1.11.1. Habitat quality

Habitat quality variables in our studies included variables quantifying essential resources needed by butterflies and variables characterizing vegetation structure and composition. Quantifying essential resources seems in many cases a good proxy for habitat quality (Mortelliti et al., 2010). Essential resources and conditions needed by butterflies are larval host plants, flowering nectar plants, vegetation structures for roosting, mate finding and hibernation, and micro-climatic conditions.

Presence and abundance of **larval host-plants** represent the most essential resource for butterflies. For studies on individual butterfly species the abundance of host plants often represents an important explanatory variable (Krauss et al., 2005; Sawchik et al., 2003). However, not only host plant abundance is important but also host plant growth form and growing conditions (Thomas et al., 2001). For studies on butterfly communities, host plant availability is more difficult to quantify since each species has one or more specific host plants. Moreover, for many butterfly species feeding on Poaceae host plant preferences are not well known. At the community level, host plant availability can be estimated by for example the percentage cover of larval host plants or the number of host plant species (Villemey et al., 2015).

We included the presence of host plants as explanatory variables in chapter 3 (edge habitats) and 4 (deciduous woodlands). Host plants used by butterflies were based on Lafranchis (2000) and field observations. Grasses were not identified to species, but their percentage cover was estimated. For the analyses of butterfly richness and community composition in deciduous woodland fragments (chapter 4), we identified dicot host plants at the species or genus level, while grasses other than *Molinia caerulea* and *Pseudarrhenatherum longifolium*, the two dominant species, were merged together into a single category. To reduce the number of explanatory host plant variables we performed a Principal Component Analysis (PCA) on the relative abundance of host plants, expressed as the proportion of transects per site with the host plant. The site positions on the first two axes of PCA were used to express variation in host plant composition among sites.

For most butterfly species **flowering nectar plants** represent an essential food resource for the adult stage. Different measures are used in literature to quantify nectar availability: from simple semi-quantitative estimates (e.g. no, low, medium or high flower abundance (Schneider and Fry, 2001)), percentage cover of flowering plants (Ouin et al., 2004), number of flowers (Clausen et al., 2001; Feber et al., 1996; Steffan-Dewenter and Tscharntke, 1997) to sophisticated methods weighting flower abundances by butterfly species' preferences (Krämer et al., 2012). In our studies we followed the method proposed by Clausen et al. (2001). Flower abundance was estimated per plant family or per plant species. The number of flower units was estimated in every section using the following abundance classes: 1-25, 26-50, 51-100, 101-200, 201-400, 401-800 and 800-1600 flower units. We noted only plant species known to be used by butterflies as nectar plants (Ebert and Rennwald 1991; van Halder personal observations).

Vegetation structure and **composition** reflect environmental conditions and historical factors, such as microclimatic conditions and land-use intensity (Sawchik et al., 2003). We estimated for our study sites the cover of dominant plant species in the herbaceous and shrub layer. Dominant plant species indicate for example variation in soil humidity and management.

1.11.2. Landscape mapping and landscape metrics

Land-use types in the two study areas were mapped in a GIS (Arcview 3.3, ESRI) using aerial colour photos with a resolution of 50 cm as background layer, followed by field verification. Twelve different land-use types that could be identified on these aerial photos and that seem ecologically relevant were mapped (see Figure 24):

- five classes of pine stands: herbaceous clearcuts, shrubby clearcuts, young pines (canopy height < 7 m), mid-class pines (canopy height 7-15 m) and older pines (canopy height >15 m),
- two semi-natural habitats: deciduous woodlands (isolated patches or riparian forests) and firebreaks (including powerlines),
- five other land-use types: hedgerows, meadows, crops, roads and urban areas.

Landscape metrics were calculated within circular buffers from the centre of the sampled plots, using Fragstats 3.3 in raster version and a cell size of 2.5 m (McGarigal et al., 2002, see Figure 28).

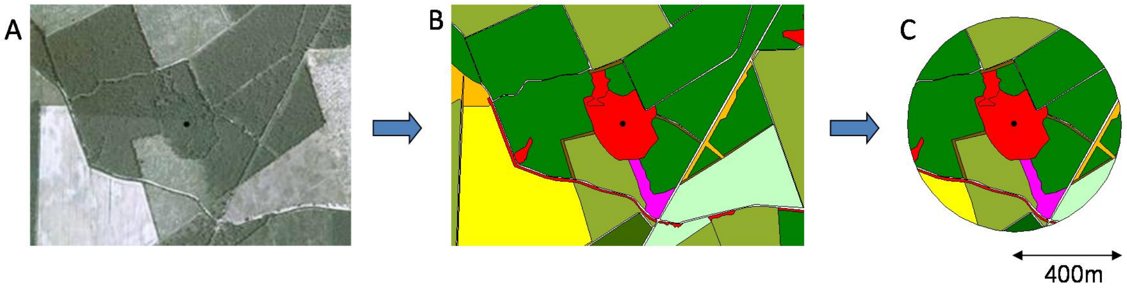

Figure 28. Procedure for calculation of landscape metrics. A) Aerial photo of the landscape around a sampled woodland (the center of the woodland is indicated with a dot). B) Landscape mapping based on 12 land-use types using aerial photos as background (see Figure 24 for legend). C) Around each sampled site a circular buffer was created for which landscape metrics were calculated in Fragstats (after rasterization, not shown in the figure).

Landscape composition was represented by the percentage cover of the seven main habitat types (i.e. the five classes of pine stands, deciduous woodlands and firebreaks). We also calculated several metrics reflecting landscape heterogeneity and configuration. We used the Shannon Diversity Index (SHDI), the Shannon Eveness Index (SHEI) and the Patch Richness Density (PRD) as metrics of landscape compositional heterogeneity and the SHAPE index (i.e. complexity of patch shape compared to a standard shape (square) of the same size), the Patch Density (PD) and Edge Density (ED) as metrics for landscape configuration (McGarigal et al., 2002).

For the study on deciduous woodlands (chapter 4) we mapped all the deciduous woodlands in a buffer of 1000 m around each site to calculate deciduous woodland area in a buffer of 500 and 1000 m and the area of the sampled fragment.

1.12. References chapter 1

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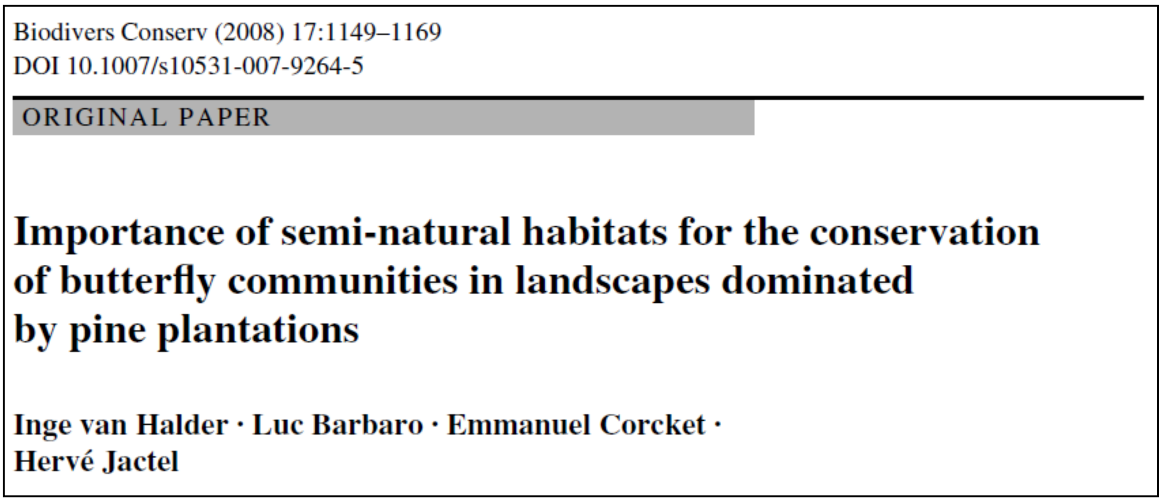
2. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations

Coenonympa oedippus



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ORIGINAL PAPER

Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations

Inge van Halder · Luc Barbaro · Emmanuel Corcket ·
Hervé Jactel

2.1. Résumé en français

L'importance des habitats semi-naturels pour la conservation des papillons de jour dans les paysages dominés par des plantations de pins

Inge van Halder, Luc Barbaro, Emmanuel Corcket & Hervé Jactel

Mots-clés : Papillons de jour, assemblages, forêts de feuillus, pare-feux, habitat, paysage, *Pinus pinaster*, forêts de plantations

A cause de leur gestion sylvicole intensive, de leur structure et de leur composition simplifiées, les plantations forestières sont considérées comme contribuant moins à la conservation de la biodiversité que les forêts semi-naturelles. Par contre il est admis que les forêts de plantation peuvent aider à l'amélioration de la biodiversité en servant d'habitats complémentaires, en augmentant la connectivité entre fragments de forêts semi-naturelles ou en assurant un rôle de tampon pour diminuer l'effet des perturbations anthropiques autour de ces habitats semi-naturels. La conservation de la biodiversité dans les paysages dominés par des forêts de plantation peut, par contre, aussi dépendre de la présence de milieux semi-naturels.

Nous avons utilisé les papillons de jour comme modèle biologique pour vérifier ces assertions. En particulier nous avons cherché à identifier les facteurs clés, à la fois au niveau local et au niveau du paysage, déterminant les patrons d'occurrence des espèces de papillons de jour dans les paysages dominés par les forêts de plantation. Les questions suivantes ont été posées :

- Est-ce que la richesse spécifique et la composition des communautés de papillons de jour diffèrent selon les types d'habitats présents dans un paysage de forêt de plantation ?
- Quelle est la contribution des habitats semi-naturels, comme les forêts de feuillus et les pare-feux, à la diversité en papillons de jour dans ces paysages ?
- Quelle est l'importance relative de la composition de la végétation, du type d'habitat et des caractéristiques du paysage pour la composition des communautés de papillons de jour ?

L'étude a été conduite dans le massif forestier des Landes de Gascogne dans le sud-ouest de la France. Ce massif constitue le plus grand massif de plantions en Europe avec un million d'hectares de peuplements purs de pin maritime (*Pinus pinaster*). Les forêts de feuillus sont rares et apparaissent comme des îlots de quelques hectares ou sous forme de ripisylves. Les milieux ouverts sont principalement constitués par des coupes rases, des pare-feux et des grandes zones de maïsiculture. Nous avons échantillonné les papillons de jour dans 83 parcelles appartenant à sept types d'habitats : cinq stades de la rotation sylvicole des plantations de pins (coupe-rases herbacées, coupes rases arbustives, jeunes pins, pins d'âge moyen et pins âgés), des forêts de feuillus et des pare-feux. Les effets des variables de qualité des patches d'habitat, du type d'habitat et de composition et configuration du paysage sur la richesse, la composition des assemblages et les espèces individuelles

de papillons ont été analysés avec des ANOVA, des Analyses Canoniques des Correspondances (ACC) partielles et par la méthode Indval.

Au total 44 espèces de papillons de jour ont été observées dans les 83 parcelles. La richesse et l'abondance en papillons étaient significativement plus élevées dans les pare-feux que dans les autres types de milieux (Figure 1). Parmi les 33 espèces avec plus de 5 individus observés, 18 avaient une valeur Indval significative: trois espèces étaient caractéristiques des forêts de feuillus et dix des pare-feux, par contre, aucune espèce n'était caractéristique des parcelles de pins. L'Analyse Factorielle des Correspondances (AFC, Figure 2) a montré sur le premier axe une nette séparation entre les assemblages présents dans les forêts de feuillus d'un côté et les plantations de pins et les pare-feux de l'autre. La sélection des variables au niveau du plot, du type d'habitat et du paysage en ACC a permis de sélectionner respectivement six, quatre et quatre variables significatives pour ces trois niveaux d'organisation. Ces variables au niveau plot, habitat et paysage expliquaient respectivement 27.5 %, 17.4% et 18.0 % de la variance dans la composition des communautés (Figure 3). La décomposition de la variance en effets indépendants et confondus pour ces trois niveaux a montré un effet indépendant de 12.8 %, 5.1 % et 6.7 % pour respectivement les variables plot, habitat et paysage (Figure 3).

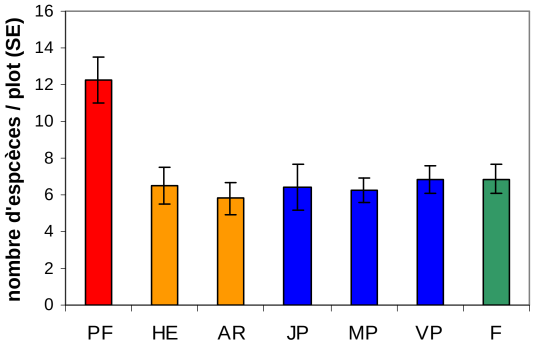

Figure1. Nombre moyen d'espèces par plot (± SE) dans les sept types de milieux. PF- pare-feux, HE – coupe-rases herbacées, AR – coupe-rases arbustives, JP – jeunes pins, MP- pins d'âge moyen, VP – vieux pins, F- forêts de feuillus.

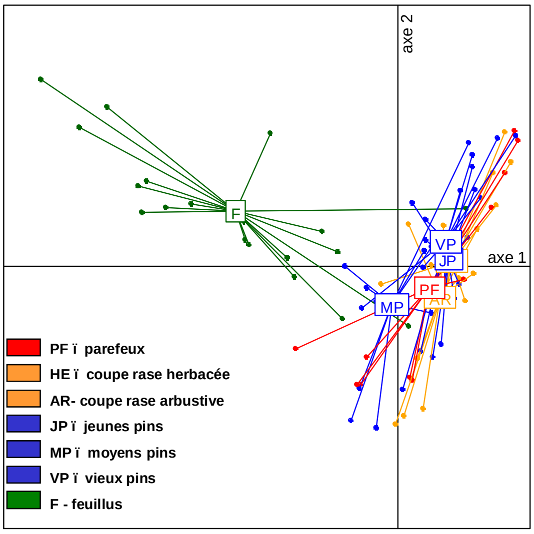

Figure 2. Position des sites sur les deux premiers axes de l'Analyse Factorielle de Correspondances.

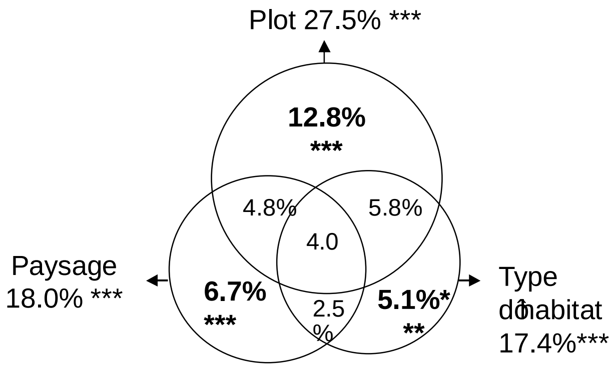

Figure 3 Décomposition de la variance dans les assemblages de papillons de jour expliquée par des variables au niveau plot, habitat et paysage.

Les résultats montrent donc **l'importance des milieux semi-naturels** dans les paysages dominés par des plantations de pins pour la conservation de la biodiversité des papillons. Les **pare-feux** et les **forêts de feuillus** se caractérisent par la présence d'espèces de papillons pas ou peu observées dans les plantations de pins, montrant une plus grande richesse spécifique dans les pare-feux que dans les autres types d'habitats. Malgré le fait que cette étude a été conduite dans un grand massif forestier, le nombre d'espèces forestières et leur abondance étaient faibles et ces espèces se trouvaient principalement dans les forêts de feuillus, indiquant que les plantations de pins ne sont pas un habitat favorable pour les papillons forestiers. Les espèces en régression en France ou en Europe étaient plus abondantes dans les pare-feux (par exemple *Coenomympha oedippus, Heteropterus morpheus* et *Euphydryas aurinia*), mais cependant n'étaient pas absentes des peuplements de pins. Les parcelles de pins hébergeaient une communauté de papillons en partie comparable à certains pare-feux, mais avec moins d'espèces. Les assemblages de papillons dans les pins peuvent donc être considérés comme des assemblages appauvris de ceux des pare-feux. Ces derniers sont probablement à leur tour une version appauvrie des assemblages de papillons des landes ouvertes qui existaient avant les travaux de drainage et la plantation massive des pins entreprises au XIXème siècle en Aquitaine.

La **composition de la végétation herbacée, liée directement à l'humidité de sol**, expliquait une partie importante de la composition des assemblages de papillons dans les pare-feux et les plantations de pins. Ce n'est donc pas l'âge du peuplement de pin qui est important pour les papillons, mais la composition de la végétation du sous-bois. La présence de certaines espèces de papillons à la fois dans les pare-feux et dans les parcelles de pins semble donc indiquer que les plantations de pins ont un rôle d'habitat de substitution ou de refuge pour ces papillons.

Les variables mesurées au niveau du plot et le type d'habitat expliquaient une partie importante de la variance dans la composition des assemblages de papillons, mais les variables paysages expliquaient également une partie indépendante avec notamment un effet indépendant du taux de recouvrement par les milieux semi-naturels, les forêts de feuillus et les pare-feux, ainsi que de la densité en lisières, confirmant donc l'importance des analyses multi-échelles pour expliquer les patrons de biodiversité.

Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations

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Abstract

While the area of plantation forests continues to increase worldwide, their contribution to the conservation of biodiversity is still controversial. There is a particular concern on the central role played by natural habitat remnants embedded within the plantation matrix in conserving species-rich insect communities. We surveyed butterflies in maritime pine plantation landscapes in south-western France in 83 plots belonging to seven habitat types (five successional stages of pine stands, native deciduous woodlands and herbaceous firebreaks). The effect of plot, habitat and landscape attributes on butterfly species richness, community composition and individual species were analysed with a General Linear Model (GLM), partial Canonical Correspondence Analysis (CCA) and the IndVal method. The most important factors determining butterfly diversity and community composition were the presence of semi-natural habitats (deciduous woodlands and firebreaks) at the landscape scale and the composition of understorey vegetation at the plot scale. Pure effects of plot variables explained the largest part of community variation (12.8%), but landscape factors explained an additional, independent part (6.7%). Firebreaks were characterized by a higher species richness and both firebreaks and deciduous woodlands harboured species not or rarely found in pine stands. Despite the forest-dominated landscape, typical forest butterflies were rare and mainly found in the deciduous woodlands. Threatened species, such as *Coenonympha oedippus* and *Euphydryas aurinia,* were found in pine stands and in firebreaks, but were more abundant in the latter. In the studied plantation forest, the conservation of butterflies depends mainly on the preservation of semi-natural habitats, an adequate understorey management and the maintenance of soil moisture levels.

Key words Butterflies, Communities, Deciduous woodlands, Firebreaks, Habitat, Landscape, *Pinus pinaster*, Plantation forests

2.2. Introduction

Plantation forests with their intensive silvicultural management and simplified structure and composition are often considered less valuable for biodiversity conservation than natural forests (Hartley, 2002). Many, but not all studies comparing plantations to more natural forests have indeed shown an impoverished flora and fauna in plantations (Carnus et al., 2006; Lindenmayer and Hobbs, 2004; Moore and Allen, 1999). However, forest management in plantation forests is not incompatible with biodiversity conservation and possibilities exist to enhance their biodiversity (Carey, 2003; Carnus et al., 2006; Hartley, 2002; Kerr, 1999). Apart from providing a habitat, plantation forests can also have beneficial effects as landscape matrix elements by increasing the connectivity of natural forest remnants (Aberg et al., 1995) or by acting as a buffer to mitigate negative edge effects for forest interior species (Aune et al., 2005; Fischer et al., 2006). Biodiversity conservation in plantation landscapes will however also depend on the presence of more natural habitat elements, such as wetlands or late successional stages of remnant forest, within the plantation matrix (Fischer et al., 2006; Lindenmayer and Hobbs, 2004).

Conserving biodiversity in plantation forests implies the identification of explanatory, environmental factors that determine patterns of species occurrences. Since species respond to environmental factors at different, interacting scales (from the micro-habitat and habitat to the landscape and regional scale) multi-scale approaches are required to analyse these causal mechanisms (Cushman and McGarigal, 2002; Wiens, 1989). In this study we analysed the effect of factors at both the local and landscape scale on butterfly diversity in pine plantation landscapes. Butterflies were chosen because they are easy to identify in surveys and include species with different habitat preferences and dispersal capacities and show therefore different responses to habitat and landscape features (Dennis, 1992; Thomas, 1995). Moreover, a large number of butterfly species are declining at an alarming rate through substantial parts of their European range and conservation measures are urgently needed (van Swaay and Warren, 1999).

During their life cycle most butterfly species need complementary resources (hostplants for larvae, nectar plants for adults, roosting-, resting- and overwintering-sites, favourable microclimatological conditions) resulting in very direct relationships with habitat characteristics such as vegetation composition and management (Dennis et al., 2003). For many taxa, including butterflies, habitat characteristics alone are often insufficient to predict species presence or abundance and landscape characteristics can provide additional explanatory information (Bergman et al., 2004; Jeanneret et al., 2003a; Krauss et al., 2003; Mazerolle and Villard, 1999; Stefanescu et al., 2004). Many butterfly studies conducted at the landscape scale have focussed on the effect of patch size and isolation and have used the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) or the metapopulation theory (Hanski, 1999) to explain species richness or population dynamics, respectively (Anthes et al., 2003; Baguette et al., 2000; Steffan-Dewenter and Tscharntke, 2000; Thomas and Harrison, 1992). Both theories assume clearly delimited habitats surrounded by uniformly unsuitable habitat (the landscape matrix). However landscape matrices are not entirely hostile and the ‘mosaic concept’ (Duelli, 1997; Wiens, 1995) can offer an alternative to explain species richness. In this concept species richness increases with the number of biotope types per unit area, the number of patches, the edge length and the proportion of natural and semi-natural areas

(Duelli, 1997). Many butterfly species are found along edges or use resources in different vegetation types (Dennis et al., 2006) thus supporting the mosaic concept. Positive effects of patch density on butterfly diversity has been demonstrated by Schneider and Fry (2001) and Debinski et al. (2001). Dunning et al. (1992) described these effects of landscape context in terms of landscape complementation and supplementation, corresponding to the use of patches with non-substitutable or substitutable resources, respectively. Landscape effects found to be linked with species diversity will also depend on the scale of the analysed landscape; shorter distances will be more related to landscape complementation / supplementation and mosaic concepts (Schneider and Fry, 2001; Weibull et al., 2000) and larger scales to metapopulation functioning and habitat thresholds (Bergman et al., 2004).

The aim of this study was therefore to identify key factors at both the habitat and landscape level that drive butterfly diversity in plantation forests, and that can be used by forest managers and landscape planners to maintain or restore butterfly diversity. We address the following questions:

- Do habitat types in a pine plantation landscape differ in butterfly species richness and composition?
- What is the contribution of semi-natural and open habitats such as oak woodland remnants and herbaceous firebreaks to butterfly diversity in pine plantation landscapes?
- What is the relative importance of understorey vegetation composition, habitat-type and landscape attributes on butterfly community composition?

2.3. Methods

Study area and plot selection

The study was carried out in South-West France in the 'Landes de Gascogne' (Figure 4), a region covering one million ha and dominated by plantations of native maritime pine (*Pinus pinaster*). Silvicultural management of the pine stands is intensive, including soil preparation and fertilisation before seeding or planting, mechanical understorey removal and four thinning operations within the 40-50 year rotation cycle (Trichet et al., 1999). Deciduous woodlands are rare and found along rivers or as scattered patches of a few hectares. They are generally dominated by *Quercus robur*, on dry sites by *Q. pyrenaica* and along rivers by *Alnus glutinosa* and *Q. robur.* Open areas in the landscape are mainly represented by large maize fields, pine clearcuts, firebreaks and powerlines.

The whole region is covered by nutrient poor, acid podzol soils with a pH of 3.5-5.5 (Trichet et al., 1999). Differences in soil moisture have an important effect on the understorey vegetation composition in forest stands: in wet conditions *Molinia caerulea* is dominant with presence of *Erica tetralix*, intermediate conditions are characterized by dominance of *Pteridium aquilinum* and *Ulex europaeus* and in dry condition *Calluna vulgaris* and *Erica cinerea* dominate (Timbal and Maizeret, 1998). Firebreaks and powerlines can have a heathland vegetation as described above or a grassland vegetation, dominated by for example *Holcus lanatus* or *Anthoxanthum odoratum*. Management of firebreaks and powerlines is very diverse. In the studied region the usefulness of firebreaks in preventing forest fires is considered doubtful and only firebreaks that are classified in a fire prevention scheme are mown once a year in summer. Other, private firebreaks are mown less often (every 4-8 years) or are progressively transformed to pine plantations. Management of powerlines is in general extensive (every 4-8 years) and aims at suppressing the regrowth of woody species, but in some cases they are mown annually. Firebreaks and powerlines typically have a width of about 15-100 m.

Within the 'Landes de Gascogne' two study sites were selected: Tagon (5000 ha), situated 35 km southwest of Bordeaux and Solferino (10500 ha), located 65 km to the south of Tagon (Figure 4). Both sites are dominated by maritime pine plantations, present similar types of soils, and include different degrees of landscape fragmentation and heterogeneity. A total of 83 plots were selected in the two sites (Figure 4, Table 1) belonging to seven different habitat types. These seven habitat types were defined a priori and represent the main land-use types within the forested landscape as well as being habitat types of ecological relevance to butterflies. Five of them were related to successional stages of maritime pine plantations: herbaceous clearcuts, shrubby clearcuts, young pines (canopy height < 7 m), mid-class pines (canopy height 7-15 m) and older pines (canopy height >15 m).

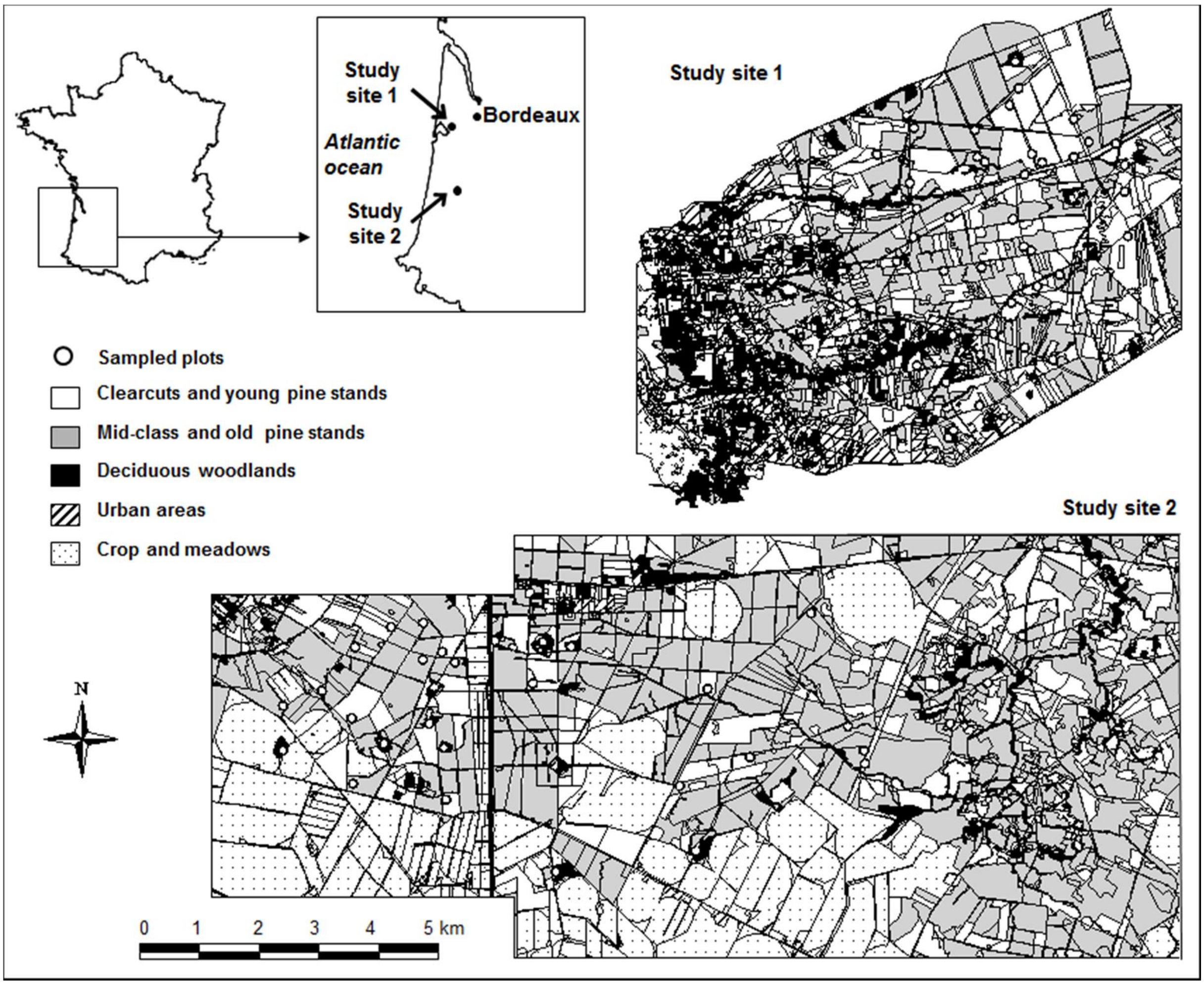

Figure 4. Map of the two study sites in the south-west of France and location of the sampled plots within each site. The polygon boundaries represent the edges of landscape elements such as stand edges or edges of roads. Firebreaks are the very narrow polygons between some stands or along some roads and at the scale of the figure cannot be separately indicated since they occupy only a small percentage of the total landscape.

The two other habitat types were deciduous woodlands (isolated patches or riparian forests) and firebreaks or powerlines (hereafter called firebreaks). Plots with different types of understorey vegetation (humid, mesic, dry) were selected for each habitat type.

Butterfly sampling

Butterflies were recorded in the 83 plots using the line-transect method (Pollard and Yates 1993). In each plot a transect of eight sections of 50 m long was laid out and butterflies were counted within 2.5 m on each side of the transect line and 5 m ahead of the recorder. Species were identified by sight or caught and released for species difficult to identify (e.g. *Thymelicus* species). Each plot was visited four times between May 14th and September 4th 2004. Surveys were conducted between 10:00 and 18:00 hours and only during appropriate weather conditions (temperature > 20°C, cloudless or just a few clouds and wind speed < Force 5 Beaufort). The order of the plots and habitat types surveyed was randomized per visiting period and visits to the two sites alternated. For data analysis the total number of individuals per species was pooled over the four visits and eight sections for each plot.

Butterfly species were classified as typical forest or non-forest species. Limits between forest and non-forest species are not strict, but we defined as forest species those whose adults and immature stages are more often found within forests than in open habitats (Ebert and Rennwald, 1991). We also attributed a European and national threat status to all native species, excluding migrants such as *Vanessa cardui* (van Swaay and Warren, 1999). For the European status we used the list of threatened species cited in the Red Data Book of European Butterflies (van Swaay and Warren, 1999). In this Data Book the IUCN criteria, which are based on population declines over a 10 year period, were adjusted to butterfly data using a roughly equivalent distribution decline over a 25 year period. Species with a decrease of at least 20% are classified as threatened, and depending on their total decrease and present distribution classed as critically endangered, endangered or vulnerable. Species with a decrease of 15-20% and a present distribution of less than 1% of Europe are also classified as vulnerable. For the French national status we calculated the distribution trend by dividing the number of departments where a species was not seen after 1980, but was present before 1980, by the total number of departments where the species was ever seen (Lafranchis, 2000). Species with a distribution decrease of at least 30% were classified as ‘nationally threatened’, assuming that these species are vulnerable at a national scale. We used a less severe threshold to compensate for the lack of data in several departments (Lafranchis, 2000). Butterfly species are named in the text are according to Karsholt and Razowski (1996).

Plot variables

We measured a set of potential explanatory variables at both the plot and landscape scale in order to relate butterfly species richness and community composition to environment. At the plot scale three types of variables were measured: flower abundance, vegetation composition of the herbaceous and shrub layer and soil moisture (Table 1). Flower abundance was measured to estimate the availability of nectar, the most common food source for adult butterflies in temperate areas (Ebert and Rennwald, 1991; Shreeve, 1992). Flower abundance was estimated during each of the four butterfly surveys using the method described by Clausen et al. (2001). Only plant species known to be used by butterflies as nectar plants were noted (Ebert and Rennwald 1991; van Halder personal observations). Flower abundance was estimated per plant family or per species for abundant and easily identifiable species. The number of flower units was estimated in every section using the following abundance classes: 1-25, 26-50, 51-100, 101-200, 201-400, 401-800 and 800-1600 flower units (Clausen et al., 2001). For data analysis the midvalues of each class were summed over the eight sections, the four visits and the different flower species or families. Total flower abundance was log-transformed to reduce the effect of outliers and because we hypothesized a non-linear relation between butterfly and flower abundance.

At the end of the field season understorey vegetation composition was recorded in a representative section within each plot. The vegetation was divided into a herbaceous layer (< 0.7 m) and a shrub layer (0.7 -7 m) and for each layer the % cover of the main vegetation components was estimated as the relative foliage area projected on a horizontal plane.

Soil moisture was estimated once between May and July 2004 at two points in each plot at a depth of 50 cm using a relative scale from 0 to 4, based on tactile and visual criteria. We used this estimation method because it can be used on soil samples extracted with an auger, a very easy and quick method, whereas measurements with a probe at 50 cm depth would have needed to dig a soil profile of at least 50 cm deep. We measured volumic soil moisture using a Theta Probe type ML2x (Delta-T Devices Ltd, Cambridge, United Kingdom) with 12 replications per class to test the relationship between moisture estimates and measures. There were significant changes in measured soil moisture between our relative classes (ANOVA, F = 78.4, $P < 0.001$). The scale from 0 to 4 corresponds to a mean soil moisture of 4.0%, 12.8%, 19.6%, 44.4% and 62.6%, respectively.

Landscape variables

Land-use types in the two study sites were mapped in a GIS (Arcview 3.3, ESRI) using aerial colour photos with a resolution of 50 cm as background layer. Photos dated from 2000 and 2002 for the Tagon and Solferino region respectively and patch attributes were verified in the field. Twelve different land-use types that could be identified on these aerial photos were mapped: the seven surveyed habitat types and five rarer land-use types: hedgerows, meadows, crops, roads and urban areas. Landscape metrics were calculated within circular buffers with a radius of 400 m (circa 50 ha), from the centre of the sampled plots, using Fragstats 3.3 in raster version and a cell size of 2.5 m (McGarigal et al., 2002). Since the surveyed patch is (partly) included in our buffer the calculated metrics represent a combination of patch and landscape characteristics (Fahrig, 2003). For most butterfly species in temperate areas 400 m is considered a moderate dispersal distance (Maes and Van Dyck, 1999) and could therefore reveal ecologically relevant landscape relations. Larger buffers were not analysed because overlap between buffers would increase collinearity of data. Within each buffer the percentage cover of the seven main habitat types was calculated as well as several metrics reflecting landscape heterogeneity and fragmentation (Table 1). We used the Shannon Diversity Index (SHDI), the Shannon Eveness Index (SHEI) and the Patch Richness Density (PRD) as metrics of landscape heterogeneity and the SHAPE index, the Patch Density (PD) and Edge Density (ED) as metrics for landscape fragmentation (McGarigal et al., 2002). Studies on birds, spiders and carabids in the same area have shown an effect of landscape composition and landscape structure (patch size, Edge Density and Shannon Diversity Index) on species composition and richness (Barbaro et al., 2005). Landscape effects on butterflies have been analysed in several studies showing an effect of landscape composition (Jeanneret et al., 2003a; Schneider and Fry, 2001; B. Söderström et al., 2001;

Stefanescu et al., 2004), landscape fragmentation (Schneider and Fry, 2001) and landscape heterogeneity (Jeanneret et al., 2003a; Krauss et al., 2003; Weibull et al., 2000).

Table 1 Plot and landscape variables used in GLM and CCA analyses. Mean values are given per habitat type. Abbreviations for habitat types: FB - firebreaks; PP1 - herbaceous clearcuts; PP2 - shrubby clearcuts; PP3 - young pine stands (< 7 m), PP4 - mid-class pine stands (7-15 m); PP5 - older pine stands (> 15 m); DW - deciduous woodlands. Landscape variables were measured in a 50 hectare circle (including the inventoried plot).

		FB	PP1	PP2	PP3	PP4	PP5	DW
Acronym	Description	12 plots	10 plots	10 plots	10 plots	11 plots	11 plots	19 plots
PLOT VARIABLES								
Nectar	log (number of flowers +1)	7.8	6.0	6.9	6.8	5.4	6.1	3.5
%Soil	% bare soil	13.7	29.1	28.2	9.6	26.1	16.4	33.4
%Paqu	% *Pteridium aquilinum*	1.5	12.5	3.0	17.2	7.3	16.8	20.2
%Mcae	% *Molinia caerulea*	28.3	42.3	22.7	29.2	35.6	52.5	10.4
%Grass	% other grass species	40.0	14.7	10.4	20.9	8.3	8.9	19.7
%Dicots	% herbaceous dicotyledons	7.2	2.1	1.7	0.9	1.4	1.0	1.0
%Erica	% Ericaceae <0.7m	6.9	5.1	15.7	15.4	12.7	7.4	1.0
%Umin	% *Ulex minor* <0.7m	1.3	1.5	1.5	9.0	1.4	2.0	0.1
%Oth-her	% other plants herbaceous layer	1.5	1.4	3.8	1.8	4.0	1.1	14.8
%Ueur	% *Ulex europaeus* >0.7m	1.2	1.4	14.1	3.1	7.6	2.7	0.3
%Faln	% *Frangula alnus* >0.7m	0.8	3.0	6.9	3.9	7.5	5.0	1.1
%Esco	% *Erica scoparia* >0.7m	0.6	0.3	1.9	1.2	3.8	6.5	0.8
%Oth-shrub	% other shrubs >0.7m	3.2	1.7	5.8	0.5	2.5	1.5	20.3
Moisture	Soil moisture at 50 cm (classes 0-4)	1.7	2.2	1.4	1.7	1.5	1.8	1.3
LANDSCAPE VARIABLES								
%FB	% firebreaks	7.2	1.1	1.9	2.2	3.2	2.0	2.1
%PP1	% herbaceous clearcuts	1.7	27.0	3.1	2.1	1.7	4.4	6.4
%PP2	% shrubby clearcuts	16.0	7.9	22.2	8.1	4.4	9.2	8.0
%PP3	% young pine stands (< 7 m)	26.8	11.1	15.6	33.2	10.0	18.2	14.6
%PP4	% mid-class pine stands (7-15 m)	26.2	28.6	21.1	33.5	55.7	21.0	16.5
%PP5	% older pine stands (> 15 m)	10.6	17.4	27.8	14.0	13.9	32.1	17.6
%DW	% deciduous/mixed woodland	6.9	2.6	4.7	1.5	3.0	2.4	16.5
SHDI	Shannon Diversity Index	1.6	1.4	1.5	1.4	1.2	1.5	1.6
SHEI	Shannon Eveness Index	0.75	0.71	0.74	0.68	0.60	0.75	0.73
PRD	Patch Richness Density	15.9	14.5	14.5	14.7	14.1	14.8	17.8
SHAPE	SHAPE index	2.1	1.9	2.0	1.9	1.9	1.9	2.0
ED	Edge Density (edge length in m / ha)	229.3	180.5	203.1	193.3	184.9	193.2	224.8
PD	Patch Density (patches / 100 ha)	56.0	41.8	49.3	46.9	40.7	44.5	57.0

Data analysis

Analyses were performed at different levels of biodiversity (species richness, single species abundances and composition of species assemblages) using hierarchical sets of explanatory variables: habitat type, plot variables and landscape variables. The effect of habitat type on number of species and total abundance of butterflies was tested by a one-way ANOVA, followed by Tukey's post hoc test. Total abundance of butterflies was log-transformed to improve normality of residuals. Species richness was analysed with a general linear model (GLM), using site, habitat and their interaction as categorical variables, and plot and landscape variables as continuous variables. Quadratic terms of plot and landscape variables were added to examine the possibility of curvilinear relationships between explanatory variables and species richness. We used a forward stepwise selection procedure ($p < 0.05$ for inclusion) to build the model. The possible interaction between selected categorical and continuous variables was tested in a forward procedure with the selected variables and their interaction.

To identify species characteristic for a habitat type or a group of habitat types we used the Indicator Value (IndVal) method (Dufrêne and Legendre, 1997). Indicator species can be defined as species found mostly in a certain habitat type and present in the majority of sites of that type. To incorporate these two criteria the IndVal index multiplies the relative abundance of a species in a habitat (mean abundance in a habitat divided by the sum of mean abundances in all habitats) with the frequency of occurrence in that habitat. The index is calculated for each habitat and the indicator value of a species corresponds to the largest IndVal value observed over the different habitats. The index is maximum (100%) when the individuals of a species are only observed in one habitat type and in all sites of that habitat. The indicator value of a species can be calculated for each level of a hierarchic site typology. The level where the species reaches its maximum IndVal index can be considered as the 'best' clustering level for that species (Dufrêne and Legendre, 1997). This procedure distinguishes between generalist species (maximum IndVal at a higher cluster level) and stenotopic species (maximum at lower levels). In our Indval analysis we used a hierarchic site typology based on the habitat types we had distinguished a priori. The clustering of groups in the hierarchy was based on their stand structure similarity. The first level groups all sites and permits identification of species that have higher indicator values for all samples than for any sample subset (generalist species). The second level separates open habitats from forested habitats, in the next steps the open habitats are separated in herbaceous and shrubby habitats, the forested habitats in pine stands and deciduous woodlands and so on (see Figure 6 for separations in further steps). This classification tests if species are characteristic for a specific clustering of predefined habitat types. The statistical significance of the index was estimated at each level of the hierarchy by a random reallocation procedure of plots among plot groups based on 999 permutations (Dufrêne and Legendre, 1997). Species present with less than five individuals were excluded from analysis.

Canonical Correspondence Analysis (CCA) was used to relate environmental variables to species assemblages (Palmer, 1993; Ter Braak, 1986). CCA is an ordination technique for multivariate direct gradient analysis in which the ordination axes of a Correspondence Analysis (CA) are constrained to be linear combinations of the environmental variables (Ter Braak, 1986). The % of variance in the species data set that is 'explained' by the environmental variables can be calculated by dividing the inertia of the canonical axes by the total inertia of the CA and this % represents an overall method of CCA fit. We tested the explanatory effects of three sets of variables in separate CCA analyses: the 7 habitat types, the 14 plot variables and the 13 landscape variables (see Table 1). For each set significant variables were selected in a forward stepwise procedure based on the additional variation explained by each variable ($P<0.05$ for inclusion). Next, we combined the selected variables in one CCA model and calculated the variation explained independently and jointly by the different sets of variables by performing several partial CCA analyses (Borcard et al., 1992; Cushman and McGarigal, 2002). In a partial CCA the pure effect of a variable or a group of variables is calculated after eliminating the variance due to other variables (the covariables). The different parts of the variation partitioning were calculated following the formulas given by Cushman and McGarigal (2002). Finally, we determined for each variable if it explained a significant part of variation when the variables in the two other subsets were used as covariables. Significance of the additional effect of each variable during the forward selection procedure and of the different (partial) CCA models was tested with 999

Monte Carlo permutations. In CA and (partial) CCA rare species represented by less than five individuals were omitted (Jongman et al., 1995). ANOVA and GLM were calculated with STATISTICA 7.1, CA and (partial) CCA with CANOCO 4.5 software.

2.4. Results

Species richness and abundance of individual species

A total of 2750 individuals belonging to 44 species were recorded in the 83 plots (see Table 2). The number of species varied from 2 to 22 per plot and the number of individuals from 2 to 154. Most abundant species, with more than 200 individuals, were in decreasing order *Pyronia tithonus*, *Maniola jurtina, Coenonympha oedippus*, *Lycaena phlaeas*, *Minois dryas*, *Coenonympha pamphilus* and *Cupido argiades*. Among the 44 recorded species seven can be characterized as typical forest-species: *Gonepteryx rhamni*, *Neozephyrus quercus*, *Satyrium ilicis, Limenitis camilla*, *Limenitis reducta*, *Argynnis paphia* and *Pararge aegeria* (Ebert and Rennwald, 1991). Only two of them (*P. aegeria* and *G. rhamni*) were relatively abundant (181 and 95 individuals respectively), for all others less than 15 individuals were observed. Two species are listed as threatened in Europe: *C. oedippus* (critically endangered) and *Euphydryas aurinia* (vulnerable) (van Swaay and Warren, 1999). With 236 and 118 individuals respectively these two species belong to the 10 most common species observed in this study. Seven species can be considered as nationally threatened: *Heteropterus morpheus, Boloria selene*, *Arethusana arethusa, Hipparchia statilinus*, *Hipparchia semele*, *M. dryas* and *C. oedippus* (Table 2).

The mean species richness was significantly higher in the firebreaks than in all other habitat types (ANOVA, N=83, F=5.32, *P*<0.001, Figure 5). The total abundance showed the same pattern with a significantly higher mean number of individuals in the firebreaks (81.6 ± 11.7 individuals/plot (mean ± SE)) than in the other habitats (mean abundance varying from 20.2 ± 4.4 to 30.7 ± 7.9; ANOVA, N=83, F=5.53, *P*<0.001). The deciduous woodland patches had the highest mean richness of typical

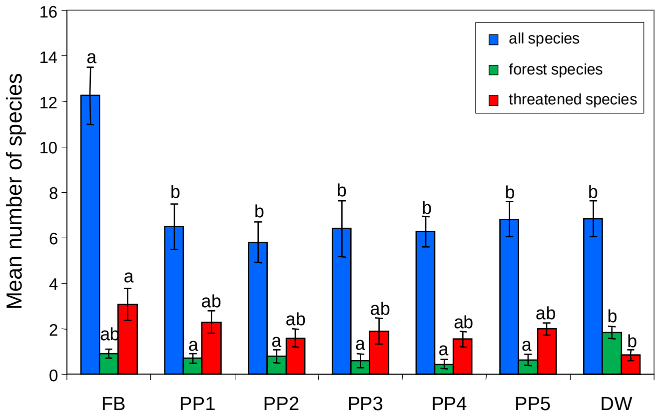

Figure 5. Mean species richness (± standard error) per habitat type of all butterfly species, forest species and threatened species. Bars of the same colour sharing no letter are significantly different (Tukey test, *P*<0.05). Habitat types: FB - firebreaks, PP1 - herbaceous clearcuts, PP2 - shrubby clearcuts, PP3 - young pine stands, PP4 - mid-class pine stands, PP5 - older pine stands, DW - deciduous woodlands.

Table 2. List of butterfly species observed in the 83 plots, the total number of observed individuals per species, the mean number of individuals per habitat type, their European and national threat status and their classification as a forest species. Species are ordered by their total abundance. Abbreviations for habitat types: FB - firebreaks; PP1 - herbaceous clearcuts; PP2 - shrubby clearcuts; PP3 - young pine stands (< 7 m), PP4 - mid-class pine stands (7-15 m); PP5 - older pine stands (> 15 m); DW - deciduous woodlands. European threat status: CR = Critically Endangered, VU = Vulnerable; National threat status (in France): T = Threatened.

Species	Total abundance	FB	PP1	PP2	PP3	PP4	PP5	DW	European threat status	National threat status	forest species
Pyronia tithonus	469	11.5	1.4	2.2	9.7	6.7	5.6	3.3			
Maniola jurtina	239	7.8	0.3	0.3	0.7	2.5	0.5	5.2			
Coenonympha oedippus	236	5.3	5.5	2.2	3.6	0.6	4.5	0.2	CR	T	
Lycaena phlaeas	227	6.4	0.7	1.6	0.9	4.7	4.1	1.1			
Minois dryas	218	4.8	3.9	3.6	3.6	1.7	2.6	0.1		T	
Coenonympha pamphilus	217	5.8	3.1	4.5	3.5	0.8	1.6	0.5			
Cupido argiades	202	11.3	1.7	1.5	2.8	0.1	0.5	0.1			
Pararge aegeria	181	0.0	0.0	0.0	0.1	0.3	0.1	9.3			forest
Euphydryas aurinia	118	7.2	0.7	0.2	0.6	0.1	0.5	0.6	VU		
Gonepteryx rhamni	95	1.3	1.5	0.8	1.2	1.2	0.6	1.3			forest
Hipparchia statilinus	79	3.2	0.3	1.2	0.3	0.3	1.7	0.1		T	
Heteropterus morpheus	56	1.9	0.6	0.7	1.0	0.5	0.4	0.1		T	
Aricia agestis	46	0.4	0.3	0.0	0.0	0.7	0.9	1.1			
Ochlodes venata	46	0.2	0.2	0.1	1.0	0.5	1.2	0.6			
Coenonympha arcania	45	0.0	0.1	0.0	0.7	0.6	0.9	1.1			
Polyommatus icarus	43	2.7	0.0	0.3	0.1	0.1	0.2	0.2			
Thymelicus lineola	37	2.8	0.0	0.0	0.1	0.0	0.0	0.2			
Hipparchia semele	30	0.2	0.2	0.0	0.1	0.9	0.2	0.7		T	
Melitaea cinxia	17	1.4	0.0	0.0	0.0	0.0	0.0	0.0			
Colias croceus	16	1.2	0.0	0.2	0.0	0.0	0.0	0.0			
Limenitis reducta	15	0.4	0.1	0.2	0.0	0.0	0.0	0.4			forest
Boloria selene	12	0.8	0.0	0.0	0.0	0.0	0.0	0.2		T	
Argynnis paphia	11	0.0	0.0	0.1	0.0	0.0	0.0	0.5			forest
Lycaena alciphron	11	0.1	0.1	0.1	0.0	0.0	0.5	0.1			
Brintesia circe	10	0.3	0.1	0.1	0.0	0.0	0.2	0.1			
Thymelicus sylvestris	8	0.5	0.0	0.0	0.2	0.0	0.0	0.0			
Callophrys rubi	7	0.2	0.0	0.1	0.2	0.2	0.0	0.0			
Melitaea athalia	7	0.1	0.0	0.0	0.0	0.0	0.3	0.2			
Pyrgus malvoides	7	0.5	0.1	0.0	0.0	0.0	0.0	0.0			
Satyrium ilicis	7	0.1	0.0	0.1	0.1	0.0	0.4	0.0			forest
Arethusana arethusa	5	0.3	0.0	0.0	0.1	0.0	0.0	0.0		T	
Neozephyrus quercus	5	0.0	0.0	0.0	0.0	0.0	0.0	0.3			forest
Pieris rapae	5	0.1	0.0	0.1	0.0	0.0	0.0	0.2			
Lampides boeticus	4	0.1	0.2	0.0	0.1	0.0	0.0	0.0			
Erynnis tages	3	0.2	0.0	0.0	0.0	0.0	0.0	0.1			
Pieris napi	3	0.0	0.0	0.0	0.0	0.0	0.0	0.2			
Vanessa atalanta	3	0.0	0.0	0.0	0.0	0.0	0.0	0.2			
Boloria dia	2	0.2	0.0	0.0	0.0	0.0	0.0	0.0			
Celastrina argiolus	2	0.0	0.0	0.0	0.0	0.1	0.0	0.1			
Iphiclides podalirius	2	0.2	0.0	0.0	0.0	0.0	0.0	0.0			
Lasiommata megera	1	0.0	0.0	0.0	0.0	0.0	0.0	0.1			
Limenitis camilla	1	0.0	0.0	0.0	0.0	0.0	0.0	0.1			forest
Pieris brassicae	1	0.0	0.0	0.0	0.0	0.0	0.0	0.1			
Vanessa cardui	1	0.0	0.0	0.0	0.0	0.0	0.0	0.1			

forest species (Figure 5), which was significantly higher than that of the other habitat types (ANOVA, N=83, F=4.37, *P*<0.001), with the exception of the firebreaks. The number of threatened species was significantly higher in the firebreaks than in the deciduous woodland patches (ANOVA, N=83, F=3.09, *P*=0.009, Figure 5), but did not differ significantly from that in the pine stands. Forward selection of variables in GLM resulted in the selection of both habitat and landscape variables that explained 47.1% of species richness variation (F=7.22 , *P*<0.001). The mean species richness per plot depended on the habitat type and was positively correlated with the availability of nectar in the understorey vegetation of the plot and the % cover of young pine stands (quadratic term) in the surrounding landscape and negatively correlated with the % herbaceous clearcuts in the landscape. In a forward selection procedure of these variables and the three interactions between habitat and the continuous variables no interaction terms were selected.

Among the 33 species analysed 18 had a significant IndVal index at one or several levels of the typology and eight species had their maximum value at the first level regrouping all plots (Figure 6). Three species had their maximum value in deciduous woodlands and 10 species in firebreaks. Three species were characteristic for open sites and two for forested sites, but no species were characteristic for pine stands at lower levels of the hierarchic typology (Figure 6).

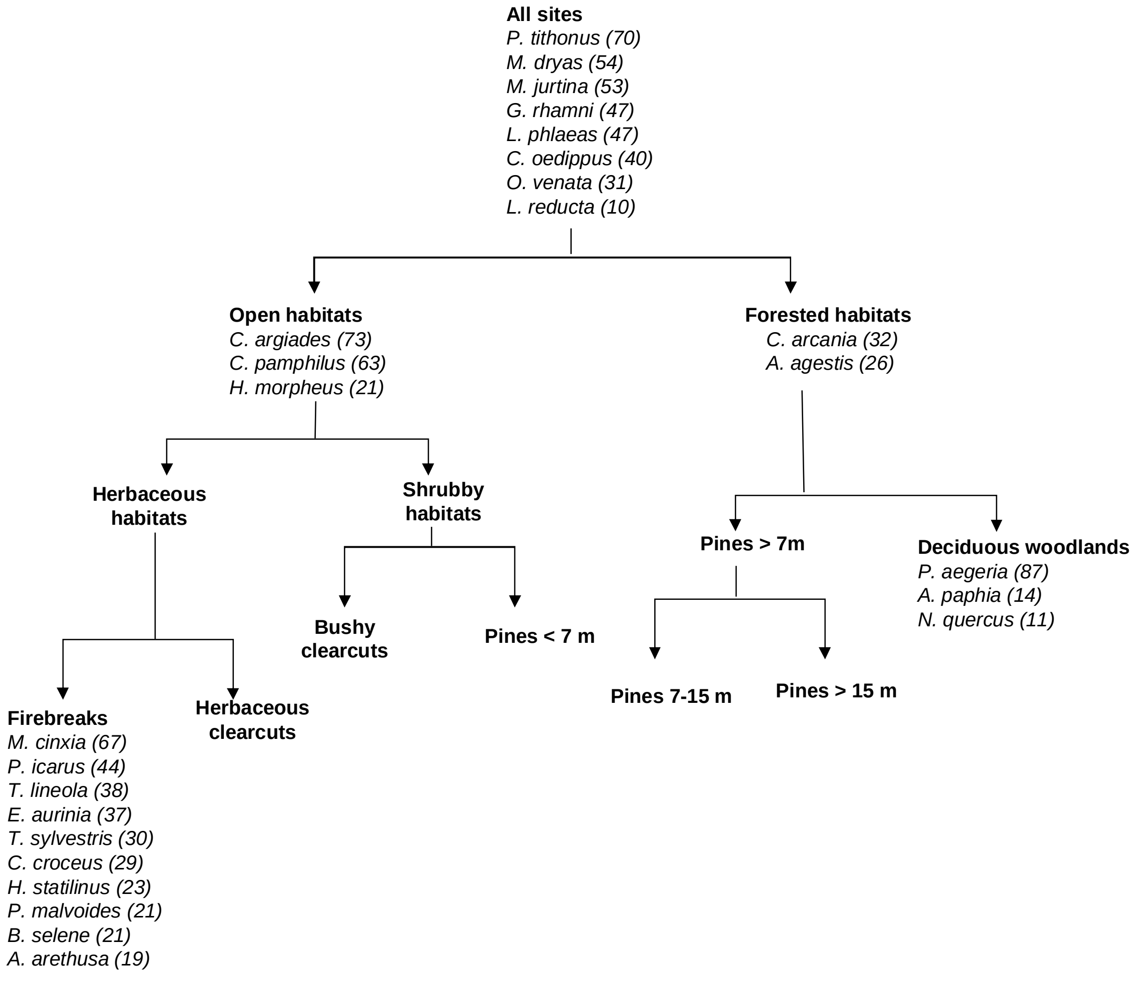

Figure 6. Indicator species for the different levels of the hierarchic site typology. Species are only mentioned at the level where they have their maximum, significant indicator value (indicator value between parentheses).

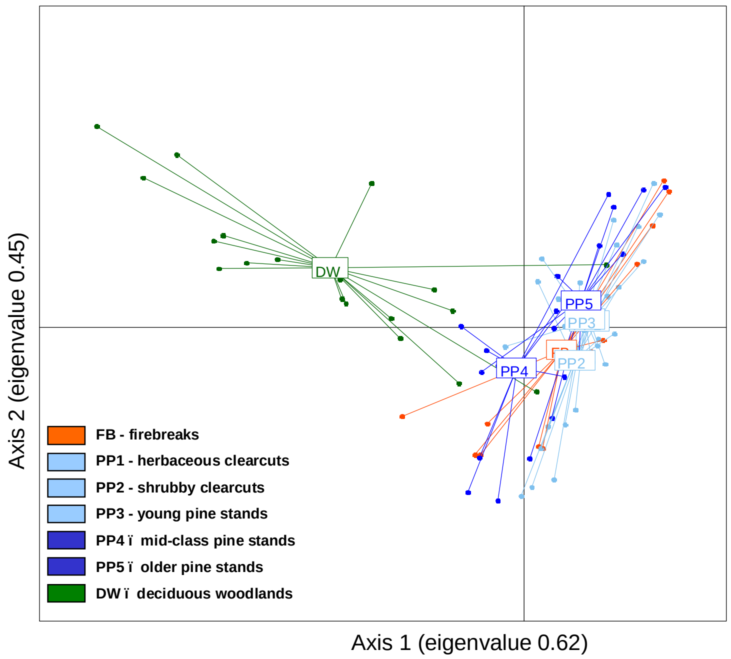

Figure 7. Correspondence Analysis ordination of the 83 inventoried plots (axes 1 and 2). The position of the name of each habitat type indicates the mean position of plots belonging to that habitat type. Different colours indicate the position of the different plot types.

Composition of species communities

The eigenvalues of the first two axes of a Correspondence Analysis (CA) on a 33 species × 83 plots matrix, were respectively 0.62 and 0.45; further axes had an eigenvalue of 0.29 or less (total inertia of CA was 3.83). The first axis separated the deciduous woodland plots from the other plots; the second axis did not show a clear separation between the different pine stands, clearcuts and firebreaks (Figure 7).

In the CCA with seven habitat types as environmental variables, three significant variables were retained (Table 3), which explained together 17.4% of total CA inertia (*P*=0.001). The first axis (eigenvalue 0.44) was correlated with the deciduous woodland habitat; the second axis was mainly related to firebreaks and had an eigenvalue of only 0.16.

In the CCA with 14 plot variables as environmental variables, six significant variables (Table 3) were retained by the forward selection procedure, which explained 27.5% of total variation (*P*=0.001). The eigenvalues of the first two axes were 0.45 and 0.33, respectively. The second axis opposed sites dominated by *M. caerulea* to sites with a high cover of herbaceous dicotyledons and *U. europaeus*, and a higher nectar abundance.

Forward selection procedures of landscape variables in CCA resulted in the selection of four significant landscape variables (Table 3), which explained 18.0% of total variation (*P*=0.001). The first two CCA axes had eigenvalues of 0.28 and 0.19. The first axis was correlated with the amount of deciduous woodlands in the landscape, the second axis opposed landscapes with a high cover of firebreaks to landscapes with a high cover of shrubby clearcuts.

Canonical Correspondence Analysis with these 13 selected variables combined explained 41.7% of species variation (*P*=0.001). Examination of the CCA plot (Figure 8) shows that the first axis opposed forest species such as *P. aegeria, A. paphia, N. quercus* and *L. reducta* which were associated with deciduous woodlands (DW and %DW) to species found in pine stands and firebreaks (for example *C. oedippus*, *M. dryas* and *C. argiades*). Best correlated with the second axis were the percentage cover of *M. caerulea* (%Mcae) in the plot and the percentage shrubby clearcuts (%PP2) in the landscape on the positive side of this axis and the percentage cover of herbaceous dicotyledons (%Dicots), of *U. europaeus* (%Ueur), the flower abundance (Nectar) and the percentage of firebreaks in the landscape (%FB) on the negative side. The second axis is therefore mainly correlated with the vegetation composition in pine stands and firebreaks. Species such as *C. oedippus, H. morpheus* and *M. dryas* were found in open pine stands and firebreaks with a high cover of *M. caerulea* and located in landscapes with a high cover of clearcuts. Species at the opposite end of the second axis were more abundant in stands with *U. europaeus* or were found in plots (mostly firebreaks) with higher % dicotyledons. The third axis (eigenvalue 0.21) opposed the firebreaks (axis positively correlated with FB, %FB and ED) to the pine stands (correlated with PP4, %Ueur). Positively associated with this axis were for example *E. aurinia, T.lineola* and *Melitaea cinxia.*

Table 3 Selected variables per variable subset in order of selection during the stepwise selection procedure in CCA, the additional variance explained by each variable at the time of inclusion, the % variance explained by each variable subset and the % variation explained by each variable using the variables in the two other subsets as covariables (partial CCA) and the associated probability (*P*). ns - not significant (*P* > 0.05).

Variable	Additional % explained in forward selection	% variation explained per variable set	% explained when 2 other subsets used as covariables	*P*
HABITAT TYPE		17.4		
DW (deciduous woodlands)	11.2		1.9	0.002
FB (firebreaks)	4.2		2.2	0.001
PP4 (mid-class pine stands)	1.9		1.0	ns
PLOT VARIABLES		27.5		
%Mcae (% *Molinia caerulea)*	9.3		5.1	0.001
%Oth-shrub (% other shrubs)	8.0		1.8	0.018
Nectar	4.0		1.9	0.007
%Ueur (% *Ulex europaeus)*	2.4		2.7	0.001
%Paqu (% *Pteridium aquilinum)*	2.1		2.1	0.006
%Dicots (% herbaceous dicotyledons)	1.7		2.5	0.002
LANDSCAPE VARIABLES		18.0		
%DW (% deciduous/mixed woodlands)	6.8		2.4	0.003
%PP2 (% shrubby clearcuts)	5.1		1.0	ns
%FB (% firebreaks)	3.9		1.6	0.025
ED (Edge Density)	2.2		2.3	0.002

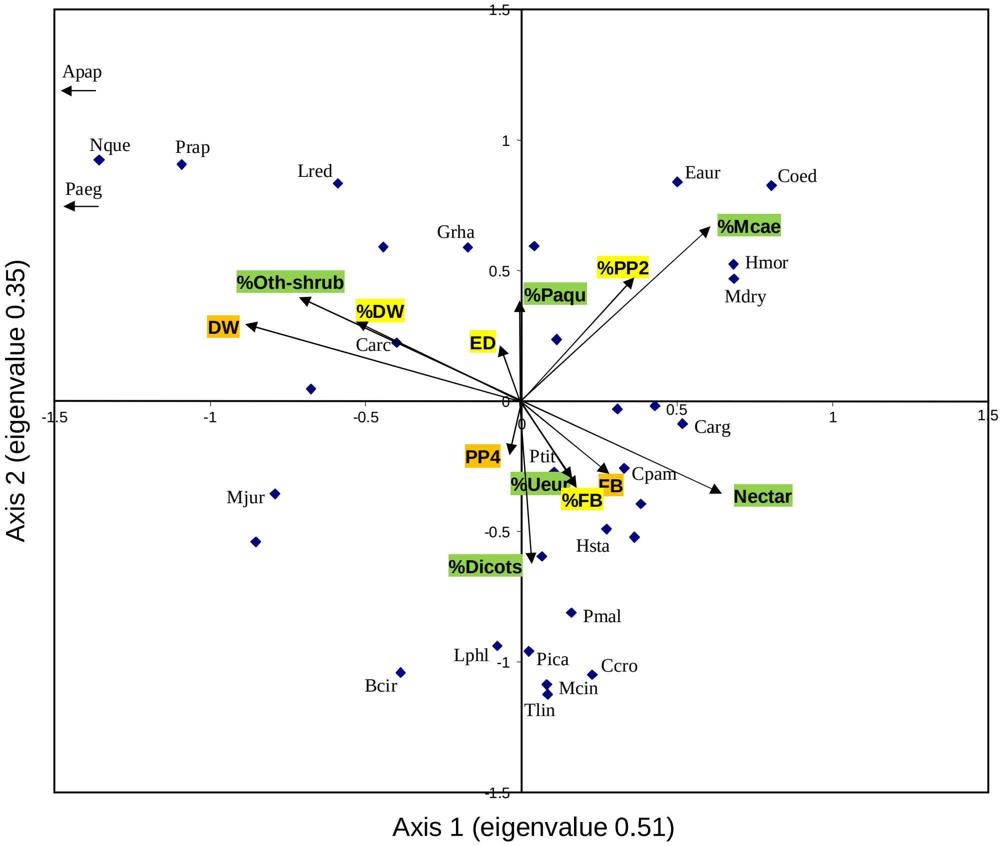

Figure 8. Canonical Correspondence Analysis ordination biplot (axes 1 and 2) with plot (green), habitat (orange) and landscape (yellow) variables represented by arrows and butterfly species by diamonds. Names of butterfly species are indicated only for species that are explained for more than 25% by the CCA. For legend of environmental variables see Table 1. Butterfly species: Apap: *Argynnis paphia;* Bcir*: Brintesia circe;* Carc: *Coenonympha arcania;* Carg: *Cupido argiades;* Ccro: *Colias croceus;* Coed: *Coenonympha oedippus;* Cpam: *Coenonympha pamphilus;* Eaur: *Euphydryas aurinia;* Grha: *Gonepteryx rhamni;* Hmor: *Heteropterus morpheus;* Hsta: *Hipparchia statilinus;* Lphl: *Lycaena phlaeas;* Lred: *Limenitis reducta;* Mcin: *Melitaea cinxia*; Mdry: *Minois dryas;* Mjur: *Maniola jurtina;* Nque: *Neozephyrus quercus;* Paeg: *Pararge aegeria*; Pica*: Polyommatus icarus;* Pmal: *Pyrgus malvoides*; Prap*: Pieris rapae;* Ptit: *Pyronia tithonus;* Tlin: *Thymelicus lineola.*

The decomposition of the variation in independent and confounded effects of the three variable sub-sets is shown in Figure 9. The pure effects of plot variables, habitat-types and landscape features accounted for 12.8%, 5.1% and 6.7% of variation respectively (all significant *P*=0.001). All variable sub-sets provided an independent, additional contribution to the explained variation, but the independent effect of plot variables was the most important. Analysis of the independent effect of each variable, after controlling for the variation explained by the other two subsets, revealed a significant effect of most variables (Table 3). Only the habitat type mid-class pines (PP4) and the landscape variable % shrubby clearcuts (%PP2) were no longer significant.

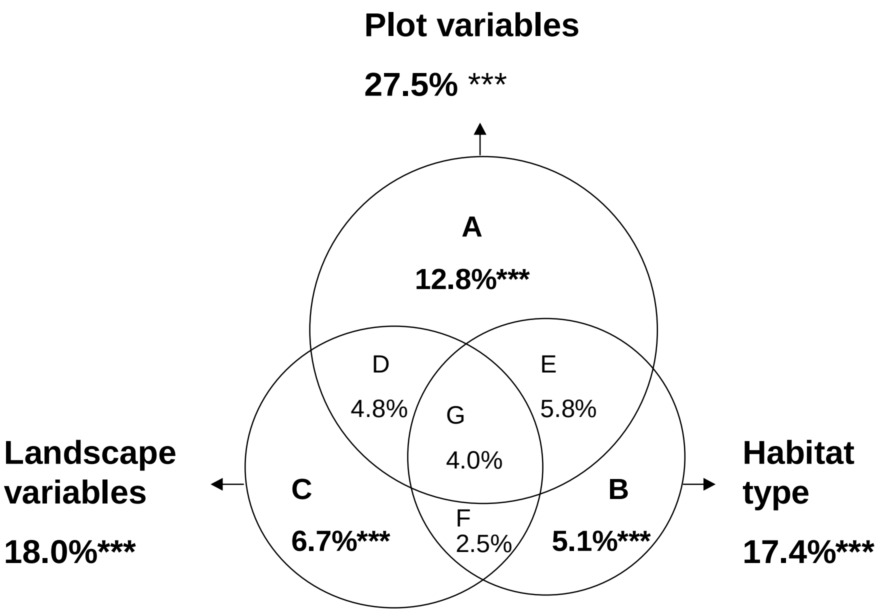

Figure 9. Decomposition of the variance in butterfly community structure explained by plot variables, habitat type and landscape variables in independent and confounded effects using several partial CCA's. Parts A, B and C represent the independent effects of plot, habitat and landscape variables, respectively; parts D, E, F and G indicate the joint effects. Significance levels are based on 999 Monte Carlo permutations: * *P*=0.001. The area of each circle is proportional to the variance explained by that group of variables. The total variance explained by the three sets of variables is 41.7 %.**

2.5. Discussion

Conserving biodiversity in plantation forests is becoming increasingly necessary because the area of planted forests continues to increase worldwide. In Europe, for example, the area of plantation forests augmented from 8.6 to 10.5 million hectares in the period of 1990-2005 (FAO, 2007). One conservation option is to improve biodiversity within stands by adapting stand management (Kerr, 1999; Lindenmayer and Hobbs, 2004). However, large-scale intensive stand management may impede the presence of many species, and the role of semi-natural habitat remnants within plantation landscapes may be essential (Fischer et al., 2006; Lindenmayer and Hobbs, 2004).

Importance of semi-natural habitats in plantation landscapes

This study confirms the importance of semi-natural habitats for butterflies in pine plantation landscapes. Both herbaceous firebreaks and deciduous woodlands were characterized by the presence of butterfly species not or rarely found in pine stands. Firebreaks were more species rich than the other habitat types and several butterfly species were almost exclusively found in firebreaks (e.g. *M. cinxia, P. icarus, T. lineola* and *E. aurinia*). The higher species richness of firebreaks might be largely attributable to their more diverse herbaceous vegetation, providing a greater and more diverse flower abundance (nectar) and hostplants not or rarely found in forest stands, such as *Plantago lanceolata* and herbaceous Fabaceae. Microclimate and especially high insolation alone does not seem to explain differences in butterfly richness since open areas such as clearcuts had a lower species richness than firebreaks.

Deciduous woodlands were also characterized by the presence of several characteristic species. *P. aegeria* was very typical for deciduous plots and together with *A. paphia* and *N. quercus* formed a group of species associated with deciduous woodlands. Although our study was performed in a well-forested region the number and abundance of typical forest species was low and these species were mainly present in deciduous woodland patches. This study confirms thereby the fact that coniferous forests do not represent a suitable habitat type for most forest butterflies (Ebert and Rennwald, 1991). Deciduous woodlands, on the contrary, provide hostplants for butterfly species feeding on broadleaved trees (e.g. *Quercus* sp. for *N. quercus*), have a more diverse herbaceous vegetation (with *Viola* sp. for *A. paphia*), offer a more varied structure for mate finding behaviour and probably provide more spatial variation in microclimate than pine plantations. These differences between deciduous woodlands and pine stands are due to their different tree composition but also to their different management. Plantation stands are typically characterized by a uniform and intensive management, whereas management of deciduous woodlands is more variable in time and space allowing a greater structural diversity.

Although the butterfly communities of pine stands seem to resemble to those of firebreaks (Figure 7), they harbour only half the number of species compared to firebreaks and no characteristic species. Apparently butterfly communities of pine stands represent an impoverished version of firebreak communities. The different successional stages of pine stands show no clear differences in butterfly community composition but several species (e.g. *C. oedippus*, *M. dryas* and *O. venata*) were less abundant in mid-class pines than in young and older pine stands because of higher canopy cover.

Relative effects of plot and landscape variables

Comparing the independent effect of plot, habitat and landscape variables revealed clearly the important effect of understorey vegetation on butterfly communities. Butterfly species show preferences for certain vegetation types and specific growing conditions of their hostplants and it is therefore logical that local factors are the most important for this taxonomic group (Thomas et al., 2001). The composition of understorey vegetation explained differences in butterfly community structure that were not explained by habitat type. The most important plot variable was the *M. caerulea* cover. This grass species dominates in sites with a high soil moisture and the second axis of the CCA is explained by a gradient in vegetation composition related to soil moisture. A group of species (*C. oedippus*, *H. morpheus* and *M. dryas*) was positively associated with sites dominated by *M. caerulea*, their main hostplant in the studied region. Cover by *U. europaeus* and by dicotyledons were best correlated with the opposite side of the second axis. The *U. europaeus* cover is however not directly related to the butterfly species (as hostplant or nectar plant) but moderate cover by this shrub characterizes drier pine stands, with butterfly species such as *L. phlaeas* and *H. statilinus.* Cover by dicotyledons, that may be nectar- or hostplants for several species, was higher in herbaceous firebreaks than in other habitat types and was associated with the presence of *L. phlaeas, P. icarus, T. lineola, M. cinxia* and *C. croceus*.

The proportion of explained variance in CCA is low, but this is a common feature in multivariate analysis of ecological communities (Aviron et al., 2005; Jeanneret et al., 2003b; Schweiger et al., 2005; Titeux et al., 2004). The aim of CCA is to identify important environmental variables and even low percentages might be informative (Ter Braak, 1986). By introducing more environmental variables, the proportion of explained variance will necessarily increase, but for a meaningful analysis the number of environmental variables should not be more than c.10% of the number of plots (Lebreton et al., 1988). A part of the unexplained variance in our study may be due to variables that were not measured, such as intra-plot variation in vegetation composition and canopy cover, or differences in management regimes.

Landscape attributes explained an independent part both in partial CCA analysis and in GLM modelling, thereby confirming that different organisation levels should be considered when explaining species abundance patterns (Wiens, 1989). In partial CCA the only significant landscape composition variables were the percentage cover of deciduous woodlands and firebreaks. Since the surveyed plot was included in the calculation of landscape metrics, this effect of habitat amount can either be an effect of habitat patch size or an effect of landscape supplementation, i.e. the use of several, similar patches within a landscape (Dunning et al., 1992). Larger patches or more patches tend to supply a greater diversity of environmental conditions and support more species. A positive effect of woodland area within 1 km on butterfly diversity was also demonstrated by Shreeve and Mason (1980) and by Baz and Garcia-Boyero (1995). Edge density explained also a significant, independent part of community variation. A high edge density may be positive for species using herbaceous strips along stand edges or for multi-habitat species (habitat complementation) (Duelli, 1997). A positive or negative effect of increased edge density and the associated fragmentation will however also depend on the observed species and the studied landscape type. Butterfly species characteristic for large woodlands are probably sensitive to fragmentation, but these species are very rare or absent in our study area.

The relatively low percentage of variation explained by landscape variables (18.0%, independent effect 6.7%) can be due to several factors. Possible landscape effects may be masked by the important variation in plot types (different stand types and understorey vegetation) compared to the variation in landscapes. To study landscape effects more accurately, we suggest the selection of the same plot type in a range of landscapes differing in composition and structure (Bergman et al., 2004). This may also permit to separate effects of landscape composition and fragmentation. Analysing the landscape at larger scales might also reveal additional effects. However, butterfly studies that examined the effect of different buffer sizes show contradictory results (Bergman et al., 2004; Krauss et al., 2003; Weibull et al., 2000). Differences in landscape types and their associated key factors may be responsible for these contradictions. Finally, landscape analysis also depends on the accuracy and choice of the patch typology. A patch typology based on a combination of stand type and understorey vegetation might have better described difference in habitat quality for the studied butterfly species. It would also have allowed the establishment of species (or guild) specific habitat maps (Li and Wu, 2004) and to reveal more or less isolated habitat patches that do not appear in the current typology. Such a typology can however not be based exclusively on aerial photos.

The presence of threatened species

Threatened butterfly species, such as *C. oedippus*, *M. dryas*, *H. morpheus* and *H. statilinus,* were observed both in pine stands and firebreaks, but they were more abundant in the latter. Firebreaks can therefore function as an essential reservoir/source in the landscape. Wahlberg et al. (2002) demonstrated in Finland that the continued presence of meadows was necessary for the survival of *E. aurinia*, a species occurring both in meadows and in clearcuts. Firebreaks may play the same role in our dynamic landscape. It seems however likely that the large areas of pine stands play a role as alternative habitat and refugium for species occurring both in firebreaks and pine stands, that they improve landscape connectivity and that they buffer the semi-natural habitats (Aberg et al., 1995; Aune et al., 2005; Lindenmayer and Franklin, 2002; Lindenmayer and Hobbs, 2004). The presence of threatened butterfly species in a landscape dominated by pine plantations argues for their potential conservation value. The 'Landes de Gascogne' forest is characterized by oligotrophic habitat conditions occurring over large areas; conditions that tend to disappear under agricultural and urbanisation pressure elsewhere. Typical butterflies of nutrient poor habitats are therefore threatened in several European countries, but are still occurring regularly in the studied region.

Nevertheless, this study does not show the possible negative effects of pine plantations on butterfly species present before the massive afforestation carried out in 1850's, when the landscape was dominated by large, mainly wet heathlands. It seems likely that several butterfly species might have seriously declined as a consequence of the huge habitat transformation. Some of these species such as *Maculinea alcon*, *Plebejus argus* and *P. idas* are very rare in the Landes de Gascogne forest and survive nowadays in isolated areas of heathland vegetation (military zones and some firebreaks). The nowadays relatively rich firebreaks may thus represent an impoverished version of the original species pool of large heathlands.

How to improve butterfly diversity in plantation forests

The enhancement of biodiversity within plantation forests should include measures to promote woodland habitats for forest species, but should also include measures to retain rare or specialist species of pre-planting habitats (Oxbrough et al., 2006). In the study area, forest butterflies were mainly found in deciduous woodlands and their presence was correlated with the extent of these woodlands, suggesting that habitat thresholds may exist. Bergman et al. (2004), for example, showed a sharp increase in occupancy probability for several butterfly species when the cover of deciduous forest/semi-natural grassland was higher than values between 2 to 12%. Our analyses do not provide an estimation of how much deciduous woodland is needed to conserve characteristic species. Species such as *A. paphia* and *L. reducta* were more abundant in larger deciduous woodlands, but these were also the more varied and humid riparian forests so that the effect of habitat quality and quantity are difficult to separate.

In our study area rare or threatened species were most abundant in firebreaks and the conservation and management of open spaces can be considered as an important technique of nature conservation within plantations (Gittings et al., 2006). In the Republic of Ireland, for example, all grant-aided afforestation should contain 5-10 % open space (Gittings et al., 2006). Recommendations for an optimal width of firebreaks for butterflies are difficult to give, based on the results of our study. For the 12 surveyed firebreaks, with a width varying from 15-90 m, no significant relation between species richness and firebreak width could be demonstrated. Oxbrough et al. (2006) showed for ground dwelling spiders that open spaces of less than 15 m wide did not support an open spider fauna due to the influence of the tree canopy. This suggests that firebreaks of 15 m may already be large enough to harbour a fauna of open spaces. The minimal width depends also on the neighbourhood of the firebreak (e.g. bordered by a high forest stand or by a road) and its orientation, which will affect the light conditions (Ferris and Carter, 2000). The actual management of firebreaks in the studied area is very variable (varying from annual mowing to about once every 8 years) and this variation is partly responsible for their diverse butterfly composition. The vegetation diversity within firebreaks can be increased and the temporarily negative impact of management reduced by a more varied management regime within firebreaks. For wide forest rides Ferris and Carter (2000) recommend a system with three different intervention frequencies. Comparable systems could be used in firebreaks, creating a more natural forest edge and by maintaining the largest part of the firebreak as herbaceous vegetation with a varied structure and composition.

The fact that composition of understorey vegetation explained the largest part of butterfly community composition implies that management within pine stands (e.g. removal of shrub layer, thinning, soil preparation before planting) and other habitats will directly affect butterfly diversity. In the Landes de Gascogne forest butterfly composition was most strongly influenced by differences in vegetation composition related to soil humidity. Maintaining existing humidity gradients and conserving the wet areas in the landscape are therefore decisive measures in conserving butterfly diversity in all habitat types, especially because silvicultural and agricultural practices tend to decrease soil moisture. Within-stand variation in canopy cover or understorey vegetation was not measured in this study, but field observations showed that butterflies were more abundant in gaps or in parts of stands with a lower canopy cover. Maintaining this variation within pine stands will therefore be profitable for butterflies. The positive effect of more open pine stands on butterfly species richness and composition has also been demonstrated in *Pinus ponderosa* (Waltz and Covington, 2004) and *Pinus edulis / Juniperus monosperma* forests (Kleintjes et al., 2004). This effect was attributed to a higher light intensity (Waltz and Covington, 2004) or to an increase in understorey cover (Kleintjes et al., 2004). Field observations also suggested the importance of variation in understorey vegetation composition. Most of the observed butterflies depend on herbaceous plants as hostplants, but some use shrubs or trees. Stand management to create a varied understorey vegetation dominated by herbs but with presence of some shrubs or deciduous trees seems most beneficial for butterflies. A more varied management of understorey vegetation (managing only one row out of two as observed in some stands) will favour vegetation diversity.

2.6. Conclusion

Three factors appear to have an important effect on butterfly richness and community composition in the studied pine plantation landscape: the presence of deciduous woodlands, the presence of firebreaks and the variation in understorey vegetation, related to both soil moisture and management practices. Explanatory factors measured at the local scale (plot vegetation and habitat type) explained the largest part of community variation, but landscape factors explained an additional, independent part. This confirms the importance of multi-scale analyses to explain patterns of biodiversity. Our study demonstrates the importance of interstitial habitats at the landscape level and shows that stand management can influence butterfly diversity, mainly by maintaining a diverse herbaceous layer.

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2.7. References chapter 2

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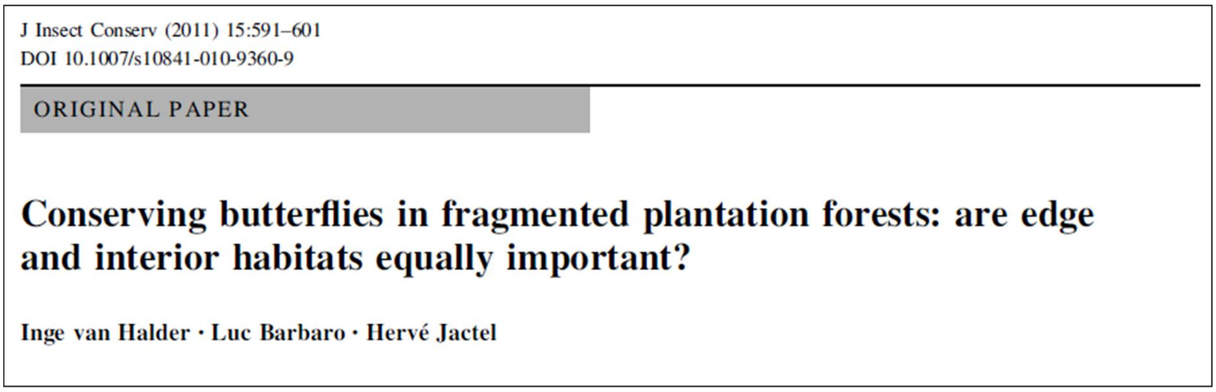
3. Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important?

Euphydryas aurinia



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ORIGINAL PAPER

Conserving butterflies in fragmented plantation forests: are edge and interior habitats equally important?

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3.1. Résumé en français

Rôle des lisières et de l'intérieur des habitats pour la conservation des papillons de jour dans les forêts de plantation fragmentées

Inge van Halder, Luc Barbaro, Hervé Jactel

Les paysages fragmentés se caractérisent par une grande longueur de lisières entre habitats, une longueur qui augmente exponentiellement avec la diminution de la taille des fragments. Les réponses des espèces aux lisières sont utiles à connaître pour mieux comprendre la dynamique des espèces dans des paysages en mosaïque. Cette réponse à l’effet de lisière peut être positive, négative ou neutre selon les espèces et les mécanismes les plus importants qui expliquent cette réponse sont la distribution des ressources et les interactions biotiques.

Pour identifier les facteurs déterminant les patrons de biodiversité, nous avons donc étudié les réponses des papillons de jour à différentes types de lisières dans un massif forestier dominés par des plantations de pins, en posant plus spécifiquement les questions suivantes :

- Est-ce que la richesse en espèces, l’abondance individuelle des espèces et la composition des assemblages sont différentes entre la lisière et l’intérieur des habitats ?
- Est-ce que ces différences dépendent du type d’habitat ?
- Quelles sont les variables environnementales aux niveaux local et paysager qui expliquent la présence des espèces en lisière ?

L’étude a été conduite dans le massif forestier des Landes de Gascogne. Ce massif est dominé par des plantations de pin maritime (*Pinus pinaster*). Les forêts de feuillus sont rares et apparaissent comme des îlots de quelques hectares ou sous forme de ripisylves. Les milieux ouverts sont principalement constitués par des coupes rases, des pare-feux et des grandes zones de maïsiculture. Les papillons de jour ont été inventoriés simultanément le long de la lisière et à l’intérieur (Figure 1) de 68 parcelles appartenant à quatre types d’habitat : 11 pare-feux herbacés, 26 parcelles de coupes rases et de jeunes pins (hauteur < 7m), 18 plantations de pins plus âgés (hauteur > 7m) et 13 forêts de feuillus. Les différences entre assemblages ont été analysées avec des tests de MRPP (multi-response permutation procedure) en utilisant la distance de dissimilarité de Bray-Curtis. Des modèles logistiques ont été utilisés pour évaluer l’importance respective des variables locales et paysagères et de l’abondance de la même espèce à l'intérieur de l‘habitat adjacent pour la présence des différentes espèces en lisière.

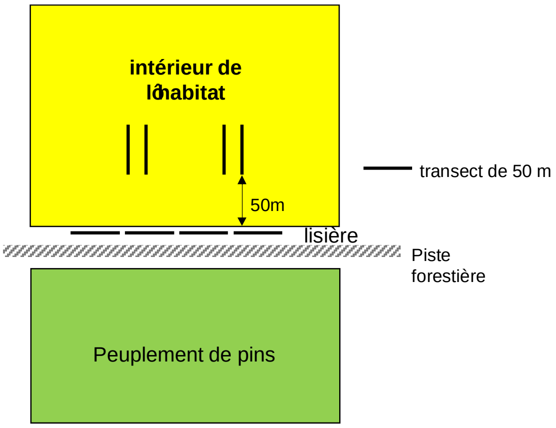

Figure 1. Position des transects à l'intérieur et en lisières des parcelles pour l'inventaire des papillons de jour.

Au total 47 espèces de papillons de jour ont été observées. Le nombre d'espèces était plus élevé en lisière qu'à l'intérieur des habitats. Cet effet était surtout dû à la plus grande richesse le long des lisières des parcelles de pins comparée avec l'intérieur de ces parcelles (Figure 2). La composition des assemblages de papillons de jour était également différente entre lisière et intérieur des habitats pour les parcelles de pins et les forêts de feuillus, mais pas pour les pare-feux. Parmi les 23 espèces de papillons les plus abondantes, sept étaient significativement plus abondantes dans une ou plusieurs types de lisières, cinq étaient plus abondantes à l'intérieur et onze espèces ne montraient pas de préférence. Les modèles logistiques par espèce ont mis en évidence l'importance des variables de qualité d'habitat, comme l'abondance des fleurs nectarifères et des plantes-hôtes pour les chenilles, mais également l'effet de l'abondance de la même espèce à l'intérieur de la parcelle adjacente à la lisière.

Pour plusieurs espèces de papillons de jour les lisières peuvent représenter des habitats à part entière. Nos résultats montrent également que beaucoup d'espèces peuvent se trouver dans plusieurs types d'habitats, probablement pour trouver des ressources complémentaires ou supplémentaires, y compris des conditions microclimatiques permettant d'échapper aux températures élevées en été. L'utilisation des lisières et des intérieurs de différents types d'habitats est probablement un processus majeur pour la survie dans les paysages en mosaïque, ce qui souligne l'importance de l'hétérogénéité du paysage pour la conservation des papillons de jour.

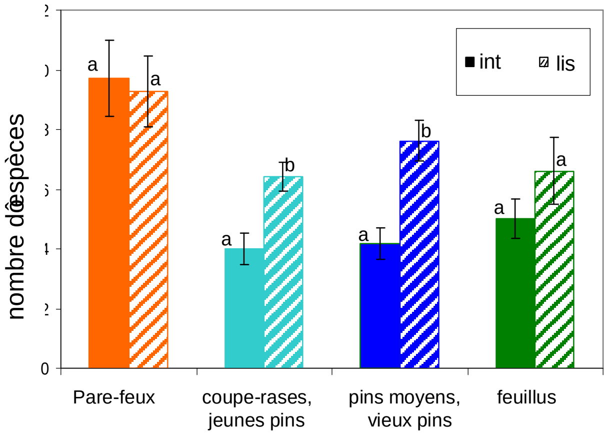

Figure 2. Nombre moyen d'espèces (±SE) de papillons de jour à l'intérieur (int) en en lisière (lis) par type d'habitat. Des lettres différentes par type d'habitat indiquent des différences significatives (P<0.05) entre intérieur et lisière.

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Abstract

Edge effects are increasing in forest-dominated landscapes worldwide, due to increased fragmentation by other land uses. Understanding how species respond to edges is therefore critical to define adequate conservation measures. We compared the relative importance of interior and edge habitats for butterflies in a landscape composed of even-aged pine plantations interspersed with semi-natural habitats. Butterfly assemblages were surveyed simultaneously at the edge and the interior of 68 patches belonging to four main habitat types: herbaceous firebreaks, clearcuts and young pine stands, older pine stands, and deciduous woodlands. Butterfly species richness was higher at edges than in interior habitats, especially for pine stands. Assemblage composition differed significantly between edge and interior habitats, except for firebreaks. Of the 23 most abundant butterfly species, seven were significantly more abundant in one or all edge habitat types, five in interior habitats, and 11 species showed no edge-interior preference. Modelling the presence of individual species in edge habitats revealed the importance of habitat variables such as the abundance of nectar and host-plants, but also of the abundance of the same species in the adjacent interior habitat. Moreover, our results suggest that most species use several, different habitat types to find supplementary or complementary resources, including micro-climatic refuges to escape hot temperatures during summer. The use of adjacent edge and interior habitats by butterflies is probably a key process in such mosaic landscapes and underlines the importance of landscape heterogeneity for butterfly conservation.

Key-words

Complementation, Edge-effect, *Pinus pinaster,* Supplementation

3.2. Introduction

Fragmented landscapes are characterised by small habitat patches, with an exponentially increasing amount of habitat edges when patch size decreases (Fletcher, 2005). The response of species to habitat edges and their subsequent dispersal behaviour is critical to our understanding of species dynamics in fragmented landscapes. Species either avoid edges, are more abundant near edges, or show no edge preference. Edge responses are species-specific and highly dependent on the type of edge encountered (Ewers and Didham, 2006; Ries and Sisk, 2004). The most important mechanisms that determine the individual species responses to habitat edges are the distribution of resources and the interactions between different species (Ries et al., 2004). Species that specialise on resources found only in interior habitat will generally avoid edges where habitat quality, predation risk or micro-climate are less favourable. These negative edge effects have been demonstrated for various taxa, including birds (Fletcher, 2005), small mammals (Stevens and Husband, 1998), herpetofauna (Lehtinen et al., 2003) and insects (Spector and Ayzama, 2003), see also Ries et al. (2004) for a review. In fragmented landscapes these ‘interior species’ may be negatively affected by the higher edge to interior ratio and could, with ongoing fragmentation, become extinct as fragment size decreases.

In contrast, positive edge effects on abundance of individual species have also been reported, for example for birds (Ries et al., 2004), spiders (Downie et al., 1996) and insects (Duelli et al., 2002; Ries and Sisk, 2008). Species richness is often highest at habitat edges (Ewers and Didham, 2006) and is thought to be caused by three mechanisms: (i) by spillover effects where individuals mix as they disperse between adjacent habitat patches, (ii) by the presence of resources at the edge that are rare or absent in adjacent patches, and (iii) by increased access to complementary resources that are located in two adjacent patches (Dunning et al., 1992; Ries and Sisk, 2004). Species behaviour at edges is also an important factor that affects dispersal through the landscape. For example, edge avoidance behaviour may hinder dispersal between different patch type (Haynes and Cronin, 2006; Ries and Debinski, 2001; Schtickzelle and Baguette, 2003), but could improve dispersal along corridors bordered by ‘hostile’ edges (Haddad, 1999; Sutcliffe and Thomas, 1996).

In the present study we investigated the responses of butterflies to different edge types in a landscape dominated by pine plantation forests. The area of plantation forests is increasing worldwide and there is much debate about their role in biodiversity conservation compared to other land uses. Plantations can contribute to conservation by providing complementary and supplementary habitats and by increasing forest connectivity at the landscape scale (Brockerhoff et al., 2008). This study was conducted in Europe’s largest plantation forest, located in the south-west of France. Within this forest several internationally threatened butterfly species occur, as well in pine stands as in firebreaks with a heathland vegetation (van Halder et al., 2008). Previous studies in woodlands, along hedgerows or at field boundaries indicate that many butterfly species use the resources provided by diverse vegetation and sheltered sunny microclimatic conditions that are found at edges (Dover and Sparks, 2000; Dover, 1996; Greatorex-Davies et al., 1993). Butterfly diversity along woodland edges can be high, including typical forest species, edge species and grassland species (Feber et al., 2001; Ferris and Carter, 2000; Robertson et al., 1995). However, studies that compare butterfly abundance between forest interiors and forest edges are rare (Ries and Sisk, 2008), especially in plantation forests. Planted forests are often characterised by a high edge length (Niemela et al., 2007), but these edges are not always of high quality for biodiversity conservation. In planted forests most edges are abrupt and many edges are exposed edges along open habitats (e.g., edges of clearcuts or young stands). Within these landscapes dominated by plantation stands semi-natural habitat types, such as deciduous woodland fragments, play an important role in butterfly conservation (van Halder et al., 2008). Their edges may be of equal importance compared to plantation stand edges or may be characterized by a unique edge species assemblage.

We addressed the following questions to analyse the interior-edge patterns of butterfly diversity in pine plantation landscapes and to establish the role of edge habitats in conserving butterflies: (i) Are there differences in butterfly species richness, individual species abundance, and assemblage composition between the interior and edge of habitat patches? (ii) Do these differences depend on the type of habitat? (iii) What are the important environmental factors at the habitat and landscape scale that drive the presence of individual butterfly species in edge habitats?

3.3. Materials and methods

Study area

The study was conducted in the south-west of France in the Landes de Gascogne forest. This region is dominated by plantations of even-aged, native maritime pine (*Pinus pinaster*) stands that cover 1 million hectares and is the largest plantation forest in Europe. Soils are nutrient-poor, acidic podzols. Soil moisture greatly affects vegetation composition; *Molinia caerulea* dominates on wet sites, *Pteridium aquilinum* and *Ulex europaeus* in intermediate conditions, and *Calluna vulgaris* and *Erica cinerea* on dry sites. In this heavily modified landscape deciduous woodlands (along rivers, and as patches of a few hectares) and herbaceous firebreaks and powerlines (hereafter resumed as firebreaks) are the most important remnants of semi-natural vegetation. Deciduous woodlands are generally dominated by *Quercus robur* except on dry sites where *Quercus pyrenaica* occurs. Along rivers the vegetation is dominated by a mixture of *Alnus glutinosa* and *Q. robur.* Firebreaks have either a wet to dry heathland vegetation or a grassland vegetation. Management of firebreaks to suppress the growth of woody species is conducted every 4-8 years, however in some cases they are mown annually. The forested landscape is dissected by a dense network of sandy forest tracks that create many forest edges. Within this landscape two study sites were selected: Tagon (5,000 ha), situated 35 km southwest of Bordeaux and Solferino (10,500 ha), located 65 km to the south of Tagon.

Butterfly counts

Butterflies were surveyed in 68 patches of four habitat types: 26 open pine stands (clearcuts and young pines with a canopy height < 7 m), 18 closed canopy pine stands (canopy height > 7 m), 13 deciduous woodlands (isolated patches or riparian forests) and 11 firebreaks. The mean size of the surveyed open and closed pine stands was 8.8 and 10.7 ha respectively, whereas the deciduous woodland patches had a mean size of 3.4 ha. The surveyed firebreaks had a mean width of 40 m.

Butterfly surveys were conducted both inside the habitat patch (interior habitat) and along its edge (edge habitat) using the line-transect method (Pollard and Yates, 1993). Within the patch interior four transects of 50 m long and 5 m wide were laid out and butterflies were counted within this strip. In pine stands these sections were located at 50 m from the stand edge and were also at least 50 m away from the other edges (Figure 3). In deciduous woodland patches sections were in general at 50 m from the edge, except in a few small woodland patches. In firebreaks the sections were laid out in the length of the firebreak, in the middle of its width. To survey the edge habitat four sections of 50 m were located at the edge of each surveyed interior habitat (Figure 3). The edge habitat always consisted of a herbaceous strip with some shrub development along the stand edge, and was bordered by a sandy forest track of about three meters wide. The opposite habitat type on the other side of the forest track was always an open or closed pine stand. The two types of opposite habitat, open or closed pine stand, were evenly distributed for each inventoried habitat type.

Each section was sampled four times (between May 14th and September 4th 2004) during appropriate weather conditions (temperature > 20°C, cloudless or just a few clouds and wind speed < 5 Beaufort). Butterfly species were identified by sight or caught and released for species difficult to identify. For data analysis the total number of individuals per species was pooled over the four visits and the four transects of each habitat (i.e. edge or interior habitat). Butterfly species are named in the text according to Karsholt & Razowski (1996).

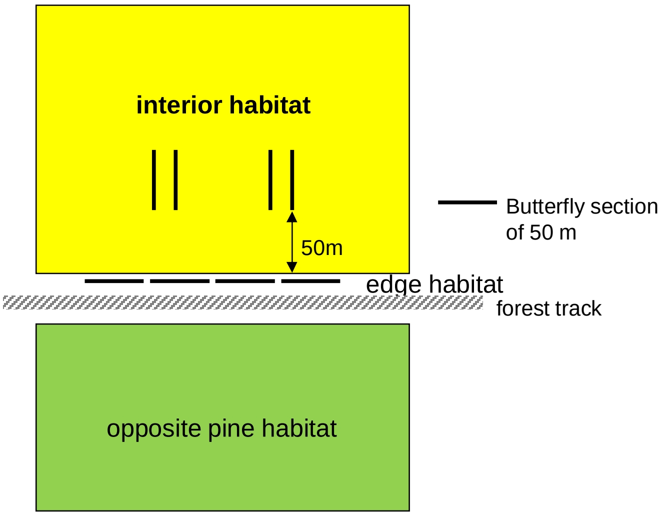

Figure 3. Position of the four butterfly sections in the interior habitat and in the edge habitat in pine stands.

Environmental variables

In order to interpret butterfly diversity, we measured several variables characterising the edge and interior habitat and the surrounding landscape (Table 1). At the habitat edge and interior we measured important resources for butterflies, such as nectar-plants for adults, vegetation structure, and insolation. Flower abundance of plant species known to be used by butterflies was used as an estimate of nectar availability (Ebert and Rennwald, 1991; van Halder personal observations). Since Ericaceae were the most important nectar source we separated nectar availability into two groups: Ericaceae and other nectar plants. At each sampling period the number of flowers was estimated per transect using seven classes (Clausen et al., 2001; van Halder et al., 2008). For data analysis we summed, for each sampling period, the midvalues of each class over the four transects. Since each butterfly species only flies during a short period of the year we calculated for each species the flower abundance during its flying period by summing the flower abundances for the sampling periods where at least 90% of the individuals of that butterfly species were seen. Flower abundance was log-transformed to reduce the effect of outliers and because we hypothesized a non-linear relationship between butterfly and flower abundances. In autumn the presence of dicotyledonous host-plants of the observed butterfly species were recorded for each transect of the edge habitat. Host plants used by butterflies were based on Lafranchis (2000) and field observations. Grasses were not identified to species, but their percentage cover was estimated. To describe vegetation structure we estimated the percent vegetation cover in the edge and the interior habitat in two height tiers (herbaceous vegetation (< 0.7 m) and the shrub layer (0.7 -7 m)). The percentage cover of the main vegetation components of the herbaceous layer (grasses, dicotyledons, *Ulex minor*, Ericaceae) was estimated to calculate a Shannon Diversity Index. Insolation was estimated in 8 classes (1 - sunny to 8 - very shady with no direct sun) and incorporated both the exposition of the edge (Clausen et al., 2001), tree height and canopy cover.

Table 1. Mean values of habitat and landscape variables per patch type. *P* = the *P*-value of a pairwise t-test between interior and edge habitats for each patch type: * *P*<0.05; ** *P*<0.01; * *P*<0.001.**

		Firebreaks			Open pine stands			Closed pine stands			Deciduous woodlands		
Acronym	Description	interior	edge	*P*	interior	edge	*P*	interior	edge	*P*	interior	edge	*P*
Habitat variables													
Sun	Insolation	7.8	8.0		7.0	7.7	*	2.4	5.0	***	1.3	4.5	**
Nec *Erica*	nectar ericaceae (ln)	3.0	4.0		4.5	6.1	*	3.5	5.5	*	0.9	2.0	
Nec Other	nectar other plants (ln)	6.4	6.2		3.4	5.5	***	3.5	5.7	***	1.5	5.5	**
%Grass	% cover grasses	68.2	62.3		46.7	50.0		52.7	52.4		25.3	44.0	*
%Herb	% cover herbaceous layer	83.5	84.5		64.2	72.5		68.3	76.4		48.4	63.5	*
%Shrub	% cover shrubs	5.5	12.2		23.3	9.3	***	19.4	9.5	*	23.3	19.5	
SHDIherb	SHDI herbaceous layer	0.48	0.66		0.53	0.71	*	0.35	0.68	***	0.26	0.54	**
Landscape variables (buffer of 200 m around edge habitat)													
%FB	% firebreaks		14.7			1.2			1.2			2.9	
%OP	% open pine stands		39.5			54.0			22.7			25.8	
%CP	% closed pine stands		38.3			40.7			68.8			28.4	
%DW	% deciduous woodlands		3.3			0.5			2.1			32.6	
ED	Edge Densitiy		265.9			204.6			226.5			243.1	
SHDI	Shannon Diversity Index		1.3			1.1			1.0			1.4	

At the landscape level, we mapped major land-use types in GIS (Arcview 3.3, ESRI) using aerial colour photos with a resolution of 50 cm, followed by field verification. The following 12 land-use types were distinguished: five stages of pine stands (from clearcuts to older pines), deciduous woodlands, firebreaks, hedgerows, meadows, crops, roads and constructed areas. Landscape metrics were calculated within circular buffers with a radius of 200 m, from the centre of the sampled edge, using Fragstats 3.3 in raster version. We used a relatively small buffer size to quantify the landscape composition and structure directly around the sampled edge. This buffer area is expected to contribute most to butterfly movements between the sampled edge and the surrounding landscape. Within each buffer the percentage cover of the four inventoried habitat types was calculated, as well as the Edge Density (i.e. length of all edge segments per hectare) and the Shannon Diversity Index (SHDI) (McGarigal et al., 2002) (see Table 1). We selected these landscape metrics because they are ecological meaningful and are known to affect butterfly diversity (Krauss et al., 2003; van Halder et al., 2008; Weibull et al., 2000).

Data analysis

For environmental variables, differences between interior and edge habitats were analysed per habitat type with a paired t-test. For butterfly species richness, the effects of habitat type and of edge vs. interior were tested with a two-way ANOVA. For the edge samples separately the effect of the edge habitat type and the pine habitat type on the opposite side was tested with a two-way ANOVA. The effect of habitat type on species richness in interior samples was tested with a one-way ANOVA. Significant habitat effects were analysed by Tukey's HSD tests. Differences in butterfly species richness between interior and edge habitats per habitat type were tested with paired t-tests. To meet the assumptions of normality and equal variance butterfly species richness data were Box-Cox transformed, and normality and equal variance were verified using the Shapiro-Wilk and Bartlett test respectively. Differences in assemblage composition were assessed by non-metric multi-dimensional scaling (NMDS) using a Bray-Curtis dissimilarity matrix (Clarke, 1993). The Bray-Curtis distance metrics was chosen because it provides a meaningful measure of dissimilarity in community structure (McArdle and Anderson, 2001). Pairwise differences in assemblage composition were tested with multi-response permutation procedure (MRPP) (Zimmerman et al., 1985). MRPP is a non-parametric method useful to test for differences (e.g., in assemblage composition) between predefined groups. MRPP tests were also based on the Bray-Curtis distance. The significance of the null hypothesis of no difference was assessed by a Monte Carlo permutation procedure with 1000 permutations. We tested for differences in assemblage composition between interior and edge habitat for all habitat types combined and for each habitat type. For edge habitats separately we tested for differences between edge types and we compared species assemblages between edges with open and closed pine stands as opposite habitat type. Butterfly abundance data were log transformed to reduce the effect of some very abundant species. Three open pine stands with no butterflies in the interior habitats where omitted from NMDS and MRPP analyses where interior data were used. Paired Wilcoxon signed rank-tests were used to compare differences in abundance of individual species between edge and interior habitats. Only species with more than 15 individuals were analysed. The effect of environmental variables on the presence of individual species in edge habitats was investigated with logistic regression models. The explanatory variables included both habitat and landscape variables (Table 1), and the abundance of the same butterfly species in the adjacent, paired interior habitat. The latter variable would indicate a degree of butterfly exchange between the edge and interior of the same habitat patch. We used Akaike's information criterion (AIC) as the selection criterion in a backward and forward selection procedure.

All analyses were performed with the R software (R Development Core Team, 2007). We used the package car for ANOVA, MASS for NMDS, vegan for MRPP, stats for stepwise logistic regressions (glm) and exactRankTests for the paired Wilcoxon tests.

3.4. Results

Butterfly species richness

A total of 47 butterfly species and 2886 individuals were observed throughout the four sampling periods. In the interior habitats 40 species were observed (1094 individuals) and in the edge habitats 44 species (1792 individuals). Species that were absent in interior or in edge habitats were rare species with less than 13 individuals observed. Two-way ANOVA revealed that edge habitats were significantly richer in butterfly species (7.2 ± 0.4 species (mean ± SE)) than interior habitats (5.2 ± 0.4 species), (n=136, F= 11.93, P<0.001, Figure 4). It also revealed a significant effect of habitat type (n=136, F= 9.80, P<0.001) and no interaction (n=136, F= 2.22, P=0.09). Tukey's HSD tests showed that firebreaks were significantly richer in butterfly species than the other three habitat types (all $P \leq 0.01$). For edge samples taken separately, the two-way ANOVA showed no effect of habitat type (n=68, F=2.15, P=0.10) and no effect of the opposite habitat type (n=68, F=0.45, P=0.51). For interior samples the one-way ANOVA indicated a significant overall effect of habitat type on butterfly species richness (n =68, F= 9.36, P<0.001), with a higher species richness in firebreaks than in the other three habitat types (Tukey's HSD tests, all P < 0.01). The comparison of edge and interior habitats per habitat type showed that edges of open and closed pine stands had significantly more butterfly species than the paired habitat interiors (t = 4.84, d.f. = 25 for open pine stands, t=5.01, d.f.=17 for closed pine stands, both P < 0.001). There was no difference in species richness between edge and interior habitats for firebreaks and deciduous woodlands (Figure 4).

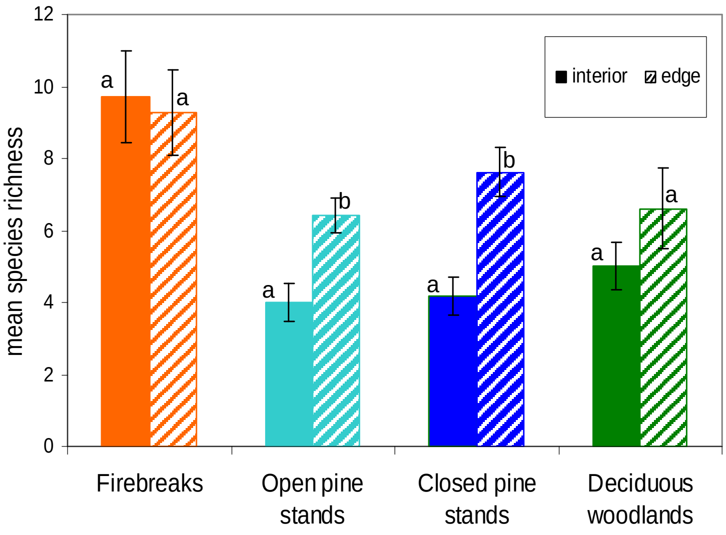

Figure 4. Mean species richness (± SE) of butterflies in edge and interior habitats per habitat patch type. Different letters per habitat patch type indicate significant differences between interior and edge habitats for that particular patch type (*P*<0.05, pairwise t-test per patch type).

Butterfly assemblages

The MRRP indicated a significant (A = 0.018, P<0.001) difference in butterfly assemblages between interior and edge habitats. Similarly MRPP tests per habitat type also showed significant differences between interior and edge habitats for deciduous woodlands (A=0.028, P=0.018), open pine stands

(A=0.027, *P*<0.001) and closed pine stands (A= 0.035, *P* = 0.002), Figure 5), but not for the comparison between interiors and edges of firebreaks (A = -0.005, *P* = 0.61). Butterfly assemblages of firebreak interiors were however different from the other edge types (all P<0.005). Similarly, pairwise comparisons of the different edges types showed significant differences in almost all cases (A≥0.02, P≤ 0.01), except for the comparison between edges of closed and open pine stands (A=-0.003 , *P*=0.67). MRRP tests showed an overall effect of the opposite habitat type (A=0.011, *P*= 0.003) when all edges were combined, but separate tests per edge type showed no effect of the opposite edge type (*P*> 0.10 in all cases).

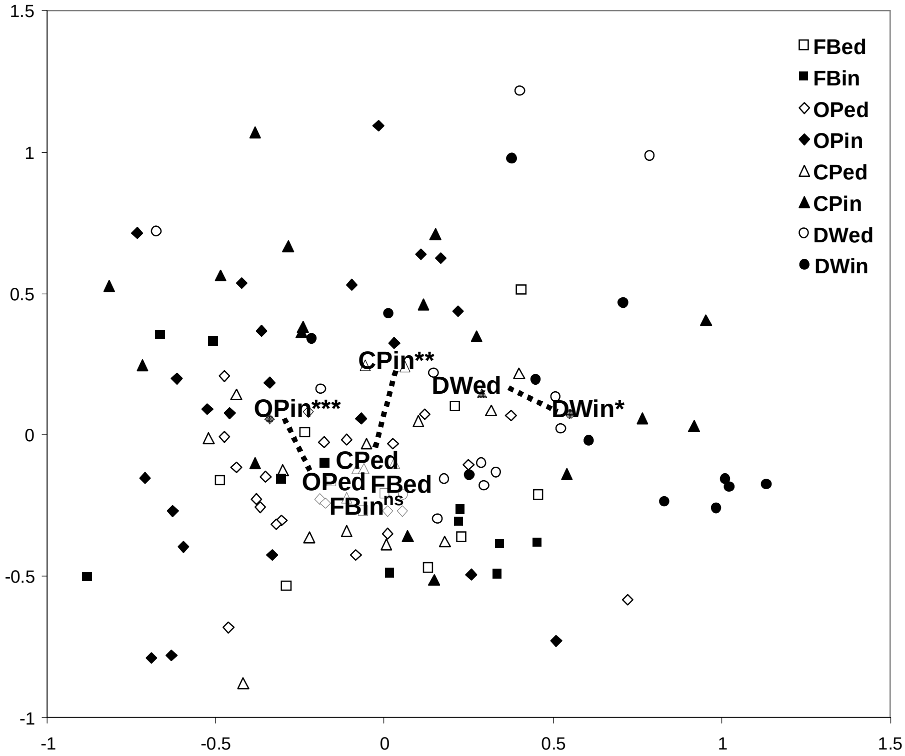

Figure5. NMDS ordination plot based on Bray-Curtis distances. Each point represents an edge habitat (open symbols) or interior habitat (closed symbols). The position of the names of the habitat types indicates the centre of all plots of the corresponding type. Pairwise differences between edge and interior habitats per habitat type were tested with MRPP (* *P*<0.05; ** *P*<0.01; * *P*<0.001, ns not significant). FBed – firebreak edges, FBin – firebreak interiors, OPed - open pine stand edges, OPin – open pine stand interiors, CPed – closed pine stand edges, CPin – closed pine stand interiors, DWed - deciduous woodland edges, DWin – deciduous woodland interiors. Two-dimension stress = 0.27.**

Individual butterfly species

Paired Wilcoxon tests of edge-interior habitat preferences of the 23 most abundant species showed that seven species were significantly more abundant in one or more edge habitat types, five species were significantly more abundant in one or more interior habitats, and eleven species showed no preference (Table 2). The analyses per habitat type showed that 'edge species' occurred mostly in open pine stands and that only one species was more abundant at firebreak edges than in their interiors. 'Interior species' were not associated with a particular habitat type (Table 2). The results of the logistic regression with environmental variables to explain butterfly abundance in edge habitats are shown in Table 3. For 18 out of 23 species a significant model could be constructed but the percentage explained deviance differed between species. Both habitat and landscape variables were significant components of the models. The most important habitat variables were the abundance of nectar flowers and host plants, whereas the percentage cover of firebreaks and closed pine stands were most important landscape variables. The abundance of a butterfly species in the adjacent interior habitat was an important determinant of edge abundance for almost half of the species tested. In Annex 1 ecological information is presented for the 23 most abundant butterfly species (Barbaro and van Halder, 2009; Bink, 1992; Lafranchis, 2000).

Table 2. Total abundance (Total abun) of butterfly species in interior and edge habitats (only species with ≥ 15 individuals are mentioned). Per species the mean abundance in all interior and edge habitats is given, as well as per patch type. int= interior. *P* = the *P*-value of a pairwise Wilcoxon test between interior and edge habitats: * *P*<0.05; ** *P*<0.01; * *P*<0.001. Species are ordered in three groups according to their preference for edge habitats, interior habitats or no preference, respectively. (ed) = significant preference for edge; (in) = significant preference for interior.**

Species	Total abun	All habitats			Firebreaks			Open pine stands			Closed pine stands			Deciduous woodlands		
		int	edge	*P*	int	edge	*P*	int	edge	*P*	int	edge	*P*	int	edge	*P*
More abundant in edge habitats																
Pyronia tithonus	694	2.1	8.1	*** (ed)	4.7	10.9	** (ed)	0.9	6.4	*** (ed)	2.3	12.1	*** (ed)	1.8	3.8	
Coenonympha pamphilus	425	1.4	4.9	*** (ed)	3.3	3.6		1.7	6.7	*** (ed)	0.8	5.6	** (ed)	0.1	1.3	* (ed)
Lycaena phlaeas	253	1.5	2.2	* (ed)	3.3	3.3		0.4	1.4	* (ed)	2.4	2.0		1.0	3.2	* (ed)
Maniola jurtina	201	1.3	1.6		3.9	5.4		0.2	0.8	* (ed)	0.7	0.6		2.3	1.6	
Hipparchia statilinus	106	0.5	1.1	* (ed)	1.4	0.7		0.2	1.5	** (ed)	0.7	1.3		0.0	0.3	
Aricia agestis	46	0.3	0.3		0.4	0.1		0.0	0.3	* (ed)	0.4	0.3		0.9	0.6	
Thymelicus sylvestris	28	0.1	0.3	* (ed)	0.5	0.8		0.0	0.1		0.0	0.4		0.0	0.2	
More abundant in interior habitats																
Coenonympha oedippus	135	1.6	0.4	*** (in)	2.1	1.0		2.1	0.3	** (in)	1.7	0.3	* (in)	0.2	0.2	
Cupido argiades	103	1.0	0.5		4.8	1.0	* (in)	0.6	0.7		0.1	0.1		0.0	0.2	
Euphydryas aurinia	84	0.8	0.4		3.8	1.0	* (in)	0.2	0.3		0.1	0.2		0.4	0.4	
Pararge aegeria	63	0.7	0.2	* (in)	0.0	0.0		0.0	0.1		0.1	0.0		3.6	1.0	* (in)
Heteropterus morpheus	29	0.3	0.1	* (in)	0.8	0.5		0.2	0.0		0.3	0.2		0.0	0.0	
No significant differences																
Minois dryas	175	1.2	1.4		1.6	0.8		1.7	1.9		0.9	1.9		0.1	0.2	
Gonepteryx rhamni	107	0.7	0.9		0.7	0.6		0.5	0.8		0.6	1.1		1.0	1.0	
Polyommatus icarus	65	0.4	0.6		2.0	2.3		0.0	0.5		0.1	0.2		0.0	0.1	
Thymelicus lineola	50	0.4	0.4		2.3	1.7		0.0	0.0		0.0	0.0		0.1	0.4	
Ochlodes venata	47	0.2	0.5		0.1	0.1		0.2	0.2		0.3	1.1		0.3	0.5	
Coenonympha arcania	44	0.3	0.4		0.0	0.0		0.2	0.3		0.4	0.9		0.7	0.0	
Hipparchia semele	30	0.2	0.3		0.0	0.0		0.1	0.2		0.3	0.7		0.3	0.2	
Limenitis reducta	26	0.1	0.2		0.5	0.5		0.0	0.1		0.0	0.2		0.4	0.4	
Colias croceus	26	0.1	0.3		0.7	0.3		0.0	0.3		0.0	0.4		0.0	0.0	
Melitaea cinxia	17	0.1	0.1		0.8	0.6		0.0	0.0		0.0	0.0		0.0	0.1	
Brintesia circe	15	0.1	0.1		0.2	0.7		0.0	0.0		0.0	0.1		0.2	0.1	

Table 3. Habitat and landscape variables selected in logistic regression models for butterfly species in edge habitats. Butterfly species are grouped according to their preference for edge or interior habitats (based on Table 2). See Table 1 for abbreviations of habitat and landscape variables, SP-INT = abundance same butterfly species in interior habitat, % DEV = % explained deviance, * *P*<0.05; ** *P*<0.01; * *P*<0.001.**

	habitat variables							landscape variables									
	Sun	Nec Erica	Nec Other	Host plant	% Herb	% Shrub	SHDI herb	% FB	% OP	% CP	% DW	ED	SHDI	SP-INT	% DEV	*P*
More abundant in edge habitats																
P. tithonus		x		x										x	39.7	***
C. pamphilus		x		x					x						16.2	**
L. phlaeas	x			x					x	x		x			27.3	***
M. jurtina								x		x		x		x	22.9	***
H. statilinus		x										x		x	26.2	***
T. sylvestris		x	x												22.8	***
More abundant in interior habitats																
C. oedippus					x					x				x	27.0	***
C. argiades				x				x							17.9	**
E. aurinia			x		x		x	x					x	x	38.0	***
P. aegeria		x													15.8	*
No significant differences																
M. dryas			x								x	x		x	30.1	***
G. rhamni			x				x						x		15.6	**
P. icarus		x		x				x					x		32.0	***
O. venata			x							x				x	15.8	**
H. semele						x		x							18.4	*
A. reducta			x	x							x				23.9	**
C. croceus				x						x	x				18.3	**
B. circe								x						x	23.1	**

3.5. Discussion

Overall, edge habitats had a higher species richness and distinctly different butterfly assemblages compared to adjacent interior habitats. These differences were most pronounced at the edge of pine stands, but were not apparent at firebreaks. The differences in butterfly richness and species composition between edge and interior habitats can be related to the observed differences in vegetation composition and nectar abundance (Dover, 1996; Kuussaari et al., 2007), as well as in insolation for closed stands. Our results are consistent with other studies that show the importance of forest edges for butterflies (Ferris and Carter, 2000; Kuussaari et al., 2007; Ohwaki et al., 2007).

Edge species

Although many species are often more abundant at edges, identifying real edge species, i.e. species that need resources only found at edges, is difficult and such obligate edge species are rare. Duelli et al. (1990) showed that of the 113 tested species of carabids, staphylinids and spiders in an agricultural landscape only two were obligate edge species. Similarly Paquet et al. (2006) found no bird species strictly indicative of edge habitats in a woodland-farmland landscape. Most bird species considered to prefer forest edges in agricultural landscapes are in fact early-successional species that could not find shrubland conditions apart from the edges of forest fragments (Imbeau et al., 2003).

Although obligate edge species are rare, some butterfly examples do exist. In Sweden, Bergman (1999) showed that *Lopinga achine* is restricted to a narrow zone along forest edges that harboured more host plants, and corresponded to a zone of higher egg survival compared to adjacent open habitat or shaded woodland. In Finland *Euphydryas maturna* is restricted to south facing forest edges where it finds a warm microclimate, suitable host plants, and in adjacent clearcuts nectar sources and perching sites for males (Wahlberg, 2001).

Most species that were more abundant at edges in our study are classified as grassland or heathland species (Asher et al., 2001; Ebert and Rennwald, 1991; Lafranchis, 2000), which is reflected in the herbaceous vegetation that dominated the sampled edges. For several species in this group, such as *Pyronia tithonus, Coenonympha pamphilus* and *Thymelus sylvestris*, the studied edges can be considered as a habitat since all essential resources are present at edges. The results of the logistic regressions confirmed that for these species habitat characteristics were important, notably nectar and host plants. These edge preferring species were rare in adjacent pine stands and their presence in interior habitat is probably a spill-over effect. Other butterfly species, such as *Neozephyrus quercus, Satyrium ilicis, Limenitis reducta, Celastrina argiolus, Iphiclides podalirius*, that are often observed along woodland edges or hedgerows in Europe (Dover and Sparks, 2000; Ebert and Rennwald, 1991) were rare in our survey. We think that their rareness may be attributed to the sharp edge boundaries at our study sites that lack a developed tree and shrub zone.

Role of edges versus interiors for butterflies

Plantation forests are generally considered to have little or no value as habitat for butterflies apart from stand edges (Asher et al., 2001; Ferris and Carter, 2000). Plantation forests have broad similarities with agricultural landscapes where linear elements such as hedgerows and grass verges are known to be important for butterflies (Clausen et al., 2001; Feber et al., 1996) and where crops represent non-habitat. In contrast to previous work we showed that interior portions of plantation forest stands harbour some butterfly species and that they are an important habitat for one of Europe's most threatened species, *Coenonympha oedippus* (van Swaay and Warren, 1999). The presence of species at edges but also inside some or all habitat types, the overlap in species composition between edge and interior habitats and the frequent selection in GLMs of the species abundance in the habitat interior next to the edge raises questions regarding the relative importance of these different elements in providing resources to butterflies. The most important resources for butterflies are host plants, nectar plants, vegetation structure and micro-climate (related to thermoregulation and survival of different stages) (Dennis et al., 2003; Hardy et al., 2007; Tudor et al., 2004). In landscapes composed of a mosaic of different habitat types the presence of particular butterfly species may depend on the presence of a certain resource in several, nearby habitat patches (landscape supplementation) or on the presence of different resources in different habitat patches (landscape complementation) (Dunning et al., 1992).

In our study many species were observed as well at edges as in interior habitats of one or several habitat types. At firebreaks these species may find the same resources in edge and interior habitats (supplementation), but this seems less plausible for contrasted edges such as of older pine stands and deciduous woodlands. In such cases the use of different resources in adjacent habitats seems more probable. The use of different vegetation types for ovipositing, nectar feeding or resting has been demonstrated for several butterfly species, e.g. for *Leptidea sinapis* (Wiklund, 1977) and

Maniola jurtina (Ouin et al., 2004). In our study nectar abundance was greater at edges than in interior habitats, and this may explain the presence of for example *Gonepteryx rhamni* in edge habitats even though its host plant *Frangula alnus* occurs in the interior of pine stands.

Selection for specific microclimatological conditions might also explain the presence of species at edges and inside habitats. Depending on the weather conditions butterflies will select specific vegetation structures to provide shelter (Dennis and Sparks, 2006), a warmer microclimate (Shreeve, 1984), or will use the shade of trees to prevent overheating in summer (Vanreusel et al., 2007). In this study several species were observed inside shady, closed stands where no apparent nectar or host plants were present. For example, the presence of *Aricia agestis* and *Hipparchia semele* in these forested stands seemed related to daily movements to escape unfavourable conditions in open habitats during hot weather. Furthermore, *M. jurtina* that is normally characterized as a grassland butterfly (Dennis, 2004) was regularly associated with the interior of shady deciduous woodlands. *M. jurtina* showed a clear seasonal pattern and was found in firebreaks and edges at the beginning and end of the flying period and in the middle of the flight season in deciduous woodland habitat. This pattern of multi-habitat use corresponds with an estivation in shady habitats in the middle of the flight season to avoid hot temperatures, as was observed in Italy and southern Germany (Ebert and Rennwald, 1991).

Edges versus firebreaks as butterfly habitats

Our results showed that butterfly species richness and assemblage composition were similar between firebreak interiors and their edges, but that the species composition of firebreak interiors and edges differed from that of other edge types. This suggests that firebreaks have a distinct role in butterfly conservation compared to stand edge habitats. Similarly, Ockinger and Smith (Öckinger and Smith, 2007) demonstrated that field margins with a perennial grassland vegetation close to semi-natural grasslands had higher butterfly species richness than field margins farther away and that these grasslands acted as source populations for surrounding field margins. In our study area firebreaks are very likely to play a similar role as source habitat and may have a positive effect on butterfly diversity in nearby stand edges. For most butterfly species the resources used in firebreaks and at stand edges are probably quite similar and supplementation of resources could explain the simultaneous presence of species in these elements. Moreover species can use firebreaks or their edges as a refuge when one of them is disturbed by management. Firebreaks are less drained and less frequently managed than edge habitats which may explain the higher abundance of some species (*Euphydryas aurinia, Coenonympha oedippus, Heteropterus morpheus* and *Cupido argiades*) associated with humid, *Molinia caerulea* dominated, heathland vegetations in firebreak interiors compared to edge habitats.

3.6. Conclusions and implications for conservation

Our study highlights the importance of edge habitat for the conservation of butterfly diversity in fragmented plantation forest landscapes. Stand edges and small open areas in forests are essential for woodland butterflies, as well as for other arthropods such as carabids or spiders (Barbaro et al., 2005; Lin et al., 2007). Compared to other open habitats such as clearcuts and young pine stands, edges were richer in butterfly species and supported a different assemblage.

Habitat quality and management of edges have a strong effect on butterfly presence and abundance (Ferris and Carter 2000). The lack of typical forest edge species in our study suggests that improving the structure of edges by developing a more soft edge with shrubs, may further increase the conservation value of edges. Maintaining and creating edges in forested landscapes will have a small impact on forestry economics, while favouring many butterfly species. However conservation management of edges does not mean that stand interiors can be neglected. *C. oedippus*, an in Europe critically endangered species, was more abundant inside habitat patches than at their edges and several other species used stand interiors as part of their habitat. The use of several patch types by a species may be a frequent phenomenon in fragmented forests and other mosaic landscapes, and it can be a necessary mechanism for species survival in these landscapes. Maintenance of a diversity of habitat types through small-scale landscape heterogeneity seems therefore an important strategy for butterfly conservation.

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3.7. References chapter 3

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3.8. Annex 1

Ecological information for the 23 most abundant species. Species are ordered as in Table 2 by their edge-interior preference. Main habitats based on Lafranchis (2000); mobility based on Bink (1992); host plants (in study area) based on Bink (1992), Lafranchis (2000) and personal observations; polyphagy level: mono - one plant species, strongly oligo - one genus, oligo - one family, poly - more than one family (groups based on Tscharntke et al. 2002); adult food sources based on Bink (1992), national distribution: % of French departments with presence of species (Lafranchis 2000); % national regression calculated by dividing the number of departments where a species was not seen after 1980, but was present before 1980, by the total number of departments where the species was ever seen (Lafranchis 2000).

Species	Main habitats	Mobility	Host plants	Polyphagy level	Adult food sources	National distribution	% National regression
More abundant in edge habitats							
Pyronia tithonus	hedges, forest edges, grasslands	sedentary	Poaceae	oligo	nectar	100	0
Coenonympha pamphilus	grasslands, open forests	sedentary	Poaceae	oligo	nectar	100	0
Lycaena phlaeas	open habitats	rather sedentary	*Rumex* sp.	strongly oligo	nectar	100	0
Maniola jurtina	grasslands, open forests	rather sedentary	Poaceae	oligo	nectar	100	0
Hipparchia statilinus	dry grasslands, heathland, dunes, open forests	sedentary	Poaceae	oligo	nectar	42	39
Aricia agestis	dry grasslands, forest edges and open forests	rather sedentary	*Geranium* sp., *Helianthemum* sp.	poly	nectar	96	3
Thymelicus sylvestris	grasslands (with scattered trees)	sedentary	Poaceae	oligo	nectar	89	10
More abundant in interior habitats							
Coenonympha oedippus	wet grasslands,heathlands and forest edges	highly sedentary	*Molinia caerulea*	mono	nectar, honeydew	10	55
Cupido argiades	grasslands, wetlands, heathlands	rather sedentary	Fabaceae	oligo	nectar	64	28
Euphydryas aurinia	grasslands, forest edges, peatlands	very sedentary	*Succisa pratensis, Scabiosa columbaria, Lonicera periclymenum*	oligo	nectar	82	17
Pararge aegeria	forest, forest edges	rather sedentary	Poaceae	oligo	nectar, fruit, tree sap	100	0
Heteropterus morpheus	wet heathlands, peatlands, open forests, forest edges	very sedentary	*Molinia caerulea*	mono	nectar	39	30
No significant differences							
Minois dryas	grasslands, wet heathlands, open forests, forest edges	sedentary	*Molinia caerulea*	oligo	nectar	47	32
Gonepteryx rhamni	forest edges, open forests,	mobile	*Frangula alnus*	mono	nectar	100	0

	grasslands, shrublands						
Polyommatus icarus	open habitats, heathlands, open forests	rather sedentary	Fabaceae	oligo	nectar	100	0
Thymelicus lineola	grasslands	rather sedentary	Poaceae	oligo	nectar	89	10
Ochlodes venata	hedges, forest edges, grasslands	rather sedentary	Poaceae	oligo	nectar	97	2
Coenonympha arcania	forest edges, hedges, grasslands, open forests	sedentary	Poaceae	oligo	nectar	89	9
Hipparchia semele	dry grasslands, heathlands, dunes and forests	rather sedentary	Poaceae	oligo	nectar, tree sap	63	36
Limenitis reducta	hedges, forest edges, shrublands, open forests	rather sedentary	*Lonicera periclymenum*	mono	nectar	72	22
Colias croceus	open habitats	migrant	Fabaceae	oligo	nectar	98	2
Melitaea cinxia	dry grasslands and shrublands	sedentary	*Plantago lanceolata*	mono	nectar	82	17
Brintesia circe	open forests, shrublands, forest edges, grasslands	rather sedentary	Poaceae	oligo	nectar	64	15

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

Argynnis paphia

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

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4.1. Résumé en français

La qualité de l'habitat domine sur les effets de fragmentation pour expliquer la diversité en papillons de jour dans les fragments de forêts feuillues

Inge van Halder, Jean-Yves Barnagaud,·Hervé Jactel,·Luc Barbaro

L'effet de la fragmentation des habitats forestiers comprend à la fois un effet de diminution de surface de la tache d'habitat et de l'augmentation de l'isolement spatial entre ces taches d'habitat. Des méta-analyses et revues bibliographiques montrent globalement un effet négatif de la fragmentation, mais ces analyses montrent également que la fragmentation n'explique qu'une partie seulement de la variation de la richesse spécifique. D'autres facteurs, comme la qualité et l'hétérogénéité de l'habitat, ainsi que la composition et configuration de la matrice paysagère, peuvent avoir un effet équivalent. De plus, les effets de ces différents facteurs semblent espèce-spécifiques, dépendant des traits de vie des espèces concernées.

Pour vérifier ces hypothèses, nous avons analysé l'effet de la qualité, de la surface et de l'isolement des fragments de forêts de feuillus sur la diversité en papillons de jour. Ces fragments de feuillus sont situés dans une matrice de plantations de pins et hébergent un assemblage typique de papillons de jour dans la zone d'étude (chapitre 2). Nous avons également échantillonné, dans la même zone, les papillons de jour dans des ripisylves où nous supposions trouver le pool d'espèces complet de papillons forestiers. Nous avons en particulier testé les prédictions suivantes :

- La diversité en papillons forestiers augmente avec la surface, la connectivité et la qualité du fragment de feuillus.
- Les assemblages de papillons dans les fragments isolés et de petite taille se caractérisent par des espèces mobiles, avec une large gamme d'habitats, polyphages, de petite taille et avec une capacité de reproduction importante.
- Les ripisylves se distinguent des fragments de feuillus par une richesse en espèces de papillons plus élevée et par une composition taxonomique et fonctionnelle des assemblages différente de ceux des fragments, avec dans les ripisylves relativement plus d'espèces spécialistes, sédentaires, de grande taille et avec une capacité de reproduction plus faible.

Nous avons échantillonné les papillons de jour dans 36 fragments de forêts de feuillus avec des gradients indépendants de surface des fragments (0.3 à 12 ha) et d'isolement spatial (surface de forêts de feuillus de 0 à 23 ha dans une zone tampon de 1000 m autour du fragment). En complément, nous avons échantillonné 8 ripisylves qui diffèrent des fragments, non seulement par leur surface, mais également par leur qualité d'habitat pour les papillons. Nous avons analysé l'effet de la surface, de l'isolement et de la qualité des fragments sur la richesse en papillons toutes espèces confondues, sur la richesse en papillons forestiers, sur la composition des assemblages et sur différents traits moyennés des assemblages.

Au total 43 espèces de papillons de jour ont été observées dans les 44 sites. Parmi ces espèces six peuvent être considérés comme forestières et correspondent à 20% des effectifs observés. Pour les 36 fragments de feuillus il n'y avait ni un effet de la surface ni de l'isolement sur la richesse en espèces totales, en espèces forestières, sur la composition des assemblages et sur les traits moyennés des assemblages. Par contre, la composition en plantes-hôtes dans le sous-bois expliquait une partie de la variation de la richesse en espèces forestières. Trois variables de qualité de l'habitat (nectar, composition en plantes-hôtes et recouvrement arbustif) expliquaient également une partie de la variance (14.4%) dans la composition des assemblages.

La comparaison entre fragments feuillus et ripisylves montrait que les ripisylves étaient plus riches en espèces forestières (Figure 1) et hébergeaient des assemblages d'espèces différents. Les Analyses Canoniques de Correspondances montraient que le type d'habitat (fragments vs. ripisylve) expliquait 9.5 % de la variance des assemblages et que quatre variables de qualité d'habitat expliquaient 19.3 % de la variance, avec 5.8 % en commun entre ces deux groupes de variables. En plus, quatre des six traits moyennés variaient significativement entre fragments et ripisylves, avec dans les ripisylves des assemblages avec relativement plus d'espèces mobiles, de grande taille, avec une plus faible gamme d'habitats et une plus faible tolérance thermique (Figure 2).

Dans notre zone d'étude, l'effet de la surface et de l'isolement des fragments sur la diversité en papillons semble donc être masqué par des différences en termes de qualité d'habitat et par la composition de la matrice paysagère. La **qualité de l'habitat**, notamment la composition en plantes hôtes dans le sous-bois, semble un facteur essentiel pour la survie des papillons de jour. La surface et la qualité des habitats déterminent, toutes deux, la taille des populations de papillons de manière complémentaire.

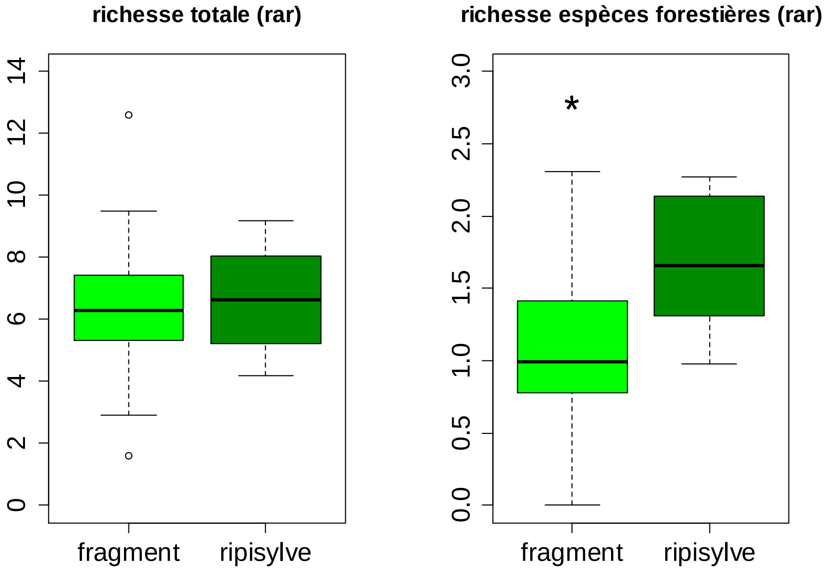

Figure 1. Valeurs médianes et extrêmes pour la richesse totale et en espèces forestières (raréfiées par le nombre de transects) dans les fragments de forêts de feuillus et les ripisylves. * indique que la richesse est significativement différente entre types d'habitat (t-test, *P*< 0.05).

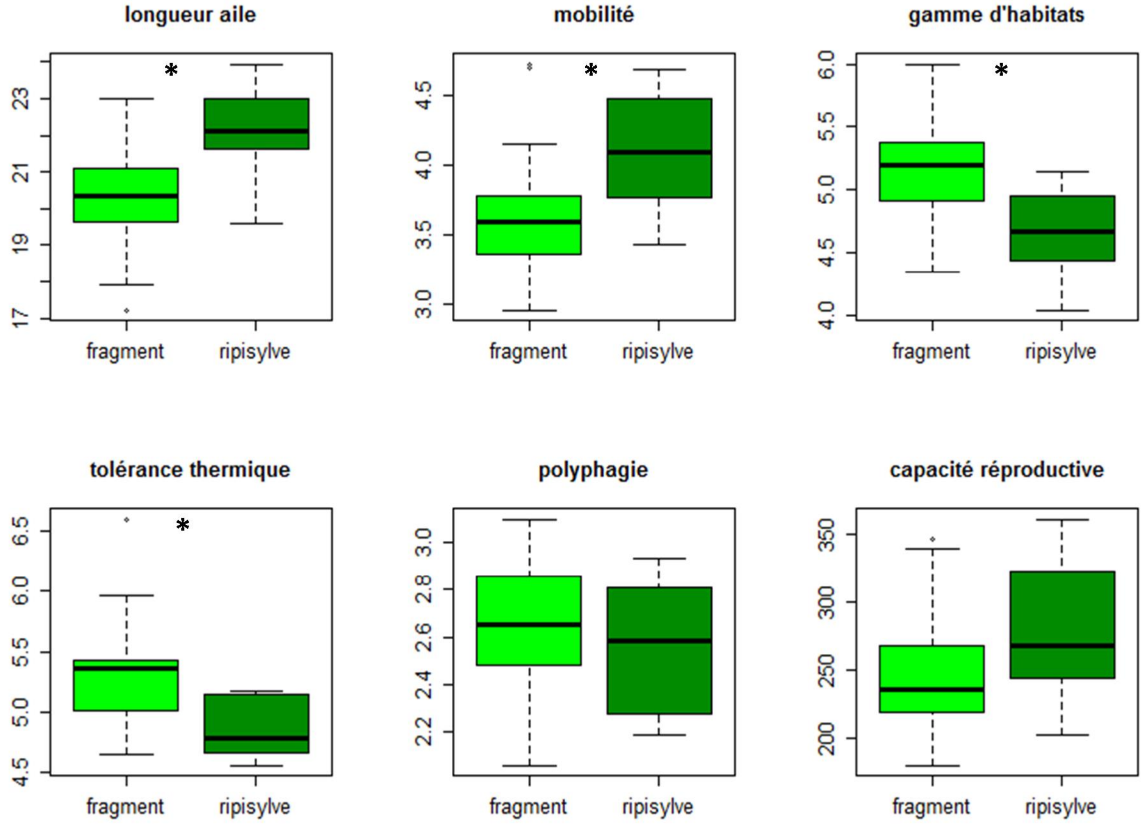

Figure 2. Valeurs médianes et extrêmes pour des traits moyennés des assemblages de papillons de jour dans les fragments et les ripisylves. * indique que le trait moyenné était significativement différent entre types d'habitats (t-test, $P< 0.05$).

La **composition de la matrice** peut également modifier les effets de la fragmentation. Il semble probable que les papillons puissent trouver des ressources supplémentaires et/ou complémentaires dans une matrice composée de plantations de pins, que la matrice puisse favoriser des mouvements d'individus entre fragments et que les espèces de la matrice puissent entrer dans les fragments de feuillus.

Les résultats montrent également **l'importance des ripisylves** pour la conservation des espèces de papillons forestiers. Les assemblages dans les ripisylves contiennent plus d'espèces forestières avec une plus grande spécialisation d'habitat et des tolérances thermiques plus étroites. Pour ces espèces spécialistes les fragments de feuillus semblent donc en dessous des seuils de qualité et/ou de surface nécessaires au maintien de populations viables. Par contre, les assemblages dans les ripisylves comprenaient aussi plus d'espèces mobiles et de grande taille, deux traits corrélés entre eux chez les papillons. Cette plus grande mobilité pourrait donc être liée à la présence d'espèces de grande taille, qui ont également besoin de surfaces d'habitats plus grandes pour se maintenir mais elle pourrait aussi indiquer que la dispersion n'est pas un facteur limitant dans les paysages étudiés pour les espèces de papillons actuellement présentes.

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

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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.

Keywords: Community-Weighted Mean traits, Forest patch area, Landscape matrix, Lepidoptera Rhopalocera, Pine plantation, Woodland connectivity

4.2. 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., 2002b).

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 favours movements between distant habitat fragments, and is therefore 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 colonisation 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 & 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 harbour 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 harbour 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 harbour 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.

4.3. Material and methods

Study sites

The study sites were located in the Landes de Gascogne forest in south-western France, an area of 10.000 km² 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 to 20 hectares, 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.

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., 2015b). For analyses, the number of individuals per species were summed over the four visits per transect. Since the number of transects differed between sites, we calculated for each site a sample-based, rarefied species richness for all species and for the subsample of forest species, designed on the basis of van Swaay et al. (2006). We used the minimum number of transects surveyed per fragment (five) to calculate for all sites an estimated species richness by performing 999 resamplings of five transects over the total number of transects per site and calculating a mean species richness over all resamplings. The nomenclature of the butterfly species follows the Fauna Europaea (2015).

Deciduous fragment area and isolation

We mapped and calculated the area of all deciduous forest fragments (including mixtures with more than 50% deciduous trees) in a buffer of 1000 m around each sampled fragment in a GIS (ArcGIS10, ESRI), using aerial orthophotographs from 2002 or 2004 as background layer. We quantified connectivity as the area of deciduous fragments in a buffer of 500 m and 1000 m, excluding the area of the surveyed fragment itself. This connectivity measure is simple, regularly used (Öckinger et al., 2010) and has shown to perform relatively well as it is correlated with immigration rates towards the surveyed fragment (Bender et al., 2003).

Habitat quality

We considered several habitat quality variables reflecting the availability of critical resources and conditions for butterflies: flowering nectar plants, larval host plants and vegetation structures, which provide suitable microclimates or physical sites for the entire butterfly life cycle (Dennis et al., 2003). For each transect and each survey date, we estimated the abundance of nectariferous plant flowers, at the family level, using seven abundance classes (1-25, 26-50, 51-100, 101-200, 201-400, 401-800, 801-1600 flowers (Clausen et al., 2001; van Halder et al., 2008)). For data analysis we summed the mid-values of each class per transect for the four visits and we calculated a mean value per site, which was log-transformed to reduce the effect of outliers.

We recorded the presence of larval host plants along the transect, based on a list of host plants published by Lafranchis (2000) and completed by personal field observations. We identified dicot host plants at the species or genus level, while grasses other than *Molinia caerulea* and *Pseudarrhenatherum longifolium*, the two dominant species, were merged together into a single category. To reduce the number of explanatory host plant variables we performed a Principal Component Analysis (PCA) on the relative abundance of host plants, expressed as the proportion of transects per site with the host plant. The first two axes were used to express variation in host plant composition between sites and correspond to 18.3% and 13.9% explained variance respectively. The first axis (*host-axis1*) opposed fragments dominated by *M. caerulea* (negative values) and *Viola* spp, *Urtica dioica* and *other grass species* (positive values). Riparian forests were mainly found at the positive side of this axis. The negative side of the second axis (*host-axis2*) was dominated by *Plantago lanceolata, P. longifolium* and *Trifolium* spp while positive values corresponded to *Ilex aquifolium* (see Appendix A). Forest habitat structure was quantified through the mean percentage cover of trees, shrubs, ferns and herbaceous plants per transect. Seven variables of habitat quality were eventually used in the analyses (*nectar, host-axis1, host-axis2, %trees, %shrubs, %ferns, %herbs*). For the 36 deciduous fragments, fragment area and isolation were not correlated with habitat quality variables with the exception of *host_axis1* that was correlated with the quantity of deciduous forest in the 500 m and 1000 m buffer ($r=0.64$, $P<0.001$ and $r=0.59$, $P<0.001$ respectively). Riparian forests differed significantly in host plant composition (*host-axis1*) and had a higher shrub cover than forest fragments (Wilcoxon, $P<0.001$ and $P=0.018$ respectively).

Butterfly traits and Community-Weighted Mean trait values

We selected six traits considered to affect species sensitivity to fragmentation: wing size, mobility, reproductive capacity, habitat range, thermal tolerance and larval host plant range (Barbaro and van Halder, 2009; Ewers and Didham, 2006; Henle et al., 2004; Öckinger et al., 2010). The last three traits reflect ecological specialization, and wing size was used as a proxy for body size. Trait values were based on Bink (1992). Relationships between species traits were first analyzed with a PCA in order to summarize the correlations among traits and identify trait combinations related to forest species. The first two axes of the PCA of the species-trait matrix accounted for 65.0 % of total variance. Two groups of correlated traits could be distinguished (see Appendix B). Wing size, mobility and reproductive rate were positively correlated (corresponding to axis 1) and habitat range, thermal tolerance and host-plant range were positively correlated (axis 2). Forest species were characterized by a narrow habitat range, a narrow thermal tolerance and narrow host-plant range compared to non-forest species (Wilcoxon test, P<0.05). We further calculated for each forest fragment and trait a Community-Weighted Mean (hereafter CWM) trait index for the community present at a site, similar to the Community Specialization Index defined in Devictor et al. (2008). For example, the 'CWM mobility' for a fragment *j* was given by

$$CWMmobility_j = \frac{\sum_{i=1}^{n} a_{ij}\left(SMI_i\right)}{\sum_{i=1}^{n} a_{ij}}$$

where *n* is the total number of species recorded at the fragment, a_{ij} is the abundance of species *i* in plot *j* and SMI_i its mobility. A high CWM mobility thus indicates that the community is dominated by individuals belonging to mobile species. We computed in the same way averaged community indices for the other traits (Table 1).

Table 1. Description of butterfly species traits used in the analyses and their range of values in the dataset. The traits are based on Bink (1992), unless otherwise stated.

Trait	Description of trait	range of trait values in the dataset
Wing size	Length of the forewing in mm, used as a proxy for body size.	11-37
Mobility	Mobility of butterflies in 9 classes (from highly sedentary to extremely mobile)	2-9
Habitat range	Number of different ecosystems in which the species is normally observed among a total of 10 ecosystems from closed forests to open grasslands.	3-8
Thermal tolerance	Adult tolerance to temperature extremes in 9 classes (from extremely sensitive to very tolerant to temperature extremes).	1-9
Larval host plant specificity	Larval host plant specialisation in 4 classes (host plants belonging to either one species (1), one genus (2), one family (3) or more than one family (4)). Host plants based on Bink (1992), Lafranchis (2000) and local observations.	1-4
Reproductive capacity	Maximum number of eggs laid per female.	61-1100

Data analyses

For the 36 fragments we analyzed the separate effect of habitat area, isolation and quality on rarefied total richness and rarefied forest species richness of butterflies using linear models with a Gaussian distribution. We used a forward selection procedure to select significant habitat quality variables (*P* <0.05 for inclusion). We used Canonical Correspondence Analysis (CCA) to relate habitat area, isolation and quality to the composition of butterfly species assemblages (Jongman et al., 1995). Separate CCAs were used to test the distinct effects of deciduous woodland area, isolation and habitat quality, using a forward selection procedure for the habitat quality variables based on the additional variation explained by each variable at each step (*P* < 0.05 for inclusion). We then combined significant variables in an overall CCA and calculated their combined and pure effects (defined as the effect of a variable after eliminating the variance due to other variables) with partial CCA (Cushman and McGarigal, 2002). We tested the significance of the effect of each variable and of the different partial CCAs with 999 permutations. We omitted species present in less than four sites in CA and (partial) CCA and log(x+1)-transformed species abundances (Jongman et al., 1995). We used linear models with a Gaussian distribution to test the relationships between each Community-Weighted Mean trait value and fragment area and isolation. For all analyses we tested the effect of fragment area and isolation as non-transformed and log-transformed explanatory variables and for the isolation metrics in the landscape buffer of 500 m and 1000 m.

We performed t-tests to analyze if forest fragments differed from riparian forests in rarefied total species richness, rarefied forest species richness and CWM trait values. We analyzed differences in community composition between fragments and riparian forests with CCA using two sets of explanatory variables: forest type (fragment versus riparian) and the habitat quality variables. As for the forest fragments, we selected habitat quality variables with a forward selection procedure and we calculated the pure and combined effect of variables as described above. We performed all analyses in R version 2.15.0. We used the package “rich” for calculating rarefied richness (Rossi, 2011) and vegan for CA and CCA analyses (Oksanen et al., 2011).

4.4. Results

Forest specialist butterflies

A total of 2542 individuals belonging to 43 butterfly species were observed in the 44 deciduous woodlands during the four visits (Appendix D and E). Among them, six species can be classified as forest specialists (van Swaay et al., 2006): silver washed fritillary (*Argynnis paphia*), white admiral (*Limenitis camilla*), southern white admiral (*Limenitis reducta*), purple hairstreak (*Favonius quercus*), speckled wood (*Pararge aegeria*) and ilex hairstreak (*Satyrium ilicis*). The white admiral was exclusively found in the riparian forests, while the other species occurred in both forest fragments and riparian forests. These six forest species were represented by 521 individuals corresponding to 20.5 % of the total number of observed butterflies.

Butterfly diversity in forest fragments

The rarefied total richness and rarefied forest species richness were not significantly correlated with fragment area nor with fragment isolation in the 36 forest remnants (see Appendix C). *Host_axis2* (i.e. the second axis of the host-plant PCA) was the single significant habitat quality variable explaining the rarefied forest species richness (F=5.02, P=0.032, R^2=0.13); yet, no habitat quality variable was significantly related to the total rarefied species richness.

In the CA of the forest fragments × butterfly species matrix, the first two axes accounted for 25.3% of the total inertia. Fragment area and isolation did not influence the ordination of butterfly communities in the CCA, while three habitat quality variables were retained by the forward selection procedure (*nectar, host-axis2* and *%shrub*) and explained together 14.4% of the inertia (P=0.001). The different CWM trait values were not significantly related with fragment area nor with fragment isolation.

These results were consistent even if fragment area or isolation were log-transformed or whether isolation was calculated in the landscape buffer of 500 m or 1000 m.

Comparing butterfly communities in deciduous fragments vs. riparian forests

The rarefied total species richness was not different between fragments and riparian forests. By contrast, the rarefied richness of forest species was significantly higher in riparian forests (*t*=-3.32, *P*=0.007, Figure 3).

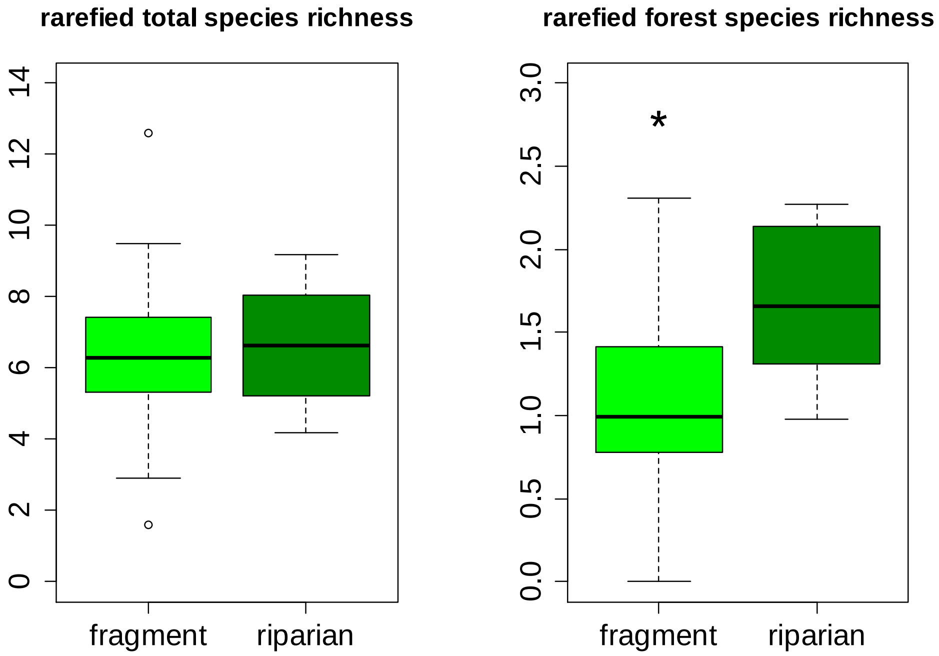

Figure 3. Median and extreme values for rarefied total butterfly species richness and rarefied forest butterfly species richness of deciduous fragments *vs*. deciduous riparian forests. * indicates that the richness is significantly different between habitat types (t test, P<0.05).

The first two axes of the CA of the forest habitats × butterfly species matrix corresponded to 25.5% of total inertia. CCA showed that fragment type (fragment *vs*. riparian) explained 9.5% of total inertia (*P*=0.001). Axis 1 showed a clear separation between the fragments and the riparian sites. For example, the forest species *A. paphia* and *L. camilla* were associated with the riparian forests (Figure 4). Four habitat quality variables were selected by the forward procedure: *host-axis1, nectar, %shrub* and *host-axis2,* which explained together 19.3% of total inertia (*P*=0.001). *Host-axis1, %shrub* and *nectar* were correlated with the first axis and high values of these variables corresponded to the riparian sites. *Host-axis2* was linked to the second CCA axis (Figure 4). Partial CCA of the conditioned effect of habitat type on the four selected habitat quality variables showed that the pure effect of habitat quality explained the largest proportion of total inertia (13.6% ; *P*=0.002). The pure effect of habitat type was 3.7% (*P*=0.016) and the joint effect of habitat quality and type explained 5.8% of total inertia.

Four of the six tested CWM traits differed significantly between fragments and riparian forests (Appendix F). Community habitat range and thermal tolerance were lower in the riparian forests and community wing size and mobility were higher in riparian forests than in the fragments (Figure 5).

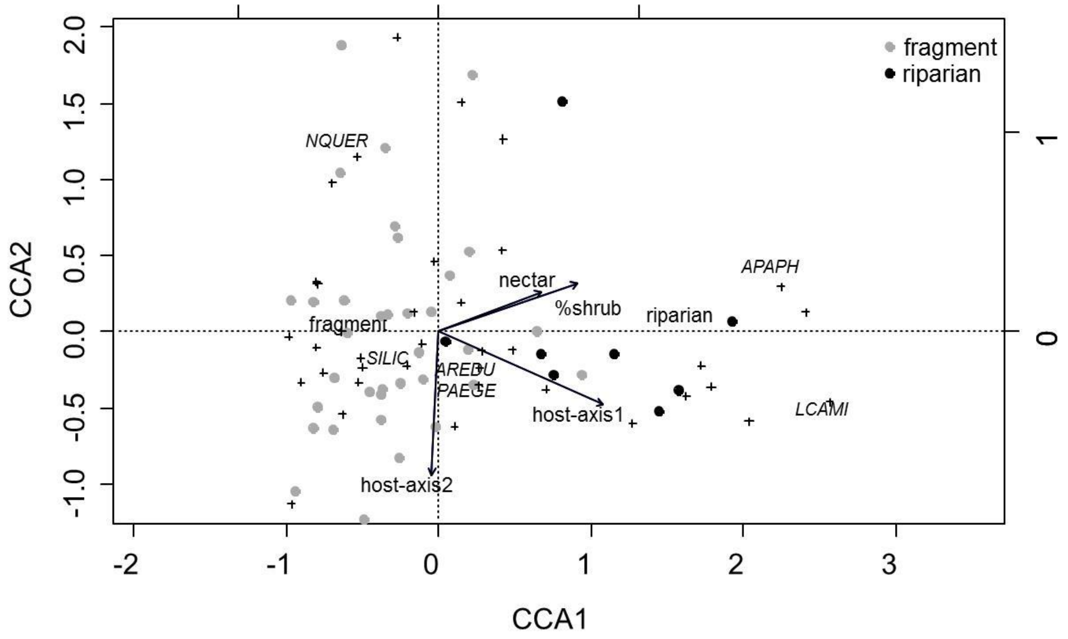

Figure 4. The first two axes of the Canonical Correspondence Analysis ordination with position of deciduous fragments (grey dots), deciduous riparian forests (black dots), butterfly species (crosses) and selected significant environmental variables. Continuous habitat quality variables are indicated by arrows (host-axis1, host-axis2, nectar, %shrub) and habitat type (fragment *vs*. riparian) by class centroids. For clarity only names of forest butterfly species are indicated: *APAPH - Argynnis paphia, LCAMI - Limenitis camilla, LREDU - Limenitis reducta, FQUER - Favonius quercus, PAEGE - Pararge aegeria, SILIC- Satyrium ilicis.*

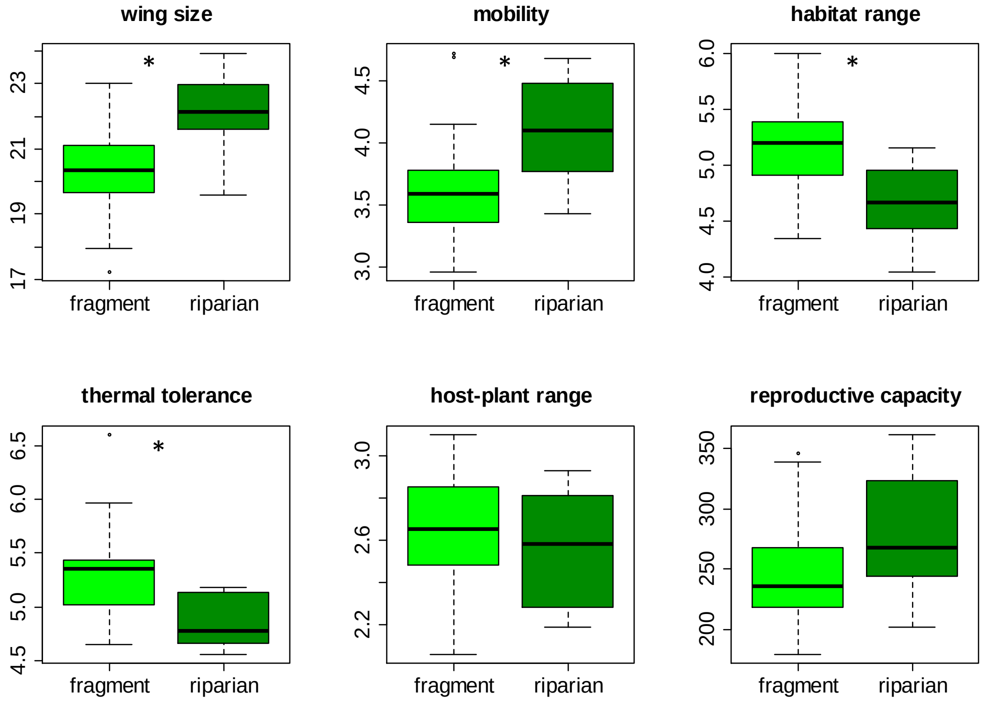

Figure 5. Median and extreme values for Community-Weighted Mean trait values of butterfly communities in deciduous fragments *vs*. deciduous riparian forests for wing size, mobility, habitat range, thermal tolerance, host-plant rang and reproductive capacity (see Table 1 for description of traits). * indicates that Community-weighted mean traits values are significantly different between habitat types (t test, P<0.05).

4.5. Discussion

The composition and richness of butterfly communities was influenced by habitat quality of forest fragments, but neither by their area nor isolation. Even the richness of forest specialists, which are more likely to be affected by forest fragmentation, did not increase with increasing deciduous fragment area or connectivity. This result contrasts with positive effects of habitat area and connectivity synthesized for different taxa by Prugh et al. (2008) and for butterflies by Ockinger et al. (2010). The effect of area and isolation may be blurred by various other factors, including habitat quality, edge effects, matrix effects and altered trophic interactions (Ewers and Didham, 2006; Prevedello and Vieira, 2010; Prugh et al., 2008; Sweaney et al., 2014). Alternatively the range of variation in fragment area and connectivity may have been too narrow to allow detecting their effect on butterfly diversity.

In contrast to area and isolation, habitat quality explained a significant part of forest butterfly richness and community composition in deciduous forest fragments. Habitat quality has been considered among the three most important environmental factors, together with patch area and isolation, to explain butterfly diversity patterns (Fleishman et al., 2002; Thomas et al., 2001; WallisDeVries and Ens, 2010). Among the variables measuring habitat quality in our study, host plant composition played a significant role for forest species richness and community composition, confirming that larval requirements are key factors for quantifying butterfly habitat quality (Thomas et al., 2001). Butterfly species in high quality habitats have higher intrinsic population growth rates and densities thereby enhancing species long-term persistence (Thomas et al., 2001). Habitat quality and area both affect population size and species occurrence thus in a complementary way.

The composition of the landscape matrix surrounding habitat patches can also enhance or mitigate the effects of habitat fragmentation on species diversity (Dover and Settele, 2009; Eycott et al., 2012; Öckinger et al., 2012). In our study deciduous forest fragments were embedded in a matrix of pine plantations that can influence ecological processes differently compared to an agricultural matrix. The pine plantation matrix can provide alternative resources and habitats, increase landscape connectivity and provide a buffer against adverse conditions (Brockerhoff et al. 2008). Resources like nectar plants, as well as several host plant for larvae, can be found in the pine-dominated matrix (van Halder et al., 2011). Ockinger et al. (2012) showed that the effect of grassland fragmentation for butterflies decreased with increasing forest cover in the surrounding landscape. They attributed this effect to the availability of additional resources and a possible higher dispersal in the forest-dominated matrix while edge effects were more negative in the agricultural matrix. It seems likely that these positive effects of a forested landscape matrix will be even more important for forest butterflies compared to the grassland species pool studied by Ockinger et al. (2012). Likewise, Eycott et al. (2012) showed in a meta-analysis that species movements were facilitated in a matrix more similar to species' habitat structure. A forested landscape matrix should thus be more permeable to forest butterfly movements than an intensive agricultural matrix (Chardon et al., 2003; Dover and Settele, 2009) and ecotones like forest edges and forest roads might also provide effective corridors for dispersion, both for forest and generalists species.

Besides that generalist butterfly species and some forest specialists use additional resources and habitats in the plantation forest matrix, reciprocally matrix-species may use deciduous forest fragments as part of their habitat (Liivamägi et al., 2014), for example as microclimatic refuges during warmer periods (van Halder et al., 2011). Accordingly, in our study area, pine plantations and their edges are not empty but harbor as many butterfly species as deciduous forests (van Halder et al., 2011, 2008). However our study design did not allow testing the effects of matrix composition since all sites were included in the same matrix type.

Area and isolation effects are expected to apply primarily to habitat specialists because of their low ability to exploit resources found in the matrix (Öckinger et al., 2010; Steffan-Dewenter and Tscharntke, 2000). We failed to find any support for this prediction in our data, as forest species richness was unaffected by fragment area and isolation. Six species were classified as forest species according to van Swaay et al. (2006). The classification of species as habitat specialists is debatable and may depend on spatial scale (*e.g*. Europe *vs*. local), biogeographical region, and other habitat types locally available. In a previous study in the same region (van Halder et al., 2008), we compared butterfly assemblages occurring in seven different habitat types: deciduous forests, firebreaks and five stages of pine plantations (herbaceous clearcuts, shrubby clearcuts, young pine stands, mid-class pine stands and older pine stands). Results from this study confirm that three out of six species qualified as forest specialists (*P. aegeria, A. paphia* and *F. quercus*) were significantly more present in deciduous forests than in pine stands (van Halder et al., 2008). The fourth species, *L. reducta*, was more abundant in deciduous woodlands than in pine stands, but occurred also in firebreaks, *S. ilicis* showed no clear preference and *L. camilla* was only observed once, so it was impossible to classify its habitat preference. Furthermore, the ordination of species according to their traits showed that the selected six forest species significantly differed in trait combinations compared to the other observed species (Appendix B).

Forest species richness was higher in riparian forests than in deciduous fragments and communities were different, pointing out the importance of this habitat for butterfly conservation in human-modified landscapes. Riparian forests are key habitats that should not be harvested because the remaining fragments of deciduous forests in plantation-dominated landscapes can not provide substitutive habitats for all forest butterflies. Here, distinct butterfly assemblages occurring in riparian forests and fragments were mainly attributed to differences in habitat quality, confirming that it is a primary determinant of butterfly persistence.

CWM trait values were unaffected by changes in deciduous woodland patch area or isolation. By contrast, four out of six community traits differed between riparian forests and deciduous fragments, underlying that these two habitats host functionally distinct butterfly communities. Both thermal and habitat specialization were higher for butterfly communities in riparian forests compared to isolated fragments. Riparian forests had indeed a higher proportion of forest species with narrower habitat range and thermal tolerance than non-forest species. These forests are therefore of great importance for conserving northern butterfly species at southern latitudes in a climate warming context (Devictor et al., 2012). As expected, species occurring in riparian forests had on average larger wing size than those of fragments, but we found no support for lower mean community mobility in highly-connected riparian forests. Higher mean butterfly mobility in riparian forest may be caused by the positive correlation with wing size (Stevens et al., 2013), but can also suggest that limitations to dispersal imposed by isolation are not primary determinants of functional turnover in butterfly communities in such mosaic landscapes.

4.6. Conclusions

Habitat quality affected the richness and composition of butterfly communities in deciduous forest fragments more than area and isolation. Even small or isolated fragments in conifer plantation matrices would have a good conservation value for forest species, provided that their habitats are of high quality, with for example several larval host plant species. However, riparian forests appear as even better for the maintenance of butterfly biodiversity. In particular, species with a narrow habitat range and sensitive to extreme temperatures were more abundant in riparian forests suggesting that, for these specialists, fragments were below minimum threshold values of habitat amount and quality. It also indicates that riparian forests might play the role of climatic refuges for woodland butterflies sensitive to climate warming, favoring their maintenance at low-latitude limits.

Acknowledgements
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4.7. References chapter 4

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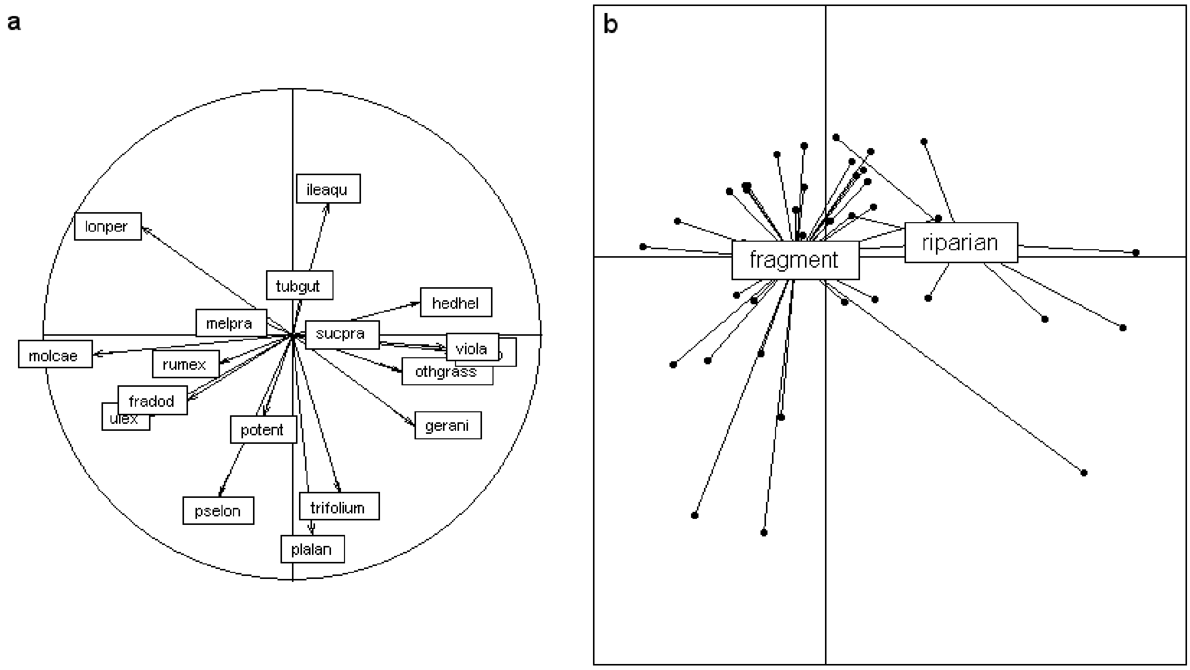
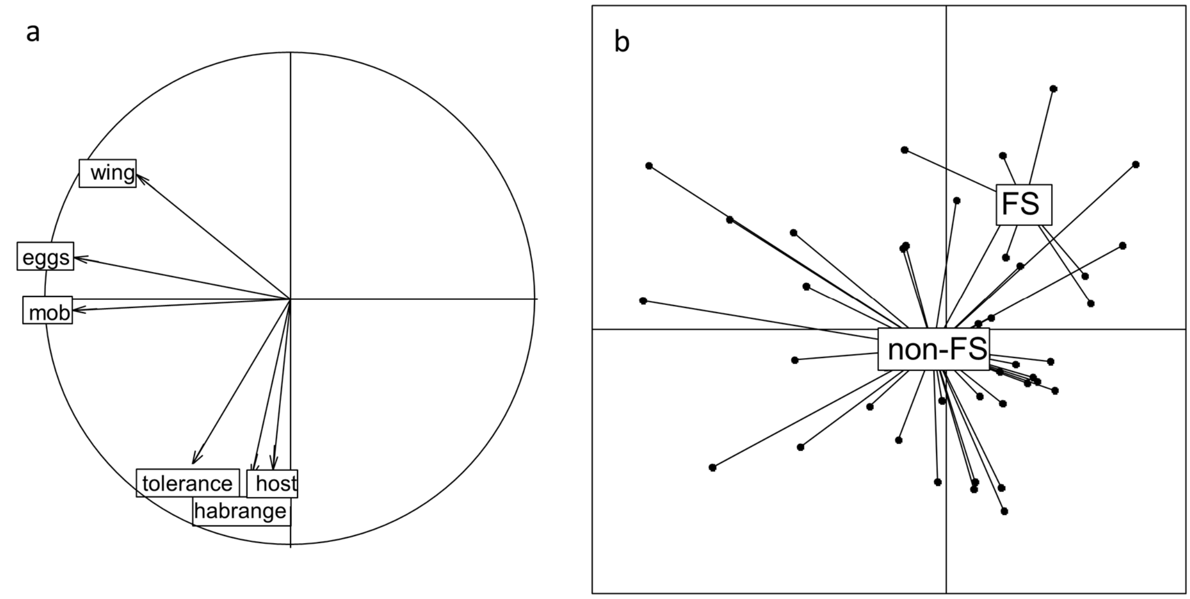
4.9. Appendixes

Appendix A



PCA biplot of the relative abundance of butterfly host-plants in fragments and riparian forests wit a) position of the host-plants and b) position of the fragments and riparian forests. Abbrevations of plant species or genera: fradod - *Frangula dodonei*; gerani - *Geranium* spp.; hedhel - *Hedera helix*; ileaqu - *Ilex aquifolium*; lonper - *Lonicera periclymenum*; melpra - *Melampyrum pratense*; molcae - *Molinia caerulea*; othgrass - other grass species; plalan - *Plantago lanceolata*; potent - *Potentilla* spp.; pselon - *Pseudarrhenatherum longifolium*; rumex - *Rumex* spp.; sucpra - *Succisa pratensis*; trifolium - *Trifolium* spp.; tubgut - *Tuberaria guttata*; ulex - *Ulex* spp.; urtdio - *Urtica dioica*; viola - *Viola* spp.

Appendix B



PCA biplot for relationships between species traits with a) position of traits and b) position of butterfly forest species (FS) and non-forest species (non-FS). Abbreviations for traits: wing – wing size; eggs – reproductive capacity; mob – mobility; tolerance – thermal tolerance; host - larval host-plant range; habrange – habitat range. See Table 1 for description of traits.

Appendix C

Results of linear models for the independent effect of habitat area and isolation on rarefied total butterfly species richness and rarefied forest butterfly species richness for the 36 deciduous forest fragments. As isolation metric we used the area of deciduous forest in a buffer of 500 or 1000 m, excluding the area of the sampled fragment.

response variable	explanatory variables	F	*P*
rarefied total richness	area	0.358	0.554
	LOG (area)	0.001	0.974
	isolation 500m	0.002	0.964
	LOG (isolation 500m)	0.057	0.812
	isolation 1000m	0.001	0.970
	LOG (isolation 500m)	0.444	0.509
rarefied forest species richness	area	0.228	0.636
	LOG (area)	0.003	0.958
	isolation 500m	0.155	0.696
	LOG (isolation 500m)	0.082	0.776
	isolation 1000m	0.044	0.835
	LOG (isolation 500m)	0.433	0.515

Appendix D

List of the 43 butterfly species observed in the 44 sites with the area of each deciduous fragment. Total abundance, frequency and abundance per site are given. Species names are according to Fauna Europeae (http://www.faunaeur.org/index.php, consulted 8 June 2015).

Species		**site**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**
		area (ha)	0.27	0.32	0.43	0.44	0.52	0.56	0.65	0.72	0.73	0.99	1.03	1.18	1.71	1.76	2.06	2.14	2.21	2.64	2.77	2.89	3.51	3.56
Forest species	abundance	frequency																						
Pararge aegeria	365	38	0	0	1	1	2	8	0	0	8	8	15	0	6	2	3	4	1	1	15	21	10	8
Limenitis reducta	47	23	0	0	1	0	0	0	0	0	4	1	2	0	1	0	1	1	1	0	1	0	0	1
Favonius quercus	37	13	0	0	0	0	6	0	1	2	0	0	0	0	2	1	0	0	0	3	0	0	0	0
Argynnis paphia	34	10	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Satyrium ilicis	32	20	1	0	2	0	2	0	0	1	2	1	3	0	0	0	1	1	1	1	1	0	0	0
Limenitis camilla	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Non-forest species (matrix)																								
Pyronia tithonus	360	40	7	0	1	13	20	2	10	6	6	6	0	6	9	1	2	22	4	3	8	5	3	13
Maniola jurtina	327	39	3	3	2	1	8	4	1	23	1	1	0	0	4	10	0	0	0	3	11	3	15	5
Gonepteryx rhamni	183	28	0	0	1	0	1	0	1	7	5	0	2	3	5	0	0	6	0	1	0	4	0	0
Melitaea athalia	117	10	1	0	0	0	1	0	0	0	0	0	0	0	6	23	1	0	0	0	0	0	0	0
Minois dryas	109	24	0	0	0	19	2	2	0	7	1	1	15	0	0	0	6	11	0	4	6	0	0	2
Coenonympha pamphilus	108	30	0	2	0	3	6	2	3	0	0	1	5	0	0	0	1	7	2	1	3	7	3	2
Euphydryas aurinia	108	17	0	0	0	0	0	0	0	1	13	0	14	1	2	0	7	9	6	2	0	0	0	0
Lycaena phlaeas	94	30	0	0	1	1	11	0	1	7	0	0	0	1	0	2	11	3	0	1	2	1	2	5
Celastrina argiolus	82	31	0	0	1	0	3	0	0	0	2	3	4	1	5	2	3	0	0	0	1	1	2	0
Coenonympha arcania	74	15	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	3	0	5
Hipparchia semele	60	18	0	0	0	0	2	2	2	0	0	0	2	0	0	0	0	0	0	9	4	1	0	5
Aricia agestis	56	19	0	0	0	2	2	0	0	10	0	0	0	0	0	1	0	0	0	0	7	1	0	9
Ochlodes sylvanus	56	23	1	0	0	0	2	0	0	1	0	1	1	0	0	4	1	0	5	1	2	0	3	0
Hipparchia statilinus	39	20	0	0	0	1	10	2	0	0	0	2	0	0	2	1	1	3	0	0	3	0	0	1
Brintesia circe	36	16	1	0	0	0	5	2	0	3	0	1	0	0	0	0	0	0	0	1	5	0	0	1
Lycaena alciphron	35	17	0	0	0	0	4	0	2	1	0	0	0	1	1	3	0	0	4	0	1	1	0	0
Melanargia galathea	24	10	0	0	0	0	0	0	1	0	1	0	0	1	4	0	0	0	0	1	3	0	0	0
Lasiommata megera	20	8	1	0	0	2	1	0	0	0	0	0	2	0	0	0	0	3	0	0	3	0	0	0
Thymelicus sylvestris	19	11	0	0	0	0	0	0	3	0	0	0	0	1	3	2	0	1	1	0	0	1	0	0
Vanessa atalanta	12	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Aglais io	11	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Coenonympha oedippus	10	6	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	2	2	0	0	0	0
Heteropterus morpheus	10	7	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0	2	0	0	0	0
Pieris rapae	10	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonia c-album	9	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieris brassicae	8	7	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Melitaea cinxia	7	3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymelicus lineola	7	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieris napi	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callophrys rubi	5	4	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0
Nymphalis polychloros	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cupido argiades	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
Polyommatus icarus	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Colias crocea	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Iphiclides podalirius	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argynnis adippe	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Papilio machaon	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Appendix D (continued)

Species	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**
	3.65	3.74	4.22	4.40	5.05	5.19	5.20	5.54	5.76	6.03	6.33	8.71	9.61	11.46	riparian	riparian	riparian	riparian	riparian	riparian	riparian	riparian
Forest species																						
Pararge aegeria	2	10	14	8	0	4	22	14	3	10	19	1	8	2	24	33	12	9	26	1	22	7
Limenitis reducta	0	1	0	1	1	0	0	0	7	1	2	2	1	0	2	0	4	0	3	0	1	7
Favonius quercus	3	1	0	3	0	1	0	0	0	0	0	10	0	0	0	0	0	0	1	3	0	0
Argynnis paphia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	2	6	3	13	3	0	2
Satyrium ilicis	1	5	0	0	1	1	0	0	1	0	2	0	0	0	2	2	0	0	0	0	0	0
Limenitis camilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	0	0	1
Non-forest species (matrix)																						
Pyronia tithonus	2	13	5	30	1	1	0	19	14	1	24	3	3	20	7	0	4	4	3	6	30	23
Maniola jurtina	1	1	2	1	8	4	21	2	3	47	36	9	14	7	14	4	8	12	5	16	2	12
Gonepteryx rhamni	2	1	0	0	1	12	37	2	8	6	2	0	4	0	10	1	30	3	16	1	0	11
Melitaea athalia	0	27	0	0	30	0	0	0	0	0	0	0	0	0	0	2	0	0	11	15	0	0
Minois dryas	0	1	0	12	1	1	0	0	4	0	2	6	0	0	1	0	1	1	0	1	0	2
Coenonympha pamphilus	2	8	4	4	0	0	8	8	1	2	3	8	4	0	0	0	0	1	0	1	3	3
Euphydryas aurinia	1	11	0	2	22	0	0	0	12	0	0	0	0	1	0	0	3	1	0	0	0	0

Lycaena phlaeas	2	5	0	7	0	4	6	1	3	2	0	1	4	0	3	2	1	0	1	0	2	1
Celastrina argiolus	1	2	3	4	2	5	6	2	1	0	0	1	1	0	7	2	5	3	4	1	1	3
Coenonympha arcania	0	9	6	1	0	0	1	2	3	0	16	0	0	0	0	0	0	1	0	4	3	16
Hipparchia semele	0	1	5	6	1	0	0	1	2	0	1	9	0	2	0	0	0	0	0	0	0	5
Aricia agestis	0	0	1	1	0	2	4	6	1	2	2	2	0	0	0	0	1	1	1	0	0	0
Ochlodes sylvanus	6	1	3	0	0	3	3	0	3	0	2	0	0	1	0	0	8	2	0	1	0	1
Hipparchia statilinus	0	1	1	1	2	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	3
Brintesia circe	0	0	2	1	2	0	1	1	0	0	1	7	0	0	0	0	0	0	0	0	0	2
Lycaena alciphron	1	1	0	1	0	0	1	2	0	7	0	3	0	0	0	0	0	0	0	0	0	1
Melanargia galathea	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7	2	3
Lasiommata megera	0	1	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thymelicus sylvestris	0	0	0	0	0	0	1	0	1	0	0	0	4	0	0	0	0	0	0	0	0	1
Vanessa atalanta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	1	0	0	1	0	3
Aglais io	0	1	0	0	0	1	1	0	0	0	0	0	1	0	2	0	1	0	2	0	0	1
Coenonympha oedippus	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Heteropterus morpheus	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Pieris rapae	0	0	0	0	0	1	0	0	2	0	0	0	0	0	1	2	0	0	2	0	0	2
Polygonia c-album	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	2	0	1	1	0	1
Pieris brassicae	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	2	0	0	1	0	0	0
Melitaea cinxia	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	1	0
Thymelicus lineola	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Pieris napi	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	2	0	0	0
Callophrys rubi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nymphalis polychloros	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Cupido argiades	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyommatus icarus	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
Colias crocea	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Iphiclides podalirius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Argynnis adippe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Papilio machaon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix E

List of the 43 butterfly species observed in the 44 sites and grouped as forest species and non-forest species with the total abundance and the number of individuals observed at each visit.

	Total abundance	visit 1	visit 2	visit 3	visit 4
Forest species					
Pararge aegeria	365	152	90	58	65
Limenitis reducta	47	12	4	23	8
Favonius quercus	37	0	9	26	2
Argynnis paphia	34	2	16	7	9
Satyrium ilicis	32	8	24	0	0
Limenitis camilla	6	1	5	0	0
Non-forest species (matrix)					
Pyronia tithonus	360	0	19	250	91
Maniola jurtina	327	105	149	27	46
Gonepteryx rhamni	183	19	120	24	20
Melitaea athalia	117	19	98	0	0
Minois dryas	109	0	5	90	14
Coenonympha pamphilus	108	67	27	5	9
Euphydryas aurinia	108	107	1	0	0
Lycaena phlaeas	94	3	44	25	22
Celastrina argiolus	82	10	33	27	12
Coenonympha arcania	74	34	40	0	0
Hipparchia semele	60	0	8	34	18
Aricia agestis	56	1	11	16	28
Ochlodes sylvanus	56	6	48	2	0
Hipparchia statilinus	39	0	2	0	37
Brintesia circe	36	0	12	14	10
Lycaena alciphron	35	19	16	0	0
Melanargia galathea	24	0	22	2	0
Lasiommata megera	20	8	0	9	3
Thymelicus sylvestris	19	0	19	0	0
Vanessa atalanta	12	8	0	2	2
Aglais io	11	2	9	0	0
Coenonympha oedippus	10	0	8	2	0
Heteropterus morpheus	10	0	9	1	0
Pieris rapae	10	0	5	3	2
Polygonia c-album	9	4	3	0	2
Pieris brassicae	8	1	7	0	0
Melitaea cinxia	7	6	0	0	1
Thymelicus lineola	7	0	7	0	0
Pieris napi	6	2	4	0	0
Callophrys rubi	5	4	1	0	0
Cupido argiades	4	3	0	1	0
Nymphalis polychloros	4	2	2	0	0
Polyommatus icarus	4	4	0	0	0

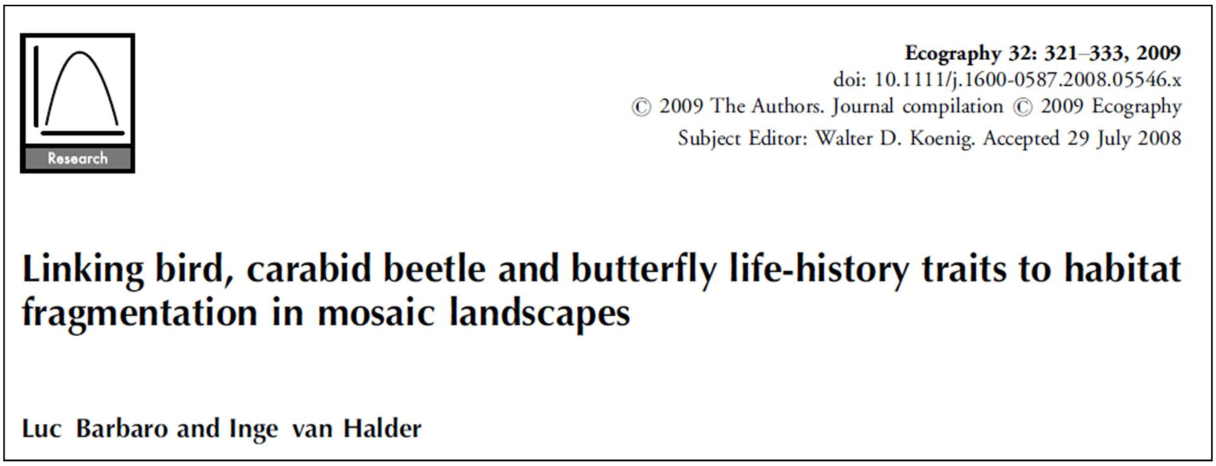
Colias crocea	3	1	1	0	1
Iphiclides podalirius	2	0	0	1	1
Argynnis adippe	1	0	1	0	0
Papilio machaon	1	0	0	1	0
	2542	610	879	650	403

Appendix F

Results of t-tests for differences in Community-Weighted Mean (CWM) trait values between habitat types (fragments *vs.* riparian forests). P values <0.05 are indicated in bold. See Table 1 for a description of the traits.

CWM trait	t	*P*
Wing size	**-3.491**	**0.006**
Mobilty	**-2.704**	**0.024**
Habitat range	**3.245**	**0.008**
Thermal toleranc	**3.925**	**0.001**
Larval host-plant range	0.914	0.383
Reproductive capacity	-1.811	0.105

5. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes



Research

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Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes

Luc Barbaro and Inge van Halder

5.1. Résumé en français

Relier les traits de vie des oiseaux, des coléoptères carabiques et des papillons de jour à la fragmentation des habitats

L’objectif de cette partie était d’évaluer l’influence de la composition et de la configuration du paysage sur la distribution des traits de vie au sein des communautés d’oiseaux, de coléoptères carabiques et de papillons de jour dans les paysages en mosaïque dominés par les forêts de plantation dans le massif de Landes de Gascogne.

Les oiseaux, les carabiques et les papillons ont été échantillonnés dans, respectivement, 287, 244 et 81 plots appartenant à différent types d'habitats : coupe-rases herbacées, coupe-rases arbustives, jeunes peuplements de pins, peuplements matures de pins, forêts de feuillus, pare-feux et prairies. Nous avons renseigné pour chaque espèce dans les trois taxa échantillonnés 12 traits biologiques et écologiques caractérisant la rareté, l’origine biogéographique, la taille, la guilde trophique, la capacité de dispersion, le potentiel reproductif et la phénologie. Nous avons utilisé une méthode d’ordination à trois tableaux, l’analyse RLQ, pour relier directement les traits des oiseaux, carabiques et papillons au même jeu de métriques paysagères calculées dans des buffers de 400 m autour des points d’échantillonnage.

Les analyses RLQ montrent des corrélations significatives entre traits de vie et configuration du paysage pour les trois taxa. Les espèces à enjeu de conservation des trois taxa se caractérisent par une combinaison de traits qui les rend particulièrement sensibles à la fragmentation des milieux ouverts à l’échelle du paysage. Ces traits sont: une faible productivité, une taille intermédiaire, une aire de distribution géographique restreinte, une phénologie tardive et un mode d’alimentation au sol pour les oiseaux ; une taille intermédiaire, une activité adulte printanière, une distribution à tendance nordique, et une période de reproduction estivale pour les carabiques ; et une aire de distribution restreinte, un hivernage sous forme d’œufs ou de chenilles, une faible mobilité, une spécialisation alimentaire et une courte période de vol pour les papillons. La prise en compte des traits apporte une perspective fonctionnelle à la définition de mesures de conservation adéquates pour les espèces menacées d’oiseaux, de carabiques et de papillons de jour dans les paysages forestiers en mosaïque.

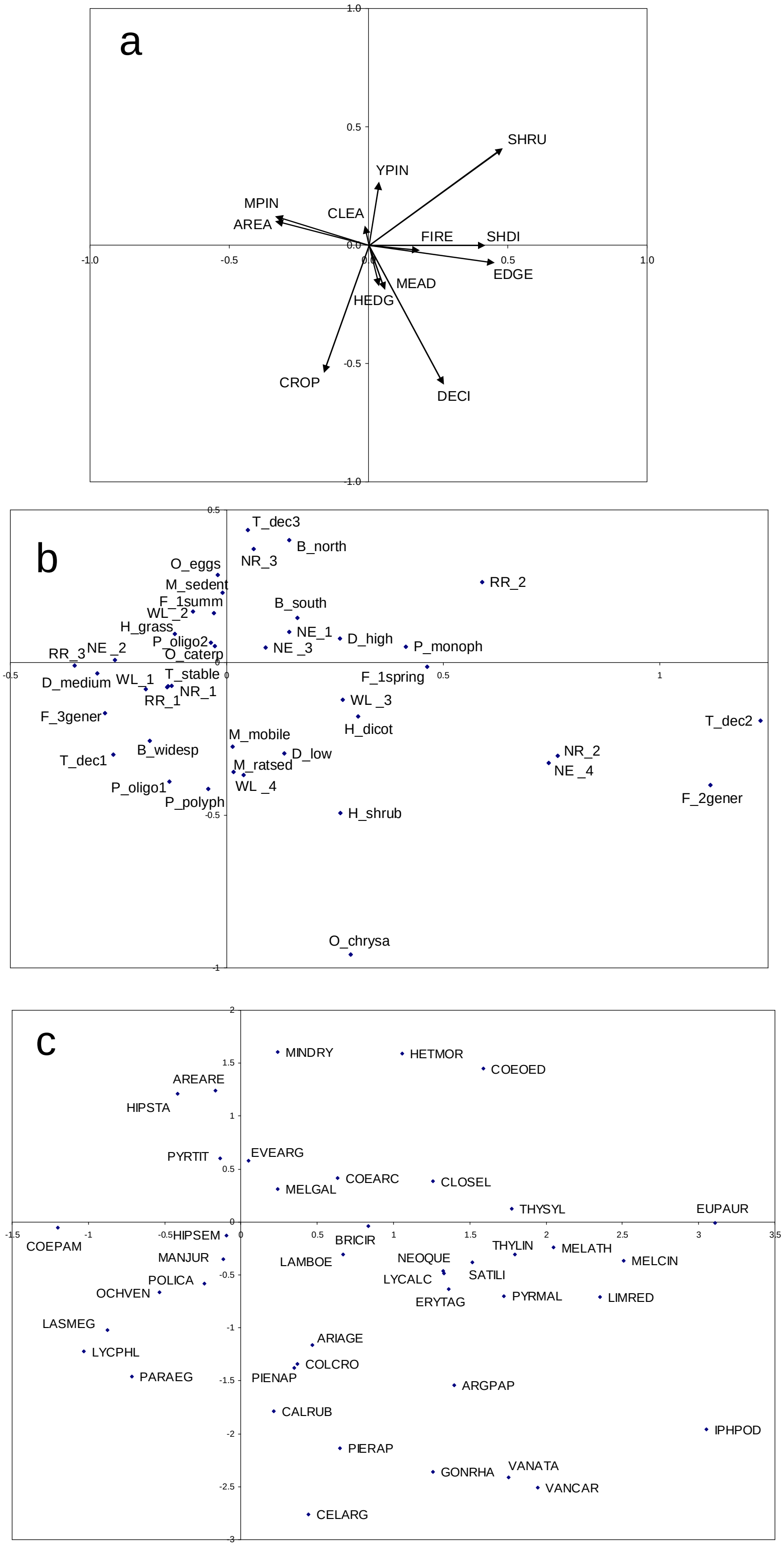

Figure 1. Représentation graphique des coordonnées RLQ pour (a) les variables paysagères (b) les traits de vie et (c) les espèces de papillons de jour. Voir Annexe C pour les codes de traits de vie. Les codes des espèces de papillons sont constitués des trois premières lettres du nom scientifique du genre et de l'espèce, e.g., MINDRY = *Minois dryas*.

Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes

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Abstract

The goal of the present study is to assess how landscape configuration influenced the distribution of life traits across bird, carabid beetle and butterfly communities of mosaic forest landscapes in south-western France. A set of 12 traits was selected for each species, characterizing rarity, biogeographical distribution, body size, trophic guild, dispersal power, reproductive potential and phenology. We used a three-table ordination method, RLQ analysis, to link directly bird, beetle and butterfly traits to the same set of landscape metrics calculated in 400 m-radius buffers around sample points. RLQ analyses showed significant associations between life-history traits and landscape configuration for all three taxonomical groups. Threatened species from all groups were characterized by a combination of life traits that makes them especially sensitive to the fragmentation of herbaceous and shrub-dominated habitats at the landscape scale. These key life traits were low productivity, intermediate body mass, restricted geographic range, late phenology and ground gleaning for threatened birds, intermediate body size, spring adult activity, northern distribution and summer breeding period for threatened carabids, and restricted range, overwintering as eggs or larvae, low mobility, monophagy and short flight periods for threatened butterflies. Focusing on species life traits can provide a functional perspective, which helps to determine adequate measures for the conservation of threatened species and communities of several taxonomical groups in mosaic landscapes.

5.2. Introduction

A major consequence of global change on biodiversity is the biotic homogenization of species communities through the gradual replacement of native taxa by non-indigenous species (McKinney and Lockwood, 1999). Species communities are thus increasingly composed of generalists, whereas specialists show a general decline (Julliard et al., 2004; Kotze and O'hara, 2003; Warren et al., 2001). At the functional level, declining species are expected to share particular life-history traits, such as large size, low fecundity, rarity, slow dispersal or high specialization, irrespective of taxonomy (Cofre et al., 2007; McKinney and Lockwood, 1999). These functional types of species will be affected more than others by habitat loss and fragmentation (Davies et al., 2000; Ewers and Didham, 2006). The knowledge of which traits make a species sensitive to habitat fragmentation may consequently be a useful tool for the identification of target groups of species in applied conservation biology (Samways and Lu, 2007; Summerville et al., 2006). The following traits have proved to be relevant predictors of species sensitivity to fragmentation: population size and fluctuation, competition and disturbance sensitivity, micro-habitat specialization, matrix use, rarity and biogeographic position (Henle et al., 2004). Other traits such as dispersal ability, body size or trophic position may also predict species response to fragmentation, depending on scale and interactions with other traits (Baguette and Van Dyck, 2007; Davies et al., 2000). Focusing on the distribution of life-history traits across environmental gradients instead of species themselves allows generalizing the results for both theoretical and applied purposes (McGill et al., 2006). Moreover, some authors have stated that ecosystem functioning depends more strongly on functional diversity, i.e. the value and range of species traits, than species richness per se (Diaz and Cabido, 2001). Conserving functional diversity at the landscape level may consequently help to maintain large-scale and long-term ecosystem processes by functional compensations between species (Loreau et al., 2003; Tscharntke et al., 2008). As a result, the relevance of life-history trait-based methods to analyze species responses to disturbance is increasingly acknowledged (Cole et al., 2002; Bo Söderström et al., 2001; Summerville et al., 2006). There is actually a need for multiscale and multitaxa approaches taking into account the distinct responses of different species guilds to landscape structure and composition (Cushman et al., 2008; Grand et al., 2004). However, to date few studies have attempted to directly link landscape attributes to the distribution of a set of species life traits (Hausner et al., 2003; Ribera et al., 2001). Here, we examined how landscape structure and composition could be related to the distribution of bird, carabid beetle and butterfly traits in mosaic landscapes dominated by maritime pine *Pinus pinaster* plantation forests in south-western France.

The maritime pine plantations of south-western France represent a good example of production landscapes harbouring an important animal biodiversity. Previous studies have demonstrated the importance of maintaining semi-natural habitat patches embedded within the pine plantation matrix (firebreaks, heathlands, meadows and deciduous woodlands) for the long-term conservation of threatened species (Barbaro et al., 2007; van Halder et al., 2008). Such 'islets' probably act as key habitats (e.g., for feeding, wintering, or breeding requirements) in the life cycle of a large range of sensitive species that may be lost in case of increasing landscape homogenization (Duelli and Obrist, 2003; Purtauf et al., 2005; Tscharntke et al., 2002a). In plantation forests, management actions should be compatible with the conservation of keystone and threatened species, as well as functional diversity, through the maintenance of a structurally complex landscape matrix including patches and corridors of native vegetation (Fischer et al., 2006). However, little information exists about the management of landscape mosaics for the conservation of several species having contrasting responses to the same landscape configurations (Holzkämper et al., 2006). In the present work, we aimed at linking directly the distribution of life-history traits in bird, carabid beetle and butterfly communities to the same set of explanatory variables characterizing landscape structure and composition. Our goal was to define functional groups of species sharing similar life traits and similar responses to environmental variables, regardless of their taxonomic status. We performed a set of RLQ analyses, a three-table ordination method that allows a direct ordination of species life traits according to various environmental variables through the link provided by the site x species table (Cleary et al., 2007; Dolédec et al., 1996; Hausner et al., 2003; Mellado et al., 2008; Ribera et al., 2001). We used a multitaxa data set collected in the same study area in order to define conservation priorities from a functional, rather than only taxonomical, point of view. Our main objective was to identify, across a wide range of organisms, which combination of life-history traits make species sensitive to habitat loss and fragmentation in mosaic landscapes.

5.3. Methods

Study area

The study was located in plantation forests that cover around 1 million ha in the Landes de Gascogne region, south-western France. The landscape is dominated by even-aged stands of native maritime pine with a rotation cycle of 40-50 years. Such a forest management creates mosaic landscapes composed of even-aged pine stands interspersed with recent clearcuts covered by grassland or heathland vegetation, and fragments of semi-natural habitats. The most important semi-natural elements of the landscape are herbaceous or shrubby firebreaks and remnants of deciduous woodlands dominated by *Quercus robur, Q. pyrenaica* and *Betula pendula* occurring along rivers or as patches of a few hectares. Three areas were selected for species surveys and GIS-mapping of land cover types: Tagon (5000 ha, 44°40’N, 0°57’W), Cestas (8000 ha, 44°44’N, 0°46’W) and Solferino (10500 ha, 44°08’N, 0°55’W). The nine main land cover types represented in the regional landscape included four stages of the rotation cycle in maritime pine plantations (herbaceous clearcut, shrubby clearcut, young pine (<7 m) and mature pine stands (>7 m), four semi-natural habitats (hay meadow, herbaceous firebreak, deciduous woodland and deciduous hedgerow), and crops (maize field).

Species surveys

Species surveys were performed using a stratified sampling design according to the main land cover types cited above, except crops that were not sampled (see Barbaro et al. 2007 and van Halder et al. 2008 for a detailed description of the sampling design). We surveyed bird communities at 287 sampling plots using point-counts with unlimited distance (Bibby et al., 2000). Two censuses per year were performed, the first during the early breeding season (early April to mid-May) and the second during the late breeding season (mid-May to late June) in 2002-2003. There was a systematic permutation of first and second census between the two observers involved, in order to eliminate a potential observer effect. Points were established at least 400 m apart to avoid double counting, and each visit lasted 20 min, within 5 h after sunrise and avoiding adverse weather conditions such as strong wind and heavy rain (Bibby et al., 2000). We recorded all birds heard and seen except waterbirds, raptors and aerial feeders (swallows and swifts). We used a semi-quantitative abundance index ranging from 0.5 for a non-singing bird to a maximum score of 5, each territorial male or pair being noted as 1. The maximum score obtained between the two visits was the species abundance index used in further analyses (Hausner et al., 2003).

We sampled carabid beetles at 244 sampling plots using pitfall traps, a standardized sampling method allowing the comparison of ground-dwelling beetle assemblages at different sites when it is not necessary to know the actual species abundances (Rainio and Niemelä, 2003). We used removable glass traps (opening diameter = 9 cm, volume = 500 ml) levelled to the soil surface and covered with wood plates supported by four nails to protect traps from rain (Purtauf et al., 2005). Each trap was filled with a solution of quaternary ammonium diluted at 25 % and collected every three weeks. Trapping went continuously from April to October in 2002-2003. The number of individuals caught in a given trap during the entire trapping period was pooled for data analyses (Cole et al., 2002).

Butterflies were surveyed in 81 plots using line-transects (Pollard and Yates, 1993). Within each plot and along its edge, a 400 m-long and 5 m-wide linear transect was laid out and all butterflies were counted within this strip. Each plot was visited four times (between mid-May and early September of 2004) during appropriate weather conditions (t°C >20, cloudless or just a few clouds and wind speed <5 Beaufort). Butterfly species were identified by sight or caught and released after determination for species difficult to identify. We pooled the total number of individuals per species over the two transects for each plot (interior and edge) and the four visits for data analyses. Interior and edge counts were summed because we aimed at linking species assemblages and life traits to landscape metrics rather than local habitat variables, and sampling only stand interiors would have underestimated the abundance of several species more abundant at stand edges than in the interiors (Ohwaki et al., 2007).

Life-history traits

We selected a set of 12 life-history traits that were expected to be good predictors of species response to fragmentation for the three taxonomical groups (Henle et al., 2004). We used only traits for which detailed and complete information has been published for all species recorded. Although it was not possible to use the same traits and categories for the three species groups, we aimed at characterizing the main life attributes regarding 1) rarity and biogeographical distribution, 2) trophic guild, 3) breeding parameters, 4) body size or mass, 5) mobility, and 6) phenology (Annex A-C). For the three taxa, we retained four attributes related to rarity, biogeography and conservation status (Kotze and O'Hara 2003): 1) overall population trend at the national level, 2) national and 3) regional rarities, defined as the percentage of national or regional range where the species is present, and 4) biogeographic position of the European range (northern, widespread or southern).

Species conservation status was evaluated with the most updated data available for birds (Julliard and Jiguet, 2005) and butterflies (Lafranchis, 2000) at the national and regional levels. For carabid beetles, we estimated conservation status (trend and rarity) at the European level using red-list data because complete information was not available at the French national level (Turin, 2000), and the regional rarity was defined according to Tessier (2000). Data on other life-history attributes were taken from Cramp et al. (1994) for birds, Turin (2000) and Ribera et al. (2001) for carabids, Bink (1992) and Lafranchis (2000) for butterflies. We used categories defined in Laiolo et al. (2004) for bird foraging techniques, and Tscharntke et al. (2002) for butterfly polyphagy levels. Additional data on butterfly life traits that are relevant at the regional level (regional rarity, local flying period, local polyphagy and host plant categories) were recorded by van Halder and Jourdain (unpubl. data). Finally, the number of categories per trait was also partly determined by the number of species that shared the same category, in order to keep a balanced number of species per category (Annex A-D).

Landscape metrics

The three study regions were GIS-mapped (ArcView, ESRI, USA) according to land-use types using aerial colour photographs (summer 2000 and 2002) with a resolution of 50 cm as background layer, followed by field validation. We distinguished 10 land cover types on these maps: the eight surveyed habitats plus croplands and urban areas. The latter type was not used in further analyses because urbanization pressure is still low in these forest-dominated landscapes and the percentage cover of urban areas is negligible. Landscape metrics were calculated within 400 m-radius circular buffers (50.3 ha), from the center of the sampled plots, using Fragstats 3.3 in raster version and a cell size of 2.5 m (McGarigal et al., 2002). As we aimed at relating species life traits to the same landscape metrics for the three sampled groups, we used a distance of 400 m because it is ecologically meaningful for these three (Weibull et al., 2003). A distance of 400 m is actually above the mean foraging or dispersal distances for most bird and carabid species involved in the present study (Barbaro et al., 2008; Paradis et al., 1998; Riecken and Raths, 1996). Within each buffer, we calculated the following metrics characterizing both composition and configuration of the landscape: the percentage cover of the nine main land cover types, edge density (in $m.ha^{-1}$), mean patch area (in ha) and the Shannon index of habitat diversity (McGarigal et al., 2002). The selection procedure used for landscape metrics is fully described in previous works (Barbaro et al., 2007; van Halder et al., 2008).

Data analysis

The methodological question of directly linking life traits of species to environmental variables through the ordination of the species abundance matrix was resolved by Doledec et al. (1996). They named RLQ analysis a generalization of co-inertia analysis (Dray et al., 2003) for analysing the joint structure of three-table data sets where R is the matrix of p environmental variables recorded at m sites, L is the matrix of k species abundances noted at m sites, and Q the matrix of n life traits characterizing the k species (Ribera et al., 2001). In such a design, R, L, and Q tables are linked both by their m rows (sites) and k columns (species), and the ordination of the L-species table represents the link between the R-environment table and the Q-trait table (Dolédec et al., 1996). The first step of RLQ analysis is the separate analyses of R, L and Q-tables. The L-species abundance tables of bird, beetle and butterfly species were first analysed by Correspondence Analyses (CA), after eliminating the rare species recorded with less than 10 individuals for birds and less than 5 individuals for beetles and butterflies (Cleary et al., 2007; Ribera et al., 2001). We consequently analysed final data tables of 287 sites x 52 species for birds, 244 sites x 45 species for carabids and 81 sites x 42 species for butterflies. The R-environment tables were analysed by normed Principal Correspondence Analyses

(PCA) with CA site scores used as row weighting to allow the coupling of R and L (Hausner et al., 2003). The Q-trait tables were analysed by Multiple Correspondence Analyses (MCA) using CA species scores for column weighting. When the L-table is analysed by way of a CA, RLQ analysis aims at selecting ordination axes that maximize the covariance between linear combinations of the columns of R- and Q-tables (Dolédec et al., 1996). RLQ analysis is a doubly constrained ordination where the stand scores in the R-table constrain the stand scores in the L-table, and the species scores in the Q-table constrain the species scores in the L-table (Hausner et al., 2003). The overall significance of the relationships between landscape variables of the R-tables and species traits of the Q-tables was assessed by a Monte-Carlo test with 1000 permutations on total inertia of the RLQ analyses (Dolédec et al., 1996). We compared the total inertia of the three RLQ analyses with the inertia of unconstrained separate analyses of R, L and Q to evaluate the percentage of the variation in separate analyses taken into account by the RLQ analysis on the main ordination axes (Hausner et al., 2003). RLQ analyses were performed using the 'ade4' package in R software (Dray and Dufour, 2007).

5.4. Results

Birds

There was a significant overall association between bird species traits and landscape variables (permutation test, $P < 0.001$). The first two axes of RLQ analysis accounted for most of the variance of the corresponding axes in the separate analyses of landscape metrics, species traits and species composition tables (Table 1). The landscape variables that correlated best with the first axis were mean patch area on the negative side and edge density and deciduous wood cover on the positive side (Table 2 and Figure 2a). It matched a landscape fragmentation gradient from mosaics dominated by large open habitats (young pines, crops and clearcuts) to more diverse mosaics with semi-natural habitat fragments including deciduous woods, hedgerows and meadows. The species traits showing the highest correlation ratios with the first axis were foraging technique, national and regional rarities, nest location and migration status (Table 3). Rare and threatened species (RR_3, NR_3, T_londec) of mid size and low productivity (BM_3, CS_1) having either northern or southern distributions (B_north, B_south) and being mostly ground gleaners and tropical migrants (F_grglean, M_tromig) were associated with the less fragmented open habitats of the younger stages of the silvicultural cycle (Figure 2b). They included *Anthus campestris* or *Lanius collurio* as typical species (Figure 2c). Fragmented landscape mosaics with deciduous woods and meadows were associated with ground probers, bark foragers, cavity nesters and early breeders of high productivity, including both large species such as *Turdus merula* and smaller species such as *Parus major* (Figure 2c). These species are not threatened (T_increa, NR_1, RR_1) and resident or temperate migrants (M_resid, M_temmig). The second axis was related to a gradient of landscape composition from mosaics including non-forest habitats (crops and meadows) to mosaics dominated by continuous mature plantations (Figure 2a). The species traits correlated with this axis were foraging technique, clutch size and body mass (Table 3). Small canopy gleaners with high productivity and small home ranges (BM_1, F_caglea, CS_3, H_small) tended to occur in landscapes dominated by continuous pine plantations, whereas large ground foragers or seed eaters with low productivity (CS_1, BM_3, D_graniv, F_grprob) were preferably found in landscapes where plantations are mixed with other non-forest habitats (Figure 2b). Typical species included *Phylloscopus collybita* or *Parus cristatus* on one side, and *Lullula arborea* or *Streptopelia turtur* on the other side (Figure 2c).

Table 1. Results of RLQ analyses and comparison with the separate analyses. R/RLQ represents the percentage of the variance of the separate analysis of R (landscape variables table) accounted for by each of the first two ordination axes of the RLQ analyses. L/RLQ is the same for the separate analysis of L (species composition table) and Q/RLQ is the same for the separate analysis of Q (species traits table). It is calculated as the ratio of the axis eigenvalue of RLQ analysis on the corresponding axis eigenvalue of separate analysis.

	Birds		Carabid beetles		Butterflies	
RLQ axes	F1	F2	F1	F2	F1	F2
Eigenvalue	0.043	0.01	0.206	0.091	0.057	0.04
Covariance	0.207	0.102	0.454	0.302	0.239	0.199
Correlation	0.226	0.152	0.371	0.403	0.266	0.289
R/RLQ	86.3	89.9	89.8	88.5	92.3	86.6
L/RLQ	45.4	40.1	42.1	47.3	43.7	56
Q/RLQ	73.5	79.1	60.7	79.2	57.1	67.6

Table 2. Correlations between landscape variables and RLQ axes for birds, carabid beetles and butterflies. Highest correlation values are indicated in bold.

Landscape variables	Abbrev.	F1-Bird	F2-Bird	F1-Beet	F2-Beet	F1-Butt	F2-Butt
Edge density (m.ha-1)	EDGE	**0.41**	0.01	**0.45**	-0.13	**0.46**	-0.07
Mean patch area (ha)	AREA	**-0.43**	0.15	**-0.43**	0.18	**-0.35**	0.11
Shannon diversity index	SHDI	0.30	0.05	0.29	-0.15	**0.43**	0.01
Firebreak cover (%)	FIRE	-0.12	0.01	-0.30	0.29	0.19	-0.02
Meadow cover (%)	MEAD	0.28	**0.38**	0.25	**0.46**	0.06	-0.20
Crop cover (%)	CROP	-0.14	0.33	0.04	-0.01	-0.16	**-0.54**
Clearcut cover (%)	CLEA	-0.24	0.26	-0.09	-0.11	-0.01	0.09
Shrubland cover (%)	SHRU	0.11	-0.25	-0.08	-0.04	**0.48**	**0.42**
Young pine cover (%)	YPIN	**-0.37**	0.20	**-0.40**	0.22	0.04	0.27
Mature pine cover (%)	MPIN	-0.07	**-0.69**	-0.08	**-0.61**	-0.33	0.13
Deciduous wood cover (%)	DECI	**0.42**	0.09	**0.35**	0.21	0.27	**-0.59**
Hedgerow cover (%)	HEDG	0.23	0.26	0.26	**0.39**	0.04	-0.18

Carabid beetles

The RLQ analysis showed a significant association between life traits of carabid beetles and landscape variables (permutation test, $P < 0.001$). The first two axes accounted for a large part of the variance in the separate analyses of environment, traits and species tables (Table 1). The first axis had the highest correlations with edge density on the positive side, and mean patch area and young pine cover on the negative side (Table 2 and Figure 3a). As with the bird trait analysis, it was related to a gradient of landscape fragmentation. The highest correlation ratios were obtained for regional rarity, biogeography and activity period (Table 3 and Figure 3b). Regionally common species (RR_1, RR_2) of southern distribution (B_south) and active in summer and autumn (P_sumaut) were associated to fragmented landscapes with deciduous woods (e.g., *Carabus purpurascens* or *Pterostichus madidus*). On the contrary, regionally rare and declining species (T_declin, RR_3, RR_4) of northern distribution (B_north), often active in late spring (P_latspr), were more abundant in less fragmented landscapes with young pine plantations and firebreaks (e.g., *Harpalus rufipalpis* or *Poecilus versicolor*, Fig. 3c). The second axis of the RLQ analysis was correlated with mature pine cover on the negative side,

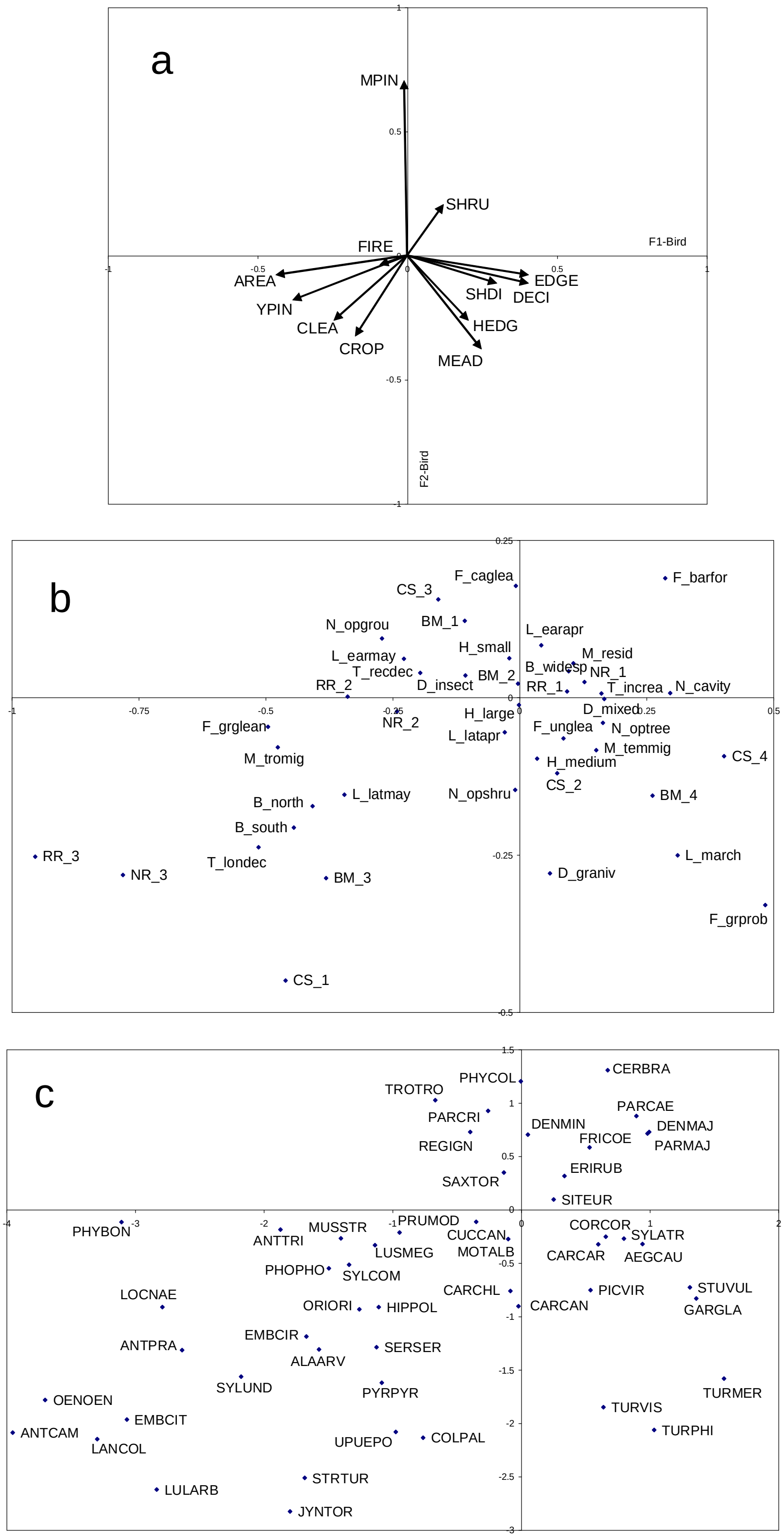

Fig. 2 Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) bird species. See Annex A for the codes of life traits and Table 2 for landscape variables. Abbreviations of bird species names use the first three letters of genus and species scientific names, e.g. PHYBON = *Phylloscopus bonelli*.

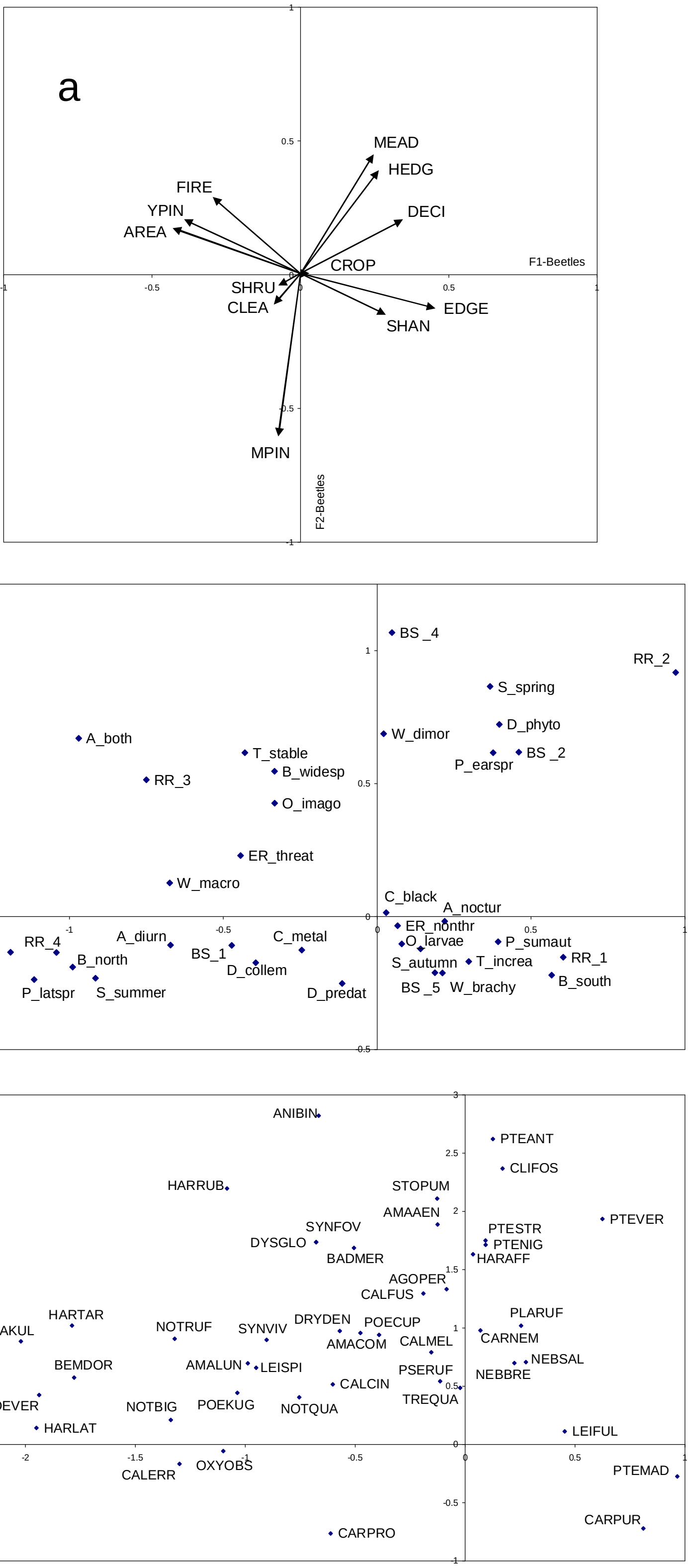

Fig. 3. Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) carabid beetle species. See Annex B for the codes of life traits and Table 2 for landscape variables Abbreviations of beetle species names use the first three letters of genus and species scientific names, e.g., HARRUF = *Harpalus rufipalpis*.

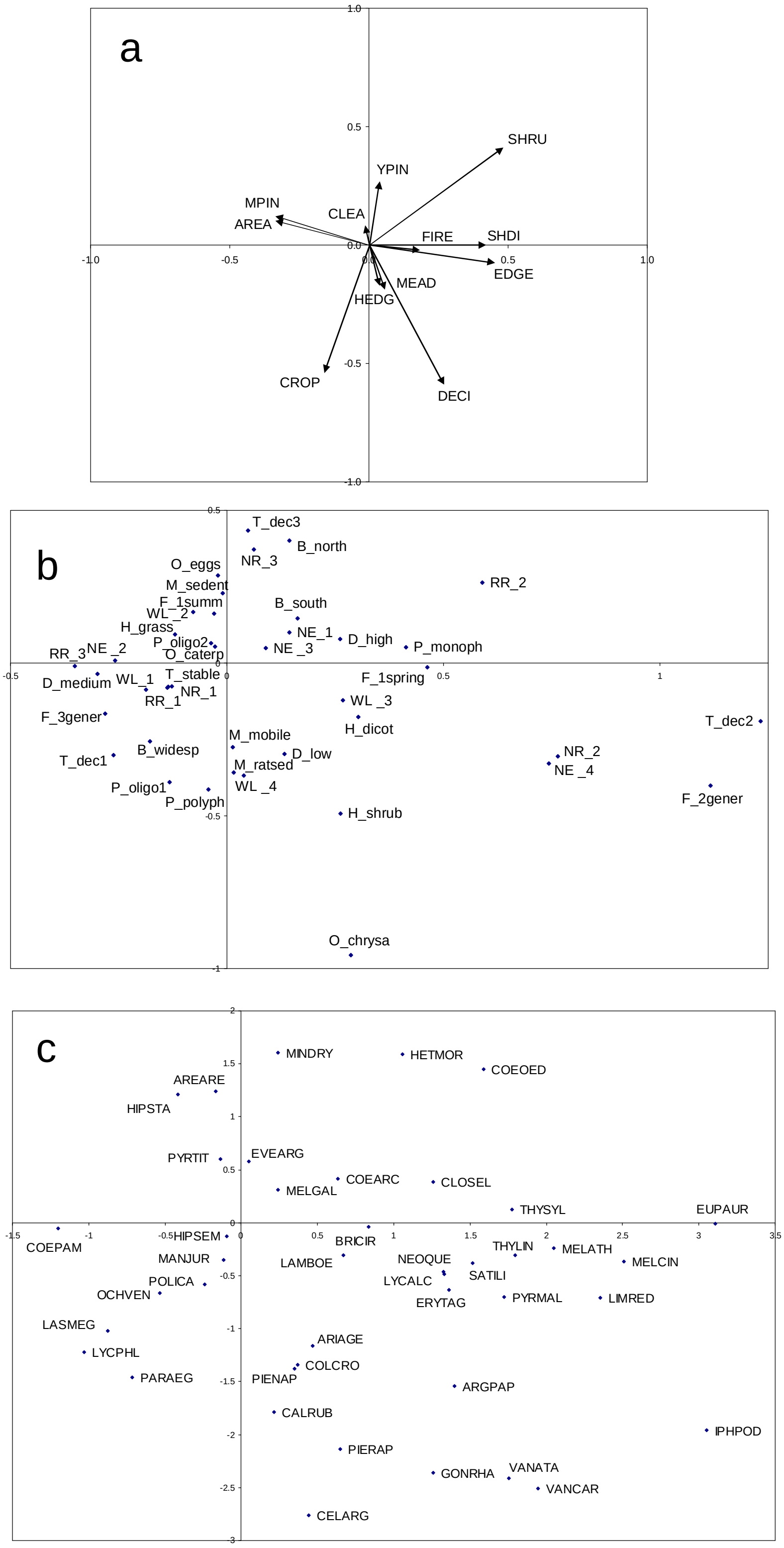

Fig. 4. Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) butterfly species. See Annex C for the codes of life traits. Abbreviations of butterfly species names use the first three letters of genus and species scientific names, e.g., MINDRY = *Minois dryas*.

meadow cover and hedgerow cover on the positive side. This axis was hence similar to the landscape composition gradient obtained for the analysis of bird traits (Figure 3a). The best correlation ratios for beetle traits on this axis were obtained for body size, diet and breeding season (Table 3). Large predatory and brachypterous autumn breeders (BS_5, D_predat, W_brachy, S_autumn) tended to prefer landscape mosaics dominated by continuous mature pine plantations, whereas small phytophagous and dimorphic spring breeders (BS_4, D_phyto, W_dimor, S_spring) occurred preferably in heterogeneous landscape mosaics including semi-natural herbaceous habitats, such as firebreaks and meadows (Figures 3b and c).

Table 3. Correlation ratios between life traits and RLQ axes for birds, carabid beetles and butterflies. Highest correlation ratios are indicated in bold.

Bird life traits	F1	F2	Beetle life traits	F1	F2	Butterfly life traits	F1	F2
National trend	0.1	0.04	European trend	0.13	0.14	National trend	**0.27**	**0.18**
National rarity	**0.12**	0.03	European rarity	0.01	0.01	National rarity	0.13	0.16
Regional rarity	**0.12**	0.02	Regional rarity	**0.3**	0.12	Regional rarity	**0.2**	0.07
Biogeography	0.09	0.06	Biogeography	**0.19**	0.14	Biogeography	0.06	**0.24**
Foraging	**0.2**	**0.23**	Daily activity	0.08	0.03	Polyphagy level	0.04	0.09
Diet	0.04	0.05	Diet	0.03	**0.22**	Host plant type	0.07	0.09
Nest location	**0.12**	0.06	Overwintering	0.01	0.05	Overwintering	0.02	**0.33**
Home range	0.01	0.04	Body color	0.01	0.01	Pop. density	0.15	0.04
Clutch size	0.09	**0.19**	Breeding season	0.08	**0.16**	Number of eggs	**0.17**	0.04
Body mass	0.06	**0.12**	Body size	0.09	**0.24**	Wing length	0.06	0.11
Migration	**0.12**	0.04	Wing developm.	0.06	0.13	Mobility	0	**0.29**
Laying date	0.06	0.11	Activity period	**0.21**	0.11	Flying period	**0.19**	0.09

Butterflies

There was a significant overall association between butterfly life traits and landscape variables (permutation test, P < 0.001). The first two axes of the RLQ analysis accounted for a large part of the variance in the separate analyses of tables (Table 1). The first axis was correlated with shrubland cover, edge density and Shannon diversity index on the positive side, mean patch area and mature pine cover on the negative side (Table 2 and Figure 4a). The main gradient of landscape structure is therefore slightly different for butterflies than for birds and beetles, opposing landscape mosaics dominated by large and homogeneous mature pine plantations with diverse and fragmented mosaics including open habitats (shrublands and firebreaks). On this axis, national trend, regional rarity, flying period and number of eggs had the highest correlation ratios (Table 3 and Figure 4b). Nationally declining species with one spring generation or two generations and high egg productivity (T_dec2, F_2gener, NR_2, NE_4, F_1spring) tended to occur in fragmented landscape mosaics with high diversity, whereas regionally rare to common species with three flight generations and mid to low productivity (RR_3, NE_2, F_3gener, RR_1) preferred plantation-dominated mosaics with low habitat diversity and low fragmentation. The first species group included *Euphydryas aurinia* or *Melitaea cinxia*, and the second group included *Coenonympha pamphilus* or *Lasiommata megera* (Figure 4c). The second axis matched a landscape composition gradient since it was negatively correlated with deciduous woodland cover and crop cover, and positively with shrubland cover (Table 2 and Figure 4a). The species traits with highest correlation ratios were overwintering, mobility, biogeography and national trend (Table 3). Large, widespread, polyphagous and mobile species overwintering as chrysalis or imago, and using shrub or tree as host plant (O_chrysa, H_shrub, P_polyph, WL_4, B_widesp, M_mobile, M_ratsed) were associated with landscape mosaics where pine plantations are fragmented by other land uses such as cropland or deciduous woodland (Figure 4b). This species group typically included *Vanessa cardui* or *Gonepteryx rhamni* (Figure 4c). On the contrary, nationally rare and large-scale declining species with northern or southern distribution, being sedentary, rather small, overwintering as eggs or young caterpillar and flying in one summer generation (T_dec3, B_north, NR_3, O_eggs, M_sedent, WL_2, B_south, F_1summ) were preferably found in landscape mosaics including open habitats created by the silvicultural cycle, i.e., secondary shrublands and young pine plantations (Figure 4b). Species associated with this group were *Coenonympha oedippus* or *Heteropterus morpheus* (Figure 4c).

5.5. Discussion

The three taxonomical groups showed a consistent pattern in the distribution of life-history traits on the main gradients of landscape structure and composition. RLQ analyses allowed to identify a combination of species traits sensitive to environmental changes that may represent useful indicators of large-scale impacts of human activities, such as forestry and agriculture, on the conservation of biodiversity (Cleary et al., 2007; Hausner et al., 2003; Mellado et al., 2008; Ribera et al., 2001). Habitat fragmentation and composition in the mosaic landscapes of the study area were directly related to species attributes characterizing rarity and biogeography, trophic guild, body size, mobility, reproductive potential and phenology. Moreover, the life attributes related to species conservation status were correlated with the gradients of landscape configuration for the three taxonomical groups studied. Birds of conservation concern showed a consistent and negative response to the landscape-scale fragmentation of open habitats and were largely restricted to landscape mosaics with the highest cover of young pine plantations and clearcuts. They tended to avoid both landscapes dominated by continuous mature pine plantations and fragmented landscapes with high habitat diversity including deciduous woodlands and meadows. They were characterized by low productivity, rather large body mass (25-50g), restricted biogeographic range (either northern or southern), late phenology, and their foraging technique was mainly ground gleaning. Threatened carabid beetles were likewise restricted to the less fragmented landscape mosaics, preferring those with high cover of young pine plantations and herbaceous firebreaks. As noticed for threatened birds, they avoided continuous mature plantations as well as heterogeneous mosaics with deciduous woods and meadows. These species tended to share intermediate body size, spring adult activity, northern biogeographic distribution and summer breeding period. The butterflies of highest conservation concern seemed to be less sensitive to landscape fragmentation but they depended more on the occurrence of particular habitats, favouring shrublands, young pine plantations and firebreaks against mature pine plantations, crops and deciduous woods. Associated life traits were restricted range, overwintering as eggs or young larvae, low mobility, monophagy and short flight period.

Rarity and biogeography

Species life attributes related to the degree of rarity in a given area, or to the restriction of biogeographical range, have proven to be good predictors of species sensitivity to environmental changes, such as habitat fragmentation (Cofre et al., 2007; Kotze and O'hara, 2003). Species with a restricted distribution range often show strong negative responses to forest fragmentation (Cleary et al., 2007; Ohwaki et al., 2007). However, rare species should be used with care because the rarity of a given taxon is not a good indicator for the occurrence of other rare taxa (Grand et al., 2004). Populations close to the margins of the species range are also more likely to experience long-term declines than those close to the range core (Warren et al., 2001). We found that birds, butterflies and carabid beetles with northern distribution in Europe, and therefore close to their southern range limit in south-western France, favoured landscapes with less fragmented open habitats, i.e., large grasslands and heathlands. These northern species are probably more prone to decline than others in the context of current global change (Hampe and Petit, 2005; Julliard et al., 2004). Moreover, the past landscape in the study region was mostly composed of large patches of grasslands and heathlands before the general afforestation process in the middle of the 19th century (Barbaro et al., 2007). The current landscape can therefore be viewed as the result of long-term and large-scale fragmentation of the past open habitats, and homogenization of previously patchy and heterogeneous vegetation, by modern intensive forestry. As elsewhere in Europe where semi-natural grasslands and heathlands have seriously decreased during the last decades, the species with unfavourable conservation status occurring in the study area were mostly grass-shrubland specialists (Duelli and Obrist, 2003; Bo Söderström et al., 2001; Warren et al., 2001).

Trophic guild

The use of trophic guilds in understanding species responses to disturbance or habitat fragmentation is widely used by ecologists (Cleary et al., 2007; Purtauf et al., 2005; Tscharntke et al., 2002a), although the results obtained are not always consistent with theoretical predictions (Henle et al., 2004). In the present work, bird foraging technique was clearly dependent on landscape configuration. Large ground insectivore gleaners responded negatively to open-habitat fragmentation, whereas ground probers and seed eaters favoured high landscape diversity, including meadows and deciduous woodlands. Granivore abundance is known to increase significantly following human disturbance, whereas large ground insectivores are often negatively affected by grazing or logging (Cleary et al., 2007; Bo Söderström et al., 2001; Tscharntke et al., 2008). For carabid beetles, habitat fragmentation tends to affect predators more strongly than phytophagous species (Davies et al., 2000), which benefit from surrounding landscape diversity, especially semi-natural grasslands (Purtauf et al., 2005; Ribera et al., 2001; Weibull et al., 2003). We found a similar pattern, with seed-eating carabids being associated with meadows and deciduous woods in the surrounding matrix. For butterflies, high landscape diversity and presence of shrublands and firebreaks favoured monophagous species, whereas polyphagous species were associated with the presence of crops and deciduous woodlands in the surrounding landscape. This is consistent with other studies showing the higher sensitivity of monophagous butterflies to habitat loss (Ohwaki et al., 2007; Tscharntke et al., 2002a).

Body size and mobility

Body size and dispersal ability may also be good predictors of species sensitivity to landscape fragmentation, although generally interacting with other correlated traits (Baguette and Van Dyck, 2007; Henle et al., 2004). Large carabid beetles are known to be more fragmentation-sensitive than smaller species because of their lower dispersal ability (Kotze and O'hara, 2003; Rainio and Niemelä, 2003). Large birds are also negatively affected by forest fragmentation (Cleary et al., 2007), although a recent review on tropical agroecosystems failed to detect higher sensitivity to landscape composition in large birds (Tscharntke et al., 2008). Here, we did not detect a negative effect of overall landscape fragmentation on large birds, carabids and butterflies, but instead a positive effect of landscape diversity, the largest species preferring the most diverse landscape mosaics including deciduous woodlands and meadows. However, this is probably due to the naturally patchy and heterogeneous vegetation in the study area compared to most of the studies dealing with habitat fragmentation. Long-distance migrating birds and macropterous carabids tended to be more fragmentation-sensitive than their less mobile counterparts (resident and short-distance migrant birds and brachypterous carabids), whereas mobile butterflies were more dependent on landscape composition, especially on the presence of crops and deciduous woodlands. For butterflies and carabids, high mobility is considered to be an adaptation to disturbed habitats and is generally expected to prevent species from decline (Ribera et al., 2001; Warren et al., 2001). However, strong flight can also be a key trait for rare butterflies, as a compensation for extreme habitat specialization and scarcity of the host-plant (Samways and Lu, 2007). For birds, long-distance migrants have declined more than short-distance migrants since 1970, indicating higher sensitivity to habitat loss (Sanderson et al., 2006). Greater dispersal ability can lead to greater vulnerability to fragmentation among species, especially in case of greater mortality during dispersal, as demonstrated, e.g., for amphibians (Cushman, 2006). Dispersal is however not a species-specific fixed trait but varies with landscape configuration, because mobility can increase in populations inhabiting more fragmented landscapes (Baguette and Van Dyck, 2007).

Reproductive potential and phenology

Breeding parameters such as a low reproductive potential may also indicate a higher sensitivity to habitat fragmentation (Henle et al., 2004), and is generally correlated with a large body mass and a low dispersal ability (Baguette and Van Dyck, 2007; Kotze and O'hara, 2003). Here we found evidence that birds with both a low productivity and a late phenology were associated with a low fragmentation of open habitats at the landscape scale. For carabid beetles and butterflies, breeding phenology and overwintering mode appeared to be key indicator traits for species responses to landscape configuration. Summer-breeding carabids were associated with low fragmented open habitats, whereas spring breeders were favoured by the presence of meadows and hedgerows. Spring breeders are known to benefit from increasing grassland cover in the surrounding landscape (Weibull et al., 2003), since they usually hibernate as adults, migrate into the fields from surrounding overwintering sites and establish the 'early season' carabid community (Purtauf et al., 2005). For butterflies, we found that a restricted flight period and overwintering as eggs or young larvae were good indicator traits for species response to the landscape composition gradient, which is consistent with other studies (Ohwaki et al., 2007; Summerville et al., 2006).

Life-history traits as a tool for conservation

Using life-history traits in the analysis of species responses to fragmentation helps to predict potential changes in ecosystem functioning following changes in the composition of species communities (Cole et al., 2002; Diaz and Cabido, 2001). It also allows to define functional response groups on the basis of shared life traits among species (Hausner et al., 2003; Ribera et al., 2001), and increases our ability to predict why certain species are more prone to decline than others (Henle et al., 2004). As a functional relationship exists between particular habitats and the requirements of species with particular life histories (Duelli and Obrist, 2003), life trait-based approaches therefore provide deeper insights into the processes linking species to their habitat (McGill et al., 2006; Summerville et al., 2006). Moreover, many ecosystem functions, including seed dispersal, pollination or biological control, will be affected by changes in bird and insect functional groups following modifications in landscape composition (Tscharntke et al., 2008). In the study area, some particular landscape configurations need more urgently to be preserved than others because they harbour species sharing a combination of life traits associated with unfavourable conservation status. Maintaining large fragments of grasslands and heathlands is the most adequate conservation issue for threatened species in such mosaic landscapes dominated by silviculture-dependent habitats, whereas the conservation of areas with high landscape diversity will help to maintain high levels of species richness for several taxa. The specific landscape history of the study area (i.e., the large-scale afforestation of naturally fragmented and heterogeneous habitat mosaics by modern forestry) can also explain why positive responses to fragmentation were observed for most forest species (Barbaro et al., 2007). This is also partly due to confounding factors interacting with the fragmentation process per se, especially the ability of surrounding matrix habitats to supply additional resources to forest species by complementation or supplementation, and to regulate dispersal and dispersal-related mortality (Barbaro et al., 2008; Ewers and Didham, 2006). Contradictory effects of landscape fragmentation are therefore explained by the different ways in which specialized and generalist species perceive landscape heterogeneity as a continuum of habitat or as isolated patches (Tscharntke et al., 2002a). As a result, key indicator traits of species sensitivity to habitat loss and fragmentation might become useful tools for conservation management of mosaic landscapes in the future.

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5.7. Annexes

Annex A

Categories of life-history traits used for bird species.

Bird species traits	Categories	Code
National trend	1. Increasing or stable	T_increa
	2. Recently declining	T_recdec
	3. Long-term declining	T_londec
National rarity (% range)	1. > 95 %	NR_1
	2. 75-95 %	NR_2
	3. < 75 %	NR_3
Regional rarity (% range)	1. > 95 %	RR_1
	2. 75-95 %	RR_2
	3. < 75 %	RR_3
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Foraging technique	1. Ground prober	F_grprob
	2. Ground gleaner	F_grglean
	3. Understory gleaner	F_unglea
	4. Canopy foliage gleaner/hawker	F_caglea
	5. Bark forager	F_barfor
Diet	1. Insectivore	D_insect
	2. Mixed diet	D_mixed
	3. Granivore	D_graniv
Nest location	1. Cavity (tree or others)	N_cavity
	2. Open in tree	N_optree
	3. Open in shrub	N_opshru
	4. Open on ground	N_opgrou
Home-range size	1. Small (< 1 ha)	H_small
	2. Medium (1-4 ha)	H_medium
	3. Large (> 4 ha)	H_large
Clutch size	1. ≤ 3 eggs	CS_1
	2. 4 eggs	CS_2
	3. 5-6 eggs	CS_3
	4. ≥ 7 eggs	CS_4
Body mass (g)	1. ≤ 14 g	BM_1
	2. 15-24 g	BM_2
	3. 25-49 g	BM_3
	4. ≥ 50 g	BM_4
Migration status	1. Resident	M_resid
	2. Temperate migrant	M_temmig
	3. Tropical migrant	M_tromig
Average laying date	1. March	L_march
	2. Early April	L_earapr
	3. Late April	L_latapr
	4. Early May	L_earmay
	5. Late May and June	L_latmay

Life trait data taken from Cramp et al. (1994), Söderström et al. (2001), Laiolo et al. (2004), Julliard and Jiguet (2005)

Annex B

Categories of life-history traits used for carabid beetle species.

Carabid species traits	Categories	Code
European trend	1. Increasing	T_increa
	2. Stable	T_stable
	3. Declining	T_declin
European rarity	1. Non-threatened	ER_nonthr
	2. Threatened	ER_threat
Regional rarity	1. > 15 regional data	RR_1
	2. 10-15 regional data	RR_2
	3. 4-9 regional data	RR_3
	4. < 3 regional data	RR_4
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Daily activity	1. Diurnal	A_diurn
	2. Both diurnal/nocturnal	A_both
	3. Nocturnal	A_noctur
Diet	1. Collembola	D_collem
	2. Generalist predators	D_predat
	3. Phytophagous or mixed	D_phyto
Overwintering	1. Imago only	O_imago
	2. Imago and larvae	O_larvae
Body color	1. Black or pale brown	C_black
	2. Metallic	C_metal
Breeding season	1. Spring breeder	S_spring
	2. Summer breeder	S_summer
	3. Autumn breeder	S_autumn
Body size (mm)	1. < 6 mm	BS_1
	2. 6-7.9 mm	BS _2
	3. 8-9.9 mm	BS _3
	4. 10-11.9 mm	BS _4
	5. ≥ 12 mm	BS _5
Wing development	1. Brachypterous	W_brachy
	2. Dimorphic	W_dimor
	3. Macropterous	W_macro
Adult activity period	1. Early spring	P_earspr
	2. Late spring	P_latspr
	3. Summer/autumn	P_sumaut

Life trait data taken from Dufrêne and Baguette (1989), Tessier (2000), Turin (2000) and Ribera et al. (2001)

Annex C

Categories of life-history traits used for butterfly species.

Butterfly species traits	Categories	Code
National trend	1. Stable	T_stable
	2. 1-10 % decline	T_dec1
	3. 10-25 % decline	T_dec2
	4. 25-55 % decline	T_dec3
National rarity (% range)	1. > 95 %	NR_1
	2. 75-95 %	NR_2
	3. < 75 %	NR_3
Regional rarity (% range)	1. 40-85 local districts	RR_1
	2. 20-40 local districts	RR_2
	3. 1-20 local districts	RR_3
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Polyphagy level	1. Monophagous	P_monoph
	2. Strongly oligophagous	P_oligo1
	3. Oligophagous	P_oligo2
	4. Polyphagous	P_polyph
Host plant type	1. Grasses	H_grass
	2. Herbaceous dicots	H_dicot
	3. Shrub or tree	H_shrub
Overwintering	1. Eggs or young caterpillar	O_eggs
	2. Mature caterpillar	O_caterp
	3. Chrysalis or imago	O_chrysa
Population density (ind.ha^{-1})	1. Low (< 4 ind.ha^{-1})	D_low
	2. Medium (4-16 ind.ha^{-1})	D_medium
	3. High (> 16 ind.ha^{-1})	D_high
Number of eggs	1. < 100 eggs	NE_1
	2. 100-200 eggs	NE _2
	3. 200-400 eggs	NE _3
	4. > 400 eggs	NE _4
Wing length (mm)	1. ≤ 14 mm	WL_1
	2. 15-19 mm	WL _2
	3. 20-24 mm	WL _3
	4. ≥ 25 mm	WL _4
Mobility	1. Sedentary	M_sedent
	2. Rather sedentary	M_ratsed
	3. Mobile	M_mobile
Flying period	1. 1 generation (spring)	F_1spring
	2. 1 generation (summer)	F_1summ
	3. 2 generations	F_2gener
	4. 3 generations	F_3gener

Life trait data obtained from Bink (1992), Lafranchis (2000) and van Halder and Jourdain (unpubl. data), see Annex D.

Annex D

Table of 12 life-history traits for the 42 butterfly species. See Annex C for trait and category codes.

Abbrev.	Species name	Trend	Natio	Regio	Biog	Poly	Host	Over	Dens	Eggs	Wing	Mobil	Perio
PYRMAL	*Pyrgus malvae*	3	3	3	1	3	2	3	2	1	1	1	3
ERYTAG	*Erynnis tages*	2	2	2	2	3	2	2	2	1	1	1	3
HETMOR	*Heteropterus morpheus*	4	3	2	3	1	1	2	3	2	2	1	1
THYSYL	*Thymelicus sylvestris*	3	2	2	2	3	1	1	3	2	1	1	1
THYLIN	*Thymelicus lineola*	3	2	2	2	3	1	1	3	2	1	2	1
OCHVEN	*Ochlodes venata*	2	1	1	2	3	1	2	2	1	1	2	1
IPHPOD	*Iphiclides podalirius*	3	2	2	3	3	3	3	1	2	4	2	3
PIERAP	*Pieris rapae*	1	1	2	2	4	2	3	2	4	4	3	4
PIENAP	*Pieris napi*	1	1	2	2	3	2	3	2	3	3	2	4
COLCRO	*Colias croceus*	2	1	1	1	3	2	2	1	4	4	3	4
GONRHA	*Gonepteryx rhamni*	1	1	1	2	1	3	3	1	4	4	3	1
NEOQUE	*Neozephyrus quercus*	3	2	3	2	2	3	1	3	1	2	1	2
SATILI	*Satyrium ilicis*	3	2	3	1	2	3	1	2	1	2	1	1
CALRUB	*Callophrys rubi*	2	1	2	2	4	2	3	2	2	1	2	1
LYCPHL	*Lycaena phleas*	1	1	1	2	2	2	2	2	2	1	2	4
LYCALC	*Lycaena alciphron*	3	3	3	1	2	2	2	1	3	2	2	1
LAMBOE	*Lampides boeticus*	4	3	2	1	3	2	3	1	2	2	3	4
CELARG	*Celastrina argiolus*	2	1	1	2	4	3	3	1	2	1	2	3
EVEARG	*Everes argiades*	4	3	2	3	3	2	2	2	2	1	2	4
ARIAGE	*Aricia agestis*	2	2	1	1	4	2	2	3	3	1	2	4
POLICA	*Polyommatus icarus*	1	1	1	2	3	2	2	3	3	2	2	4
LIMRED	*Limenitis reducta*	3	3	2	1	1	3	2	2	2	4	2	3
VANCAR	*Vanessa cardui*	1	1	2	2	4	2	3	1	4	4	3	3
VANATA	*Vanessa atalanta*	1	1	1	2	1	2	3	1	4	4	3	3
ARGPAP	*Argynnis paphia*	2	2	2	2	2	2	1	1	4	4	2	2
CLOSEL	*Clossiana selene*	4	3	3	3	2	2	2	3	3	3	1	3
MELCIN	*Melitaea cinxia*	3	2	1	1	1	2	2	2	3	2	1	3
MELATH	*Mellicta athalia*	3	2	3	2	1	2	2	3	3	2	1	1
EUPAUR	*Euphydryas aurinia*	3	2	2	1	3	2	2	3	4	2	1	1
MELGAL	*Melanargia galathea*	2	1	1	3	3	1	1	3	1	4	1	1
BRICIR	*Brintesia circe*	3	3	3	1	3	1	1	1	3	4	2	2
AREARE	*Arethusana arethusa*	4	3	3	1	3	1	1	2	3	3	1	2
HIPSEM	*Hipparchia semele*	4	3	3	2	3	1	2	2	4	4	2	2
HIPSTA	*Hipparchia statilinus*	4	3	3	1	3	1	1	2	2	3	1	2
MINDRY	*Minois dryas*	4	3	2	3	3	1	1	2	2	3	1	2
MANJUR	*Maniola jurtina*	1	1	1	2	3	1	2	3	3	3	2	2
PYRTIT	*Pyronia tithonus*	1	1	1	1	3	1	2	3	3	2	1	2
COEPAM	*Coenonympha pamphilus*	1	1	1	2	3	1	2	2	2	2	1	4
COEARC	*Coenonympha arcania*	2	2	3	3	3	1	2	3	1	2	1	1
COEOED	*Coenonympha oedippus*	4	3	2	3	1	1	2	3	1	3	1	1
PARAEG	*Pararge aegeria*	1	1	1	2	3	1	3	2	2	3	2	4
LASMEG	*Lasiommata megera*	2	1	3	2	3	1	2	1	2	3	2	4

6. Discussion

Ochlodes venata

6.1. Butterfly communities in mosaic pine plantation landscapes: the effect of local and landscape factors

6.1.1. Conservation value of different habitats in plantation mosaics

The debate whether plantations are ‘biological deserts’ or valuable habitats for flora and fauna is still ongoing (Bremer and Farley, 2010). The outcome depends greatly on the habitat type with which plantations are compared, the composition and structure of plantations and the land use history (Berndt et al., 2008). Plantations are likely to contribute positively to species richness when compared with degraded land or agricultural crops, particularly when native tree species are used (Bremer and Farley, 2010; Brockerhoff et al., 2008). When plantations are compared to mature, semi-natural forests, the biodiversity value of plantations is in general lower (Brockerhoff et al., 2008). Plantations may however represent favorable habitat for particular species groups. Clearcutting and succeeding plantation creates temporary, open habitats for early successional species that may be threatened elsewhere (Paquet et al., 2006). Biodiversity conservation in plantation landscapes may, however, also depend on the presence of more natural habitat elements in the plantation matrix, such as wetlands or late successional stages of remnant forest (Berndt et al., 2008; Burgar et al., 2015; Fischer et al., 2006; Lindenmayer and Hobbs, 2004).

The results of our studies highlighted the importance of interstitial, permanent semi-natural habitat patches for butterfly conservation in landscapes dominated by pine plantations. Fragments of **deciduous forests** harbored a specific butterfly community characterized by forest species, **firebreaks** were species-rich and harbored several threatened species and **forest edges** were always richer in species than their interiors. However, our results also demonstrated that butterflies are not absent from the **pine plantations**.

Forest butterfly species were mainly associated with **deciduous woodlands**. However, comparison of small deciduous fragments with riparian deciduous forests showed that the latter habitat type was more suitable to forest butterflies. Forest butterflies were however relatively rare in the study area, even when only deciduous forests were considered. The scarcity of forest butterfly species may be due to the effect of a long history of deciduous forest loss and fragmentation, which may have caused the loss of specialist forest butterfly species. One can assume that the remaining species are the ones that can cope with the intense deciduous forest fragmentation or that are capable of using complementary or supplementary resources in the pine plantation matrix. The scarcity of forest butterflies seems also partly caused by the nutrient-poor, sandy soils that do not allow the development of a diverse understory vegetation containing their host plants.

➔ *Forest specialist butterflies are mainly found in deciduous woodlands and notably in riparian forests*

Firebreaks were the habitat type with the **highest butterfly species richness**, harboring several threatened species. Updated, red list data for butterfly species at the European or national level (UICN France et al., 2012; van Swaay et al., 2010) are presented in Table 1. We do not dispose of a regional Red List for the Aquitaine region and species that are nationally threatened are not necessarily threatened at a regional level or *vice versa*. However, the region has a responsibility to protect inter-(nationally) threatened species, even if they are regionally not rare. Among the butterfly species observed in our studies (chapter 2 - 5) five are protected or are listed on red lists (Table 1). *Euphydryas aurina, Hipparchia statilinus* and *Boloria selene* were characteristic species of firebreaks, while *Coenonympha oedippus* occurred both in firebreaks and in pine stands. *Lycaena alciphron* did not show any specific habitat preferences, but was rarely observed (11 individuals). Figure 1 illustrates that these threatened species are found in different firebreaks; their presence depends on vegetation composition with species typical for humid conditions with *Molinia caerulea* (e.g., *C. oedippus*) or dry conditions (e.g., *H. statilinus*), as shown in chapter 2. Besides their importance for **threatened species**, firebreaks harbored ten **characteristic species** (highest, significant IndVal value for this habitat).

Although firebreaks are actually relatively species rich, they may represent an impoverished version of the species pool of the heathlands that existed a few centuries ago. The area of heathlands has decreased enormously due to the the massive afforestation carried out in 19th century. Some red-list species, such as *Maculinea alcon* and *M. teleius,* are nowadays very rare in the Landes of Gascogny and survive in a few, isolated areas with heathland vegetation. The current firebreaks are not only smaller in size than the heathlands, they are also drier, are managed differently and they are-linear shaped, making them more similar to large forest rides and thereby also of interest for edge species (Greatorex-Davies et al., 1993; Mullen et al., 2003).

Table 1. Butterfly species observed in the different studies in the Landes of Gascony with their classification in the European Habitat Directive, European Red data book, European Red list and French national red list.

Species	European Habitat Directive	European Red Data Book (1999)	European Red List (2010) Europe	European Red List (2010) EU27	Red List France (2012)	observed number in study area
Coenonympha oedippus	II/IV	CR	EN		NT	236
Euphydryas aurinia	II	VU				118
Hipparchia statilinus			NT	NT		79
Lycaena alciphron				NT		11
Boloria selene					NT	12

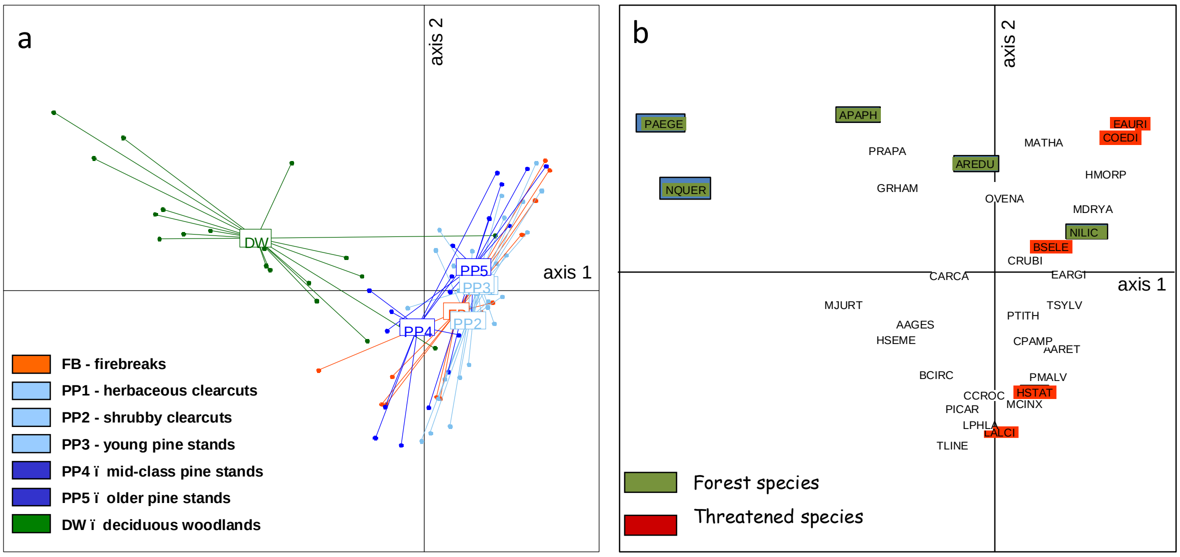

Figure 1. Correspondence Analysis ordination of the 83 inventoried plots (axes 1 and 2). (a) Position of the plots. The position of the name of each habitat type indicates the mean position of plots belonging to that habitat type. Different colours indicate the position of the different plot types. (b) Position of butterfly species, with in green forest species and in red threatened species (Table 1). Forest specialist butterfly species (green) are more often observed in deciduous woodlands (DW), while threatened species (red) are found in different firebreaks or pine plantations.

➔ *Firebreaks have the highest butterfly species richness and harbor several threatened species*

Pine plantations harbored less butterfly species than firebreaks, but were not as species-poor as expected. Their mean species richness (6,4 species/transect) was comparable to that of deciduous woodlands, but the two habitat types hosted distinct butterfly communities (Figure 1). Their community composition appeared to be an impoverished version of firebreak communities and depended mainly on vegetation composition of the understory vegetation. In the Landes of Gascony, pine stands were established mostly on open heathlands. The use of native maritime pines and the relative open canopy structure of these plantations permitting the development of a secondary heathland vegetation may explain why pine plantations harbor several heathland associated butterfly species, even including threatened species, such as *C. oedippus*.

Pine stands appeared to be an unsuitable habitat for most forest butterflies. This is likely due to their different understorey vegetation composition (i.e. secondary heathland vegetation), more simple structural composition and different microclimate, compared to deciduous forests.

Edges of pine stands were richer in butterfly species than the adjacent stand interior and harbored a different community. Edges can be a habitat or part of a habitat for butterfly species, as suggested by the frequent presence of the same species in the adjacent habitat interior. They may also play an important role for butterfly dispersal.

- ➔ ***Interstitial, semi-natural habitat patches (deciduous woodlands, firebreaks, edges) are very important for butterfly conservation in landscapes dominated by pine plantations.***
- ➔ ***However butterflies are not absent from the pine plantation stands.***

Comparable patterns for other taxonomic groups

The butterfly community patterns observed in the Landes of Gascony can be compared with those of other animal taxa, such as spiders, carabid beetles, birds (Barbaro et al., 2007, 2005) and bats (Charbonnier et al., 2016), all sampled in the same region.

Spider, carabid beetle and bird communities all responded to a comparable gradient of tree height and composition from open habitats, such as young pine stands, to mature deciduous woods (Barbaro et al., 2005). Carabid communities were species-poor in **deciduous woodlands** and only composed of generalist species. However, bird and spider species richness were higher in mature, deciduous woodlands with several characteristic bird and spider species. Likewise, bat communities were species-richer and bat activity was higher in deciduous woods than in pine plantations (Charbonnier et al., 2016). As for spiders, birds and bats, mature deciduous woodlands harbored also a distinct butterfly community. The importance of native, broadleaved forests for biodiversity as compared to coniferous plantations has also been demonstrated in other temperate countries, such as Sweden, Belgium, Ireland, Portugal, New-Zealand and Australia (Deconchat et al., 2009;, du Bus de Warnaffe and Deconchat, 2009; du Bus de Warnaffe and Lebrun, 2004; Enoksson et al., 1995; Lindenmayer and Hobbs, 2004; Oxbrough et al, 2016; Proença et al., 2010).

However, old-forest bird and carabid specialists were absent in the Landes of Gascony forests, probably because of a lack of colonization from large deciduous forests and because of the historical landscape, that was very open for centuries (Barbaro et al., 2005). The same holds for butterflies, with a low number of forest species in the region, probably caused by the same processes.

- ➔ ***Mature, deciduous woodlands harbor distinct communities of butterflies, spiders, birds, and bats in pine plantation landscapes. However, several mature-forest specialists are lacking.***

Another common point for several taxa is the importance of **open habitats**. Bird and carabid species of conservation concern were, in the Landes of Gascony, mainly found in open habitats, such as young stands, clearcuts and firebreaks (Barbaro et al., 2007, 2005). For butterflies, the presence and amount of firebreaks also appeared critical to many species. The importance of open areas for biodiversity in plantation mosaics has been observed in different countries and for several taxa, such as birds, spiders, hoverflies and carabid beetles (Butterfield et al., 1995; du Bus de Warnaffe and Lebrun, 2004; Gittings et al., 2006; Oxbrough et al., 2006; Paquet et al., 2006). For example, Paquet et al. (2006) showed that clearcut openings in plantation forests in Belgium harbored a distinct bird community. Due to the decrease in moor- and heathland cover, birds of these open areas have decreased, giving to the communities found in clearcuts a high conservation value as secondary, compensation habitats (Paquet et al., 2006). Our study system, before massive afforestation in the 19th century, consisted of extensively grazed heathland or moorland and the actual bird species community of clearcuts and young stands are considered an impoverished version of the open

heathland community. In the same region in Belgium, medium and large clearcuttings had also high conservation values for carabid beetles (du Bus de Warnaffe and Lebrun, 2004).
The biodiversity value of plantation stands may thus be found principally in young stages. Older pine stands are still too young to harbor forest species, which rely on semi-natural forests in these areas. However, clearcuts are temporary habitats and species with low mobility, like some carabid species, may not be able to cope with these spatio-temporal dynamics (du Bus de Warnaffe and Lebrun, 2004). Likewise, clearcuts do not have the same vegetation composition as more permanent habitats, such as firebreaks, making them less valuable for biodiversity than the latter habitat type (Butterfield et al., 1995).

➔ ***Open areas in plantation landscapes have a high conservation value for several taxa, such as birds, butterflies, carabids, hoverflies and spiders.***

There are however also important differences between butterflies and the other surveyed taxa. Unlike the patterns observed for birds, spiders and carabids, butterfly communities were not different between young and old pine stands but depended on understory vegetation composition. Because they are specialist herbivores, butterflies show a direct link with vegetation composition (Sawchik et al., 2003), whereas birds, spiders and carabid beetles depend more on prey abundance and have thus indirect relationships with vegetation, being more influenced by vegetation structure (Barbaro et al., 2005; Oxbrough et al., 2006).

6.1.2. Importance of habitat quality

Habitat quality had a predominant effect on composition of butterfly communities compared to habitat type and landscape variables when all habitat types were considered. For butterflies in deciduous woodland fragments it was the only variable affecting forest species richness and community composition. Several studies have observed a similar, principal effect of local variables on butterfly communities or species (e.g. Collinge et al., 2003; Krämer et al., 2012; Pöyry et al., 2009; Sawchik et al., 2003; Stoner and Joern, 2004; Wilson et al., 2015). However, some studies showed no effect of habitat quality on butterfly diversity (Flick et al., 2012; Liivamägi et al., 2014b). They may however have studied a too narrow habitat quality gradient or have overlooked essential resources for estimating patch quality (Mortelliti et al., 2010). As butterflies depend on specific larval host plants and on flowering nectar plants for the adult stage, they often show a strong relationship with vegetation attributes (Krämer et al., 2012; Sawchik et al., 2003). Furthermore, the vegetation composition also reflects environmental conditions and historical factors, such as microclimate and land-use intensity (Sawchik et al., 2003).

Important habitat quality variables in our study sites were plant species representing the variation in soil humidity, notably the cover of *Molinia caerulea.* This species is a host plant for several butterfly species (*C. oedippus, Heteropterus morpheus* and *Minois dryas),* but its cover also indicates soil humidity and management conditions. Other selected plant species, such as *Pteridium aquilinum* have no direct link with butterflies, but their presence can indicate negative conditions for some species. Selected local variables related to the presence of individual species at edges were often host-plants or abundance of nectar-plants. Likewise, in deciduous forest fragments, host plant composition had a significant effect on forest species richness and community composition. These results confirm that larval requirements are key factors for the characterization of butterfly habitat quality (Thomas et al., 2001). Using only host-plant species, Sawchik et al. (2003) could predict 48 % of variation in abundance of five grassland specialist species. Adding five more plant species, indicating ecological conditions favorable to butterflies without direct causal relationships, permitted to increase explained variation to 76 %.

Habitat quality has been considered among the three most important environmental factors, together with patch area and isolation, explaining butterfly diversity patterns (Fleishman et al., 2002; Thomas et al., 2001; WallisDeVries and Ens, 2010). Butterfly species in high quality habitats have higher intrinsic population growth rates and densities thereby enhancing species long-term persistence (Thomas et al., 2001). Habitat quality and area affect thus both population size and species occurrence. Habitat area combined with habitat quality is for example used in metapopulation modelling to calculate the carrying capacity of sites (Sawchik et al., 2002).

The strong effect of habitat quality on butterfly population dynamics has also direct implications for their conservation. Improving habitat quality can be a cost-effective conservation measure compared to habitat enlargement or corridor creation (Villemey et al., 2015).

- ➔ ***Habitat quality, and notably host plant composition, is as important as habitat area for butterfly conservation.***

6.1.3. Landscape effects

Although habitat quality and type explained the largest part of variation in butterfly community composition in our studies, landscape characteristics also had significant, independent effects. Three landscape variables were selected in models when different habitat types were analyzed simultaneously: % cover of **deciduous woodlands**, of **firebreaks** and the **edge density**. The first two represent the habitat amount at the landscape scale of two semi-natural habitat types that harbor characteristic species, which are rarely found in pine stands. Their influence can thus correspond to an effect of habitat amount at the landscape level (Fahrig, 2013), coupled with an effect of increased connectivity for butterfly species mainly found in these habitat types. For deciduous woodlands it can also correspond to the presence of riparian forests with a greater surface and higher habitat quality. For species using resources in different habitat types, the presence of these semi-natural habitats can correspond to an improved resource supplementation or complementation at the landscape level.

Edge density did not only affect butterfly community composition, but had also a positive effect on species richness (Rossi and van Halder, 2010; Annex 1) and appeared to be important for several butterfly edge species. The effect of edge density can correspond to a larger amount of edges, a habitat with a higher species richness than stand interiors and leading to a higher richness in stand interiors by spill-over effects or multi-habitat-use (Dunning et al., 1992; Fahrig, 2003). Edge density is also a measure of landscape heterogeneity and was positively correlated with patch richness and patch density, respectively measures of compositional and configurational heterogeneity (Fahrig et al., 2011), indicating a possible effect of landscape heterogeneity on butterfly community composition, possibly related with resource supplementation and complementation (Ouin et al., 2004; Perović et al., 2015).

- ➔ ***Butterfly community composition is affected, at the landscape scale, by the cover of deciduous woodlands and firebreaks and by the edge density, probably corresponding to effects of habitat amount and resource supplementation and complementation.***

Possible effects of patch area and isolation on butterfly species richness and composition in deciduous woodland fragments were probably less important than habitat quality and **matrix effects**. The pine plantation matrix can provide complementary and supplementary resources, can increase connectivity between deciduous fragments and can provide a buffer against adverse conditions (Brockerhoff et al., 2008). Besides that generalist butterfly species and some forest specialists use additional resources in the plantation matrix, reciprocally matrix-species may use deciduous forest fragments as part of their habitat (Liivamägi et al., 2014b), for example as microclimatic refuges during warm periods. Several studies showed a positive effect of a forested matrix on butterflies, even for grassland specialists. For example, Ockinger et al. (2012a) showed that the effect of grassland fragmentation for butterflies decreased with increasing forest cover in the surrounding landscape. They attributed this effect to the availability of additional resources and a possible higher dispersal in the forest-dominated matrix, while they supposed that edge effects were more negative in the agricultural matrix. Likewise, Villemey et al. (2015) found a positive effect of woodland cover on abundance, diversity and conservation value of butterfly communities within grasslands. This effect was even found on abundance and species richness of grassland specialists. Kramer et al. (2012) also found a positive effect of woodland cover on specialist butterflies of calcareous grasslands, but attributed this effect to a diminished emigration into the forested matrix, thereby preventing species to arrive in non-habitat grasslands that act as sinks. Furthermore, Eycott et al. (2012) showed in a meta-analysis that species movements were facilitated in a matrix more similar to the species' habitat structure. For forest butterflies, a forested matrix may thus facilitate movement compared to an intensive agricultural matrix (Chardon et al., 2003; Dover and Settele, 2009) and ecotones like forest edges might also provide effective corridors for dispersion, both for forest and generalist species.

The effects of a pine plantation matrix could not be properly tested in our studies, since we did not sample the same type of deciduous forest fragments in an agricultural matrix. It seems however very probable that a pine matrix is more favorable to butterflies to find resources, as secondary habitat and for dispersal, than a matrix composed of intensively managed, large agricultural fields.

- ➔ ***Positive matrix effects may have masked the area and isolation effects of deciduous woodland fragments on butterfly diversity.***

Landscape effects on other taxonomic groups in the Landes of Gascony Forest

Landscape variables also explained species richness, abundance or community composition of other taxa such as birds, carabids, spiders and bats in the Landes of Gascony (Barbaro et al., 2005;

Charbonnier et al., 2016). The amount of deciduous woodlands at the landscape scale appeared important for birds, carabids, spiders and bats (Barbaro et al., 2007, 2005; Charbonnier et al., 2016). Their results suggest that even small and isolated deciduous woodland patches can enhance species richness at the landscape scale. However, threatened bird and carabid species were mainly found in open areas (clearcuts and young pine stands), with specialist species preferring large open areas (Barbaro et al., 2005).

Multi-taxa studies can also reveal opposing landscape effects. For example, bird richness increased with landscape heterogeneity, whereas carabid richness decreased with fragmentation of pine plantations by other habitats (Barbaro et al., 2005). There are thus compromises to be made between positive effects of heterogeneity and negative effects of habitat fragmentation. The balance between heterogeneity/fragmentation effects measured at a certain scale will thus depend on the studied species group, and will change when other scales are considered (Tews et al., 2004).

- ➔ ***Cover of deciduous forests and open areas in plantation landscapes is favorable for several taxa, including bats, birds, butterflies, carabids and spiders.***
- ➔ ***Compromises have to be found in landscape planning to conserve species groups with different habitat requirements.***

6.1.4. Butterfly diversity and landscape models

The results of our studies revealed significant differences in butterfly community composition between deciduous woodlands, pine stands and firebreaks and between edges and forest interiors. They revealed however also similarities between different aged pine stands with a similar understory vegetation, which were an impoverished version of certain firebreak communities. All patch types in the landscape contained a certain number of species and differed more or less in their butterfly composition. The pine plantation matrix is thus not entirely hostile to butterflies, which questions the use of the ‘fragment-matrix’ model in these landscapes. It suggests that other concepts like the mosaic concept, with habitat supplementation and complementation, or a continuum model are more appropriate to explain the patterns of butterfly diversity (Didham et al., 2012; Duelli, 1997; Dunning et al., 1992; Fischer and Lindenmayer, 2006).

To illustrate the various responses of butterfly species to different patch types, we have indicated in Figure 2 for some species their mean abundance in different interior and edge patch types. *Pyronia tithonus* was more abundant in all edge types compared to their interiors and can be considered a typical ‘edge species’ in the studied landscape. *Pararge aegeria* is a typical example of a habitat specialist, occurring almost exclusively in deciduous woodlands. *C. oedippus* may, at first, seem a habitat generalist but is a specialist of humid, heathland vegetations dominated by *M. caerulea*. The species uses this vegetation type as habitat if it occurs in firebreaks or in relatively open pine stands. *Maniola jurtina* is an example of a multi-habitat species, which was observed at the beginning and end of its flying period in the grassy vegetation of firebreaks and their edges, and in mid-summer in deciduous woodlands, where the species estivates and escapes hot summer conditions. These different examples illustrate thus that each species perceives the mosaic landscape as a species-specific combination of more or less suitable patches. Within the same landscape, species occurrence patterns can thus correspond to the fragmentation model (e.g. *P. aegeria*) or to a mosaic model with habitat supplementation or complementation for multi-habitat species (e.g. *M. jurtina*) (Brotons et al., 2005; Fahrig, 2003). A continuum model in which each species or community is modelled separately seems thus the most appropriate way to explain and predict biodiversity patterns in these landscapes. As understory vegetation composition drives butterfly community composition in pine plantations and firebreaks, habitats should be mapped according to gradients in vegetation composition related to soil humidity and to openness of the tree canopy, which will provide a more realistic mapping of habitat suitability than maps based on aerial photo-interpretation. This **functional mapping** may show zones of suitable habitat (with differences in habitat quality), separated by non-habitat, but at a grain not visible on the actual landscape maps (Fahrig et al., 2011). Depending on the grain of suitable habitats, the dispersal capacity of species and differences in habitat quality, species may function as a metapopulation, as a source-sink-population or as a patchy population.

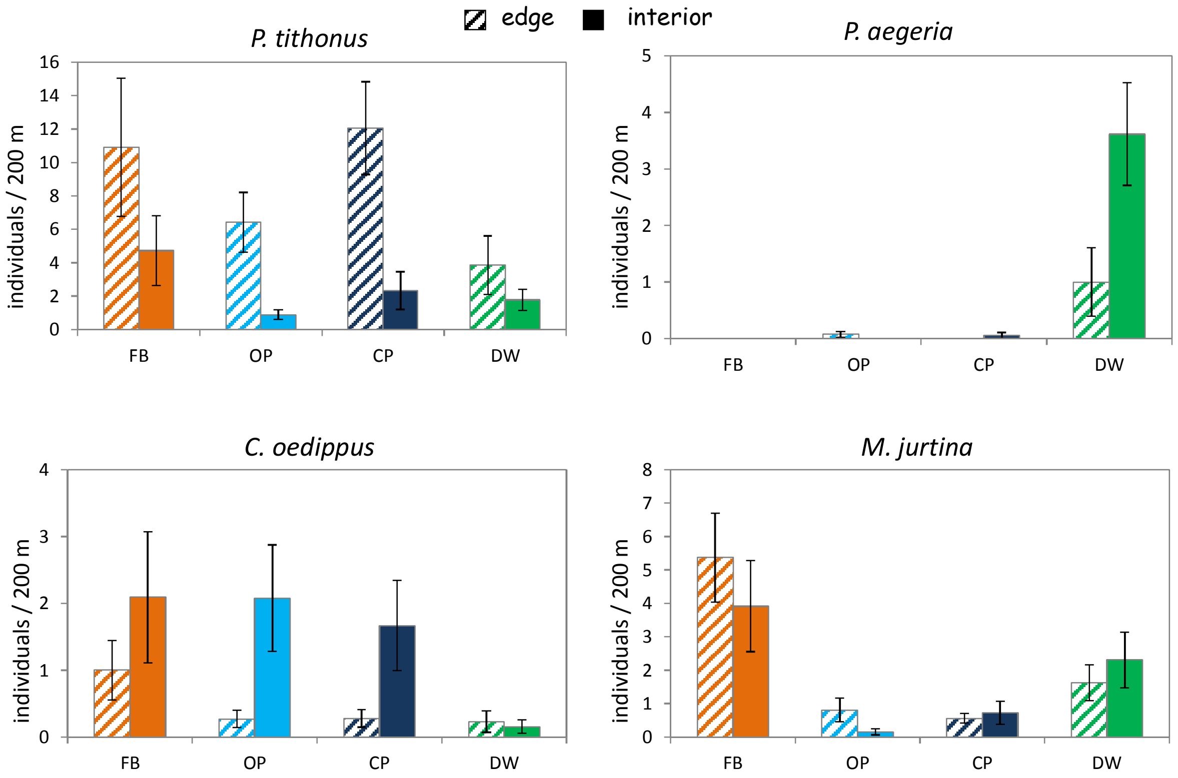

Figure 2. Mean abundance of four butterfly species in edge and interior habitats of four patch types. FB - firebreaks, OP - open, young pine stands, CP - mature pine stands, DW – deciduous woodlands.

A particularity of plantation landscapes, compared to semi-natural forests, is their dynamic character with new clearcuts being created every year. Species inhabiting certain stand age-classes have thus to track these landscape dynamics (du Bus de Warnaffe and Lebrun, 2004). For example, *E. aurinia* occurs in Finland in clearcuts and an aggregated network of clearcuts favors metapopulation survival. However the presence of permanent habitats, i.e. meadows and firebreaks, seems necessary for long-term metapopulation stability of threatened species (Butterfield et al., 1995; Wahlberg et al., 2002).

Deciduous woodlands are the habitat type with the most distinct, fragmented pattern in the landscape, suggesting a metapopulation functioning for the associated forest species. However we did not observe any effect of area or isolation on these communities, either indicating that the fragments do not delimit their habitat, that fragmentation sensitive species have already disappeared or that the remaining species can cope with the degree of fragmentation which may be mitigated by matrix effects.

- ➔ ***As many butterfly species use several, but different habitat types, a continuum model in which each species or community is modelled separately seems most appropriate to understand biodiversity patterns. These models should be based on functional landscape maps integrating species habitat requirements.***

6.1.5. Use of different landscape elements by butterflies

In our study many species were observed as well at edges as in interiors of one or several patch types. The use of different patches can be considered **multi-habitat use**, but the term is *sensu stricto* not correct. The term habitat is species specific and describes the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism (Hall et al., 1997). However the term habitat is commonly used to indicate a biotope, a vegetation type, or in landscape mapping a patch type corresponding to a land-use or land-cover.

The fact that butterflies are not restricted to one vegetation type, led Dennis et al. (2006, 2003) to argue that patch based habitat definitions do not correspond to butterfly habitats and that a resource based concept for butterfly habitat is more appropriate. Our above cited description of the habitat of *C. oedippus* (humid, heathland vegetation dominated by purple moor-grass, without trees or with an open canopy cover) includes thus different land-uses or patch types (firebreaks, open pine stands, stand edges). In this example *C. oedippus* uses the same resources in these different patch types. The use of different patch types with the same resources can be beneficial in risk spreading, but can also lead to source-sink dynamics or to ecological traps if resources in different patches are of different quality (Battin, 2004).

The term multi-habitat use seems more appropriate when species use different resources in different patch types, as is for example de case for *M. jurtina* (Figure 2). However, according to Dennis et al. (2003) it just corresponds to one habitat with different resources spatially distributed over different patches. Nectar plants and larval host plants can be present in different patch types, as shown for *Leptidea sinapis* (Wiklund, 1977) and *Maniola jurtina* (Ouin et al., 2004), and which seems to apply in our study area to, for example, *Gonepteryx rhamni* or *Argynnis paphia* which have their host-plants inside forest stands but find nectar plants in open vegetation.

Species can also select patches for their different micro-climatic conditions (Dennis and Sparks, 2006; Shreeve, 1984; Vanreusel et al., 2007). In our study sites, several species were observed inside shady, closed stands where no apparent nectar or host plants were present and that seem to be used to avoid unfavourable conditions in open habitats during hot weather. The use of these cooler patches can correspond to daily or seasonal movements.

Use of different patches can also be necessary to escape unfavourable conditions after disturbances, e.g. mowing of firebreaks or stand edges, and to find a temporary refuge in other patches (Bruppacher et al., 2016). The results of our study suggest that multi-patch use is a common practice in mosaic plantation landscapes for butterflies, where for many species the fragment-matrix dichotomy seems inappropriate. Multi-habitat use is more often described for birds, e.g. the Hoopoe *Upupa epops* in the study area (Barbaro et al., 2008), or for amphibians, with distinct overwintering and reproduction sites. It seems however to be common for insects also, for example in agricultural contexts where species overwinter in stable habitats and colonize agricultural fields yearly (Burel and Baudry, 1999).

Species that use different habitat types can be favoured by both compositional and configurational landscape heterogeneity that will facilitate access to different elements and reduce the distance between them (Fahrig, 2003; Fahrig et al., 2011). A reduced distance between patches can be particularly important for multi-habitat species with low mobility.

➔ ***Multiple habitat use by butterflies may be a frequent phenomenon in mosaic landscapes, underlining the importance of compositional and configurational landscape heterogeneity.***

6.1.6. Species traits and responses to habitat and landscape characteristics

Trait based studies are increasingly used to explain species sensitivity to local or landscape changes. Investigating how species with different trait values respond to environmental conditions, such as land-use or management practices, increases our understanding of mechanisms behind observed changes in community composition, including why some species are more threatened than others (Devictor et al., 2008; McGill et al., 2006; Mouillot et al., 2013b; Öckinger et al., 2010). For example, for butterflies, recent negative population trends and unfavorable Red List status have been attributed to traits as overwintering as eggs or larva, few annual generations and long larval development (WallisDeVries, 2014).

Our results showed that **deciduous riparian forests** differed in functional butterfly composition **from deciduous fragments**. Both thermal and habitat specialization were higher for butterfly communities in riparian forests compared to fragments. This corresponds to a higher proportion of forest species with narrower habitat range and thermal tolerance in riparian forests. These forests are therefore of importance for conserving specialized butterfly species, especially for species at their southern limits in a climate warming context (Devictor et al., 2012), such as *Limenitis camilla*, a species at high risk of extinction under climate change (Settele et al., 2008).

However we did not observe, as predicted, a lower mean community mobility in highly-connected riparian forests, but instead a higher mean mobility (see e.g. Samways and Lu (2007)). Higher mean mobility in riparian forests may be caused by the positive correlation with wing size and minimum area requirements (Baguette and Stevens, 2013; Stevens et al., 2013). It can also suggest that limitations to dispersal imposed by isolation are not primary determinants of functional turnover in butterfly communities in the studied landscapes and that sedentary forest species have already disappeared from the Landes of Gascony. This example also shows that ecological traits should be interpreted considering other, correlated traits. Species traits may have coevolved to maximize fitness under particular environmental conditions (Stevens et al., 2012).

When considering all habitat types, we showed that butterfly species of highest conservation concern were not primarily influenced by mean patch size but by the presence of particular habitats such as clearcuts, young pine stands and firebreaks. Associated traits were: restricted range, overwintering as eggs or young larvae, low mobility and short flight period. Monophagous species were associated with diverse landscapes with shrubland and firebreaks. These traits are also listed by other authors as linked to threat status (Öckinger et al., 2010; WallisDeVries, 2014).

Trait-driven responses of butterflies are also scale-dependent, which implies to use environmental variables measured at both local and landscape levels for analyzing response patterns (Dainese et al., 2015; Gilroy et al., 2015; Winqvist et al., 2014). The combination of traits linked with a negative conservation status (slow larval growth, overwintering in young stages, low mobility and low reproductive capacity), may thus simultaneously increase the sensitivity to changes in local management and to landscape fragmentation. Species with a long larval development, overwintering in immature stages and with only one generation a year are probably more sensitive to habitat disturbances, like mowing, than mobile species with a short larval development and more generations per year, which have the possibility to escape unfavorable habitat conditions. The host plant type, i.e. herbaceous plants, shrubs or trees and the overwintering site, may also explain sensitivity to management disturbances. Several forest species that use trees or shrubs as host-plants are less threatened than species whose immature stages feed on herbaceous vegetation that is more often disturbed (Warren, 1993). At the landscape scale, sedentary, monophagous, habitat specialists will be most sensitive to habitat loss and fragmentation (Öckinger et al., 2010).

- ➔ ***Butterfly communities in riparian deciduous forests show higher thermal and habitat specialization than those in deciduous fragments.***
- ➔ ***Butterflies of conservation concern are characterized by restricted range, overwintering as eggs or young larvae, low mobility and short flight period and seem influenced by the nearby presence of particular habitats such as clearcuts, young pine stands and firebreaks.***

6.1.7. Most appropriate landscape scale

There is no consensus on the optimal scale to be used in butterfly studies and field works comparing the effect of different scales show contradictory results. For example, Bergman et al. (2004), using buffers with radii of 500, 2000 and 5000 m, found only an effect on butterfly communities at the largest scale of 5000 m. This result contrasts with several other studies that observed effects at the smallest tested scales. For example, Krauss et al. (2003) and Marini et al. (2009) observed an increase in species richness with landscape diversity at the smallest scale of 250 m and 95 m respectively. A general rule based on modelling studies indicates that the radius of a landscape should be 4-9 times the median dispersal distance or 0.3-0.5 times the maximum dispersal distance (Jackson and Fahrig, 2012). The mean dispersal distance of all northwestern European butterfly species was estimated to be 200 m (Stevens et al., 2013), leading to a theoretical scale of 800 to 1800 m. However there is a large variation in dispersal distances among butterfly species and populations (Stevens et al., 2010) and landscape scale effects are thus at least species specific. Differences in optimal scales observed in butterfly studies may thus depend on the species pool studied and landscape analyses should preferably be done separately for species groups differing in mobility and habitat preferences (Olivier et al., 2016).

Differences in observed optimal scales are however more likely due to differences in landscape composition and configuration between studies and of the relative importance of ecological processes working in the studied landscapes. At short distances, processes like ressource complementation and supplementation, edge effects and spill-over effects can be important, while meta-population dynamics would rather work at larger spatial scales (Rossi and van Halder, 2010). This can also imply that if different mechanisms are working at the same time, different landscape variables may be important at different scales.

We used in our studies relative small landscape buffers of 200 and 400 m radius (chapter 2, 3 and 5), and larger scales of 500 m and 1000 m (chapter 4). The choice was related to the expected landscape mechanisms and the overlap between buffers. We also analyzed for a large number of landscape variables calculated in buffers with radii varying from 100 to 1000 m, their relationship with butterfly species richness (Rossi and van Halder, 2010, see Annex 1). Figure 3 shows the results for our two study regions separately. Responses are variable and there is no unique distance that is best related to butterfly species richness for all metrics, but in general distances of a few hundred meters show the highest correlation (Rossi and van Halder, 2010). Moreover, at large scales, buffers are generally largely overlapping, leading to similarities in landscape metrics (Pasher et al., 2013)

- ➔ ***The best landscape scale in butterfly studies is species and landscape dependent, but in general scales of a few hundred meters seem best correlated with butterfly diversity.***

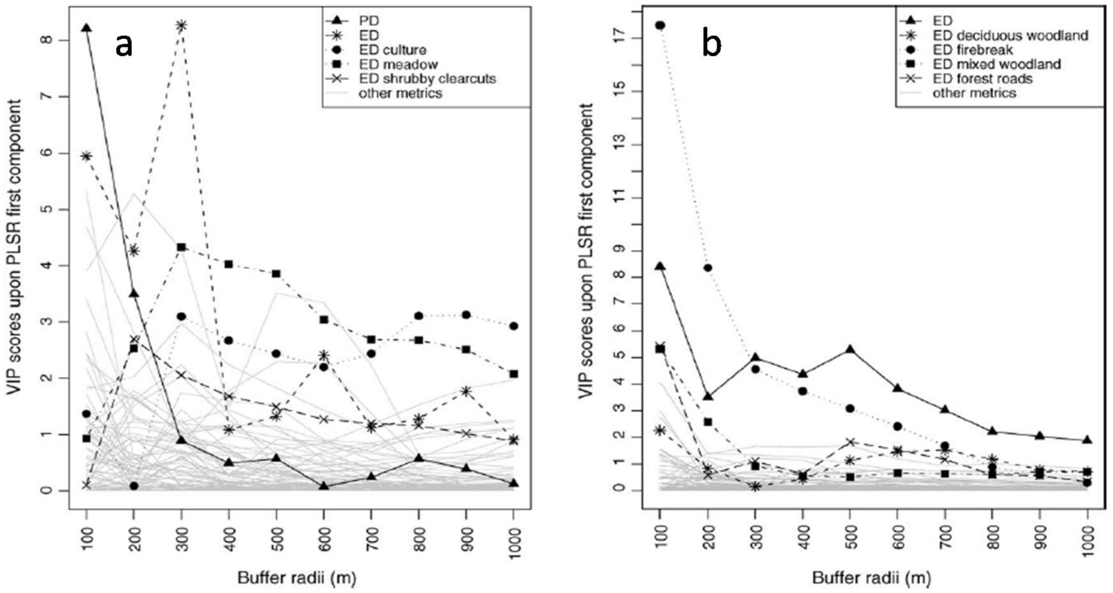

Figure 3. Output of the Partial Least Squares Regression (PLSR) linking butterfly species richness and 830 metrics describing landscape along a range of spatial scales in the site of (a) Solferino and (b) Tagon. Relationship between the VIP scores of the landscape descriptors and the spatial scale at which they are computed (Rossi and van Halder, 2010).

6.2. How to conserve butterflies in mosaic pine plantation landscapes?

Our results clearly demonstrated the importance of semi-natural habitats for butterfly conservation in mosaic landscapes dominated by pine plantations and especially the role of deciduous woodlands, firebreaks and stand edges. The conservation of these key elements is therefore primordial for the conservation of butterfly diversity, but also of other taxa such as birds, spiders and bats. Moreover, our results indicated the importance of habitat quality for butterflies, and notably the presence of host- and nectar plants in the herbaceous vegetation suggesting that appropriate management of different landscape elements is also important.

The next paragraphs describe for the different habitat types their conservation status and management recommendations.

6.2.1. Deciduous woodlands

Forest butterfly species were mainly found in deciduous woodlands. The presence of forest butterflies in deciduous fragments depended mainly on their **quality**, indicating that even small fragments can be of conservation value if they represent habitats of good quality (i.e. with abundant nectar- and host-plants).

Deciduous woodland **fragments** in the Landes of Gascony are privately owned and are maintained for hunting, mushroom- or firewood-collecting. Their future depends therefore mainly on conservation decisions of the private owner. Environmental and forest schemes (e.g. FSC, PEFC) should increase the awareness of their biodiversity value and provide incentives for their conservation and adequate management.

Riparian forests appeared to contain more forest butterfly species and specialized species, indicating their higher conservation value. A particular effort should thus be paid to maintain riparian forests in pine plantation landscapes. The larger riparian forests in the study area are part of Natura 2000 zonation, and seem relatively well protected against, for example, urbanization. However, they are also mainly privately owned and owners maintain or improve habitat quality on a voluntary basis.

Deciduous woodland management

The deciduous fragments in the Landes of Gascony are often unmanaged or are sometimes partly thinned for collecting fuel wood. In the larger riparian forests management in the corridor directly next to the river is in most cases very extensive, but neighboring stands can be managed by clearcuttings. Actual, recommended actions in these Natura 2000 riparian forests are the preservation of deciduous forests, the transformation of pine stands after clearcutting to deciduous woods and the control of invasive tree species (PNR Landes de Gascogne, 2005). Forest owners can receive financial aids for these actions by subscribing 5-year contracts. Nature protection in these areas demands thus a continuous, stimulating coordination by governmental organizations and the availability of financial aids.

Our results showed that differences in butterfly richness and community composition among deciduous fragments and between fragments and riparian forest were mainly related to understory vegetation composition, which will depend on soil type and humidity, forest history, but also on management. There is a debate over the optimal degree of intervention in (semi-)natural forests, varying from no-intervention to active management creating more open structures. This debate is linked to the reference state of forests in Europe. Disturbances such as grazing by mega-herbivores, fires, storms and floodings created probably in at least a part of the original forests much more open forest structures than in actual no-intervention forests (Sebek et al., 2015; Svenning, 2002). We did not study specifically the effect of forest management, but our field observations and the results of other studies suggest that creating heterogeneity in forest structures with a combination of closed-canopy and more open forest, clearings and rides of different size and varied internal and external edge structures would be favourable for butterfly conservation and for many other groups, such as plants, reptiles, birds and hoverflies (Fichefet et al., 2011; Greatorex-Davies et al., 1993; Robertson et al., 1995; Sebek et al., 2015).

6.2.2. Firebreaks

Firebreaks harbored twice as many butterfly species as other habitat types and threatened species were often found in this habitat type. The term ‘firebreaks’ was used in this study to indicate herbaceous or shrubby, open linear land-uses, with a width of at least 15 m (often larger) and a length of several hundred meters. They include linear elements classified as firebreaks in fire-preventing schemes, but also powerlines, open land over gaslines and former firebreaks.

The conservation of firebreaks seems much more alarming in the Landes of Gascony than that of deciduous fragments. Firebreaks that are not classified in a fire-preventing scheme are gradually transformed in pine plantations, are used for crop growing (e. g., corn or plant mixtures for deer), are ploughed annually or are kept as bare soil. It is clear that without their heathland or herbaceous vegetation much of the biodiversity value of firebreaks is lost. Since these open heathland areas do not have an economic interest for the forest owner, it is difficult to promote their conservation if they are not included in a fire-preventing scheme or a biodiversity scheme, for example through forest certification (PEFC).

The actual management of firebreaks in the Landes of Gascony is very variable (varying from annual mowing to about once every 8 years). The vegetation diversity within firebreaks can be increased and the temporarily negative impact of management can be reduced by a more diverse mowing management regime within sites (Bruppacher et al., 2016). For wide forest rides, Fichefet et al. (2011) recommend a system with different intervention frequencies varying from a yearly cut of the central area, and a less intensive management frequency of 4-8 and 8-24 years near the forest edge. Comparable systems could be used in firebreaks, creating a more natural forest edge and by maintaining the largest part of the firebreak as herbaceous and heathland vegetation with a varied structure and composition. Vegetation heterogeneity, with short and dense vegetation close together, seems important for butterflies and overall biodiversity (Bruppacher et al., 2016; Valtonen et al., 2006; Vickery and Arlettaz, 2012).

6.2.3. Stand edges

Edges of pine stands and deciduous fragments harbored higher butterfly richness than their interior and can act as habitat or part of a habitat. A management comparable to that proposed for firebreaks could be applied to edges, with a strip next to the forest track mown annually and next to the forest stand less frequently. The first lines of the pine plantation could be replaced by an area allowing growth of diverse shrubs and deciduous trees. A more diverse forest edge with deciduous trees is not only beneficial to biodiversity, but will also diminish the attacks by pine processionary moths (*Thaumetopoea pityocampa*) on pine trees (Dulaurent et al., 2012).

6.2.4. Pine stands

Pine stands were not a ‘biological desert’ and even threatened species such as *C. oedippus* were observed in young and older stands of maritime pine that have an open tree canopy permitting more sunlight to reach the understorey vegetation. The positive effect of more open pine stands on butterfly species can be due a direct, positive effect of insolation (light intensity) on butterflies or on the positive effect of insolation on the cover of the herbaceous layer, as demonstrated respectively in *Pinus ponderosa* (Waltz and Covington, 2004) and *Pinus edulis / Juniperus monosperma* forests (Kleintjes et al., 2004).

The management within pine stands (e.g. clearcutting, soil preparation before planting, removal of shrub layer, thinning) may affect directly butterflies by destroying immature stages or indirectly by altering vegetation composition. Field observations suggested the importance of variation in understorey vegetation structure and composition. Most of the observed butterflies depend on herbaceous plants as host-plants, but some use shrubs or trees. Stand management creating a diverse understorey vegetation dominated by herbs but with presence of some shrubs and deciduous trees seems most beneficial for butterflies. A more varied management of understorey vegetation (mowing only one inter-row out of two as observed in some stands) will favour vegetation diversity and in turn butterfly conservation (Bruppacher et al., 2016).

The Landes of Gascony has experienced two very severe storms (1999 and 2009) causing important forest damage. Different scenarios have been developed for the reconstitution of the forest, including shorter rotation cycles, more wood for bioenergy and the use of exotic tree species, such as *Eucalyptus* spp. (Mora et al., 2012). Shorter rotation cycles are not necessarily negative for butterflies or some other taxonomic groups, because it will lead to a larger amount of clearcuts and young stands. However it will also increase the structural homogeneity at the landscape scale. Until recently, clearcuts were left without management for a few years before planting to diminish attacks by pine weevils (*Hylobius abietis*), a practice even increased after the heavy storms. These 'fallow lands' can develop a diverse vegetation that can harbor several butterfly species such as *C. oedippus* and *E. aurinia*. However short rotation forestry may also imply a more intensive forest management with removal of stumps for bio-energy, ploughing, immediate tree planting and more drainage. Post-storm management of forest windthrow, i.e. salvage logging or set aside for natural regeneration, may affect bird and insect communities more than the windthrow itself (Zmihorski, 2010; Zmihorski and Durska, 2011). The effect of windstorm on butterfly communities remains virtually unexplored, although potentially important, by favoring open habitat species over forest specialists (Zmihorski, 2012).

6.2.5. Soil humidity gradients

An essential conclusion of the different studies was also the role of **vegetation composition** on butterfly communities, mainly determined by **soil humidity** and **management**.

The increased drainage in the Landes of Gascogny for silvicultural and agricultural purposes has led to a loss of areas with humid soil conditions, as can be demonstrated by the loss of many natural water bodies (Timbal and Maizeret, 1998). Some authors indicate a loss of 49% of wet and humid areas in the period 1983-1995 and a marked loss of wet heathlands (Guillot, 2011). These open, humid areas are of special interest to threatened butterflies and other taxa (Maizeret, 2005). Moreover, these habitat types are particularly at risk under climate change (incl. more severe and frequent droughts). Further drainage for silvicultural or agricultural purposes should thus be restricted and to mitigate climate warming effects the current network of ditches should be reduced.

6.2.6. (Missed) possibilities for biodiversity conservation in forests

Forest certification

The conservation and enhancement of biodiversity is one of the objectives of **sustainable forest management (SFM)**. Since consumers are more and more concerned about environmental issues and want to know the origin of forest related products, certification systems have been developed (e.g. Forest Stewardship Council (FSC), Programme for the Endorsement of Forest Certification (PEFC)). For example, the PEFC label indicates that management practices meet requirements for best practice in sustainable forest management, including that biodiversity of forest ecosystems is maintained or enhanced. In the Landes of Gascony, forest owners can obtain a PEFC certification by signing a statement that they follow sustainable management recommendations. It seems however that no monitoring process has been established to verify compliance with SFM rules. The certification system could, however, represent a real possibility to improve biodiversity conservation in the participating forests. However, this seems to demand a change in mentalities of forest owners and private and governmental organizations.

Financial aid after storm damage

For the reconstitution of the pine forest after the heavy storms of 1999 and 2009 the French government and the regional council have supplied financial aids. This financial program included a diversification option to favor the creation or conservation of other land uses than pine plantations. Principally, the diversification program included the plantation of deciduous trees along pine stands, the conservation of small deciduous fragments, of water bodies and of open heathland areas. This diversification program is beneficial for butterflies and other taxonomic groups and shows similarities with programs in other countries. For example in Ireland in all grant-aided afforestation 15 % of the area must be treated with particular regard to biodiversity and contain 5-10 % open space and 5-10% retained forest habitat (Gittings et al., 2006; Oxbrough et al., 2006). However application of the diversification program in the Landes of Gascony was on a voluntary basis. Among the 176,000 ha reconstituted after the storm 98.5 % were planted with pine trees, while only 1.5 % were used for diversification measures, which mainly consisted of planting deciduous trees along pine stands (J.-R. Liarçou, pers. comm.). Maintaining open areas for biodiversity thus does not seem a priority for forest owners in the region.

Other options have thus to be explored such as land assignment to ecological restoration or reintroducing the use of traditional agro-pastoral management to maintain grasslands and heathlands that are highly beneficial to a large suite of threatened species in mosaic landscapes dominated by plantation forests.

6.3. Research pespectives

6.3.1. Improving landscape description and site selection

We showed that the occurrence of butterfly species was more influenced by vegetation composition than *a priori* categories of habitat types (e.g. different tree height classes of pine stands). Moreover, habitat characterization is species- or community-specific. Constructing functional landscape maps relevant to each species or group may allow analyzing the effect of landscape composition and configuration on occurrence patterns better than using usual methods (Fahrig et al., 2011; Perović et al., 2015). Constructing these kinds of maps demands detailed knowledge about species' habitat requirements, the possibility to classify differences in habitat quality and to dispose of information at the landscape scale permitting to construct these species specific maps (e.g. vegetation data, ground water tables, management history). Species distribution models (SDM) based on species presence/absence or presence-only data and environmental data can offer the possibility to model species niches in the examined environmental dimensions and to construct habitat maps (Phillips et al., 2006; Thuiller et al., 2009).

When studying the effect of landscape variables on butterfly diversity, intrinsic collinearity between landscape metrics should be taken into account, either by statistical methods (Smith et al., 2009) or by adequate landscape selection (Pasher et al., 2013). Methods like 'moving windows' permit to calculate for a large number of potential, functional landscapes the variables of interest and to select a subset of landscapes with uncorrelated variables (Pasher et al., 2013; Perović et al., 2015) or alternatively, to select landscapes that correspond to pre-defined criteria (Villemey et al., 2015). Combination of GIS and statistical analyses furthermore enables selecting landscapes along large, crossed gradients of landscape variables and with a low spatial autocorrelation (Pasher et al., 2013).

The use of functional maps and a site selection based on the above indicated criteria will permit to better analyze the effects of landscape composition and configuration on selected species groups.

6.3.2. Multi-habitat use and mosaic landscapes

In our study many species were observed both at edges and interiors of one or several habitat types. The fact that species are found in different habitat types does not mean that they disperse between these patches if they provide the same resources. Dispersal between habitat patches is however probable when they supply complementary resources or the same resources but at different periods. Detailed capture-mark-recapture studies combined with observational studies may permit to indicate the rate of dispersal between habitat patches and the use of resources in different patch types. These observations can be linked to microclimatic measurements in different habitat types in order to analyze behavioral responses to weather conditions. Understanding these processes seems particularly important in the context of climate warming. It can also guide conservation priorities toward preservation of habitats with cooler microclimates (Suggitt et al., 2015).

Multi-habitat use may also be analyzed in an indirect way by sampling species in land mosaics differing in composition (Fahrig et al., 2011). Land mosaics have emergent properties and are not just the sum of the elements within a landscape. To study these properties, species should be sampled in different patches in each land mosaic (Bennett et al., 2006). Different studies revealed that heterogeneity of landscape elements is often positively correlated with species richness, while spatial configuration has in general less effect (Bennett et al., 2006). However, species richness is just one aspect of biodiversity and functional diversity can be related to landscape configurational heterogeneity (Perović et al., 2015)

6.3.3. From patterns to processes

Most landscape ecological studies analyze correlations between observed patterns of species richness or community composition and variables characterizing landscape composition and configuration. Relying on correlations contains the risk that correlations are consequences of correlations with other, non-measured variables or of spatial co-variation between landscape variables and response variables (Smith et al., 2009). Even if the identified landscape variables are really linked with the response variable, they are not the direct cause of observed occurrence patterns. They affect one or more biotic or abiotic mechanisms that provoke population responses, i.e. births, immigrations, deaths or emigrations (Didham et al., 2012). For example, habitat loss leads to reduced patch size and increased relative edge length, which can in turn favor the access by predators to the patch increasing mortality rates of the studied population (Ries et al., 2004). Population growth parameters can however be affected in contrasting ways by different or the same landscape variables, complicating their analysis (Didham et al., 2012). Realistic modelling of (meta)population dynamics may offer a possibility to understand these underlying mechanisms (Sawchik et al., 2002). It can also provide insight in which processes influence most meta-population survival and to propose efficient, cost-effective conservation measures (Radchuk et al., 2012).

Species traits

The use of species traits combined with functional landscape maps and improved landscape selection criteria will allow to gain more insight in the mechanisms behind occurrence and abundance patterns (Mouillot et al., 2013b; Öckinger et al., 2010). Species traits should ideally be based on measurements of local populations because traits can show important regional variation, as for example the number of annual generations or host-plant use. In the literature the list of host plants is often long (Bink, 1992; Lafranchis, 2000), but at a local scale a butterfly species can be very selective, using only one or a few host-plants. Even for a well-studied group as butterflies, host-plant use is not always known. For example, we observed *E. aurina*, a protected and well-studied species, in areas where its preferred host-plant *Succisa pratensis* was absent. Since the caterpillars of this species are gregarious and spin an easy observable silken web around the leaves of their host-plant, we discovered the apparently frequent use of *Lonicera periclymenum* as host-plant (van Halder and Jourdain, 2010; Annex 2*)*, which allowed us to better understand the occurrence pattern of the species in different habitat types in the Landes of Gascony.

6.3.4. Biotic interactions and landscape structure

Most butterfly studies focus on the ‘bottom-up’ aspects of habitat (vegetation composition and quality) while ‘top-down’ influences are generally ignored (Shaw et al., 2009). Likewise, we analyzed the effect of vegetation composition and structure on butterflies. However, other biotic interactions may have an important effect on population dynamics and in structuring butterfly communities. These biotic interactions can be separated in intra- and interspecific competition for resources and the effects of parasitoids, predators and micro-organisms (Dempster, 1983; Glen, 2004). As these organisms are also affected by changes in landscape structure, but most likely in a different way than butterflies, landscape changes will alter these biotic interactions and thus butterfly population dynamics.

Interspecific competition among butterfly species for resources is rarely studied and seems not an important factor affecting populations, probably because of niche specialization or high resource abundance.

Parasitism by parasitoids seems to be one of the most important biotic interactions affecting butterfly population dynamics. Very high levels of parasitism are mentioned in the literature, for example for *Proclossiana eunomia* (92 % of larvae parasitized by *Cotesia vestalis* (Braconidae), (Sawchik et al., 2002), for *Melitaea cinxia* (Lei and Hanski, 1997) and for *Euphydryas aurinia* (Porter 1981). Eggs, larvae and pupae of butterflies can be parasitized by generalist or specialist parasitoids, that can in turn be parasitized by hyperparasitoids, leading to complex, interacting systems (Shaw et al., 2009). Species that experience very high local parasitism or predation risks may distribute their eggs in different patches or colonize new, parasitoid free patches (Ohsaki and Sato, 1994; Petit et al., 2001). Habitat fragmentation can thus result in lower parasitism rates and higher meta-population survival. The effect of the landscape mosaic and more precisely of compositional and configurational landscape heterogeneity on parasitism rates of butterfly immature stages remains however unexplored to our knowledge.

Predation by insects, mammals or birds of different butterfly stages can also have important effects on population dynamics and can, like parasitism, depend on landscape composition and configuration. We experimentally estimated caterpillar predation by birds as the number of feeding attempts on plasticine models attached to branches of oak trees in forest patches of the Landes of Gascony. Predation rates by birds were higher at edges than in forest interiors (Barbaro et al., 2014), suggesting that in more fragmented landscapes butterflies and moths can experience higher predation rates. The same experiment was conducted in New-Zealand showing a comparable edge response, but also indicating higher predation rates in smaller patches (Barbaro et al., 2012, Figure 4).

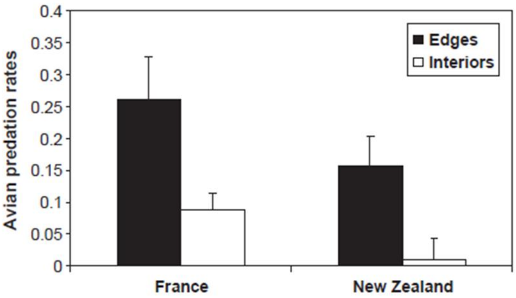

Figure 4. Mean (± SE) model predation by insectivorous birds at edge plots (black bars) and interior plots (white bars) in France (Landes of Gascony) and New-Zealand (Banks Peninsula), (Barbaro et al., 2014).

Interactions with invasive, exotic species

Invasive plant species can alter vegetation composition and thereby butterfly habitats. There are also examples of invasive insect species that cause declines of native butterfly species, especially on islands. The Speckled Wood (*Pararge aegeria*), a widespread species in Europe, was introduced in the 1970s on Madeira and is possibly threatening the Madeiran Speckled Wood (*Pararge xiphia*) (Jones and Lace, 1992). There are however many more examples of introduced parasitoids having a serious impact on endemic butterflies and moths (Benson et al., 2003; Nafus, 1993). For example, the Canary Islands Large White (*Pieris cheiranthi*) is probably declining because of the introduction of *Cotesia glomerata* (Lozan et al., 2008).

A special case of **landscape-driven parasitism** by an exotic parasitoid can be observed for the endemic New Zealand Red admiral butterfly (*Bassaris gonerilla*), that is parasitized by *Pteromalus puparum*, a pupal parasitoid introduced to control the introduced Cabbage white butterfly (*Pieris rapae*). This is a case of apparent competition, i.e. an indirect interaction among two prey species mediated by a shared predator or parasitoid (DeCesare et al., 2010). Our preliminary observations (Figure 5), made during a 3-months stay in New-Zealand, suggest an interaction between parasitism rate and forest fragmentation. The New-Zealand red admiral shows a much higher parasitism rate at forest edges near agricultural areas, where cabbage white butterflies and its parasitoids are abundant, than in the forest interior where cabbage whites are absent. This is combined with maladaptive habitat selection since female admirals prefer lush edge plants of nettles for oviposition to the forest interior. Under these circumstances invasive species and forest fragmentation interact to turn forest edges into an ecological trap for red admirals (Schlaepfer et al., 2002).

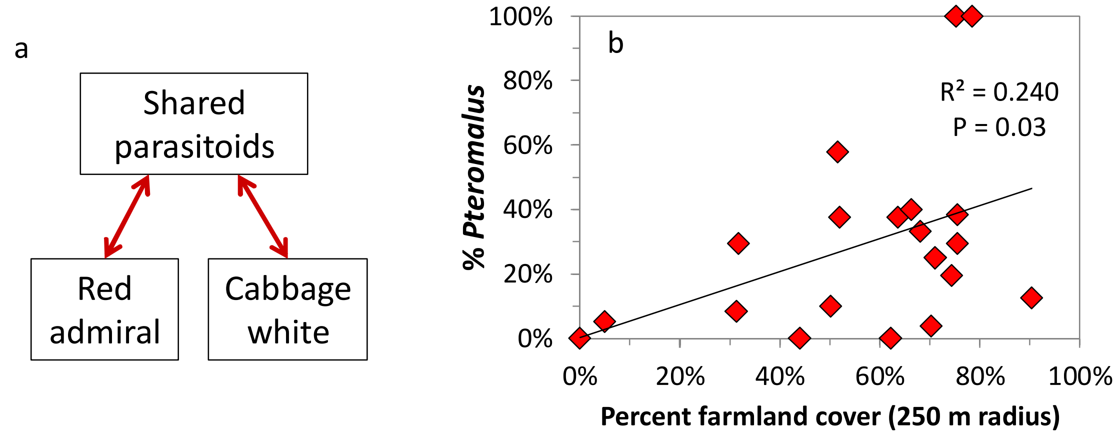

Figure 5. (a) Apparent competition between the New-Zealand Red admiral *Bassaris gonerilla* and the introduced Cabbage white *Pieris rapae* in New Zealand due to a shared, introduced pupal parasitoid and (b) relationship between the percentage parasitism of pupae of the New-Zealand red admiral by *Pteromalus puparum* and percentage farmland cover in a buffer of 250m around the point where pupae were sampled.

6.3.5. Heterogeneity as key-factor for butterfly diversity at different scales

Our studies suggest that spatial and temporal resource complementation and supplementation (use of different habitat patches) can be an important mechanism for butterfly diversity and survival in mosaic landscapes. Landscape compositional and configurational heterogeneity may thus be key factors for butterfly diversity, but also for other taxonomic groups. Moreover, heterogeneity seems important at different scales, from small-scale vegetation heterogeneity to landscape heterogeneity at the scale of species daily or life-time dispersal.

Heterogeneity can be characterized in different ways and will for example depend on land-use classification and the construction of functional maps. Moreover, species presence may not only depend on heterogeneity but also on the presence of particular habitat types. It seems promising and relevant to try to disentangle these different aspects of heterogeneity on butterflies. Including other species groups in these studies may reveal if the same mechanisms operate for different groups. Furthermore, the use of species traits can reveal the positive or negative effects of heterogeneity on species with certain trait combination, especially for trait-combinations linked with species threat status. Species sensitivity to climate change can be incorporated in these studies since heterogeneity will provide microclimatic refuges at different spatial scales.

Studies aiming to analyze the effect of heterogeneity can include behavioral studies, capture-mark-recapture studies, species surveys or the use of citizen science data. The following studies seem most relevant:

- ➔ Study on the dispersal of butterfly individuals between different, nearby habitat patches and the resource use in these patches. These studies combine capture-mark-recapture (CMR) techniques and behavioral observations, are repeated several times a day and under different weather conditions. Measurements of microclimatic conditions in different habitats can indicate if these movements correspond to behavioral responses to weather conditions.

- ➔ Study on relationships between functional landscape heterogeneity and functional butterfly community composition. The availability of more precise habitat maps will permit to select landscapes with pre-defined, independent gradients of heterogeneity and to perform surveys in these selected landscape mosaics. The use of citizen science data (atlas-data or monitoring data) may enable studying the effects of heterogeneity in different landscape types.
- ➔ Study on the effect of vegetation heterogeneity on butterflies. The effect of vegetation heterogeneity can be studied by selecting habitats with an existing heterogeneity gradient or by creating the heterogeneity gradient by different management regimes. The latter option has the advantage that gradients are controlled and that management recommendations can be provided directly. Butterfly sampling should be repeated during several years to evaluate the long-term effect of vegetation heterogeneity and management.

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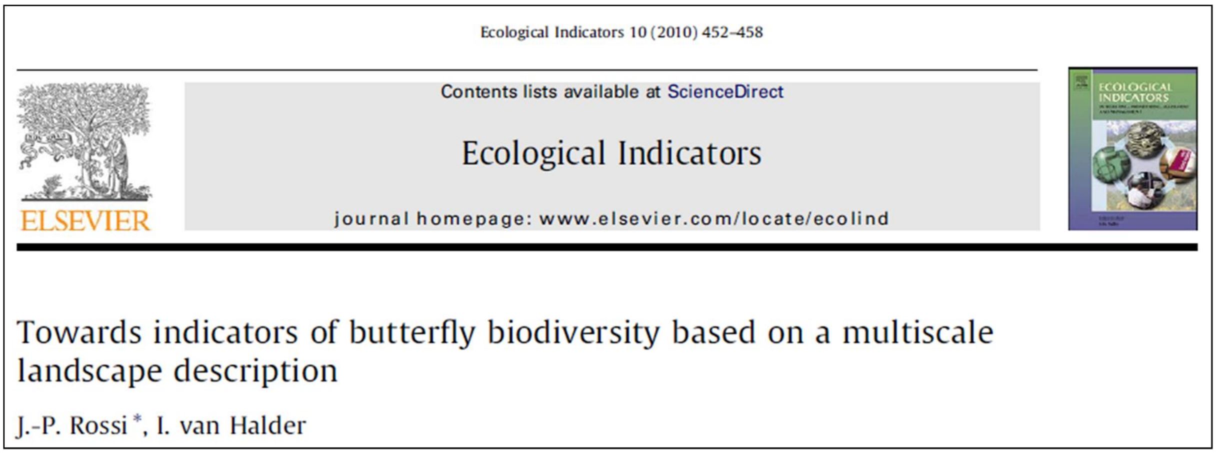
8. Annexes

Annex 1: Towards indicators of butterfly biodiversity based on a multiscale landscape description

Melitaea athalia



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Abstract

The conservation of biodiversity has gained prominence in ecological research for the last decades. Conservation actions require a measure of biodiversity such as species richness, but its assessment is very difficult, even for small areas and therefore the search for surrogates (i.e. indicators) of biodiversity has emerged as an active research topic. We investigated the relationships between butterfly species richness and landscape structure and composition in two pine plantation sites in Southwest France. We assessed the correlation between butterfly species richness and a set of 15 landscape metrics computed for 18 land-uses at 10 different spatial scales. Spatial scales were accounted for by computing landscape metrics for circular buffers with radius ranging from 100 to 1000 m. The joint use of the Partial Least Squares Regression (PLSR) and a stepwise regression procedure revealed strong correlations between butterfly species richness and various landscape metrics in both study sites. The selected landscape metrics differed from one site to another and mostly involved measures of landscape fragmentation. We found a very strong effect of the spatial scale of investigation upon the perception of the landscape–butterfly richness relationship. Our main conclusions are that (i) certain landscape attributes can potentially serve as indicators for butterfly species richness at the landscape scale; (ii) future indicators of biodiversity based on landscape features should consider various spatial scales.

Keywords: Butterfly species richness, Biodiversity, Landscape metrics, Spatial scales, Partial Least Squares Regression

Introduction

The conservation of biodiversity has gained prominence in ecological research for the last decades and it is widely recognized that large-scale habitat alteration has led to unprecedented worldwide species extinction (Pimm et al., 1995). Conservation actions require a measure of biodiversity such as species richness, but its assessment is very difficult, even for small areas. As a consequence, the search for surrogates (i.e. indicators) of biodiversity has emerged as an active research topic (Araújo et al., 2001; Prendergast and Eversham, 1997). Biodiversity indicators can be based on species richness of one or several taxonomic groups, with the assumption that the diversity of this group is correlated with that of other groups (Maes and Van Dyck, 2005). The level of correlation depends on the taxonomic resolution employed as well as the taxa themselves and the results have been contrasted so far (Similä et al., 2006). The literature contains case studies where some indicator groups have been identified (Dynesius and Zinko, 2006; Schmidt et al., 2006), but other authors reported weak correlations (Chase et al., 2000; Wolters et al., 2006) or highly spatially variable and hence unpredictable relationships (Prendergast and Eversham, 1997). A different approach consists in using habitat patch characteristics and landscape features as an indicator of species richness (Dauber et al., 2003). The basic idea is that since landscape acts upon biodiversity dynamics there must be some landscape features that can be correlated to biodiversity and eventually be used as indicators (Araújo et al., 2001).

The biodiversity at the local scale (e.g. the scale of the habitat patch) depends primarily upon local habitat characteristics but also on communities scattered across the landscape. This corresponds to the idea that local biodiversity does not only depend on local processes (e.g. local extinction) but also on processes that act over regional or biogeographical scales (e.g. migration) (Ricklefs, 1987). The effects of landscape configuration (i.e. the ''matrix effect'') correspond to a variety of processes among which dispersal, source–sink dynamics, neighborhood effects and metapopulation dynamics (Dunning et al., 1992). Fragmentation (With and King, 1999a) and matrix quality (Fahrig, 2001) can strongly affect species extinction thresholds while lacunarity alters colonization success hence the dynamics of biodiversity (With and King, 1999b). At the regional scale, the so-called γ diversity is strongly dependent on landscape composition (Dunning et al., 1992) with subsequent effects at local scales (Whittaker, 1972). The impacts of landscape are therefore multiple, and depend on the taxa examined, the scale considered and the scale at which organisms interact with their environment (Bestelmeyer et al., 2003).

Butterflies are insects that form communities including species with different habitat preferences and dispersal capacities and therefore contrasted response to landscape composition and configuration (Dennis et al., 2003). Most butterfly species need complementary resources like host plants (for larvae), nectar plants (for adults) and sites for resting or overwintering. In addition, many species use resources in different vegetation types and/or are mostly active along edges. As a consequence, there are direct and strong relationships between butterfly community structure and richness and habitat characteristics, vegetation composition and landscape (Dennis et al., 2003). Butterflies are therefore a very convenient group to study the relationships between landscape mosaic and species richness (Debinski et al., 2001; Schneider and Fry, 2001) and explore the potentials for biodiversity indicators.

Building a landscape-based indicator of butterfly biodiversity amounts to (i) describing landscape by means of relevant metrics, (ii) correlating the metrics with a biodiversity measure such as species richness. There is no way to determine a priori which scales matter to the taxa at hand (only a range of known or likely spatial scales can be suggested) and one metric may be linked to species richness at one scale while another metric would be at a different scale, therefore a large range of scales must be investigated. Another difficulty arises when choosing the landscape metrics that must be computed and used in further correlation analyses: their inner pair correlations can cause problems in the data processing (i.e. collinearity between landscape metrics) (Cushman et al., 2008; Schindler et al., 2008). Moreover, the multiscale behavior of landscape metrics themselves implies multiscale analysis to adequately characterize and monitor landscape heterogeneity (Wu, 2004). As an exemple, Zaccarelli et al. (2008) emphasized the insights gained from a multiscale approach in the establishment of regional conservation network to manage biodiversity at the regional scale. Both theoretical and empirical studies show that indicators of species richness based on landscape metrics should be multiscale although there are only few case studies (Bergman et al., 2004; Krauss et al., 2003) and some questions regarding the statistical methodology needed to tackle these issues remain to be investigated.

The aim of the present study was to explore the relationships between butterfly species richness and landscape metrics measured at different spatial scales. We based our analyses on butterfly communities sampled in two sites located in the same region (Southwestern France) where the landscape is dominated by pine plantation forests with virtually no variability in topography (van Halder et al., 2008). Our survey is a first step towards more general indicators that require more replicated studies and additional sampling in various landscape types. In this paper we explore the contribution of a multiscale view of the landscape–biodiversity relationship, concentrate on the statistical issues and introduce the use of the Partial Least Squares Regression (PLSR) (Wold et al., 2001) as a tool to design landscape-based indicators.

Materials and methods

The present study is based on data published by van Halder et al. (2008). Study sites and sampling procedures are fully described in the original paper and therefore we only provide the main information here.

Landscapes

The study was carried out in Southwestern France in the ‘‘Landes de Gascogne’’ (van Halder et al., 2008). The region covers ca. 1 million ha of plantation forest of maritime pine (*Pinus pinaster*, Aiton 1789). Landscapes are therefore dominated by pine plantations with rare deciduous woodlands mostly found along rivers (riparian forest) or as scattered patches of a few hectares. Open areas comprise maize fields, pine clear cuts and firebreaks. Soils are acid podzols (pH of 3.5–5.5). Pine forests are submitted to intensive silvicultural managements including fertilization, mechanical understorey removal and four thinning operations during the rotation cycle (van Halder et al., 2008).

Study sites

We investigated two sites (namely the ‘‘Tagon’’ and the ‘‘Solferino’’) located South West of Bordeaux and covering 5000 ha and 10,500 ha, respectively. Soils were similar but landscape composition and structure differed to a certain extent. Butterflies were studied in 33 and 46 sampling plots in Solferino and Tagon, respectively. Each plot corresponded to one of the seven main habitat types (land-uses) commonly encountered in the Landes de Gascogne (van Halder et al., 2008). Five habitat types depicted the main stages of the maritime pine plantations in Southwestern France: herbaceous and shrubby clearcuts and three size classes of pines (young pines, canopy height 7 m; mid-class pines, canopy height 7–15 m; and older pines, canopy height >15 m). Other habitats included deciduous woodlands (isolated patches or riparian forests) and firebreaks or powerlines (hereafter called firebreaks).

Sampling procedure

Butterflies were sampled using a line-transect protocol that is fully described in van Halder et al. (2008). Butterfly sampling was carried out within and at the edge of each sampling plot using two 400 m long transects. Butterflies were counted within 2.5 m on each side of the transect line and 5 m ahead of the recorder. Each plot was visited four times between May 14th and September 4th 2004.

Landscape description

Land-use types in the two study sites were mapped in a GIS based on aerial colour photos with a resolution of 50 cm as background layer. Photos dated from 2000 and 2002 for Tagon and Solferino, respectively. Field surveys were conducted to check patch attributes and correct for changes that might have occurred since the date of the photos. Aerial photos were mapped using 18 land-use categories including the 7 main habitat types.

Data analysis

Basic statistics

If both study sites hosted similar butterfly communities it would imply that all data could be analyzed as a whole. On the contrary, different communities correspond to different ‘‘sample populations’’ and as such deserve separate landscape–species richness analyses. We used a correspondence analysis (CoA) (Legendre and Legendre, 1998) to determine to which extent the community structure differed amongst the sites of Solferino and Tagon. The between-sites difference was assessed using an inertia test based on 999 randomizations (Manley, 1997). This was done using the software R and the R package ade4 (Chessel et al., 2004). We used the bootstrap to reestimate the species richness and approximate the bias in the estimator of species richness (Manly, 1997, p. 36). This allowed to compute bias-corrected species richness and the associated confidence interval (Manly, 1997). We compared the observed species richness of the two sites by means of a randomization test following Manly (1997, p. 6).

Multiscale landscape description

Landscapes were described around each sampling point using circular areas referred to as buffers. We used buffers of increasing radii so as to capture landscape features at different spatial scales. Buffers radii ranged from 100 to 1000 m. The resulting microlandscapes were described using landscape metrics reflecting both structure and composition. The metrics are listed in Table 1 and fully described in McGarigal et al. (2002). Overall, each sampling location was described using 11 landscape metrics and 4 class metrics computed for each of the 18 landscape classes, i.e. the land-use categories (Table 1). Given that we used 10 buffer sizes the resulting landscape data set comprised (11+4x18) x 10 = 830 variables.

Table 1. List of the metrics used to describe the plantation forest landscapes in two sites located in South-western France. Acronyms, names and codes correspond to the terminology of McGarigal et al. (2002). C and L respectively stands for class and landscape level metrics (see McGarigal et al., 2002, for a complete description of each metric).

Acronym	Name	Level	Code
PLAND	Proportion of landscape	C	C4
PD	Patch density	C, L	C6, L6
LPI	Largest patch index	C	C10
ED	Edge density	C, L	C8, L8
PRD	Patch richness density	L	L125
SHDI	Shannon's diversity index	L	L127
SIDI	Simpson's diversity index	L	L128
SHEI	Shannon's evenness index	L	L130
SIEI	Simpson's evenness index	L	L131
AI	Aggregation Index	L	L116
COHESION	Patch cohesion index	L	L121

Results

Relating landscape metrics to species richness

Van Halder et al. (2008) showed that the butterfly species community was strongly affected by habitat in the ''Landes de Gascogne'' and therefore this effect might obscure the relationship between species richness and surrounding landscape (matrix effect). We accounted for that difficulty by removing the average habitat effect through centering and therefore based our analyses on the habitat-centered species richness (referred to as species richness). Because the number of landscape metrics was larger than the number of objects (i.e. the sampling locations), the classical regression analyses (e.g. multiple linear regression) could not be used. Another characteristic of our data sets is that they are likely to contain many noisy, partially redundant or collinear variables (Cushman et al., 2008). Such data can be analyzed by Partial Least Squares Regression (PLSR). Basically, PLSR is a linear regression of one or more response variables **y** onto a number of principal component scores from a predictor matrix **X** but whereas principal component analysis maximizes the variance of the scores, PLSR maximizes the covariance between the scores and the response (Mevik, 2006). It is a standard tool in chemometrics where large data sets with strong collinearity are common (Wold et al., 2001) and various applications in other fields of life sciences have been published (McIntosh et al., 1996; Nguyen and Rocke, 2002). A detailed introduction to the PLSR can be found in Wold et al. (2001), Mevik and Wehrens (2007) and Martens (2001).

We used the PLSR in a design strictly similar to a multiple regression, **X** being the landscape metrics table and **y** the species richness. The computations were done using the software R and the associated package pls (Mevik and Wehrens, 2007). The PLSR leads to a statistical model linking the response variable (species richness) to all the explanatory variables and additional computations are needed in order to identify the pertinent explanatory variables (Gauchi and Chagnon, 2001). This step is important because it allows to reduce the huge initial data set to a lower number of pertinent variables that can be used in further analysis like standard multiple regressions. We used the Variable Importance in the Projection (VIP) approach described in Chong and Jun (2005) and used the threshold value of VIP = 1 for selecting the variables deemed pertinent. The computations were done using the software R and the associated function VIP.R written by Bjørn-Helge Mevik and available at http://mevik.net/work/software/VIP.R. Since the VIP approach does not include a formal statistical test, the metrics of interest were subsequently incorporated into a multiple stepwise regression with the aim to build a simple model linking landscape and species richness.

When a metric had a VIP value greater than one (for Tagon) or two (for Solferino, see Section Results) for different buffer sizes we retained the metric corresponding to the largest VIP value in order to reduce the risk of collinearity.

Species richness and inter-site variability

The two study sites harbored contrasted species richnesses ranging from 37 (Solferino) to 45 species (Tagon) (Table 2). Both uniques and singletons were low and the between-site difference in species richness remained marked when the bias-corrected estimators were considered. The difference between the observed species richness in Solferino and Tagon was significant (P=0.009, randomization test). Both sites hosted butterfly communities that differed in their richness but also in terms of community structure. The CoA showed discrepancies between the sites along axis 2 whereas axis 1 mostly conveyed within sites heterogeneity (Fig. 1). The between-site inertia test performed on CoA indicated that these differences were significant ($P= 9 \times 10^{-4}$). Thirty-three species (67.3% of the total) were common in the two sites. We concluded that the sites of Solferino and Tagon should be analyzed separately given their differences in community structure and species richness.

Table 2. Observed and estimated butterfly species richness in two sites in the ''Landes de Gascogne'' (South-western France). Singleton and unique are respectively the number of species that were represented by one individual or occurred in one sample only. Sb is the bias-corrected estimator of the species richness. LB and UB are respectively the upper and lower bounds of the species richness estimator based on 999 randomizations.

Site	S	Sb	LB	UB	Singleton	Unique	n
Solferino	37	39.9	36.9	42.9	3	6	33
Tagon	45	46.2	43.9	48.3	1	1	46
All pooled	49	50.8	48.4	53.2	3	3	79

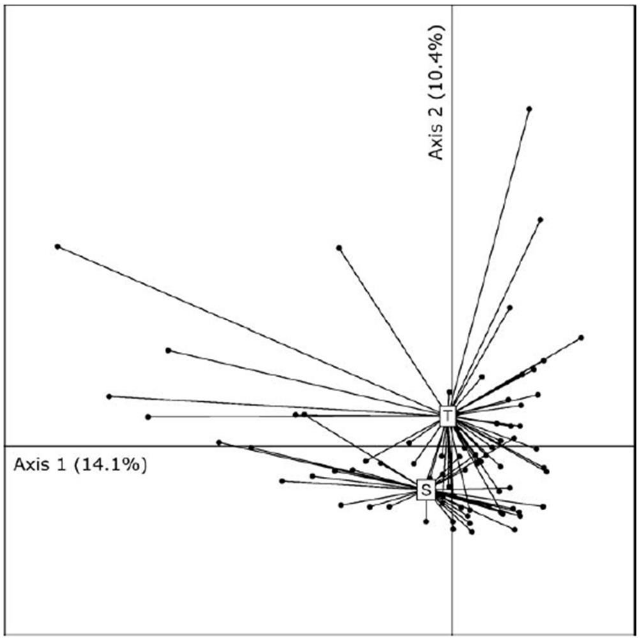

Figure 1. Correspondence analysis (CoA) of butterfly abundance data in two study sites dominated by pine plantations in Southwestern France. Projection of the sampling units upon the factorial plane 1–2. Open squares are placed at the centre of gravity of the scatter of points corresponding to each site. Lines link samples to the corresponding sites. S: Solferino. T: Tagon.

PLSR of the species richness with landscape metrics

The PLSR performed with the species richness as the response variable and the landscape metrics as explanatory variables yielded a first component (i.e. latent variable) that explained 9.6% and 30.9% of the variance of the response variable in the sites of Solferino and Tagon, respectively. The number of landscape metrics with VIP ≥1 was 131 and 47 (i.e. 15.8% and 5.6% of the 830 initial descriptors available) in Solferino and Tagon. The examination of how the VIP of a given landscape metric changed according to the buffer size (i.e. the scale considered) allowed to explicitly address the question of the effect of the spatial scale upon metric’s contribution to the model performance. The impact of the spatial scale was very clear in both Solferino and Tagon as shown in Figs. 2 and 3. These graphs revealed that the VIP of some metrics changed dramatically according to the buffer size considered. In Solferino, for instance, the importance of the edge density (ED) of the shrubby clearcuts was maximum for buffers of 200 m and tended to decrease regularly with increasing radii. The importance of the patch density (PD) decreased sharply with increasing buffer size and the edge density of the meadow was minimum for buffers ≥ 200 m, reaching its peak at 300 m and smoothly fluctuated afterwards (Fig. 2). Some landscape descriptors were clearly more strongly related to species richness when measured within small buffers like the edge density of the firebreaks and most of the other metrics measured at the site of Tagon (Fig. 3). The VIP of the edge density of deciduous woodlands decreased for buffer sizes ranging from 100 to 300 m and displayed a bell-shaped curve for larger scales (Fig. 3). Overall, the scale effect manifested itself for a large part of the landscape descriptors and the shape of the curves appeared as very variable according to the metric and the study site considered.

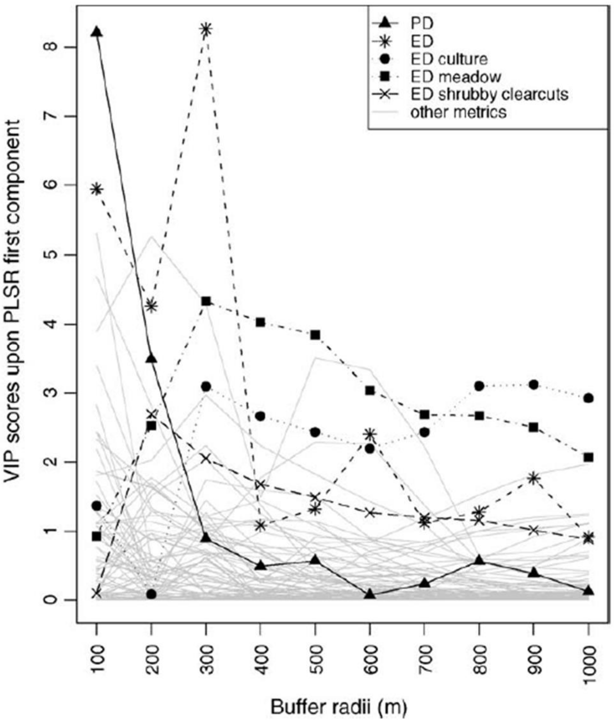

Figure 2. Output of the PLSR linking butterfly species richness and 830 metrics describing landscape along a range of spatial scales in the site of Solferino (Southwestern France). Relationship between the VIP scores of the landscape descriptors and the spatial scale at which they are computed. Changes of the VIP scores of some selected metrics according to the buffer size illustrate scale dependent fluctuations of the strength of the relationship between landscape descriptors and species richness.

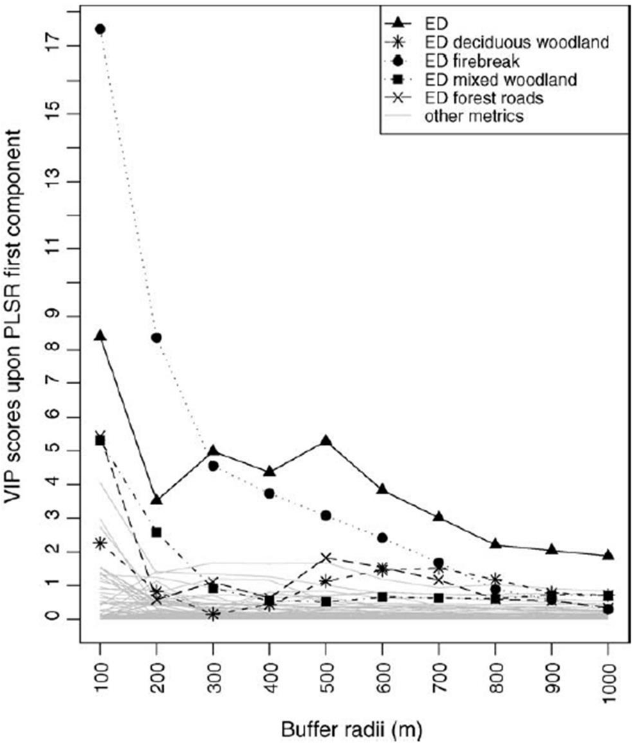

Figure 3. Output of the PLSR linking butterfly species richness and 830 metrics describing landscape along a range of spatial scales in the site of Tagon (Southwestern France). Relationship between the VIP scores of the landscape descriptors and the spatial scale at which they are computed.

Linear models linking butterfly species richness and landscape metrics

The PLSR and the VIP method led to 131 metrics of interest (i.e. VIP ≥ 1) in the site of Solferino. Since the number of objects was lower, it was impossible to use the classical regression models and we consequently used a VIP threshold of 2 which led to 17 explanatory variables. Table 3 shows the results of the models fitted for the habitat-centered richness in Solferino and Tagon. The models were significant in both cases and the proportion of explained variance (adjusted R^2) ranged from 16% to 41% in Tagon and Solferino, respectively (Table 3). The number of landscape metrics that were finally retained through the stepwise fitting was small and consisted of only one metric (the edge density of firebreaks) in the case of Tagon. In Solferino the species richness was correlated to the patch density of forest roads and of cultures, and edge density of hedges. The scales of importance as represented by the buffer sizes varied from 100 to 300 m according to the landscape metrics considered. The edge density (ED) was the only landscape level metric correlated to species richness (Solferino).

Table 3. Linear models linking landscape metrics and butterfly species richness in 2 sites in the ''Landes de Gascogne'' (Southwestern France). The habitat-centered richness (see text for details) was linearly related to various landscape metrics measured at different spatial scales. Acronym indicates the label of the landscape metrics following McGarigal et al. (2002). C and L respectively stands for class and landscape level metrics. Land-use corresponds to the landscape class name. Buffer radius indicates the radius of the circular area used to compute the landscape metrics.

	Adjusted R^2	*P*	Acronym	Level	Land-use	Buffer radius (m)	*P*
Solferino							
Habitat centered richness	0.407	0.0024					
			ED	L	-	300	0.022
			PD	C	Forest Road	100	0.031
			PD	C	Culture	100	0.035
			ED	C	Hedge	300	0.030
Tagon							
Habitat centered richness	0.156	0.018					
			ED	C	Firebreak	100	0.024

Discussion

Correlates between butterfly species richness and landscape metrics

The results reported in this work show the existence of a clear statistical correlation between butterfly species richness and certain landscape descriptors i.e. metrics. There is a wealth of literature dealing with the mechanisms at work in the community landscape relationships (see Dunning et al., 1992, and references therein). Species richness at one place can be affected by the presence and extent of patches of species rich habitat in the surroundings through the so-called ''vicinism'' or ''mass effect'' (Zonneveld, 1995). In this situation a flow of individuals originates from species rich habitat patches and allows the presence of species in neighboring habitats where they are not self-maintaining (Shmida and Wilson, 1985). This corresponds to the ''spillover effect'' by which species can be maintained in unsuitable habitat patches in the framework of source–sink dynamics (Holt, 1997). Other ecological processes affecting communities are landscape complementation and landscape supplementation (Dunning et al., 1992) that occur when individuals move to use non-substitutable or substitutable resources located in different patches. Most butterfly species use complementary resources and therefore the latter processes are likely to shape their communities and affect species richness.

The presence of species in a patch depends on the quality of the patch and on the surrounding landscape (Dauber et al., 2003). In this study we focused on landscape effects by fitting our model on the habitat-centered richness. In the site of Tagon the results clearly emphasized the importance of the firebreaks. The edge density of this habitat in the surroundings of the sampling sites affected the species richness. Interestingly, the multiscale approach adopted here indicated that the near surroundings had the strongest impact with higher correlation for buffers of 100 m radius. Firebreaks constitute rich habitats and as such sampling points corresponding to that land-use harbored the highest biodiversity (see a detailed discussion in van Halder et al., 2008). In the present study, we showed that this land-use also affected species richness when located in the vicinity of the sampling locations (at least in the close neighborhood i.e. buffers of 100 m). Firebreaks are particularly rich mostly because they are characterized by a more diversified herbaceous vegetation hence more diverse flowering species (the nectar is an important resource for adult feeding of various butterfly species) as well as more host-plants (important for larval development) (van Halder et al., 2008). The effect was maximal at small distances (100 m) but remained high for distances up to several hundred of meters (Fig. 3). The species that inhabit firebreaks and contribute to species richness of other, very different habitat types (e.g. deciduous forest patches), may mostly be found at the edges of these patches where local microclimatic conditions are more similar to that of firebreaks. Such a pattern would suggest a typical mass effect and could be properly examined in future analyses.

The data collected at the site of Solferino showed that richness was correlated to landscape edge density. This suggested that a certain level of habitat fragmentation affected butterfly species richness possibly due to increased availability of herbaceous strips along stand edges. Other metrics of significance included patch density of forest roads and cultures as well as edge density of hedges measured within buffers of 100 or 300 m. This result again suggested that open habitats or at least herbaceous strips along stand edges affected butterflies. The main difference between our study sites is that Solferino only featured a very low amount of firebreaks. This may explain the between-site differences in species richness and community structure as well as the discrepancies in the fitted models. On the other hand, it must be noted that our results showed the importance of landscape metrics that measure landscape fragmentation (edge density, patch density) in both study sites.

Scale effects

An important result of our study was the critical effect of the spatial scale at which the landscape is quantified upon our perception of landscape–biodiversity relationships. In the case of butterflies, various studies examined this relationship using different buffer sizes but led to contradictory results (Bergman et al., 2004; Krauss et al., 2003; Weibull et al., 2000). This can be explained by the diversity of ecological processes that tune the local values of species richness and the fact that they take place at various spatial and temporal scales and highly vary in function of local and historical contingencies (Belyea and Lancaster, 1999). As a consequence there is probably no a priori or general spatial scale that could be well adapted to a given taxon. The changes in the level of metrics correlation with biodiversity according to the size of the buffer was dramatic in our study. Previous studies that used different buffer sizes usually compared the performances of each buffer size (Dauber et al., 2003) whereas we identified the scale at which each metric is the most distinctly linked with species richness. The difference is essential if we consider that the importance of the metrics change dramatically and a priori unpredictably with scale. Figs. 2 and 3 clearly illustrate that there is no unique (single) buffer size for which all the metrics exhibit their best relationship with species richness. We argue that this is the manifestation of the diversity of the processes that are responsible for community dynamics as well as the multiple scales at which they act. Short-range scale effects may imply processes like mass effect or habitat complementation/supplementation. Relationships between species richness and landscape metrics quantified at larger spatial scales may rather involve other processes like metapopulation dynamics (Holt, 1997). In this study, the correlation between landscape metrics and butterfly richness was in general higher for small buffers which suggested that short-range processes were more important than long-range processes. This may be explained by the fact that our study sites are rather homogeneous (monospecific pine plantation forest) with all land-uses hosting butterflies. This is different from landscapes constituted by alternate patches of habitat and non-habitat where long-range processes like metapopulation dynamics may prevail.

Statistical issues

An important aspect of landscape analysis lies in that landscape description often involves a large number of partially redundant and strongly interrelated metrics (Cushman et al., 2008). In the type of studies we carried out, explanatory variable redundancy may be troublesome in the multiple stepwise regressions (Graham, 2003). Many problems could be avoided by selecting metrics on the basis of their universality and consistency (Cushman et al., 2008) thereby reducing the number of explanatory variables. However, using a range of buffer sizes necessarily leads to redundancy. We dealt with that problem by using the PLSR, a multivariate tool that is common in chemometrics albeit still rarely used in ecology. The PLSR is not impaired by collinear explanatory variables and as such ideally suits our needs. Another advantage is that PLSR allows to handle data sets that have more descriptors than objects which is likely to occur when numerous metrics are computed with numerous landscape classes. We believe that PLSR is a very promising approach in the field of landscape description because metrics are intrinsically redundant and often constitute very large data sets with more variables than samples. Our results indicate that the outputs of the PLSR can be used to identify those metrics that are the most consistently linked to the response variable and then other, additional data treatments can be done with that reduced set of explanatory variables.

Landscape as indicator of butterfly species richness

By working on the habitat-centered species richness we accounted for the average habitat type effect but our models could be possibly improved by adding ecological information about habitat quality. This can be done by adding plot scale variables like e.g. understorey vegetation descriptors. Van Halder et al. (2008) showed that a significant part of butterfly community variation was linked to understorey vegetation (Collinge et al., 2003). In their study, Dauber et al. (2003) showed the clear prevalence of habitat descriptors upon landscape descriptors and that the latter variables alone performed poorly as predictors of biodiversity. However, our multiscale approach allowed to built simple and significant models which may be improved by adding local descriptors of habitats. The selected landscape metrics differed according to the site considered and this can be explained by differences in the landscape composition (Solferino notably lacked firebreaks). In order to find indicators that are more generally applicable one could search landscape metrics that are related to species richness in both sites. In our landscapes some degree of fragmentation seemed to affect species richness and metrics like patch or edge density may be correlated to species richness in both sites. More generally, the feasibility of general indicators of biodiversity on the basis of landscape metrics alone remains an open question. The first point is to determine to which extent one or a few taxa can be taken as surrogates for the overall biodiversity. Various studies indicated that such surrogates are rarely found (Chase et al., 2000; Wolters et al., 2006). Our results showed that if such a group was identified, a multiscale approach could reveal the best landscape predictors. Since landscape metrics are always redundant to a large extent one may consider dropping a certain metric and adding another one, with a weaker relationship with the response variable but more easily measurable, universal or consistent (Cushman et al., 2008) for the sake of feasibility. It must be noted that our results and conclusions are highly dependent on the classification scheme used to elaborate the landscape maps. In other words, the definition of the land-use types has an extremely strong influence on the result of the landscape analysis (Turner et al., 2001) hence upon our perception of the landscape–butterfly richness relationships. Because inter-taxa species richness correlation is generally low (Wolters et al., 2006), future indicators may integrate different taxonomic groups, different habitat descriptors and allow for a multiscale landscape matrix description. Another point to consider in future research is that focusing on the total species richness may not be the best strategy. Species richness encompasses very different elements amongst which very common, rare or endangered species. These taxa obviously do not have the same value for conservation purposes which is often why indicators of biodiversity are needed (Pearman et al., 2006). Locally rare species can be very numerous (Novotnỳ and Basset, 2000; Rossi et al., 2006) and their presence is likely to be partly explained by mass effects (Novotnỳ and Basset, 2000). Therefore, using a modified value of species richness including a correction term weighting for the presence of rare species (Colwell and Coddington, 1994) may be a promising approach.

Conclusions

The present study revealed strong effects of the spatial scale at which landscape metrics are computed upon the outputs of correlative analyses aiming at relating butterfly species richness and landscape composition and structure. The consequences of these results are particularly important when searching for landscape metrics correlated to biodiversity with the aim of elaborating biodiversity indicators.

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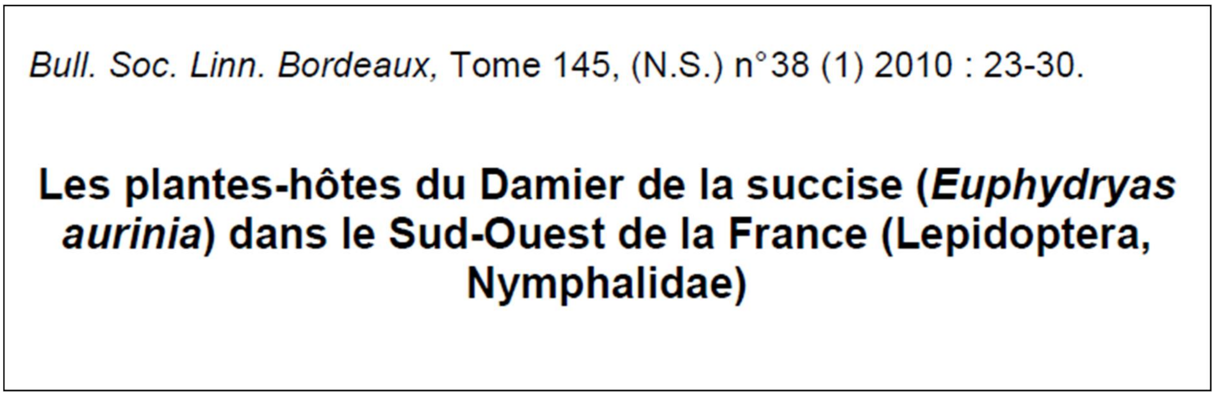
Annex 2 : Les plantes-hôtes du Damier de la succise (*Euphydryas aurinia*) dans le Sud-Ouest de la France (Lepidoptera, Nymphalidae)

Chenille du Damier de la succise (*Euphydryas aurinia*) sur succise



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Les plantes-hôtes du Damier de la succise (*Euphydryas aurinia*) dans le Sud-Ouest de la France (Lepidoptera, Nymphalidae)

Les plantes-hôtes du Damier de la succise (*Euphydryas aurinia*) dans le Sud-Ouest de la France (Lepidoptera, Nymphalidae)

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Résumé - Dans le Sud-Ouest de la France, *Euphydryas aurinia,* un papillon de jour protégé, colonise principalement deux types d’habitats : des milieux herbacés humides et des pelouses sèches. Les plantes-hôtes généralement admises pour les chenilles sont respectivement *Succisa pratensis* pour le premier type d’habitat et *Scabiosa columbaria* pour le second. Nos observations, réalisées entre 2005 et 2009 dans la partie ouest du département de la Gironde, ont montré l’utilisation fréquente d’une autre plante-hôte : *Lonicera periclymenum*. Cette partie de la Gironde est principalement occupée par des plantations de pins maritimes et les nids de chenilles ont été observés dans des coupes rases et des pare-feux dominés par la Molinie et en bordure des peuplements de pins.

Mots-clés - *Euphydryas aurinia*, *Lonicera periclymenum,* plante-hôte, plantations pin maritime, Gironde (33).

Summary - In the south-west of France the protected butterfly *Euphydryas aurinia* occurs mainly in two habitat types: humid herbaceous vegetations and dry grasslands, where it is supposed to use *Succisa pratensis* and *Scabiosa columbaria* respectively as larval host-plants. Our observations from 2005 to 2009 in the western part of the Gironde department showed the frequent use of another host-plant: *Lonicera periclymenum*. This part of the Gironde is covered by even-aged maritime pine stands. Larval nests were mainly observed in *Molinia caerulea* dominated clearcuttings and firebreaks, and at pine stand edges.

Key words: *Euphydryas aurinia*, *Lonicera periclymenum*, host-plant, maritime pine plantations, Gironde department.

Introduction

Le Damier de la succise (*Euphydryas aurinia* (ROTTEMBURG, 1775)) présente une vaste aire de répartition, qui s'étend du Maghreb, de la Péninsule ibérique et de l'Irlande à l'ouest jusqu'à la Russie et à la Corée à l'est. L'espèce est citée de la majorité des pays européens mais un déclin rapide et marqué est constaté dans beaucoup d'entre eux (VAN SWAAY & WARREN, 1999). Elle est, pour cette raison, inscrite dans l'annexe 2 de la Directive Habitats (Directive 92/43/CEE du 21 mai 1992) et bénéficie d'une stricte protection en Europe (Convention de Berne du 19 septembre 1997) et en France (Arrêté du 22 juillet 1993).

La conservation d'une espèce menacée implique une bonne connaissance de sa biologie et de ses exigences écologiques, de façon à prendre des mesures adéquates de protection et de gestion des milieux. L'identification des plante-hôtes utilisées par les chenilles est, bien sûr, primordiale pour mieux comprendre les exigences de l'espèce par rapport à son habitat.

Il nous semble qu'il existe des lacunes dans la connaissance des plantes-hôtes utilisées par *E. aurinia* dans le sud-ouest de la France. Cet article rend donc compte de nos observations relatives aux plantes-hôtes utilisées par le Damier de la succise en Gironde. Elles ne sont pas exhaustives et méritent d'être enrichies dans les années à venir.

Biologie et cycle de vie

Le Damier de la succise est une espèce univoltine qui vole, en Aquitaine, de la fin avril à la mi-juin. La femelle dépose pendant cette période, au revers des feuilles de la plante-hôte, un premier amas de plusieurs centaines d'œufs. Les éventuelles pontes suivantes sont moins importantes. Les chenilles, grégaires, consomment les feuilles de la plante-hôte et s'abritent dans un nid collectif de soie, déplacé au fur et à mesure de la consommation des feuilles. La diapause hivernale débute en fin d'été alors que les chenilles ont atteint le quatrième stade larvaire et ont tissé un nid de soie assez dense. Au printemps suivant, elles reprennent leur activité et on peut alors les observer prendre un bain de soleil sur la végétation. Elles se dispersent ensuite et poursuivent, seules, leur développement jusqu'au sixième stade larvaire (DUPONT, 2001). Lors de la nymphose, la chrysalide est suspendue dans la végétation basse.

Sous-espèces et plantes-hôtes

E. aurinia est une espèce très variable, pour laquelle beaucoup de sous-espèces et de formes ont été décrites. Le taxon peut être considéré comme une super-espèce en voie de différenciation avec des taxons géographiquement distincts qui utilisent des plantes-hôtes différentes (LAFRANCHIS, 2000a). Certains auteurs ont séparé le taxon en trois espèces : *E. aurinia* (la plus grand partie de l'Europe), *E. beckeri* (Péninsule ibérique) et *E. debilis* (Alpes et Pyrénées) (KUDRNA, 1986).

En ne retenant qu'une seule espèce, on rencontre alors en France cinq sous-espèces utilisant des plantes-hôtes appartenant aux familles des Dipsacaceae, Caprifoliaceae, Valerianaceae et Gentianaceae, toutes caractérisées par la présence de composés protecteurs, des glucosides iridoïdes (DESCIMON *et al*., 2001) :

- la sous-espèce nominale *aurinia* a une vaste répartition et est répandue sur la majeure partie de la France et de l'Europe. Elle vit en France surtout sur *Succisa pratensis* MOENCH, localement sur *Scabiosa columbaria* (L.) et *Knautia arvensis* (L.) COULT., rarement sur *Cephalaria leucantha* (L.)

SCHRAD. ex ROEM. & SCHULT., et exceptionnellement sur chèvrefeuilles (*Lonicera etrusca* SANTI dans le Lot) (LAFRANCHIS, 2000a ; WARREN, 1999). LAFRANCHIS (2000b) précise que les observations effectuées dans le Lot sur *C. leucantha* et *L. etrusca* ont été faites au printemps,

- la sous-espèce *provincialis* (Provence et Languedoc) vit sur *C. leucantha*, parfois sur *Centranthus angustifolius* (MILL.) DC.*, C. ruber* (L.) DC. et *L. etrusca* après hibernation (LAFRANCHIS, 2000a),
- les sous-espèces *debilis* (en altitude dans les Alpes) et *pyrenes-debilis* (en altitude dans l'Est des Pyrenées) vivent sur *Gentiana alpina* VILL*, G. acaulis* L. et *Succisa pratensis* (LAFRANCHIS, 2000a ; DUPONT, 2001)*,*
- la sous-espèce *beckeri* (Pyrénées-Orientales) vit sur *L. etrusca* (LAFRANCHIS, 2000a ; DUPONT, 2001). Les papillons qui volent en Espagne, des Pyrénées et monts Cantabriques jusqu'à l'Andalousie, appartiennent également à la sous-espèce *beckeri* (TOLMAN & LEWINGTON, 1999). Les plantes-hôtes sont différents chèvrefeuilles : *L. periclymenum L. hispanicum, L. etrusca* et *L. implexa* AITON (WARREN, 1999).

La liste des plantes-hôtes des différentes sous-espèces reste néanmoins à compléter et à différencier régionalement (WARREN, 1999). Des études génétiques effectuées sur des populations françaises ont montré une structuration géographique avec des groupes distincts en Provence, en Languedoc et dans le sud-ouest. Par contre, les populations qui vivent sur *S. pratensis* au sein de ces groupes dans l'Est de la France sont proches des populations du Sud-Ouest. Localisation géographique et spécialisation trophique influencent donc la structure génétique des populations (DESCIMON *et al.*, 2001).

Dans la plus grande partie de la France, y compris l'Aquitaine, vole donc la sous-espèce *E. aurinia aurinia*. La succise (*S. pratensis)* est considérée comme sa plante-hôte principale dans la région atlantique (WARREN, 1999). Selon MAZEL (1982), la sous-espèce *aurinia* vit sur *S. pratensis* et une forme xérophile de cette sous-espèce sur *S. columbaria* et *K. arvensis.* Cette forme xérophile constitue probablement une sous-espèce distincte (MAZEL, 1982). En Limousin, DELMAS *et al*. (2000) distinguent également les deux écotypes d'*E. aurinia* avec des plantes-hôtes différentes. L'écotype des prairies et landes humides utilise *S. pratensis* comme plante-hôte et l'écotype des prairies sèches, chemins forestiers et clairières utilise *S. columbaria.* En Loire-Atlantique et Vendée, *S. pratensis* semble la principale plante-hôte d'*E. aurinia* (PERREIN & GUILLOTON, 2001). Il existe néanmoins une observation en Loire-Atlantique de chenilles au dernier stade larvaire en train de consommer *L. periclymenum* près d'une prairie à *S. pratensis* (GUILLOTON, 1997 *in* PERREIN & GUILLOTON, 2001).

Répartition en Aquitaine

En Aquitaine, *E. aurinia* est citée de tous les départements (LAFRANCHIS, 2000a). En Gironde, elle est largement répandue et peut présenter des effectifs importants. Elle est fréquente dans les landes (surtout landes humides), dans les pare-feux enherbés, les bords de pistes et les prairies humides du massif forestier des Landes de Gascogne, mais aussi sur les pelouses sèches et humides de l'Entre-Deux-Mers.

En Dordogne, l'espèce est assez commune et répandue dans tout le département, sauf le secteur cristallin. Les deux écotypes (xériques et hygrophiles) semblent assez bien représentés (DELMAS & DESCHAMPS, 2008). Par contre, nous disposons de très peu de données pour le département des Landes, malgré des prospections pendant la période de vol dans différents secteurs.

Les données disponibles sur l'utilisation de plantes-hôtes en Aquitaine sont rares et concernent surtout des observations non publiées de naturalistes.

Succisa pratensis est en Gironde considérée comme la principale plante-hôte. Les chenilles ont été observées sur cette plante dans différents secteurs de ce département (communes de Bernos-Beaulac, Blanquefort, Lapouyade, Léognan, Pugnac, Saint-Morillon et Saint-Vivien-de-Blaye, communication personnelle de Sébastien Labatut).

En Dordogne, les chenilles sont également majoritairement contactées sur *S. pratensis* (communes de Agonac, Azerat, Bassillac, Beauronne, Bergerac, Echourgnac, Eymet, Ginestet, St-Germain-du-Salembre). Des individus appartenant à l'écotype xérique et utilisant *S. columbaria* ont aussi été observés, pour l'essentiel dans le quart nord-ouest du département (communes de Allemans, Mareuil, La Rochebeaucourt et Argentine, Tocane-St-Apre, Vieux-Mareuil). Sur la commune de Ginestet, des chenilles ont été observées à plusieurs reprises, consommant *Plantago lanceolata* L. et ce, malgré la présence de *S. pratensis*. Des chrysalides étaient présentes à proximité immédiate et sur *P. lanceolata* ; l'émergence d'imagos viables a pu être confirmée (les donnée relatives à la Dordogne ont été recueillies par Mikaël Paillet).

En Gironde et Dordogne, les observations mettent donc en évidence la présence de deux écotypes avec, pour plantes-hôtes principales, respectivement *S. pratensis* et *S. columbaria*. Lors de nos prospections dans la partie girondine du massif forestier des Landes de Gascogne, nous avons pourtant observé des adultes en nombre important sur des pare-feux, le long des pistes ou dans les peuplements de pins maritimes où ces deux plantes sont absentes ou peu présentes ; nous nous sommes donc interrogés sur les plantes-hôtes réellement utilisées par l'espèce dans cette partie du département.

Recherche des plantes-hôtes

Pour déterminer les plantes-hôtes d'une espèce, il est possible de suivre les femelles et d'attendre qu'elles pondent. L'observation d'une femelle en train de pondre, ou la découverte d'une ponte, peut généralement fournir une bonne indication sur la plante-hôte utilisée, mais ne suffit pas comme preuve. Il est en effet établi que, pour plusieurs espèces de Rhopalocères, les femelles peuvent pondre sur d'autres plantes à proximité de la plante-hôte. La découverte de chenilles âgées sur certaines plantes a également certaines limites parce que les chenilles matures sont souvent moins exigeantes par rapport au choix de la plante consommée que les jeunes chenilles. L'observation de jeunes chenilles avec des traces de consommation permet plus sûrement d'identifier la plante-hôte d'une espèce.

Les femelles d'*E. aurinia* pondent la plus grande part de leurs œufs en une seule fois sur la face inférieure d'une feuille. Les femelles sont alors très difficiles à repérer et l'observation des pontes est très aléatoire. Les nids de soie communautaires qui abritent les jeunes chenilles en été sont, avec un peu d'expérience, beaucoup plus faciles à trouver.

Observations relatives aux plantes-hôtes du Damier de la succise en Gironde

En 2005, nous avons observé une femelle d'*E. aurinia* en train de pondre sur *L. periclymenum* dans une clairière en forêt de feuillus à Audenge (au lieu-dit Castéra). En juillet de la même année, nous avons découvert un nid de chenilles d'*E. aurinia* sur *L. periclymenum* dans une parcelle de chêne pédonculé à Saint-Jean-d'Illac (au lieu-dit France). En 2009, dans le cadre d'un inventaire de

Rhopalocères à Caudos (Mios), nous avons d'abord observé le 16 mai une femelle en train de pondre sur *L. periclymenum* en bordure d'une parcelle de pins. Le 29 juillet, nous avons découvert, sur le même site, une quinzaine de nids de chenilles en prospectant une petite partie d'une coupe rase (surface prospectée de 30 m sur 30 m environ). Sur cette coupe rase, une lande humide dominée par la molinie s'est développée et, en l'absence d'entretien au cours des dernières années, des bourdaines et chênes pédonculés s'y sont installés. Les nids de soie se trouvaient tous sur *L. periclymenum,* qui se développe au sol parmi la molinie. Ils intégraient fréquemment d'autres plantes mais, dans tous les cas, nous avons pu constater que les feuilles de *L. periclymenum* étaient consommées. Suite à cette découverte, nous avons intensifié nos prospections dans d'autres secteurs et des nids de chenilles d'*E. aurinia* sur *L. periclymenum* ont été découverts à Louchats (lieu-dit les Abourdeyres), à Avensan (lieu-dit la Herreyre) et à Arsac (lieu-dit Chemin de Ludon). Nous avons cependant également trouvé des nids sur *S. pratensis* et *S. columbaria* (à Salles).

Photo 1. Femelle d'*Euphydryas aurinia* en train de pondre sur *Lonicera periclymenum* (Audenge, 20 mai 2005). Photo : Inge van Halder.

Ces observations effectuées dans plusieurs communes et sur plusieurs années montrent clairement que *L. periclymenum* n'est pas une plante-hôte accidentelle pour cette espèce dans notre département. Dans la partie girondine du massif forestier des Landes de Gascogne, elle semble au contraire essentielle et sa grande fréquence explique assurément la présence de populations importantes de ce papillon dans des secteurs où *S. pratensis* et *S. columbaria* sont absentes ou rares. L'utilisation fréquente et non occasionnelle de *L. periclymenum* comme plante-hôte est une donnée essentielle qui nous permet de mieux appréhender les habitats sélectionnés par cette espèce protégée et de préciser les mesures de gestion conservatoire qui lui sont favorables.

Des prospections plus systématiques seront toutefois nécessaires pour évaluer l'importance des différentes plantes-hôtes en fonction des milieux en Gironde et dans les autres départements aquitains, puis pour appréhender le rôle de ces différents types d'habitats et des plantes-hôtes associées dans la survie d'*E. aurinia* en Aquitaine. On peut ainsi supposer que des plantes-hôtes habituelles de l'espèce comme *S. pratensis* ou *S. columbaria* qui se développent fréquemment dans des secteurs fauchés très régulièrement (bords de route, prairies…) ne permettent pas, dans certains milieux et du fait de cette gestion trop intensive, de garantir la pérennité du Damier de la succise. Les pare-feux et les coupes rases proches où se développe *L. periclymenum* constitueraient alors des milieux refuges, permettant à l'espèce de se maintenir et fournissant les imagos susceptibles de coloniser les zones à nouveau favorables.

Il nous semble donc primordial, pour répondre à ces différentes questions, de poursuivre des prospections ciblées sur les plantes-hôtes du Damier de la succise, essentiellement de la mi-juillet à la mi-août, période qui semble la plus favorable à la découverte des nids de soie communautaires (dès fin août, les chenilles s'installent dans leurs nids d'hiver et les restes des nids de soie ne sont presque plus visibles sur le chèvrefeuille) tout en rappelant qu'*E. aurinia* est une espèce protégée et qu'il est impératif de ne perturber ni les chenilles ni les milieux.

Photo 2. Nid de chenilles d'*Euphydryas aurinia* sur *Lonicera periclymenum* à Caudos (commune de Mios, 29 juillet 2009). Photo : Bruno Jourdain.

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Conservation des communautés de papillons de jour dans les paysages forestiers hétérogènes : effets de la qualité, de la diversité et de la fragmentation des habitats

Alors que la superficie des forêts de plantation continue d'augmenter dans le monde, leur contribution à la conservation de la biodiversité reste controversée. L'objectif de cette thèse est d'identifier les facteurs clés, à la fois au niveau de l'habitat local et à celui du paysage, qui influent sur la diversité des papillons de jour dans les paysages en mosaïque dominés par des plantations de pins.
Les communautés de papillons ont été échantillonnées en lisière et à l'intérieur de plantations de pin maritime, pare-feux, ripisylves et fragments de forêts de feuillus variant par la taille et le degré d'isolement spatial. Les traits biologiques et écologiques des papillons ont été liés aux caractéristiques de l'habitat et aux variables paysagères.
Les éléments les plus importants pour la conservation des papillons dans les paysages dominés par les plantations de pins sont les habitats semi-naturels: forêts de feuillus, pare-feux et lisières. Les ripisylves se révèlent être les plus riches en papillons forestiers, abritant des espèces spécialisées. Les pare-feux hébergent deux fois plus d'espèces que les autres types d'habitats et sont importants pour la conservation de plusieurs espèces menacées. Toutefois les plantations de pin ne sont pas vide de papillons. La qualité de l'habitat, notamment la présence de plantes hôtes, est le facteur le plus déterminant de la composition des communautés de rhopalocères. La composition et la configuration du paysage ont également une influence importante sur la diversité des papillons. De nombreuses espèces de papillons ont été observées dans plusieurs types d'habitat suggérant que la complémentation et supplémentation des ressources soient des processus clés pour maintenir la diversité des papillons dans les paysages forestiers hétérogènes.

Mots clés : biodiversité, communautés, complémentation, lisière, forêt de plantation, fragmentation, isolement, milieux semi-naturels, surface d'habitat, traits de vie, richesse spécifique, supplémentation.

Conservation of butterfly communities in mosaic forest landscapes: effects of habitat quality, diversity and fragmentation

While the area of plantation forests continues to increase worldwide, their contribution to the conservation of biodiversity is still controversial. The aim of this thesis is to identify key habitat and landscape factors that drive butterfly diversity in mosaic landscapes dominated by pine plantations.
Butterfly communities were sampled at edges and interiors of five successional stages of pine stands, in firebreaks, riparian forests and in deciduous woodlands varying in fragment size and isolation. Biological and ecological traits of butterflies were related to habitat patch attributes and to landscape composition and configuration.
The results highlighted the critical importance of semi-natural habitats for butterfly conservation in pine plantation mosaics, i.e. deciduous woodlands, firebreaks and edges. Riparian forests were especially rich in forest butterfly species, harboring specialized species with both narrow habitat and thermal ranges. Firebreaks had twice as many species as other habitat types and were of conservation value for several threatened butterfly species. Our results also showed that pine stands were not 'free of butterflies'. Habitat quality, particularly the presence of host plants, was the most important driver of butterfly community composition. Landscape composition and configuration also influenced butterfly diversity. Many species used more than one distinct habitat type, suggesting that resource complementation and supplementation are important mechanisms of butterfly diversity persistence in pine plantation mosaics.

Keywords: biodiversity, community, complementation, ecological traits, edge-effects, fragmentation, habitat size, isolation, plantation forest, semi-natural habitats, species richness, supplementation