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Habitat from a butterfly's point of view:

How specialist butterflies map onto suitable resources.

Ph-D thesis

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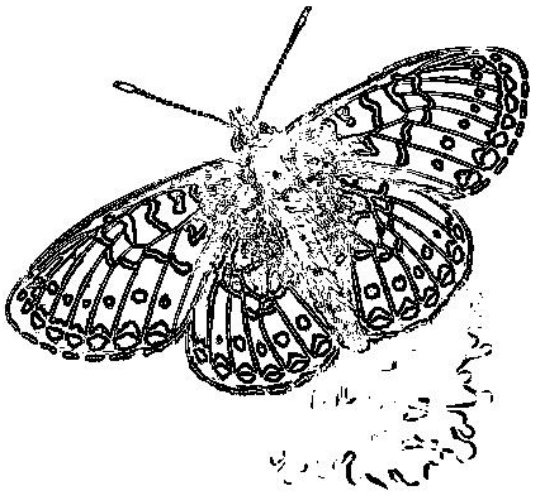

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General introduction

General introduction: illustration cover
and pictures in Figures i.8, i.9, i.10, i.11 and i.12 by Camille Turlure

Aerial pictures in Figure i.4 : Région wallone
http://cartographie.wallonie.be/NewPortailCarto

The biodiversity crisis and the need to preserve habitat

Current extinction rate of species by far exceeds historical ones and reveals that we face a major biodiversity crisis (Western 1990; Morris 1995; Olson *et al.* 2002). Human development and biodiversity are closely connected; humankind receives products and services of biodiversity and our (over)use has in turn a strong impact on biodiversity. Nowadays, biodiversity is beyond any shadow of doubt threatened by many processes: mostly by fragmentation, loss and degradation of ecosystems (Fischer 2000; Fahrig 2003; Watling and Donnely 2006; Ewers and Didham 2007), loss of connectivity between habitats (Saunders, Hobbs and Margules 1990; Kruess and Tscharntke 1994), abandonment of traditional agricultural management in semi-natural ecosystems (Pykälä 2000; Svenning 2002), introduction of invasive species (Gurevitch and Padilla 2004) and global warming (Walther *et al.* 2002; Beaumont *et al.* 2007). Moreover, the speed and magnitude of these changes enable little flexibility for organisms to respond in our modern landscapes, impacts becoming more significant for species with low adaptability and/or low mobility.

This biodiversity crisis has been considered seriously by the international community since the Rio Convention in 1992 and resulted in a global policy decision taken at the UN Summit in Johannesburg in 2002 to "significantly reduce the loss of biodiversity by 2010". But the conservation and restoration of biodiversity is a hard target to reach because there is no ideal or absolute state of biodiversity to maintain everywhere (Terrasson 1994; Génot 2003). There are also great

differences among European countries in public involvement, political and financial supports for biodiversity conservation, available data on species status and distribution. To stop the severe loss of biodiversity, political decisions have been taken in Europe from the beginning of 1980 (Margules and Pressey 2000): application of the «Birds Directive » and «Habitats Directive» (enacted in 1979 and 1992, respectively) lead to protected areas in the European network called Natura 2000 (McLean, Wight and Williams 1999; Jongman and Pungetti 2004; Jongman, Külvik and Kristiansen 2004). By listing at the same time priority habitats and species, this network jointly used two approaches: the first is a "sanctuary approach", based on the positive relationship between site area and species diversity (May 1975a; Connor and MacCoy 1979; Higgs and Usher 1980; Fahrig 2001) and the second is a "population approach" built on the conservation of populations of often threatened, endemic or specialist species (Shaffer 1981; Fontaine *et al.* 2007; Van Dyke 2008).

Conservation planning needs to effectively locate and preserve sites that accommodate remnant populations of threatened species. But this approach is not enough. To be efficient, conservation planning has also to ensure that preservation means that: (i) each protected area contains the ecological resources needed to provide population viability of each species at the local scale (Richter et al. 1997); (ii) all protected areas form a functional network at the regional scale, which guarantees the process of dispersal (and associated gene flow) and long term persistence of metapopulations (Jongman and Pungetti 2004; Wiegand, Revilla and Moloney 2005; Pressey *et al.* 2007); and (iii) management

actions needed to keep sites under favourable conditions are identified and applied (Higgs 1997).

At the local scale, habitat and population are closely connected concepts. Then, in the context of population conservation and habitat management, underlying and understanding the relationships between habitat characteristics and population distribution and abundance are fundamental (Krebs 1972; Jorge Soberon 1986) (i) to assess impact of landscape and climate changes and (ii) to develop conservation and restoration strategies. The more precisely resources needed by an organism are recognised and measured, the clearer it will become how they are affected by climate and landscape changes (Thomas *et al.* 2001b). Hence, to preserve populations of (endangered) species, it is absolutely necessary to define and conserve their habitats (Western 1990). But what exactly is the habitat of a species?

A history of habitat definitions

Many ecological studies focused on the effect of habitat fragmentation on metapopulation dynamics and survival at the regional scale. Effects at smaller scale, such as the effect of local habitat quality, have often been neglected, or habitat quality was often poorly defined (i.e. more based on assumption/subjective estimation than on reliable measures). Nevertheless, it has been demonstrated that habitat quality can play a crucial role in local population persistence, which could overrule the effect of habitat fragmentation (Dennis and Eales 1997; Thomas *et al.*

2001b; Anthes *et al.* 2003). As explained by Southwood (1977), ecology comes from the Greek word "Oikos" meaning household, or habitat. According to him, this implies that ecologists "should devote some attention to the house or habitat of the population or community they are studying" (p 337). Already 30 years ago, this suggested that habitat should be viewed as a fundamental unit and a key concept in ecology and for biodiversity conservation. Given the high frequency of the use of this concept in the literature, it should also be an "unquestioned paradigm" (Mitchell 2005), which means that it would be used and accepted by the entire scientific community (Kuhn 1996). Although it is considered as a paradigm, several definitions have been proposed in the literature, making this concept unclear, "flawed or not complete", and often offering a reductionist view on this complex concept (Haskel 1940; Mitchell 2005). Indeed, in 82% of the papers reviewed by Hall, Krausman and Morrison (1997), habitat was used vaguely and imprecisely. They also noted confusion of terms while using habitat type, habitat availability, habitat quality or habitat suitability. This questions the relevance of the concept and distorts communication among scientists and between scientists and biodiversity managers. Below, we will briefly list and criticize the most commonly used definitions in ecological researches (but see Hall, Krausman and Morrison 1997; Dennis, Shreeve and Van Dyck 2003b; Baguette and Mennechez 2004; Shreeve, Dennis and Van Dyck 2004; Dennis 2004a; Mitchell 2005; Kearney 2006; Dennis, Shreeve and Van Dyck 2006a; Dennis and Hardy 2007 for more detailed discussions on this topic). As stated by Mitchell (2005, p 638), we always "need to critically evaluate the cornerstone of our believe".

The first and more common definition of the habitat refers to an identifiable locality. There is widespread belief, and it makes intuitively sense, that habitat is ***the place where an organism lives*** (Odum 1971; Morrison, Marcot and Mannan 1998). This definition cannot be viewed as wrong, but it reduces the concept to its distribution dimension and does not offer any information on the relation between habitat and population. Hence, this definition offers little meaning for conservation perspectives.

Habitat is sometimes considered as ***the environment in its physical and chemical aspects*** (Whittaker, Levin and Root 1973). Even if this definition incorporates more quantitative notions (i.e. measurable variables) than a location only, it is still a narrow and incomplete definition as abiotic components are included, whereas resources needed by an organism can include both abiotic and biotic factors (Mitchell 2005).

Habitat is regularly ***mixed up with ecosystem or vegetational association*** (Hall, Krausman and Morrison 1997). But the ecosystem, as described by Tansley (1935), is a dynamic complex composed of plant communities, animal communities and their abiotic environment, interactions between the three leading to a functional unity. While ecosystem relates to the community level, habitat is linked to population. Hence, they are two different concepts that should not be mixed up. When defining habitat as a vegetational association, it indirectly suggests uniformity of resource composition and distribution within this association. However, resources required by a species can be distributed and exploited either in a unique spatial location or widely in the

landscape, in distinct ecosystems or vegetational associations, which is particularly the case when organisms are mobile. As a consequence, definitions based on ecosystems or vegetal associations may overestimate or underestimate both the area and the amount of habitat (Vanreusel and Van Dyck 2007). This confusion again challenges the effectiveness of the habitat definition for conservation perspectives (McLean, Wight and Williams 1999). This refers more to habitat type as a notion that can serve as a useful first step to localise a species within landscapes.

According to Forman and Gordon (1986) and Ricklefs and Miller (1999), ***habitat is a particulate, invariant and homogeneous entity, a patch that contains the necessary resources and conditions for a population to persist***. This definition contains both abiotic, biotic and spatial components, but it is still a restrictive one, leading to the attractive oversimplification of the environment in "patch" and "matrix", where the matrix is viewed as a "sea of non-habitat", empty of all resources (Dennis *et al.* 2004; Dennis, Shreeve and Van Dyck 2006a). Resources never or rarely have a homogenous or constant distribution, implying that in general habitat cannot be viewed as an invariant and homogeneous entity. This was nevertheless a useful simplification to elaborate biogeography and metapopulation theories using the few model organisms that fit this definition (i.e. specialist species with low mobility and aggregated resources for which spatial dynamics of resources is assumed to be less important than spatial dynamics of populations, such as *Proclossiana eunomia* and *Melitaea cinxia*, Hanski, Kuussaari and Nieminen 1994; Schtickzelle, Le Boulengé and Baguette 2002). As only a few natural settings and systems seem to correspond to

this simplified view, this definition is inconsistent in the real complex world (Baguette and Mennechez 2004).

Kearney (2006, p 186) also noticed that "the terms 'habitat', 'environment' and 'niche' are used inconsistently, and with some confusion, within the ecological literature on species distribution and abundance modelling". But the environment is a set of abiotic and biotic conditions without any reference to a particular organism. To be functional for a given organism, a good definition should incorporate information on the species needs and their influence on individual fitness and demographic responses. A functional definition of the habitat could be derived from the ***ecological niche concept*** initiated by Grinnel (1927), completed by Elton (1927) and finally modelled by Hutchinson (1957). Ecological niche is the intersection of ranges of tolerances for the set of resources used by a species, conceived as a multidimensional space (Hutchinson 1957, **Figure i.1**). Ecological niche is quantifiable: while the niche breadth attempts to measure specialisation of an organism using the variety and the range of resources used as indicators, the niche overlap expresses the percentage of niche space shared by two or more species using the similarity of resources used by both organisms as indicator (Ricklefs and Miller 1999). Dennis, Shreeve and Van Dyck (2006) proposed that projections of the niche axis on the real space could be "a practical solution to Hutchinson's concept of a hyperdimensional niche". In this case, the two concepts become distinct but complementary: "habitat describes real ground conditions (e.g., occupied space) whereas niche formulates biological space (vectors of influential agents)". This has led to the ***resource-based definition of the habitat***.

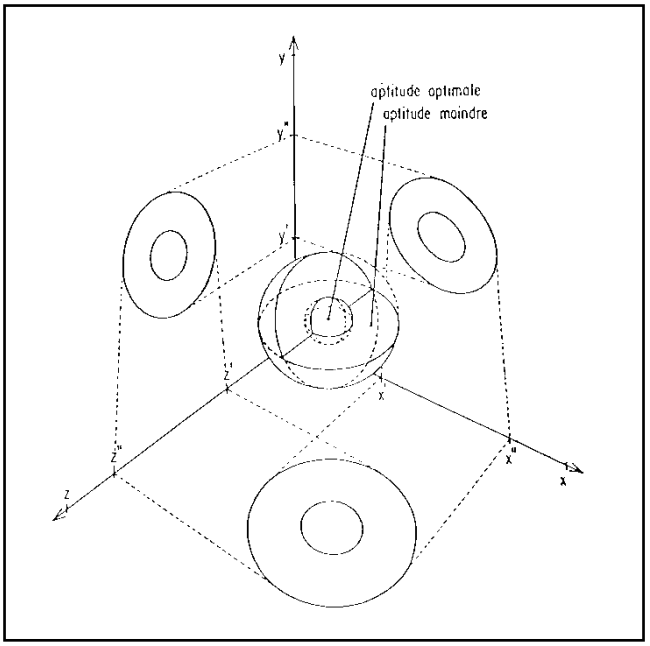


Figure i.1. Model of an hyperdimensional ecological niche in a three dimensional space and projection of this volume on two dimension plans (in Blondel 1995, from Pianka 1974).

The resource-based definition of the habitat

At such a central place in ecology, the habitat concept lacks a rigorous definition. Because such lack of precision hampers the progress in conservation biology, standard definitions of ecological terms are needed, and habitat makes no exception to that rule. Quantifying and defining habitat characteristics were required by several authors (Elton 1966; May 1975b; Hall, Krausman and Morrison 1997), taking into

account variation in space and time, i.e. habitat heterogeneity. Such variations must be related to the time scale and space use of the organism. All these characteristics are included in the alternative approach suggested by Dennis, Shreeve and Van Dyck (2003): the functional resource-based definition of the habitat. They used butterflies as model organisms to tackle this complex but widely applicable issue. Even if several definitions have been proposed and are still further used in the literature, evidence accumulates that habitat is best understood in terms of resource distributions (Dennis, Shreeve and Van Dyck 2003b; Dennis 2004b; Dennis, Shreeve and Van Dyck 2006a; Dennis and Hardy 2007). Hall, Krausman and Morrison (1997, p 175) defined habitat "as the resources and conditions present in an area that produce occupancy – including survival and reproduction - by a given organism", including migration and dispersal corridors. The definition adopted here is the following: habitat is a delimited space made of union and/or intersection of all resources (consumables and utilities) needed and influencing the fitness of the individuals of a single species population (Dennis, Shreeve and Van Dyck 2003b), producing occupancy (both survival and reproduction) (Hall, Krausman and Morrison 1997), routine individual movements assuring the link between the distinct and discontinuous resources or units of habitat (Baguette and Mennechez 2004).

Contrary to what was proposed by several authors (e.g. Hall, Krausman and Morrison 1997; Dennis, Shreeve and Van Dyck 2003b), we chose to not include corridors and enemy free space in the definition of habitat. This can be justified on several grounds. (i) Corridors are structures or particular landscape configurations that facilitate connectivity between habitats or between populations. Hence, this can be

better viewed as an attribute of the meta-habitat that allows movements of individuals within the metapopulation. (ii) Enemy free space allows reducing the pressure exerted by predators, parasites or diseases and cannot be considered as a resource (included in Dennis, Shreeve and Van Dyck 2006a): the absence of a resource is likely to lead to the absence of the organism while the absence of enemy free space is not.

Figure i.2, illustrates the definition of habitat derived from projection of the niche axes in real space for a virtual butterfly population.

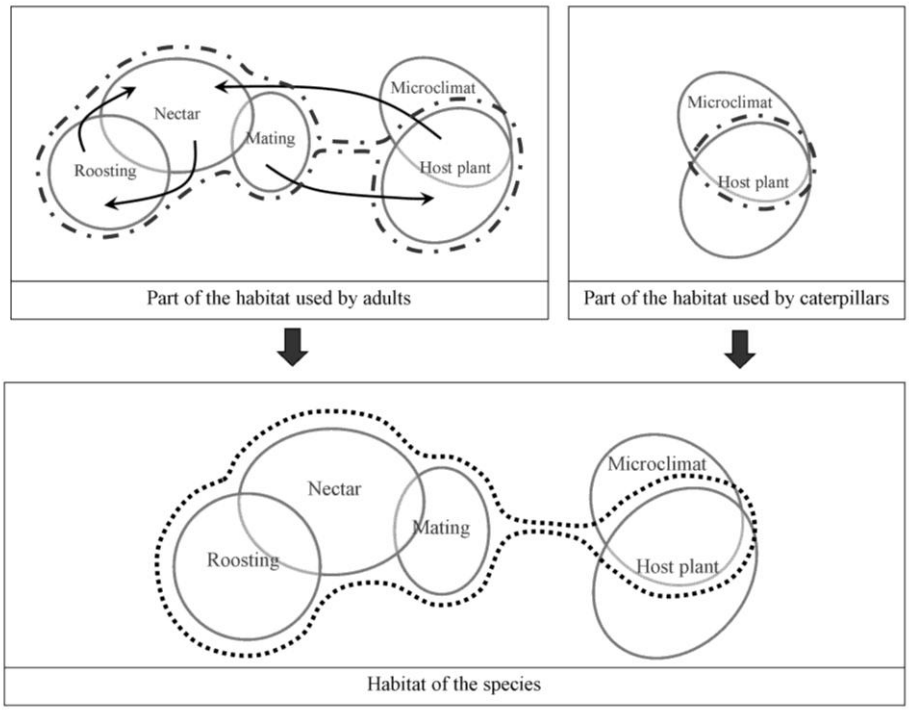


Figure i.2. Simplified representation of the habitat of a virtual butterfly population, taking into account adults and larvae requirements only. Each resource is represented by an oval grey area. Limit of the part of the habitat used by the two stages is delineated by doted and segmented lines. Black arrows represent possible movements between discontinuous resources. Habitat of the population (sum of the habitat used by caterpillars and adults) is delineated by a dotted line. (derived from figure 2 in Dennis, Shreeve and Van Dyck 2003b)

Objectives of this PhD-thesis

ᘓ General objective:

The significance of the resource-based definition has been particularly well discussed in the literature for butterflies, at least for some life stages such as adult butterflies. The importance of often neglected resources, such as roosting and mate-locating sites for adults, thermal conditions needed for caterpillars… was particularly stressed, as well as the often inappropriate distinction between habitat and matrix (Dennis 2004a). Nevertheless, the resource-based definition has rarely been tested while considering in detail the whole life cycle of an organism.

Using several butterfly species co-occurring in the same ecosystem, the main objectives of my thesis were:

(1) To define what makes up a habitat for five butterfly species in peat bogs, based on requirements of each life stage, and assess whether the resource-based definition is more appropriate than definitions based on vegetational association or host plant patches.
(2) To compare definitions of the habitat drawn for the five species and determine whether the habitat is species-specific. In other words: do the five species that co-occur in the same ecosystem or location necessarily have the same habitat?
(3) More conceptually, even if the habitat is a complex topic, with probably no single pattern, the idea is to generate a general framework, a practical guidance to recognise a species habitat.

Results from the first two objectives would help confirming or even improving the current definition.

ᔓ Scientific approach:

To reach these objectives, we introduced a two step approach based on observations of habitat use in the field (patterns) and experimental tests of organism responses under controlled conditions (processes) (**Figure i.3**). As habitat cannot be defined and mapped until we know which resources are needed and used, we searched for relationship(s) between organism presence (or abundance) and *a priori* pertinent characteristics (variables), according to butterfly biology. Because a butterfly life cycle consists of several stages, the precise identification of essential resources for eggs, larvae, pupae and adults is necessary. Then, we first measured characteristics of the individuals and the population through local presence and density of eggs, larvae, pupae and adults, total adult population size, behaviour and morphology. Secondly, we described and measured a wide array of such resources (nectar and host plant resources abundance and distribution, resting, mating and egg-laying sites, microclimatic conditions…) for the studied sympatric butterfly species. Measures of these habitat variables were done at the relevant scale for the life stages under consideration. Finally, we tested relations between organisms and habitat characteristics to model the functional habitat of each population or species.

Studies of habitat selection are often the first step in generating hypotheses about the mechanistic links between an organism and its

environment. But, observation of patterns does not mean optimal or complete utilisation of the habitat: (i) on one hand, utilisation can be limited by the choice between available conditions at the site level, (ii) on the other hand, utilisation can be underestimated simply because the population is not at maximal size (i.e., below the maximal carrying capacity). Moreover, correlations do not indicate causative relationships: pattern of use and suitability are only concordant under euchresis (Jorge Soberon 1986). Therefore, we searched for cause and effect relationships (i.e. processes) based on relations inferred from patterns.

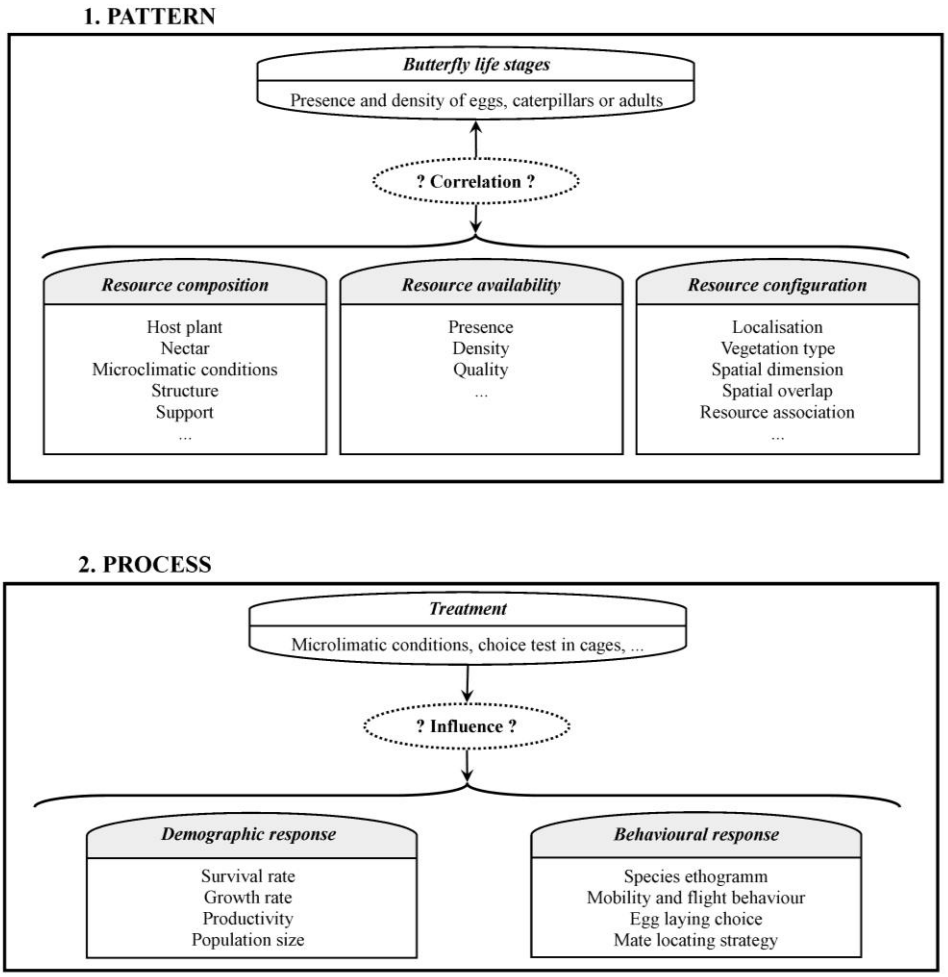


Figure i.3. Schematic representation of the general scientific approach used.

1. Patterns: we first searched for correlation between organism presence (or density) and *a priori* relevant (a)biotic characteristics of the habitat.

2. Processes: according to the results from the "pattern step", we tested mechanistic relationships between organism response (demographic and/or behavioural response) and various treatments representing variations of habitat characteristics. In the boxes are listed examples of variables used or tested in the two steps.

Study system

The two steps described previously were carried out in peat bog ecosystems. In Europe, peat bogs are considered as priority ecosystems for conservation. In Belgium, out of 60.000 ha covered by peat bogs in the past, there are now only 13.000 ha left, of which 6.000 are not drained and several hundred are still active. In Wallonia (S-Belgium), peat bogs are in general extremely damaged for several reasons (Cayron 2004): turf exploitation, forestry and intensive drainage, changes of agricultural practices (mainly abandonment of grazing, mowing and burn-beating), fires, impacts of human frequenting and eutrophication due to atmospheric pollution. Moreover, these changes may favour the development of invasive plant species such as *Molinia caerulea*, at the cost of peat bog specialist species (Limpens, Berendse and Klees 2003). Nowadays, most peat bogs are protected and managed areas.

Among the Belgian peat bogs, we selected two nature reserves (**Figure i.4**), the Fange de Pisserotte (50°13'N, 5°47'E) and the Troufferies de Libin (49°57'N, 5°19'E). Pisserotte is a 56 ha large peat bog located on the south side of the Plateau des Tailles (altitude between 550 and 605 m) and Libin is 52 ha large, located in the Plateau de Recogne (altitude: 430 m). Both sites are crossed by a river and surrounded by birch and willow forest and spruce plantations and present a mosaic of peat bog vegetation. In Pisserotte and Libin, we selected 40 and 25 zones (17 ha and 9 ha) respectively.

According to the presence and abundance of diagnostic plant species, we classified zones in different vegetation types or associations (**Figure i.4**): (1) floating mats and swamps *SW*, pioneer stages with *Sphagnum sp.*, *Eriophorum polystachion*, *Menyanthes trifoliata*, *Drosera rotundifolia*... , (2) rushes *RU* dominated by *Juncus acutiflorus*, (3) fen grasslands *FG* with various flowering plants including *Angelica sylvestris*, *Lotus pedunculatus* and *Cirsium palustris*; (4) almost monospecific short sedge fens *SF* with *Molinia caerulea*; (5) heathland *HL* with *Vaccinium sp.*, *Polytrichum sp.*, *Calluna vulgaris* and *Eriophorum vaginatum* and (6) wet meadows *WM*, mainly composed of *Deschampsia cespitosa*, *Anemone nemorosa* and *Polygonum bistorta*.

In each zone, 10 randomly placed vegetation samples (1-m^2 grid) were recorded (five in mid-June and five in mid-July, in 2005 in Pisserotte and in 2006 in Libin) to measure the abundance of each plant species (**Annex i.1**). Each sample was divided in 25 equal squares and plant abundance was estimated on the basis of its presence on each square, i.e. on a zero to 25 scale (**Figure i.5**). Then, we used a discriminant function analysis on plant species abundance to confirm the *a priori* assignment of each zone to one of the six vegetation types defined. Only 16.7% of the 400 vegetation samples from Pisserotte and 18.76% of the 250 vegetation samples from Libin were misclassified, mainly those located at the border of the zones presenting transitional vegetation.

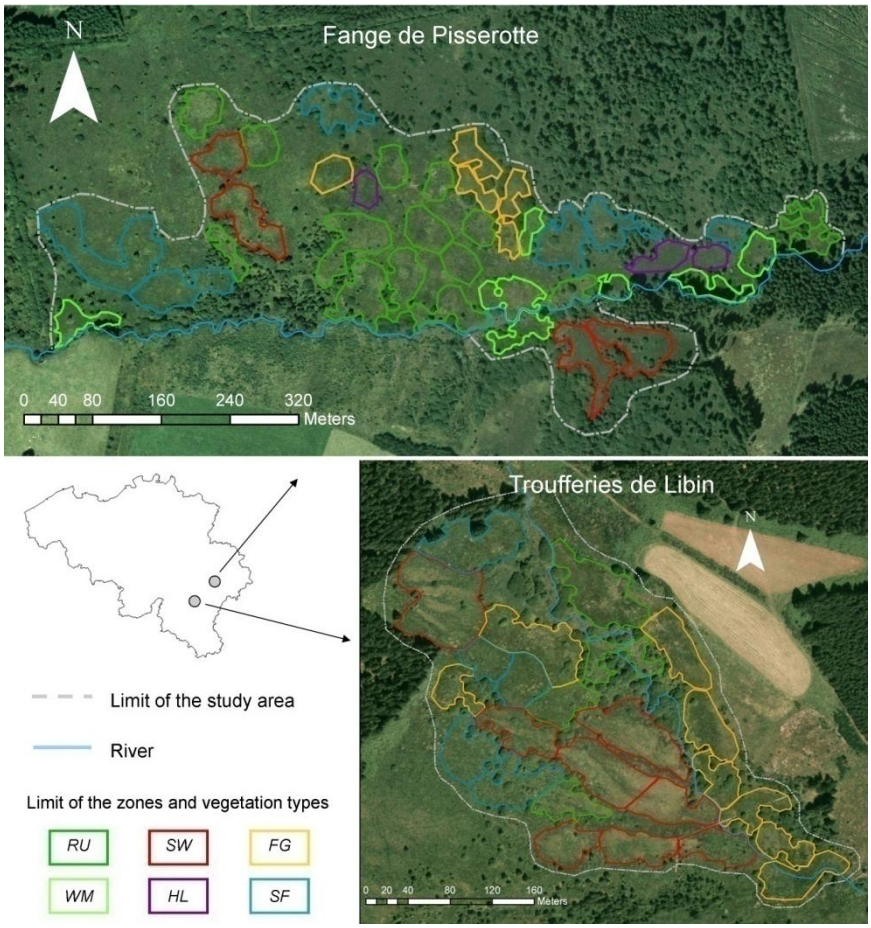


Figure i.4. Maps of the two study areas: the Fange the Pisserotte (top) and the Troufferies de Libin (bottom right). *RU*: rushes, *WM*: wet meadows, *SW*: floating mats and swamps, *HL*: heathlands, *FG*: fen grasslands, *SF* short sedge fens.

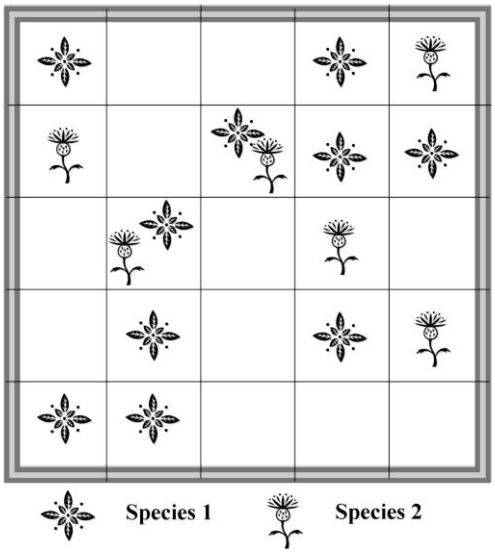
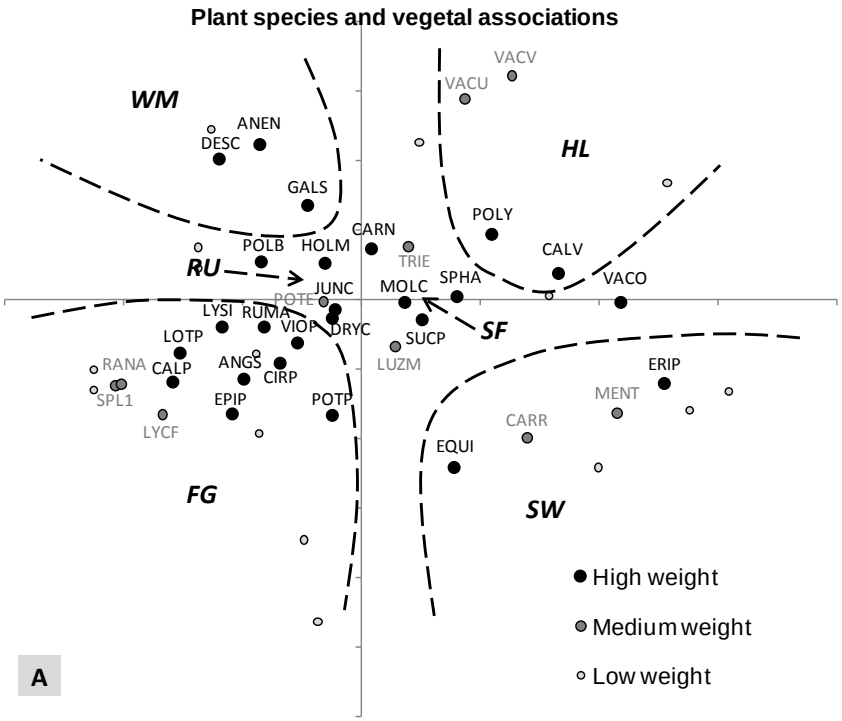
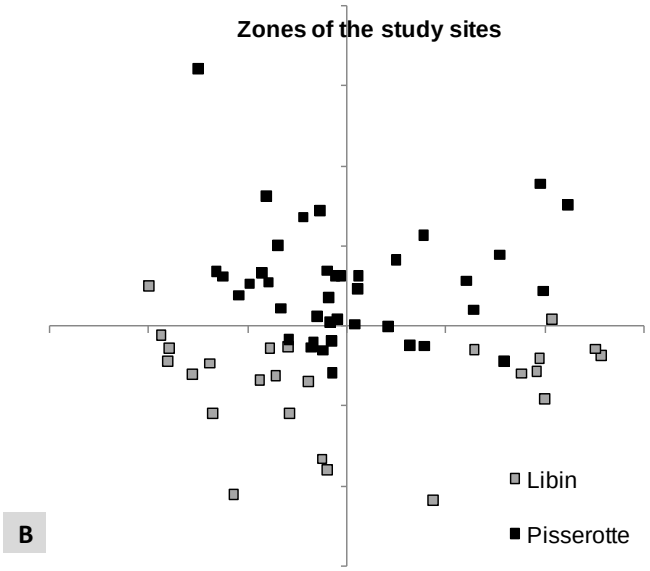


Figure i.5. Simplified representation of a vegetation sample. The 1 m^2 grid was divided in 25 equal squares and used to measure the plant abundance on the basis of its presence on each square, i.e. on a zero to 25 scale. On this example, abundances of species 1 and 2 were 10 and 6, respectively.

Associations between plant species were graphically summarised by a Detrended Correspondance Analysis (**Figure i.6**, Legendre and Legendre 1998). First, diagnostic plant species used previously for classification were among species that contributed the most to the loading of the axes. Secondly, vegetation types were clearly separated in the bidimensional graph. Fen grasslands *FG* and swamps *SW* occurred more frequently in Libin than in Pisserotte. Rushes *RU* and short sedge fens *SF* were equally represented in both sites. Wet meadows *WM* and heathland *HL* occurred only in Pisserotte. This indicated that succession from pioneer stages to heathland was more advanced in Pisserotte.

Figure i.6. Graphical representation of the DCA. **A)** Dots represented position of each plant species (for scientific names and abbreviations, see **Annex i.1**), with variation in size according to their weight on axes formation. Vegetation types were separated by dotted lines. *RU*: rushes, *WM*: wet meadows, *SW*: floating mats and swamps, *HL*: heathlands, *FG*: fen grasslands, *SF* short sedge fens. **B)** Black squares represented position of the zones of Pisserotte while grey squares represented position of the zones of Libin.


Plant species and vegetal associations
VACV
VACU
WM
ANEN
DESC
HL
GALS
POLY
CARN
POLB
HOLM
TRIE
CALV
RU
SPHA
VACO
JUNC
MOLC
POTE
LYSI
RUMA
VIOP
DRYC
SF
LOTP
SUCP
RANA
CALP
ANGS
CIRP
LUZM
ERIP
SPL1
EPIP
POTP
MENT
CARR
LYCF
EQUI
FG
SW
High weight
Medium weight
Low weight
A


Zones of the study sites
Libin
Pisserotte
B

Study species

From the butterfly community of peat bogs, we selected five study species: *Lycaena helle*, *Lycaena hippothoe*, *Proclossiana eunomia*, *Clossiana selene* and *Boloria aquilonaris*. They were chosen for both practical and biological reasons: 1) they represent a gradient from a specialist of peatbog (*B. aquilonaris*) to a generalist species (*C. selene*), according to the different ecosystems in which populations can be found, and are then likely to differ in their requirements and hence in the definition of their habitat; 2) caterpillars feed on a single host plant in the peat bog ecosystem (*Polygonum bistorta* for *L. helle* and *P. eunomia*, *Rumex acetosa* for *L. hippothoe*, *Vaccinium oxycoccos* for *B. aquilonaris* and *Viola palustris* for *C. selene*); 3) caterpillars of *P. eunomia* and *L. helle* feed on the same host plant, which offers the opportunity to test the definition of habitat based on host plant patches; 4) flight period of adults are not all overlapping (**Figure i.7**), which facilitates studying them and 5) all are at least species of regional conservation concern, for which studying the ecological requirements is directly of interest to reserve management. Distribution, adult morphology and behaviour, and egg and caterpillar characteristics (based on Bink 1992; Lafranchis 2000; Lafranchis 2004; Fichefet *et al.* 2008) are described below for each species. Except for distribution, descriptions are mainly based on observations in our study system.

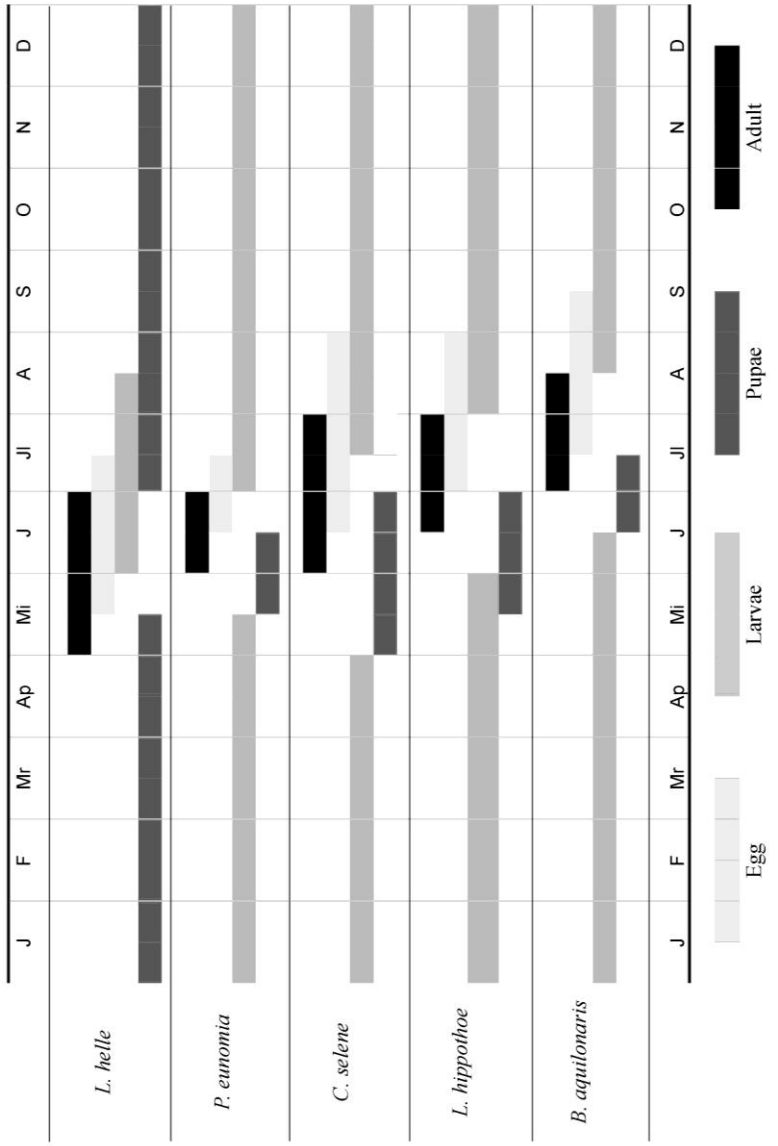


Figure i.7. Seasonal time table of the presence of the four life stages of the five study species.

Lycaena helle (Denis & Schiffermüller 1775, **Figure i.8**)

ᘓ Distribution. The violet copper *Lycaena helle* is a glacial relict butterfly species inhabiting peat bogs, wet meadows and wet clearings. *L. helle* is listed as vulnerable on the Red Data Book of European butterflies. In Belgium, distribution is confined to the Ardenne and Lorraine region, in 88 atlas squares (5 x 5 km).

ᘓ Adult morphology. Adults are small butterflies with average wingspans of 12 to 14 mm. Underside of the wings of both sexes shows a marginal series of black spots bordered by white chevrons. Upperside of the wings of males and females are markedly different. Wing coloration of the male is deep, reflecting violet, whereas females are orange and black with blue spots restricted to the borders of the wings.

ᘓ Adult behaviour. After a short patrolling flight, females land on a host plant (*P. bistorta*) leaf, walk along the leaf rib, walk backwards, just round to the underside where they quickly lay their egg singly. Males show territorial behaviour as they perch on landmarks such as bushes, small trees or tall grasses. They wait for females to mate with and engage short pursuits against intruders. At the end of the day, both males and females settle at the top of the trees to spend the night.

ᘓ Egg and caterpillar. Duration of egg and larval stages are around 9 and 21 days respectively. The green, flattened, rather slug-like caterpillars feed on the underside of host plant and pupate on the soil. This species overwinters at the pupae stage.

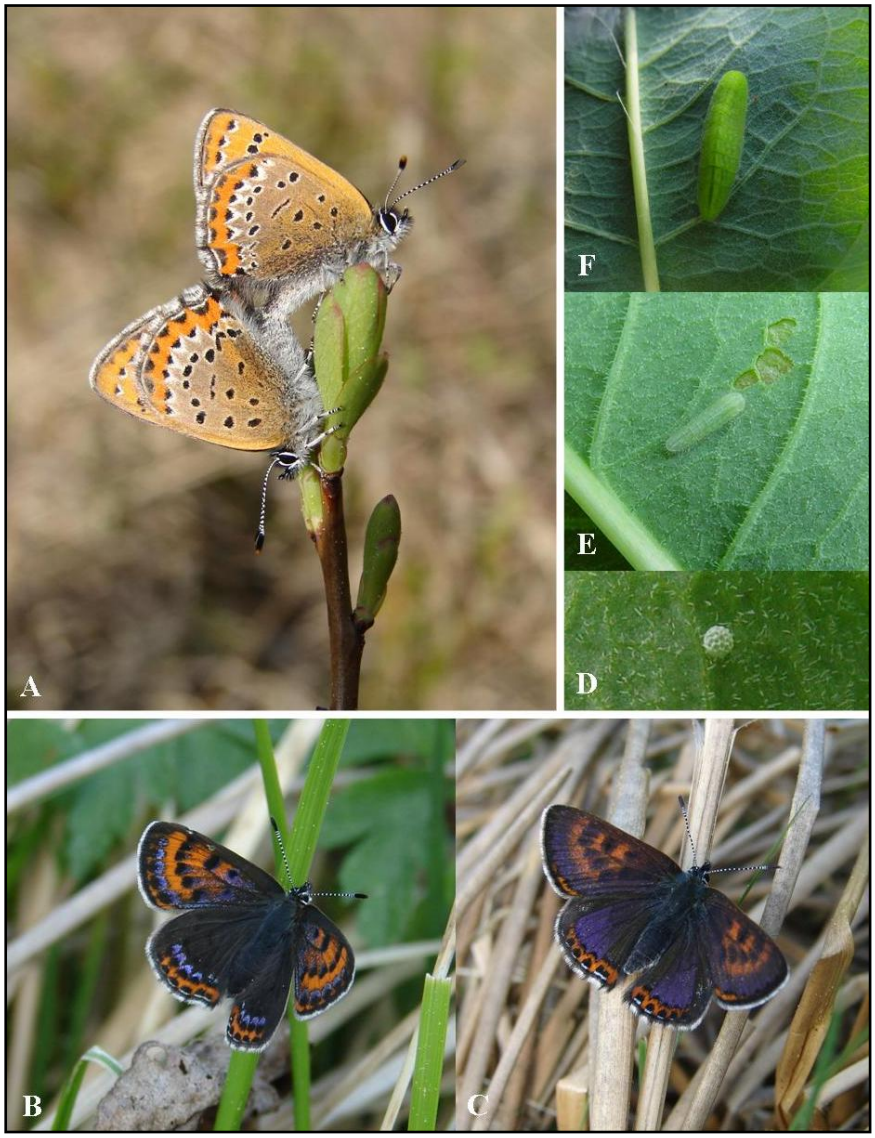


Figure i.8. *L. helle*: A. Mating adults. B. Female. C. Male. D. Three days egg under *P. bistorta* leaf. E. Second instar caterpillar under *P. bistorta* leaf. F. Last instar caterpillar under *P. bistorta* leaf.

Lycaena hippothoe (Linneaus 1761, **Figure i.9**)

ᘓ Distribution. The purple-edged copper butterfly *Lycaena hippothoe* is widespread in north Europe, but much more localized in central Europe. In Belgium, it occurs in the Ardenne and the northern part of Lorraine regions, in 53 atlas squares, and is declining. *L. hippothoe* is ecologically confined to damp meadows, clearings, peat bogs and alpine and arctic grasslands.

ᘓ Adult morphology. Adult wingspans range from 16 to 17 mm. Ground colour of the underside of the wings of both sexes is pale grey brown, with a regular row of black spots on forewing. Upperside of male wings are bright orange-red with a black margin and display a purple iridescence when basking. Upperside of female wings is dull: brown with an orange margin band on the backwing to orange with black spots on forewing.

ᘓ Adult behaviour. *L. hippothoe* males show perching behaviour in an aggressive territorial way by defending patches of nectar sources. Females lay eggs singly on the unique host plant, the sorrel *Rumex acetosa*.

ᘓ Egg and caterpillar. Duration of egg and larval stages are around 10 and 330 days respectively. Caterpillars are rounded, green, with a light red line along the back. They were observed to feed at night, on the underside of host plant leaves and pupate on the soil.

Figure i.9. *L. hippothoe*: A. Male. B. Female landing on a *R. acetosa* plant to lay her egg. C. Egg on *R. acetosa* stem. D. Third instar caterpillar.

Proclossiana eunomia (Esper 1799, **Figure i.10**)

ᘓ Distribution. The bog fritillary *Proclossiana eunomia* is a glacial relict butterfly species inhabiting peat bogs and wet hay meadows. This species is declining in European countries and its distribution in Belgium is confined to the Ardenne and Lorraine region, in 85 atlas squares.

ᘓ Adult morphology. Adult wingspan ranges from 32 to 40 mm. Upperside of the wings is very similar to other fritillaries; it has an orange background with black markings and spots. The outer portion of the wings is lined with a row of black dots followed by a row of black triangles. Upperside of the wings of females is usually darker than in males. The underside of the wings is however very distinctive: it is creamy white with light non-metallic bands and a post-discal row of white ocelli surrounded by a black rim.

ᘓ Adult behaviour. *P. eunomia* flies only in June. Males appear before females and actively patrol in host plant patches searching for emerging females. Females lay groups of eggs either under host plant (*P. bistorta*) leaves or on surrounding plants.

ᘓ Egg and caterpillar. Duration of egg and larval stages are around 14 and 320 days respectively. Third- and fourth-stage caterpillars overwinter. Some spend two winters as caterpillars (C. Turlure, personal observation).

Figure i.10. *P. eunomia*: A. Female feeding on *P. bistorta* flower. B. Groups of nine eggs on a *P. bistorta* leaf. C. Last instar caterpillar. D. Pupae.

Clossiana selene (Denis & Schiffermüller 1775, **Figure i.11**)

ᘓ Distribution. The small pearl-bordered fritillary *Clossiana selene* is widespread in central and northern Europe. It inhabits wet meadows, moorlands, peat bogs and woodlands clearings.

ᘓ Adult morphology. Adult wingspan ranges from 35 to 51 mm. As in *P. eunomia*, the upperside of the wings is bright orange with black markings on the inner half of the wings. Again, the outer portion of the wings is lined with a row of black dots and followed by a row of black triangles. Underside of the wings is yellowish orange, marked with black and brown. The hind wing has three metallic silver spots, the central silver cell being elongated. A black dot on the basal area of the hind wing can be seen on the two faces.

ᘓ Adult behaviour. Adults fly from June to August. Flight of males is very rapid. Females lay eggs on host plant (*V. palustris*) leaves or near the host plant while flying.

ᘓ Egg and caterpillar. Duration of egg and larval stages are around 8 and 330 days respectively. Caterpillars are mottled black, with yellowish spines tipped with black hairs. The spines towards the front are much longer and included in white spots.

Figure i.11. *C. selene*: A. Mating adults on *Lychnis flos-cuculi*. B. Male basking on *Juncus acutiflorus* with two white acarids on the back. C. Last instar caterpillar. D. Caterpillar habitat.

Boloria aquilonaris (Stichel 1908, **Figure i.12**)

ᘓ Distribution. The cranberry fritillary *Boloria aquilonaris* is a glacial relict butterfly species of acid peat bogs. This species is declining in European countries and its distribution in Belgium is confined to the Ardenne and Lorraine region, in 22 atlas squares.

ᘓ Adult morphology. Adult wingspan ranges from 32 to 40 mm. Hind wing apex is square in this species. Upperside of the wings in orange with black markings and the second space is marked by two opposite chevrons. Underside of the forewing is orange while underside of the hingwing is tawny brown with white spots.

ᘓ Adult behaviour. Adults fly in July and August. Females lay their eggs one by one under leaves of the host plant, *V. oxycoccos*.

ᘓ Egg and caterpillar. Duration of egg and larval stages are around 25 and 300 days respectively. Caterpillars are dark brown, with light spines and a double yellow light line along the back.

Figure i.12. *B. aquilonaris*: A. Freshly emerged female. B. Male feeding on *Potentilla palutris*. C. Egg under *Vaccinium oxycoccos* leaf. D. Last instar caterpillar. E. Caterpillar habitat.

Chapter I. Caterpillars of two study species (i.e. *P. eunomia* and *L. helle*) feed on the same unique host plant. This provides opportunity to test whether two species with very similar ecological requirements at first sight effectively, have the same habitat. In other words, we compare the relevance of the habitat definition based on the host plant only with that based on multiple adult and larval resources.

Chapter II. It is obvious that the host plant is a critical resource for caterpillars. We demonstrate that other resources, such as vegetation structure providing appropriate micro-habitat, (1) can play a functional role in caterpillar survival and growth rate and (2) have to be included in the habitat definition. This was studied on caterpillars of *B. aquilonaris* in the two study sites.

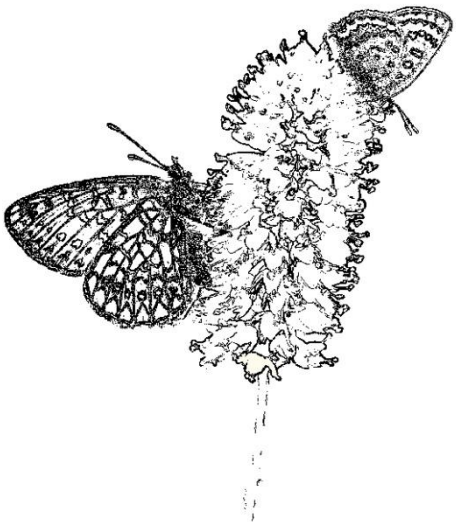
Chapter III. The way resources are distributed in a habitat can have an influence on the way they are exploited by individuals. Using data on local density and behaviour of *L. hippothoe* adults, we show that both territorial behaviour of males and localisation of appropriate micro climatic conditions for egg development can have a strong influence on egg laying choice by females.

Chapter IV. Resources needed by adult butterflies can be distributed differently between populations of the same species. Using four butterfly species (i.e. *P. eunomia*, B. *aquilonaris*, *C. selene* and *L. hippothoe*), we test (1) how resource distribution within a site may impact on movement ranges and (2) how differences in resource distribution between populations can induce differences in morphology.

Chapter V. Host plant area is commonly used as a surrogate for habitat area and expected population size in Population Viability Analysis for butterflies. Using two butterfly species (i.e. *P. eunomia* and *B. aquilonaris*) we test to what extent functional habitat area (i.e. area containing all resources needed by caterpillars in this case) provides a better estimation of the expected population size compared to host plant area.

Chapter I

Resource-based habitat definition, niche overlap and conservation of two sympatric glacial relict butterflies.



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Turlure, Van Dyck, Schtickzelle & Baguette
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Chapter I: Illustration cover by Camille Turlure

ABSTRACT.

The precise knowledge of ecological resources and conditions required by species threatened by rapidly changing environmental conditions is of prime importance for conservation biology. Transferability of this knowledge between species with similar ecological requirements is often assumed, but rarely tested. This is especially the case for glacial relict populations confined to climate-habitat traps from where they cannot move to rejoin areas with suitable environmental conditions.

Using two glacial relict butterflies as model organisms, we first quantitatively define larval and adult resource-based habitat use of each species. Secondly, we test the transferability of ecological profiles (both habitat and ecological niche) between these two species that share both the same biotope and the same host plant. Our results show that both species have markedly different ecological requirements relating to differences in life history and behavioural traits (i.e. egg-laying strategies and mate-locating behaviour). Although the two species share many ecological features, they use different functional habitats within our study site. The high degree of interspecific niche overlap should indicate a high interspecific competition. However, we argue that their co-existence can be explained by the non-limiting abundance of some resources (e.g. host plants), by the partial separation in time of adult flight periods and by the territorial behaviour of one of the species.

We discuss the following general messages: (1) functional habitat of a (threatened) species should be defined in a spatial context

corresponding to individual station keeping, and (2) quick diagnosis based on similar ecological requirements may be misleading for the design of reliable conservation and restoration strategies. Detailed mechanistic and quantitative ecological understanding of resource-use and environmental tolerances across an organism's life cycle is essential for effective conservation in changing environments, like for glacial relict species.

I.1 INTRODUCTION

Ecological networks represent the focal concept for conservation in man-shaped, fragmented landscapes (Baguette 2004; Jongman and Pungetti 2004). After island biogeography, metapopulation theory has become the major paradigm to establish ecological networks with an emphasis on large, well connected areas (Fahrig 2001). With Natura 2000 habitat network, European Habitat Directive aims to implement this philosophy (Jongman, Külvik and Kristiansen 2004).

Habitat patches are usually delineated based on vegetation types or biotopes (Hall, Krausman and Morrison 1997), e.g. using diagnostic plant species presence for particular vegetation types. Many studies addressed the issue of conservation areas selection and networks based on different criteria including the application of selection algorithms (Cabeza and Moilanen 2001). Besides the exclusive emphasis on patch area and isolation from early metapopulation work, there is now ample evidence that habitat patch quality needs to be explicitly considered as well (Thomas *et al.* 2001b; McIntire, Schultz and Crone 2007). In some systems, the importance of habitat quality may even overrule the importance of habitat configuration (Dennis and Eales 1999, Fleishman et al. 2001). There is growing concern about keeping the quality of Natura 2000 sites in favourable condition for target species. Habitat quality for target species is, however, not a simple issue as habitat is a multidimensional trait referring to the combination of interactions between the organism and its environment. Functional habitat relates to

the concept of ecological niche through the concept of resource-based habitat (Dennis, Shreeve and Van Dyck 2003b).

The recognition of ecological resources or conditions needed or tolerated by a species of conservation concern under rapidly changing environmental conditions is considered as a priority. With changes in climatic isotherms northwards, several species have expanded or shifted their range northward (Parmesan *et al.* 1999; White and Kerr 2006; Parmesan 2006). Glacial relict species are clearly exceptions to this pattern. Their populations are located in climate-habitat traps, and cannot escape in space from sites that become unsuitable. Given the very specific and discontinuous distributed environmental conditions they rely on, gradual range shifts are no option. As a consequence, conservationists have to anticipate climate-related challenges on the currently occupied sites. This implies a much more focused management of ecological resources and vegetation structures than it has traditionally been the case. Genuine adaptations to particular environmental conditions may prevent the use of surrogate data collected in the main part of their distribution range to infer reliable conservation strategies. Therefore, a detailed and quantitative ecological understanding of resource-use and environmental tolerances across the life cycle becomes a key aspect to adapt conservation programs over the coming years.

Here we address this challenging conservation topic with two co-occurring glacial relict butterfly species of peat bogs in the Belgian Ardenne: a lycaenid, the violet copper *Lycaena helle* and a nymphalid, the bog fritillary *Proclossiana eunomia*. The aim of our paper is twofold. Firstly, we quantitatively define what actually represents habitat for the

two species separately. This step encompasses the identification of spatial subsets of ecological resources and conditions within and across different vegetation types (Dennis, Shreeve and Van Dyck 2003b; Dennis, Shreeve and Van Dyck 2006a). For holometabolous insects (i.e. insects for which development includes four life stages: egg, larva, pupa and adult), this implies the study of resource-use across different life cycle stages. Secondly, we test to what extent ecological profiles can be transferred between species sharing the same biotope and host plant. Here, we relate to the theory of resource overlap, which is classic in ecology (Abrams 1980; Edwards, Heckel and Guynn 1998), but has been rarely incorporated into conservation biology.

I.2 METHODS

Study species

The violet copper *Lycaena helle* and the bog fritillary *Proclossiana eunomia* are two specialist butterfly species of peat bogs and wet hay meadows. They are declining in European countries; *L. helle* is listed as vulnerable (i.e. SPEC 3 level: species with headquarters within and outside Europe, but considered threatened in Europe) on the Red Data Book of European butterflies. In Belgium, their distribution is confined to the Ardenne and Lorraine region. *L. helle* flies from early May to the end of June and hibernates as pupa, whereas *P. eunomia* flies only in June and hibernates as caterpillar. The same single host plant of both species is the bistort *Polygonum bistorta*.

Study site

The study was carried out in the Fange de Pisserotte nature reserve (S Belgium: 50°13'N, 5°47'E) during the summers of 2005 and 2006. This 56 ha large peat bog is located on the south side of the Plateau des Tailles. It is surrounded by birch and willow forest and spruce plantations, and consists of six major vegetation types, as described from the presence of diagnostic plant species (Turlure unpubl.): (1) floating mats and swamps dominated by *Sphagnum* sp., *Menyanthes trifoliata* and *Narthecium ossifragum*; (2) rushes dominated by *Viola palustris* and *Juncus acutiflorus*; (3) fen grasslands with various flowering plants

including *Angelica sylvestris*, *Valeriana repens* and *Cirsium palustre*; (4) almost monospecific short sedge fens with *Molinia caerulea*; (5) heathland with *Vaccinium* sp. and *Calluna vulgaris*; and (6) wet meadows, mainly composed of *Deschampsia cespitosa* and *Anemone nemorosa*, along the Rolayi river in the southern part of the peat bog.

In the study area, we selected 40 zones totalling 17 ha according to two main criteria: presence of the host plant and succession stage of the zone. In each zone, 10 randomly placed vegetation samples (1-m^2 grid) were recorded (five in mid-June and five in mid-July) to measure the abundance of each plant species on a 0 to 25 scale. Then, we used a discriminant function analysis on plant species abundance (PROC DISCRIM in SAS: http://support.sas.com) to confirm the a priori assignment of each zone to one of the six vegetation types. Only 16.7% of the 400 vegetation samples were misclassified, mainly those located at the border of the zones. The host plant *P. bistorta* occurred in the six vegetation types, in 24 patches covering 163 to 2399 m^2 (**Figure I.1**, **Table I.1**).

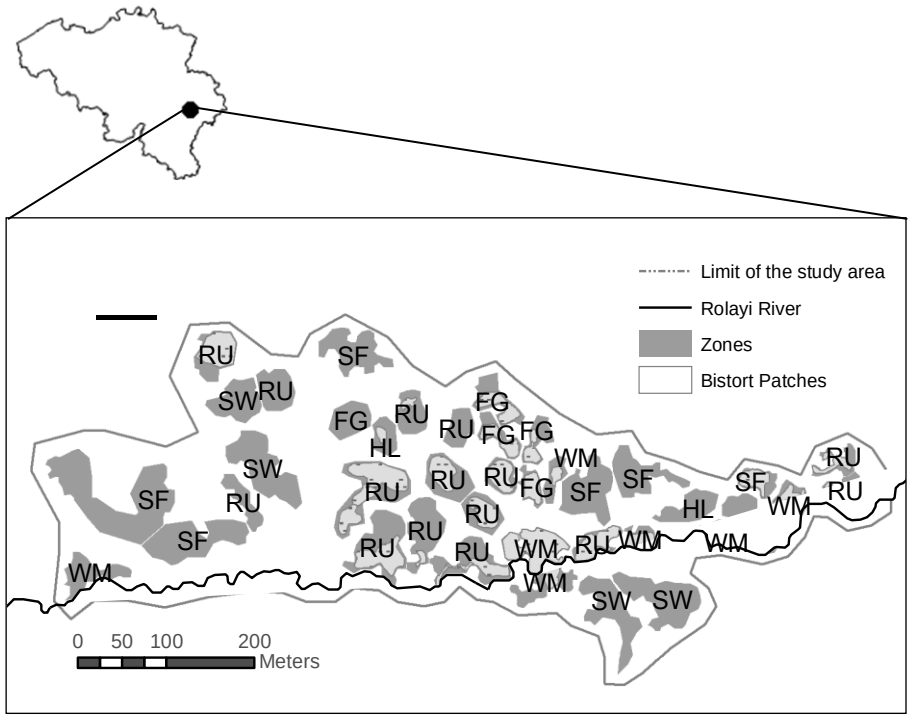


Figure I.1. Map of the study area: the plain grey areas indicate the 40 zones, the letters inside the zones indicate the vegetation type (SW = swamps, RU = rushes, WM = wet meadows, FG = fen grasslands, SF = short sedge fens, HL = heathlands) and the marbled grey areas represent the 24 host plant patches.

Table I.1. Number, area and percentage of the zones and the host plant patches in each vegetation types.

Vegetation type	Zones			Host plant patches		
	Number	Area (m^2)	%	Number	Area (m^2)	%
WM	7	10372.31	13.42	6	6660.13	27.22
SW	4	11497.57	14.87	1	416.13	1.7
RU	15	27001.53	34.93	11	13404.77	54.78
FG	5	6048.51	7.82	4	3002.27	12.27
SF	6	18928.95	24.49	1	820.61	3.35
HL	3	3456.01	4.47	1	165.14	0.67
Total	40	77304.88	100	24	24469.05	100

Caterpillars

In May and July 2005, we searched for caterpillars in all host plant patches, with a similar sampling effort, search time being proportional to host plant patch area (Pearson correlation: R = 0.55, n = 24, p = 0.004). We found 107 caterpillars of *P. eunomia* and 94 caterpillars of *L. helle* in 87 and 73 distinct plots, respectively. The number of caterpillars found in each patch did not vary with sampling effort (Pearson correlation: R = –0.24, n = 24, p = 0.24 for *P. eunomia*, R = 0.25, n = 24, p = 0.23 for *L. helle*).

For each caterpillar, we recorded the number of grass tussocks and the abundance of each plant species within a 1 m^2 plot (0 to 25 scale). We also recorded the same vegetation variables in a series of control plots within host plant patches where no caterpillar was found (73 for *P. eunomia* and 33 for *L. helle*). Local conditions of moisture,

light intensity and temperature were inferred for each of the 266 plots from the abundance-weighted mean of Ellenberg indicator values of plant species (Ellenberg 1974). As the three microclimatic variables were correlated (Pearson correlation tests: all $p < 0.001$) and to avoid multicollinearity problems in further regression models (Graham 2003), we performed a principal component analysis to create two independent variables: CLIM1 was positively correlated with light intensity and temperature; CLIM2 was positively correlated with moisture (CLIM1 and CLIM2 explained 89.63% of the variance).

We did three statistical analyses on the caterpillar data. First, χ^2 tests were used to assess the degree of matching between caterpillar abundance and the relative area of each of the six vegetation types. Secondly, logistic regressions were used to relate caterpillar presence to vegetation descriptors (i.e. host plant abundance and number of grass tussocks) and local microclimatic conditions (CLIM1 and CLIM2) using AIC-based model selection (Burnham and Anderson 2002a). To take into account model selection uncertainty, we report the AIC weight of each explanatory variable, expressing the probability that the variable influences the response (here the presence of caterpillars), and model-averaged parameter estimates and confidence limits (Burnham and Anderson 2002a). Thirdly, interspecific differences for local conditions where caterpillars were found were assessed by χ^2 for vegetation types and by ANOVA for host plant abundance, tussock abundance and microclimatic conditions.

Adults

We monitored population size and spatial structure using a mark–release–recapture (MRR) study for both species during their flight periods in 2005 and 2006. The study site was visited daily if weather permitted (i.e. no strong wind, few clouds and air temperature > 15°C). Adults were individually marked and released on the spot of capture. At each (re)capture, we recorded date and time, location (i.e. one of the 40 predefined zones), species, marking code and sex.

Demographic parameters (i.e. survival and recapture rates, daily and total population size) were inferred for each species from our MRR data using Mark software (White and Burnham 1999) according to the procedure described in Schtickzelle, Le Boulengé and Baguette (2002). Next, we analyzed population spatial structure by assessing the local frequency of each species in each of the 40 zones relative to environmental conditions by generalized linear models with AIC-based selection. Response variable was the number of (re)capture events; explanatory variables, measured at the zone level, were vegetation type (six types as described previously), woody edge structure (three classes: no edge, some nearby trees, surrounded by trees), host plant density (three classes: no, low density, high density), tussock density (three classes: no, few, many), and nectar resource abundance apart from bistort flowers (three classes: no, few, many). Classes of the last three explanatory variables resulted from a discriminant function analysis using vegetation samples of each zones. Nectar resource abundance was included for *L. helle* only, because *P. eunomia* only feeds on the host plant. Area of each zone was used as a covariate. We tested for

differences between the two species and the sexes in terms of local conditions preferred by adults (vegetation type, nectar resource abundance, host plant density, tussock density and edge structure) using χ^2 and Cochran–Mantel tests.

Niche breadth and overlap

To assess to what extent species and sexes share the use of their environmental setting, we measured the niche breadth *B* (Edwards, Heckel and Guynn 1998), for larval resources, adult resources, space used by adults (using the 40 vegetation zones), and adult presence over time (i.e. flight period). *B* was computed according to Ricklefs' equation:

$$B = \frac{1}{\sum P_i^2}$$

where P_i is the proportion of individuals in the ith state of the considered resource. *B* can range from 1 to the number of resource states. As resource states were not equal in each resource, we standardized niche breadth to 10 states. Hence, niche breadth can range from 1 to 10.

The niche overlap expresses the percentage of niche space shared by two or more organisms and may then indicate the intensity of competition for resources between organisms of a same community. We chose Schoener's index *O* to estimate niche overlap of both species:

$$O_{eh} = 1 - 0.5 \sum \left| P_{ie} - P_{ih} \right|$$

where P_{ie} and P_{ih} represent the proportion, in the *i*th state of the considered resource of *P. eunomia* and *L. helle*, respectively. Schoener's

index is the most accurate index to estimate overlaps between 7 and 85% (Linton, Davies and Wrona 1981) and it is free of assumptions about the nature of the competitive process (Abrams 1980). Wilcoxon signed rank tests were used to compare niche breadth of the two species.

Association between resources and their distribution

To analyze the spatial cohesion of the n different ecological resources in our study site, we used a multiple correspondence analysis (MCA) in SPAD Decisia ver. 5.6 software (www.spad.eu). The aim of this multivariate data analysis is to highlight associations between variables by graphic representation. Variables used for this analysis were those selected by previous analyses: i.e. vegetation type, woody edge structure, host plant density, tussock density, and nectar resource abundance for each zone (area of each zone was considered as covariable). Abundances of adult butterflies of both species (transformed in four classes of density) were added as illustrative nominal variables to the MCA. The percentage of the total variance explained by each new dimension of the representation is generally very small in MCA and we retained only dimension(s) with eigenvalues > 1/n, here 0.2 (Benzecri 1992). Then, a close position of two variables on a two-dimensional graph indicates a strong positive association between them.

I.3 RESULTS

Caterpillars

Caterpillars of both species were confined to three out of the six vegetation types within the study site: rushes, wet meadows and fen grasslands (**Figure I.2**). Caterpillars were homogeneously distributed among three vegetation types (caterpillar incidence and relative area of each vegetation type matched: *P. eunomia*: χ^2_2 = 3.61, p =0.16; *L. helle*: χ^2_2 = 0.368, p = 0.83) and this distribution did not differ between species (χ^2_2 = 1.94, p = 0.38).

At the microhabitat scale, *P. eunomia* caterpillar presence was mainly associated with moister, darker and colder conditions (i.e. lower values of CLIM1 and higher values of CLIM2), with abundant grass tussocks and higher host plant abundance (**Table I.2, Figure I.3**). *L. helle* caterpillar presence was also associated with moister conditions (i.e. higher values of CLIM2) but with a lower number of grass tussocks, and its presence was not explained by host plant abundance (**Table 2, Figure I.3**).

In addition, *P. eunomia* and *L. helle* caterpillars differed in environmental conditions in which they were found (**Figure I.3**). Compared to *L. helle*, *P. eunomia* caterpillars were found in plots with higher host plant coverage ($F_{1,158}$ = 10.56, p = 0.0014) and colder conditions ($F_{1,158}$ = 5.67, p = 0.018). There were no interspecific

differences for moisture conditions ($F_{1,158}$ = 0.07, p = 0.79), light conditions ($F_{1,158}$ = 1.76, p = 0.19) and tussock abundance ($F_{1,158}$ = 2.59, p = 0.11).

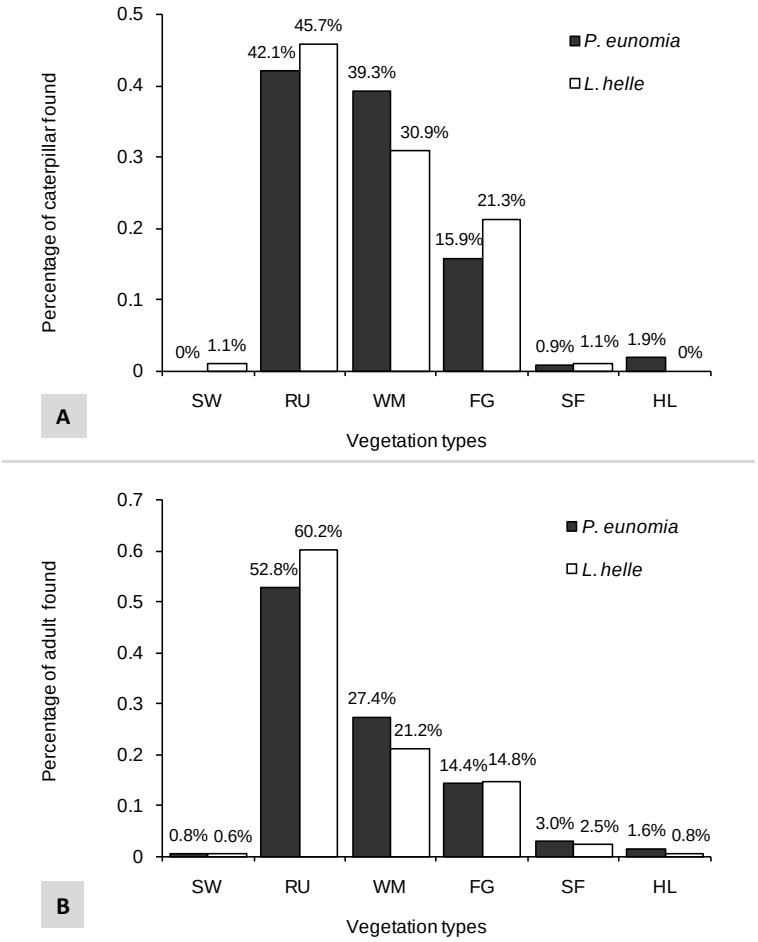
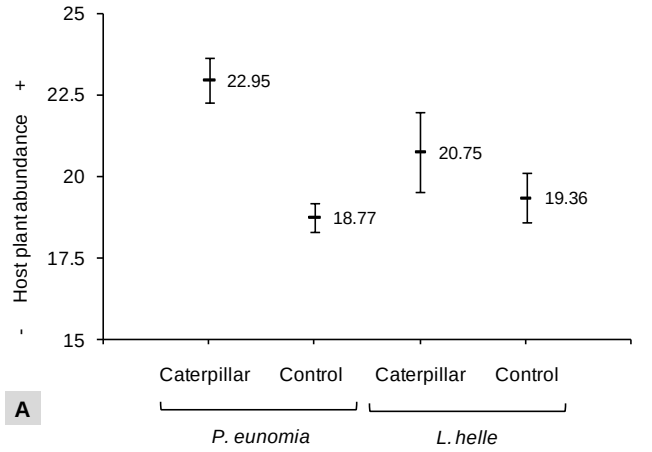


Figure I.2. Percentage of caterpillars (A) and adults (B) found in each of the six vegetation types (SW = swamps, RU = rushes, WM = wet meadows, FG = fen grasslands, SF = short sedge fens, HL = heathlands) present in the study area, in black for *P. eunomia*, and in white for *L. helle*.


25
22.5
20
17.5
15
- Host plant abundance +
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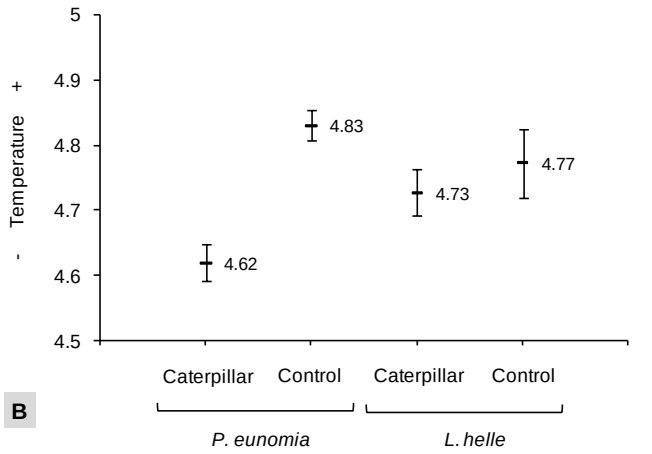
Caterpillar
Control
Caterpillar
Control
P. eunomia
L. helle

A


5
4.9
4.8
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- Temperature +
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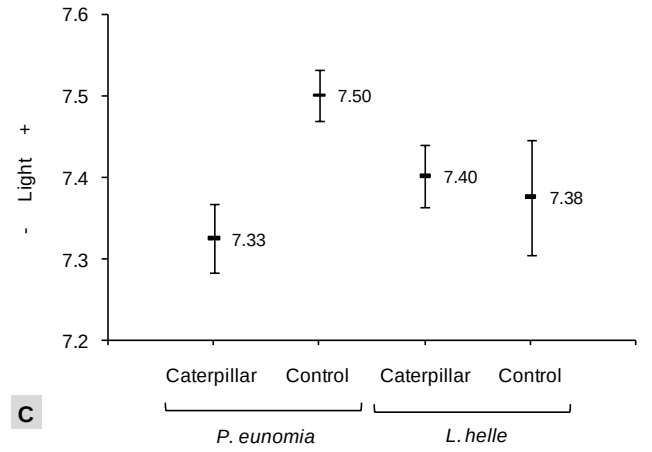
Caterpillar
Control
Caterpillar
Control
P. eunomia
L. helle

B


7.6
7.5
7.4
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- Light +
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7.38
Caterpillar
Control
Caterpillar
Control
P. eunomia
L. helle

C

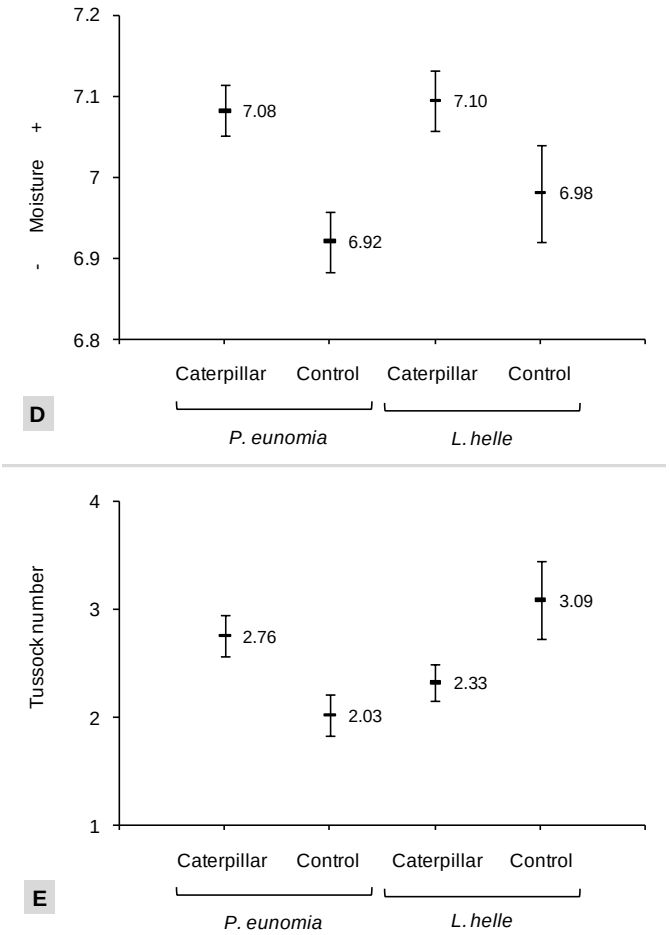


Figure I.3. *P. eunomia* caterpillar samples have moister, darker and colder conditions and higher host plant abundance compared to control samples. *L. helle* caterpillar samples have only moister conditions compared to control samples. Caterpillars of *P. eunomia* were found in places with more abundant host plant (A) and cooler temperature conditions (B) than caterpillars of *L. helle*. There were no differences in light conditions (C), moisture conditions (D) and tussock number (E) between species.

Table I.2. Logistic regressions of *P. eunomia* and *L. helle* caterpillar presence according to environmental conditions indicated that (1) *P. eunomia* caterpillar presence was mainly associated with higher host plant abundance, abundant grass tussocks, lower values of CLIM1 and higher values of CLIM2 (i.e. moister, darker and colder conditions), (2) *L. helle* caterpillar presence was above all associated with lower tussock number and higher values of CLIM2 (i.e. moister conditions). Results are based on multi-model averaging.

Species	Type	Intercept	Bistort	Tussocks	CLIM1	CLIM2
P. eunomia	Variable weight (%)	100	100	78.83	73.07	99.99
	Parameter estimate	–6.0762	0.27631	0.22081	–0.2818	0.97714
	Parameter st.e.	1.40262	0.05892	0.11538	0.16684	0.26901
L. helle	Variable weight (%)	100	28.77	83.7	61.15	97.19
	Parameter estimate	1.54378	0.00353	–0.27908	–0.25042	0.6011
	Parameter st. e.	0.78745	0.01473	0.13826	0.18452	0.28362

Adults

Basic statistics of the 35 and 20 MRR sessions of 2005 and 2006 (in total 92 and 67 h, respectively) are summarized in **Table I.3**. Average recapture probability was much higher for *P. eunomia*, and higher for males than for females in both species. Estimated population sizes were larger for *L. helle*.

Adults of *P. eunomia* exclusively fed on flowers of the host plant, whereas adults of *L. helle* used 24 different flowering plant species (mainly *Anemone nemorosa*, *Cirsium palustre*, *Vaccinium* sp. and *P. bistorta*). The flight period of *P. eunomia* matched the flowering period of *P. bistorta*, whereas the flight period of *L. helle* was longer and corresponded to the successive flowering periods of various nectar feeding plants.

Adult incidence of both species was significantly related to all tested environmental conditions: vegetation type, woody edge structure, density of tussocks, host plants and nectar plants. The relative importance of these variables was, however, species-specific (**Table I.4**). Both species were more frequently associated with rushes, short sedge fens and wet meadows than with swamps, fen grasslands and heathlands; *P. eunomia* occurred significantly more frequently in wet meadows, and less frequently in rushes and fen grasslands (χ^2_5 = 17.21, p = 0.004; Cochran–Mantel–Haentzel test value = 20.97, DF = 5, p <0.001). Most *P. eunomia* individuals were observed in zones with high host plant and tussock densities, but not necessarily with trees, whereas most *L. helle* adults were observed in zones with trees or surrounded by trees,

abundant nectar plants, but with few or no tussocks. Host plant density was not as important for *L. helle* as it was for *P. eunomia* (χ^2_2 = 17.94, p <0.001; Cochran–Mantel test value = 16.37, DF = 2, p <0.001): the host plant density did not influence the abundance of *L. helle* adults provided a minimum abundance level was reached. The presence of a woody edge (χ^2_2 = 72.64, p <0.001; Cochran–Mantel test value = 82.46, DF = 2, p <0.001) and of nectar plants (χ^2_2 = 19.61, p <0.001; Cochran–Mantel test value = 21.49, DF = 2, p <0.001) was an important variable for *L. helle*, but not for *P. eunomia*.

Table I.3. Basic statistics of mark–release–recapture done in 2005 and 2006. Estimated population sizes are shown with 95% CI. Average recapture probability was much higher for *P. eunomia* than for *L. helle* and also higher for males than for females in both species. Estimated population sizes were larger for *L. helle*.

		L. helle			***P. eunomia***		
		Males	**Females**	**Total**	**Males**	**Females**	**Total**
2005	Number of captures	268	195	463	216	164	380
	Daily recapture probability	0.8 to 17.15%			6.83 to 66.45%		
	Estimated population size	831±197	927±256	1758±367	262±17	344±79	606±81
2006	Number of captures	145	116	261	77	65	142
	Daily recapture probability	9.77%			10.62 to 55.43%		
	Estimated population size	804±281	839±510	1643±612	158±42	166±46	324±73

Niche breadth and overlap

Niche breadth tended to be smaller for *P. eunomia* but, comparison of niche breadths between species did not reach significance level (**Table I.5**; Wilcoxon signed rank test: n = 13, p = 0.33). In both species, niche breadth was the narrowest for vegetation type and host plant abundance for both adults and caterpillars, and for microclimatic temperature conditions for caterpillars. In *P. eunomia*, niche breadth was also especially narrow for nectar use. Niche breadth was a little broader for males than for females in *P. eunomia* and conversely in *L. helle*. The niche overlap between the two species was considerable (O >70% for most resources) but lower for nectar use (O = 55%) and flight period (O = 50%).

Table I.4. Results of generalised linear regressions of the incidence of *L. helle* and *P. eunomia* adults according to environmental conditions. A single model was far better than the others for each species (ΔAIC with second best model: 22.81 for *L. helle*; 95.75 for *P. eunomia*) and is presented here; no multi-model averaging was performed. For categorical explanatory variables, the estimate expresses the difference with the reference level fixed to zero. Amount of nectar plants was not included in *P. eunomia* model because this species exclusively feeds on the host plant.

Parameter & Modalities		*L. helle*				*P. eunomia*			
		Estimate	SE	Wald 95% confidence limits		Estimate	SE	Wald 95% confidence limits	
Intercept		1.909	0.212	1.494	2.325	1.491	0.149	1.198	1.783
Sex	F	–0.3686	0.068	–0.5014	–0.2357	–0.825	0.063	–0.9485	–0.7014
	M	0				0			
Vegetation type	WM	1.646	0.186	1.282	2.010	1.665	0.127	1.415	1.915
	HL	0.067	0.434	–0.7827	0.917	0.383	0.276	–0.1566	0.923
	RU	0.725	0.138	0.454	0.996	0.736	0.109	0.523	0.950
	SF	0.548	0.355	–0.1477	1.243	0.905	0.243	0.428	1.383
	SW	–2.7227	0.496	-3.695	–1.7509	–0.9606	0.270	–1.4893	–0.4319
	FG	0				0			
Bistort	0	–1.1895	0.138	–1.4594	–0.9196	–1.0288	0.119	–1.2621	–0.7955
	+	0.250	0.142	-0.027	0.528	–0.5106	0.102	–0.71	–0.3111
	++	0				0			
Edge structure	0	–2.76	0.227	–3.2042	–2.3158	1.693	0.146	1.406	1.980
	+	–1.0019	0.102	–1.2024	–0.8013	2.195	0.127	1.947	2.443
	++	0				0			
Tussock	0	1.616	0.220	1.185	2.047	–1.4637	0.132	–1.7228	–1.2045
	+	1.547	0.172	1.209	1.885	–0.6061	0.094	–0.7893	–0.4229
	++	0				0			
Nectar	0	–0.1342	0.170	–0.4681	0.200	/	/	/	/
	+	–0.7106	0.136	–0.9765	–0.4447	/	/	/	/
	++	0				/	/	/	/

Table I.5. Measures of niche breadth and overlap for resources used by adults (males and females pooled and separated), resources used by caterpillars, space used by adults (using the 40 vegetation zones), and flight period (FP) of adults.

Stage	Sex	Resource	Number of classes	Standardised niche breadth		Overlap (%)
				P. eunomia	*L. helle*	
Adults	F+M	vegetation type	6	4.435	3.8775	92.14
		edge	3	8.2771	7.1085	88.54
		host plant	3	5.4367	5.8207	93.73
		tussocks	3	7.2577	8.393	82.49
		nectar	3	5.4367	8.0587	41.26
	F	vegetation type	6	4.2556	4.1139	92.7
		edge	3	8.1002	7.4174	87.73
		host plant	3	5.1847	5.8449	93.78
		tussocks	3	7.0999	8.4975	85.17
		nectar	3	5.1847	7.819	36.14
	M	vegetation type	6	4.4805	3.6316	89.68
		edge	3	8.303	6.7913	86.92
		host plant	3	5.5499	5.7018	94.2
		tussocks	3	7.3208	8.0492	80.05
		nectar	3	5.5499	8.0606	44.04
Caterpillars		vegetation type	6	4.7018	4.2762	92.55
		host plant	19	1.852	3.2054	72.96
		tussocks	9	6.7119	5.3682	78.29
		light	16	5.9806	5.8535	77.44
		temperature	17	2.5632	3.0112	73.19
		moisture	16	5.2042	6.4924	77.34
Adults	F+M	FP 2005+2006	21	3.9535	4.3912	50
		FP 2005	9	3.8926	5.9649	50
		FP 2006	12	4.017	3.6789	18.72
Adults	F+M	space	40	3.5982	3.437	71.19
	F	space	40	2.981	3.6714	73.35
	M	space	40	3.8135	3.0562	64.78

Resources association and distribution

Different resources were not homogeneously associated across the study site. 17% of the possible associations between modalities of variables did not exist. Host plant density, nectar abundance and woody edge presence were positively correlated and increased jointly, whereas they were negatively correlated with tussock density (**Figure I.4**). Therefore, resource settings of *L. helle* were more aggregated and more widely distributed in different zones than it was the case for *P. eunomia*: nectar, bistort and trees were present in the same zones, whereas zones with high bistort density and high tussocks density were sparse. As a result, distribution of complete sets of resources for the two butterfly species was not uniform in this study site.

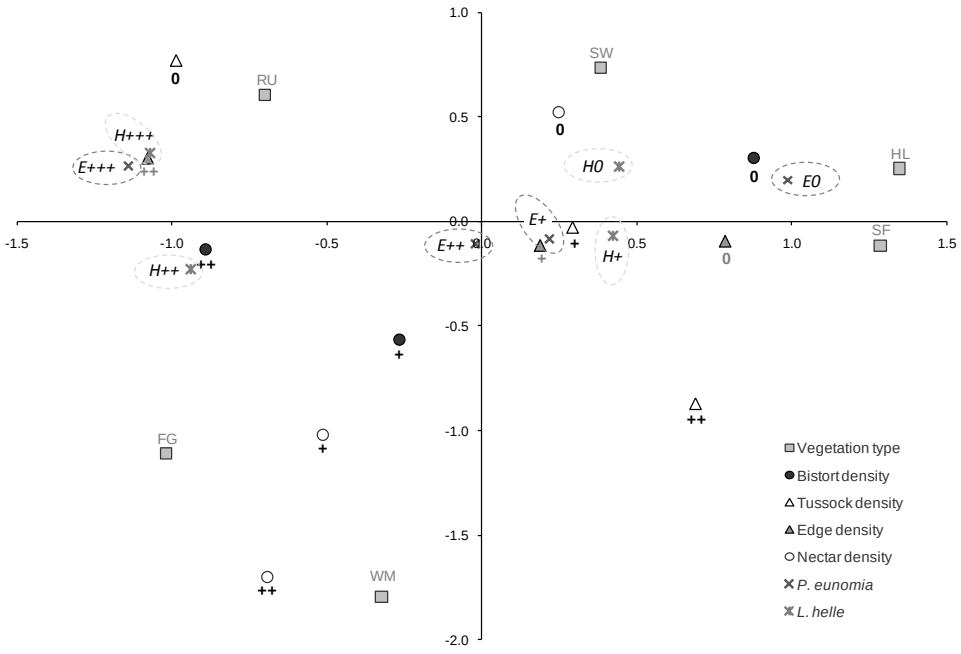


Figure I.4. Graphical representation of the multiple correspondence analysis using vegetation types (grey squares: SW = swamps, RU = rushes, WM = wet meadows, FG = fen grasslands, SF = short sedge fens, HL = heathlands), woody edge density (grey triangles), host plant density (black dots), tussock density (white triangles) and nectar resource abundance (white dots) for each zone. Classes of abundance of adult butterflies of both species were added as illustrative nominal variables (crosses with E = *P. eunomia*, crosses with H = *L. helle*). Close position of two variables on this graph indicates a strong positive association between them. Density of host plant, abundance of nectar and edge presence were positively correlated and increased jointly, whereas they were negatively correlated with tussock density.

I.4 DISCUSSION

There is an increasing tendency in ecological studies and conservation approach to focus on large scale processes (e.g. the landscape level or metapopulations). Here we demonstrate the importance of not neglecting functional micro-scales (as stated by Pe'er and Settele 2008). Although the ecological requirements of these two species, sharing the same host plant, could have been considered as similar at first sight, our results indicated significant differences in habitat use within the study site, reflecting differences in their life history traits, as we will discuss below. We focus on two major general conclusions: (1) species functional habitat should be defined in a spatial context corresponding to individual station keeping (sensus Dingle 1996), and (2) quick ecological diagnosis without taking into account ecological resource-use may be misleading to establish conservation strategies for threatened populations.

Differences in life history traits

The significant differences in resource use can be explained by differences in life history between the two species. The first main issue is egg-laying strategy. *P. eunomia* is mainly a capital breeder laying batches of 7–41 eggs, whereas *L. helle* is an income breeder laying eggs singly (Turlure unpubl.). This translates into differences for egg-laying: caterpillars of *P. eunomia* were indeed more abundant in microhabitats where the host plant was denser, which corresponds to the rather trivial assumption that aggregated consumers need more local feeding resources. Due to differences in caterpillar size, host plant biomass

consumed by one *P. eunomia* caterpillar during the last instar only, is twice as large as the biomass consumed by *L. helle* during all larval stages (Turlure unpubl.). This also connects to the contrasted egg-laying behaviour: *L. helle* is more likely being time-constrained, whereas *P. eunomia* has in principle more time for host plant selection. We also noticed a difference in time spent searching for an egg-laying substrate (12 s for *L. helle*, 63 s for *P. eunomia*, Turlure unpubl.). The difference between larval habitats relative to tussock abundance is likely to reflect physiological and behavioural differences. Smaller *L. helle* caterpillars remain under bistort leaves until the leaves are completely eaten and next they move to closer leaves with higher ground temperatures that facilitate fast pupation (cf. Bryant, Thomas and Bale 2002). Larger *P. eunomia* caterpillars spend most of their time basking on the exposed side of tussocks, move to bistort leaves to eat and then return to tussock to bask (Turlure unpubl.). Tussocks may also allow *P. eunomia* caterpillars to escape from parasitoids, predators and winter flooding (cf. Joy and Pullin 1997). These lifestyles correspond to differential larval growth rates: *L. helle* caterpillars pupate at the end of the summer, while *P. eunomia* caterpillars overwinter as second instar larvae. Accordingly, *L. helle* adults emerge several weeks before *P. eunomia*.

Another interspecific difference relates to mate-location. *L. helle* males are territorial and adopt a perching or sit-and-wait strategy, while *P. eunomia* males patrol to find potential mates. *L. helle* territories are usually established in areas where host plants are close to scrubs and trees that are used to sit and scan for passing females and males. This explains the association with trees for *L. helle* adults. *P. eunomia* adults were more frequently observed in areas with grass tussocks where males

locate freshly emerged, virgin females. The significance of trees for *L. helle* also relates to the roosting behaviour. At the end of the day, adults move to the eastern top part of trees to spend the night. This strategy probably allows individuals (males in particular) to start their activity earlier in the morning and hence to occupy more rapidly a territory (Dover, Sparks and Greatorex 1997; Dennis 2004b). Adults of *P. eunomia* usually roost on *P. bistorta* or on neighbouring herbs (Turlure unpubl.).

The significance of detailed natural history information is not always fully appreciated by conservation biologists (see for instance the insight that habitat and landscape quality matter for metapopulation persistence more than landscape spatial configuration : Thomas *et al.* 2001b, Ricketts 2001). We argue that explanations in terms of life history strategies and behaviours are far from anecdotal details, but are key aspects to understand how species at similar sites may respond differently to conservation and restoration measures. In the present study, two populations with many common ecological features have in fact different functional habitats. A quick diagnostic based on similar ecological requirements could be misleading for conservation strategies. Both species need in fact distinct structural elements in the vegetation. Cutting trees and shrubs to create more open vegetation on the one hand, and sod-cutting of tussocks to regenerate vegetations on the other, will have very different impacts on the two species (or populations). Behavioural aspects and associated structural vegetation characteristics can be as important for habitat-use and ultimately local population viability as, for example, more widely recognized ecological resources like host plants.

Niche breadth and overlap

Niche breadth was very narrow for both species, confirming their specialist nature. Specialisation was particularly pronounced at larval stage, which has rarely been shown in other studies (Smallidge, Leopold and Allen 1996). Their ecological similarity at coarser level would suggest that their distribution mainly coincides. Barascud and Descimon (1992) investigated the distribution range of both species at continental European scale and showed that *L. helle* can be found in regions where *P. eunomia* is present but the reverse was not true. At local scale, our results showed, however, the opposite relationship: *P. eunomia* populations were found in nearly every zone where the host plant occurred at reasonable density, whereas this was not the case for *L. helle*. Our quantitative, resource-based study at micro-scale suggests that *L. helle* is a more demanding species of greater conservation concern. The absence of *P. eunomia* in regions where *L. helle* is present seems mainly due to differences in colonisation routes at the end of the previous glacial period, as shown by the successful introduction of *P. eunomia* in the Morvans (northeastern France, Neve et al. 1996).

There was a high degree of niche overlap which usually indicates significant interspecific competition (Tilman 1982). However, we argue based on several lines of evidence that their coexistence is possible without competition. Firstly, food competition hypothesis at the larval stage is relaxed because host plant is not likely to be a limiting resource in this system given its high abundance and because caterpillars of the two butterfly species use it in different microclimatic conditions (Abrams 1980). Secondly, there is limited temporal overlap (<50%) in

adult flight periods, which allows a non synchronous resource utilization (Schoener 1970). Thirdly, behavioural observations showed that *L. helle* males defended their territory against intra- and interspecific intruders, including *P. eunomia* males. Mikami and Kawata (2004) suggested that interspecific territoriality may reduce interspecific competition and leads to species coexistence. Moreover, "repulsive behaviour between conspecific males (…) creates space for competing species, which promotes their coexistence (…) even when their ecological niches completely overlap" (Mikami, Kohda and Kawata 2004 p. 213). Finally, as pointed out by Schoener (1970), interpretation of comparison from contingency tables must be done cautiously as environmental variables used in the separate comparisons might be highly associated. Associations between resources artificially raise niche overlap estimation and it might be the case in our study due to the strong associations existing between some resources. Strategies of habitat selection would allow species coexistence provided that different specialised strategies have evolved in order to exploit separate habitats within the same area (Friberg et al. 2008).

Defining habitat for conservation purposes

Our results provide a first-hand opportunity to test commonly used definitions of habitats. The classical, widespread geographical habitat definition (Odum 1971) only has limited conservation and restoration interest. A more precise definition of habitat relies on the use of physionomical or phytosociological hierarchical classification (Hall, Krausman and Morrison 1997). Accordingly, habitats are mapped at a

particular level of such a classification (Baguette and Mennechez 2004). However, resources required by a species can be distributed widely in several biotopes or in several vegetation types. Moreover, the tendency to neglect small-scale habitat heterogeneity may result in management that homogenizes essential heterogeneity within and between vegetations. As a consequence, and according to species mobility and requirements, these definitions may underestimate or overestimate both the area and the amount of habitat (Dennis, Shreeve and Van Dyck 2003b; Dennis, Shreeve and Van Dyck 2006a, Vanreusel and Van Dyck 2007). The problem of overestimating the effective habitat area should receive more attention in the context of species conservation, like for the Natura 2000 program, as it may challenge the effectiveness at least in some cases (McLean, Wight and Williams 1999).

Insect herbivores habitats have often been defined as larval host plants patches. The allocation of resources during larval stages can be of major influence to holometabolous insects (Coley, Bateman and Kursar 2006). Nectar resources and non consumable resources have often been ignored (Dennis 2004a), but they are nowadays more frequently recognized as important habitat components (Loertscher, Erhardt and Zettel 2008). We have therefore adopted a functional, integrative approach to recognize habitat, by determining the precise habitat requirements for the organism instead of focusing on a single resource that is assumed to be the most important one. In our study, *P. eunomia* adults are restricted to host plant patches as the host plant is the only nectar resource used, but particular conditions are needed for the caterpillars. In this case, ecological needs of adults encompass larval needs and habitat is closely related to host plant patches. However, for *L.*

helle, we have shown that habitat is not restricted to host plant patches. The assimilation of habitat to host plant patches seems then applicable only for extremely specialist butterfly species as *P. eunomia* and *M. cinxia* (Baguette and Nève 1994; Hanski, Kuussaari and Nieminen 1994; Shreeve, Dennis and Van Dyck 2004).

From a conservation viewpoint, it is now empirically recognised that habitat is best understood in terms of resource distributions rather than in terms of surrogate variables (Dennis, Shreeve and Van Dyck 2003b; Mitchell 2005; Dennis, Shreeve and Van Dyck 2006a). Hall et al. (1997 p175) defined habitat as "the resources and conditions present in an area that produce occupancy – including survival and reproduction - by a given organism", including migration and dispersal corridors. Butterfly habitats involve more than just the presence of host plant and nectar resources; vegetation structures provide an important component for thermoregulation, resting, hibernation and locating mates. Besides this spatial component, the tempo of resource use and its variation are also important: during our two year study, we noticed that the flying period of both species were either overlapping or fully dissociated. This is why an accurate definition of required resources related to careful behavioural observations is of prime importance to design optimal conservation strategies. Moreover, the recognition of relevant spatial and temporal scales is essential (Wiens 1989; Holland, Bert and Fahrig 2004); those scales should map to the processes acting on the organism under investigation rather than being convenient to the observer or being defined according to human perception only. This, more generally, illustrates the key importance of behaviour for conservation (Sutherland 1998).

Chapter II

Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change.

Chapter II is a submitted manuscript:
Turlure, Choutt, Baguette & Van Dyck
Global Change Biology

Chapter II: Illustration cover by Camille Turlure

ABSTRACT.

Opposite to several organisms that have already shown range shifts to the north as a response to climate change, southern populations of relict species are trapped in isolated altitudinal habitats. Therefore, there is a growing interest to better understand their habitat-use, with particular attention to the thermal aspects and associated significance for their habitat management.

We address this issue by a study of larval habitat-use relative to vegetation structure and microclimate in a glacial relict butterfly of peat bog ecosystems, using a functional, resource-based approach of the habitat. We analyzed caterpillar presence and density relative to vegetation composition (reflecting gradients of humidity, temperature, and natural succession of peat bog) and to the availability and quality of thermal refuge structures for caterpillars (i.e. *Sphagnum* hummocks). We also tested survival rates of caterpillars under different temperature and humidity treatments.

We found that (1) *Boloria aquilonaris* was a specialist butterfly of early successional stages of peat bog (i.e. floating mats and swamps), (2) the lack of thermal refuge structures (i.e. *Sphagnum* hummocks) reduced the larval habitat suitability, and hence the carrying capacity of a site, and (3) a reduction of the thermal buffering ability of *Sphagnum* hummocks was observed in late-successional stages or degraded parts of peat bog. Our larval rearing experiment showed a significant impact of

temperature only on caterpillar survival; survival being higher at lower temperature.

Our field and laboratory results support the idea that the thermal environment exploited by caterpillars should be considered as a functional resource and included in a population-specific habitat definition. Appropriate management of the peat bog habitat of this glacial relict species should not exclusively focus on the larval and adult feeding resources, but also on the quality of thermal micro-environments provided by *Sphagnum* hummocks, especially in the current critical context of climate warming.

II.1 INTRODUCTION

A range of different animals and plants has been observed to shift their distribution or phenology in response to current climate change (Walther *et al.* 2002; Parmesan and Yohe 2003; Hickling *et al.* 2005; Parmesan 2006; Best *et al.* 2007). In temperate-zone thermophilous organisms, like many butterflies, regional warming may increase the thermal accessibility to a wider range of habitats across the landscape. For example, the combined effect of appropriate management and of climate warming has recently improved the availability of thermally suitable habitat for the silver-spotted skipper butterfly *Hesperia comma* in the south of the UK (Thomas *et al.* 2001a; Davies *et al.* 2005; Davies *et al.* 2006). As a result, the conservation status of the species has improved significantly. However, in the case of glacial relict species at lower latitude, the opposite scenario is likely to occur with climate warming (Franco *et al.* 2006). In these regions, their fragmented populations are typically trapped in altitudinal habitat providing little, or even no, opportunities to shift their regional range uphill (e.g., Konvicka *et al.* 2003; Wilson *et al.* 2007) or to the north (e.g., Warren *et al.* 2001; Hill *et al.* 2002; White and Kerr 2006; Pöyry *et al.* 2009). This issue significantly increases the conservation concern of glacial relict species in ecosystems like peat bogs. Hence, a better understanding of the ecological mechanisms of habitat-use causing the observed (and predicted) temporal and spatial patterns of change is a key challenge for ecologists in the era of climate change and biodiversity crisis. This includes a better understanding of the thermal properties of vegetation structures and how they can be influenced by appropriate management.

The patterns of responses by species to climate change can be detected regionally, but the ecological and evolutionary mechanisms behind them operate locally, at the level of populations and individuals. This issue is closely related to the conceptual question of what really makes up a species' habitat (Boyce and MacDonald 1999; Dennis, Shreeve and Van Dyck 2003b) and it stresses the role of the thermal dimension of habitat use and suitability (Magnuson, Croder and Medvick 1979; Sinclair *et al.* 2003). The functional resource-based approach of habitat recognizes the fundamental requirements of organisms (Dennis, Shreeve and Van Dyck 2003b; Dennis, Shreeve and Van Dyck 2006a; Turlure *et al.* 2009b), both consumables and utilities, the latter describing suitable environmental conditions as well as essential substrates rather than using vegetation types (or biotopes) as surrogates for a species' habitat (Dennis and Shreeve 2003). Especially in butterflies, non consumable resources such as temperature conditions required for larval stages have often been ignored (Dennis 2004a; Dennis 2004b), but they are likely to be important to fully understand current conservation challenges of glacial relict butterfly species.

Regional climate is filtered by local vegetation structures and substrates into a particular configuration of microclimates representing spatial and temporal thermal heterogeneity in the habitat (WallisDeVries and Van Swaay 2006; Aschcroft, Chisholm and French 2009). Herbivorous insects, such as butterflies, can respond at two levels. First, females may use thermal cues for oviposition site choice (Shreeve 1986; Talsma *et al.* 2008), which will determine the future micro-environment of the offspring (Rausher 1979; Nylin, Janz and Wedell 1996; Doak, Kareiva and Kingsolver 2006). Secondly, caterpillars may also adjust

their body temperature by moving among substrates that differ in thermal profile (Sherman and Watt 1973; Casey 1976; Bryant, Thomas and Bale 2000; Bryant, Thomas and Bale 2002). The temporal variation (or change) of a thermal environment induces a variation (or change) in the localization of the optimal thermal niche within the micro-environment (Tracy and Christian 1986). Caterpillars have a low thermal inertia; therefore small differences in ambient temperature may translate into significant changes in body temperature (Heinrich 1993). The interaction between the availability of microclimates and the behaviour of the caterpillar determines operational body temperature and, hence, the physiological conditions to grow and survive. The selection for thermally favourable microclimates is a primary mechanism of temperature control (Stevenson 1985) and has been observed for several species (see *Cydia pomonella* in Kührt, Samietz and Dorn 2005; *Eriogaster lanestris* in Joss *et al.* 1988 and Ruf and Fiedler 2002). For example, caterpillars were observed avoiding overheating by moving into less exposed sites during the hottest period of the day (Casey 1976; Frears, Chown and Webb 1997; Nice and Fordyce 2006).

In this paper, we address larval habitat-use relative to vegetation composition and microclimatic conditions in a glacial relict butterfly of the peat bog guild, the cranberry fritillary *Boloria aquilonaris*. Although adults appear to be typical heliotherm butterflies that require nectar sources and sufficiently high ambient temperature to maintain their body temperature during flight, caterpillars are thought to be particularly adapted to cool and humid environmental conditions (cf. Addo-Bediako, Chown and Gaston 2002). We particularly deal with the following hypotheses:

1. Firstly, at the ecosystem scale, we analysed the presence of *B. aquilonaris* caterpillars relative to vegetation composition in two peat bog landscapes. Being a peat bog specialist, we predict that the occurrence of caterpillars is mainly confined to host plant patches of early successional peat bog stages (i.e. more humid conditions and higher dominance by *Sphagnum* moss species).

2. Secondly, at micro environmental scale we also analysed the caterpillar density relative to vegetation composition and availability and thermal properties of the *Sphagnum* hummocks. *Sphagnum* hummocks, which form one of the structural elements of hummock/hollow complexes of the peat bog, provide a variety of micro-environments (Nungesser 2003) and it has been demonstrated that they buffer the ambient temperature into a stable and cool environment (van der Molen and Wijmstra 1994). Hence, we hypothesise that *Sphagnum* hummocks act as cold thermal refuges for the caterpillars of this glacial relict species. We predict higher caterpillar densities in (i) again host plant patches of earlier successional stage, and ii) in patches with higher degree of thermal buffering against daily temperature fluctuations by *Sphagnum* hummocks.

3. In the laboratory, we tested caterpillar survival under different conditions of temperature and humidity. This was done to confirm directly the significance of those microclimatic factors for caterpillar survival, and hence, for the functional significance of larval microhabitats provided by *Sphagnum* hummocks.

4. Some changes in vegetation composition can occurred according mainly to the decrease of the water table level: pioneer stages become gradually dominated by vascular plant species at the cost of moss species until heathlands (Mauquoy and Yeloff 2007). These changes are natural processes, but can be accelerated by nearby spruce plantations and by regional warming (Hendon and Charman 2004; Heijmans *et al.* 2008). Finally, we discuss peat bog management relative to this thermal dimension of larval habitat-use.

II.2 METHODS

Study species

The cranberry fritillary, *Boloria aquilonaris* (Stichel 1907), is a glacial relict butterfly of acid peat bogs and damp heaths (Bink 1992). Adults fly in July and eggs are laid singly on the underside of the leaves of the host plant, *Vaccinium oxycoccos*. This species has a boreo-alpine distribution, with highly fragmented populations to the south (like in Belgium). *B. aquilonaris* is listed as vulnerable on the Red Data Book of European butterflies (van Swaay and Warren 2006) and, hence, also as a species of high conservation importance in Belgium (Fichefet *et al.* 2008). Earlier studies have particularly addressed its demography, including metapopulation dynamics and population viability (Baguette 2003; Baguette and Schtickzelle 2003; Schtickzelle, WallisDeVries and Baguette 2005b).

Study sites and populations

We collected field data in two ombrotrophic peat bogs having each one population of *B. aquilonaris*: the Fange de Pisserotte nature reserve (S-Belgium: 50°13'N 5°47'E) and the Troufferies de Libin nature reserve (S-Belgium: 49°57'N 5°19'E). The host plant *V. oxycoccos*, occurred in high density in 15 (9748 m²) and 9 (10643 m^2) patches in Pisserotte and Libin, respectively. Mean host plant patch area did not differ between the study sites (t-test: t = 1.54, dF = 33, $P = 0.132$).

During the summers of 2006 and 2007, we did standard transect counts of *B. aquilonaris* adults in each site (8 and 5 repetition in Libin, and 9 and 5 repetitions in Pisserotte in 2006 and 2007, respectively). Total length of each transect repetition was 4200m for Pisserotte and 3400m for Libin. Adult transect counts were only done under suitable weather conditions that allow butterfly activity (i.e. no strong wind, few or no clouds and air temperature > 15°C). Transect length was 4200m for Pisserotte and 3400m for Libin. We calculated daily adult densities for the two populations from the transect count data by weighing the total daily number of individuals by the total transect length. These daily densities were compared by two-way crossed ANOVA. *B. aquilonaris* density was six times higher in Libin compared to Pisserotte (Site effect: $F_{1,24}$ = 3.45, P = 0.002), not significantly different between both years (Year effect: $F_{1,24}$ = 1.39, P = 0.18) and the difference in adult density between sites did not differ significantly between years (Site x Year effect: $F_{1,24}$ = 1.01, P = 0.33).

Modeling caterpillar presence

In May and June, we searched for caterpillars by visual inspection in all host plant patches (Pisserotte: 2745 and 950 minutes in 2005 and 2006, respectively; Libin: 655 and 410 minutes in 2006 and 2007, respectively). We recorded the abundance of each plant species (N_{total} = 54 species) in one square meter plots for each caterpillar found and for a series of equally sized control plots in host plant patches where no caterpillar was found (Pisserotte: 50 caterpillar plots and 30 without; Libin: 42 caterpillar plots and 5 control plots). Each plot was divided in

25 equal squares and plant abundance was computed on the basis of its presence on each square (i.e. on a zero to 25 scale). Firstly, we summarized vegetation data of all 127 plots by Detrended Correspondance Analysis (DCA, in Canoco software Version 4.5) using the abundance of the plant species (Legendre and Legendre 1998; Ter Braak and Smilauer 2002). Secondly, we calculated local conditions of moisture and temperature using abundance-weighted means of Ellenberg indicators values of plant species for each plots (Ellenberg 1974). Each plants species has been given an indicator value for moisture and temperature on a semi-quantitative scale according to the classification of Ellenberg (1974). We computed the average of these values for each plot, weighted by the mean abundance of each plant. This procedure takes advantage of the integrative character of the plant's presence over time relatively to the instantaneous character of direct but punctual measures of moisture and temperature. Thirdly, we tested correlations between vegetation composition (i.e. the first two axes of the DCA: DCA1 and DCA2) and the two microclimatic variables. Finally, logistic regressions were used to relate caterpillar presence to vegetation characteristics using AIC-based model selection (Burnham and Anderson 2002b; Anderson 2008). Predictor variables used in the model selection were the two first axes of the DCA (DCA1 and DCA2), their quadratic terms ($DCA1^2$ and $DCA2^2$) and the interactions between site and these four variables. As there was no difference in adult population densities between years (see above), data on caterpillar presence of different year were pooled in the same analysis.

Sphagnum hummocks covered by the host plant were mostly used by caterpillars

In both sites, *V. oxycoccos* (i.e. the unique host plant for the caterpillars), can be found on *Sphagnum sp*. carpets (15 % and 66 % of the host plant area in Libin and Pisserotte, respectively) or hummocks (85% and 15% of the host plant area in Libin and Pisserotte, respectively). In Pisserotte, it also growths on *Polytrichum sp.* hummocks (19 %). More than 90% of *B. aquilonaris* caterpillars were found on *Sphagnum* hummocks. As no caterpillar was ever found on host plants growing on *Polytrichum* hummocks in Pisserotte, we predicted a difference in microclimatic conditions offered by both substrates. To test this prediction, six temperature recorders were placed at three different depths of a *Sphagnum* hummock and a *Polytrichum* hummock: the first one on the top, the second one at 15 cm depth and the third one at 30 cm depth. Temperature was recorded every minute between June 26 and July 3 in 2006. We observed differences in temperature between recorder positions within the hummock and between the two hummock types.

Modeling caterpillar density

Caterpillar density relative to vegetation characteristics and microclimatic conditions was studied in the Libin population only. In May 2008, we counted caterpillars along nine caterpillar transects of 20 m length and 5 m width each. Each caterpillar transect was located in zones with high host plant density to discard any effect of host plant abundance on caterpillar density. This was done two times and

caterpillars from the first count were taken to the laboratory for a rearing experiment (see below). On each caterpillar transect, we recorded: (1) the abundance of each plant species (N_{total} = 28 species) on a zero to 25 scale in five plots of one square meter randomly spread along each caterpillar transect, (2) the total area of available *Sphagnum* hummocks in each caterpillar transect and (3) the temperature within one *Sphagnum* hummock with temperature recorders. For this last measure, we selected one representative hummock of similar size (same diameter and same height) in each caterpillar transect and we placed two temperature recorders at each hummock: one at the top and one at 20 cm depth. Temperature was recorded every 150 s between May 22 and June 23 2008.

From the temperature data, we inferred the mean temperature at the hummock surface and the thermal buffering ability of the hummock calculated as the variance of the difference between temperature on the top and inside the hummock. If temperatures at both positions vary in the same way, the difference between these two temperatures is constant. However, when the temperature inside the hummock is stable, whereas the surface temperature fluctuates, the difference between these temperatures will vary as well. Hence, the higher the variance of this difference, the better is the buffering ability of the hummock.

Similarly as before, we performed a Detrended Correspondance Analysis (DCA) on the abundance of plant species in the 45 plots along caterpillar transects. We calculated local conditions of moisture and temperature using abundance-weighted means of Ellenberg indicators values of plant species for each caterpillar transects and we tested

correlations with vegetation composition (i.e. the first two axes of the DCA). Caterpillar density was analyzed relative to the first two axes of the DCA, the total *Sphagnum* hummock area, the mean temperature at the hummock surface and the buffering ability of hummock by linear regression (using AIC-based model selection).

Caterpillar survival relative to temperature and humidity

We tested the effect of temperature and humidity on caterpillar survival in the laboratory with 136 field-collected caterpillars. Caterpillars were assigned to one of three size or age groups (T1: caterpillars prior to their final instar; T2: caterpillars at the beginning of their final instar, T3: caterpillars at the end of the final instar) and kept individually in Petri dishes. Next, we assigned each caterpillar to one of four treatment groups represented by the combination of high against low temperature and high against low humidity. Caterpillars were homogeneously distributed according to their size across the experimental treatments (χ_3^2 = 1.07, P = 0.98) to avoid biases. Low humidity treatment corresponded to one piece of *Sphagnum* in the Petri dish compared to six pieces in the case of high humidity. Half of the Petri dishes of the high humidity and of the low humidity treatment group were placed in a climate room at high temperature, and half at low temperature. To approach field conditions, both climate rooms had the same low temperature during the night (i.e., 10°C), but different temperatures during the day: 25°C for the high temperature treatment and 20°C for the low temperature treatment. These values correspond to daily average temperatures recorded on the top of hummocks. Every two days, we cleaned the Petri dishes and

provided new young *V. oxycoccos* leaves and new pieces of *Sphagnum*. We followed caterpillar survival until pupation. Emerging individuals were released in the field. We used logistic regression models to compare survival rate between the experimental treatments (temperature effect, humidity effect and crossed factors).

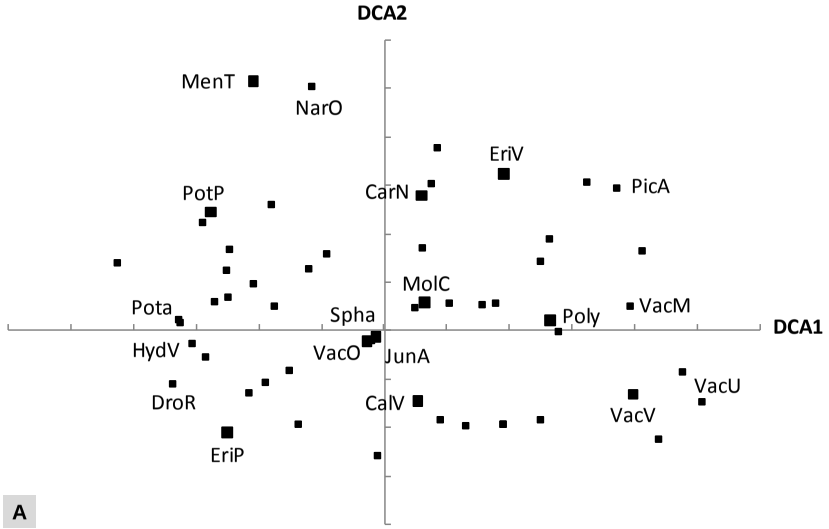
II.3 RESULTS

Caterpillar presence relative to vegetation composition

Variation in vegetation composition was summarized by DCA-analysis into two composite axes (**Figure II.1A**). The first axis (DCA1) was negatively correlated with humidity and positively with temperature (Pearson correlation tests; humidity: $P < 0.001$, R = -0.72; temperature: $P < 0.001$, R = 0.38, **Figure II.1B**). Lower values of DCA1 corresponded to the presence of hygrophilous plant species (e.g. *Hydrocotyle vulgaris*, *Potamogeton sp.* and *Drosera rotundifolia*), whereas higher values were associated with plant species that were less dependent on high humidity, as *Polytrichum sp.* and *Vaccinium* species, with colonization by young spruce trees and spruce plantations in their surroundings. The second axis (DCA2) was negatively correlated with temperature (Pearson correlation tests; humidity: $P = 0.96$, R = 0.004; temperature: $P = 0.004$, R = -0.25). This axis reflected natural succession of peat bogs, from pioneer stages (higher values) towards heathlands (lower values) (**Figure II.1B**). Overall, a larger part the Libin peat bog had more humid conditions compared to the Pisserotte peat bog and the occurrence and abundance of *Calluna vulgaris* and *Vaccinium* bushes were limited, indicating that natural succession in the former peat bog had not yet reached the heathland stage (**Figure II.1B**). The abundances of *Sphagnum sp*. and of *V. oxycoccos* were very similar in all the plots explaining their highly central position on **Figure II.1A**.

Presence of caterpillars was related by this synthetic description of the vegetation by logistic regression. Among models with the smallest AIC values, we selected the one using the fewer number of variables according to the parsimony rule (i.e. model selected: DCA1 + DCA2 + DCA2 x Site + $DCA2^2$). Accordingly, caterpillar presence was significantly related to vegetation composition **(Table II.1, Figure II.1C)**. Caterpillars were more likely to occur under more humid and cooler conditions with lower abundance of *Polytrichum sp.* (i.e., lower values of DCA1) and in pioneer stages (i.e., lower values of DCA2). The additional positive effect of $DCA2^2$ indicated that the probability of caterpillar presence along DCA2 had an optimum for lower values of DCA2. Succession towards heathland had a stronger effect on caterpillar presence in Pisserotte compared to Libin as shown by the interaction effect.

Figure II.1. A) Graphical representation of the DCA using the plant species abundance from the 92 caterpillar plots and the 35 control plots in both sites. Black squares represented position of each plant species in the bidimensional graph; bigger squares represented plant species that contributed the most to the axis formation. CalV = *Calluna vulgaris*; CarN = *Carex nigra*; DroR = *Drosera rotundifolia*; EriP = *Eriophorum polystachion*; EriV = *Eriophorum vaginatum*; HydV = *Hydrocotyle vulgaris*; JunA = *Juncus acutiflorus*; MenT = *Menyanthes trifoliata*; MolC = *Molinia caerulea*; NarO = *Nartessium ossifragum*; PicA = *Picea abies*; Poly = *Polytrichum sp.*; PotA = *Potamogeton sp.*; PotP = *Potentilla palustris*; Spha = *Sphagnum sp.*; VacM = *Vaccinium myrtilus*; VacO = *Vaccinium oxycoccos*; VacU = *Vaccinium uliginosum*. **B)** Horizontal axis (DCA1) represents a gradient of humidity and temperature and vertical axis (DCA2) represents natural succession of peat bogs, from pioneer stages to heathlands. **C)** Calculated caterpillar presence probability is represented by a grey value gradient, from high presence probability (black area) to low presence probability (light grey area), for both sites separately. Caterpillar presence was higher under more humid conditions (lower values of DCA1) and in pioneer stages (higher values of DCA2) for both sites. White points = observed caterpillar plots. White crosses = observed control plots.


DCA2
MenT
NarO
EriV
PicA
PotP
CarN
MolC
Pota
Spha
Poly
VacM
DCA1
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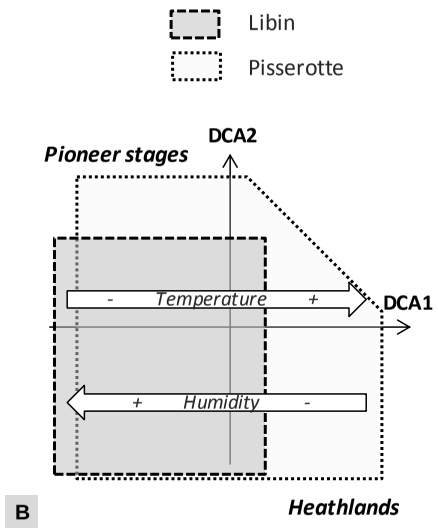
VacO
JunA
VacU
DroR
CalV
VacV
EriP
A


Libin
Pisserotte
DCA2
Pioneer stages
- Temperature +
DCA1
+ Humidity -
Heathlands
B

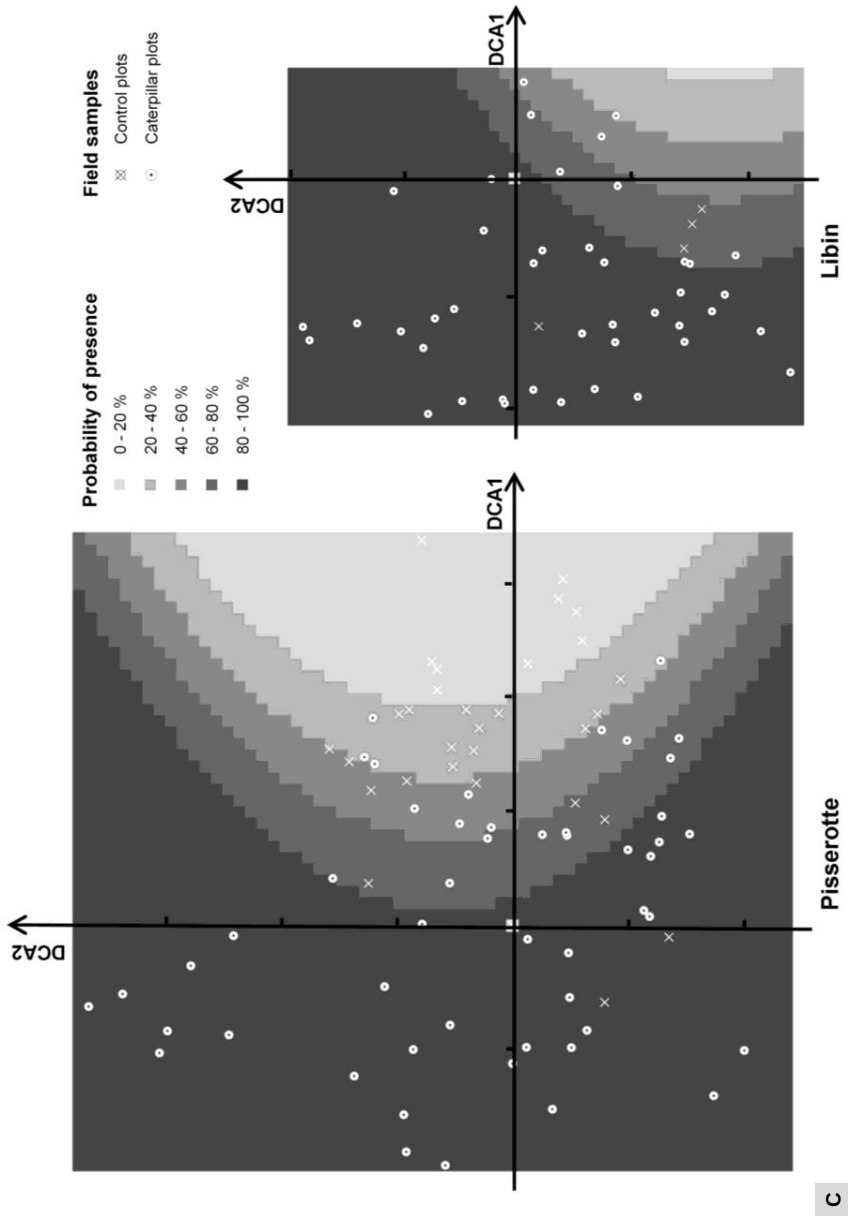

Field samples
Control plots
Caterpillar plots
Probability of presence
0 - 20 %
20 - 40 %
40 - 60 %
60 - 80 %
80 - 100 %
DCA1
DCA2
Libin
DCA1
DCA2
Pisserotte
C

Table II.1. Results of the logistic regression of *B. aquilonaris* caterpillar presence according to vegetation composition showed that caterpillars were more likely to occur under more humid and cooler conditions (lower values of DCA1) and in pioneer stages of the peat bog (lower values of DCA2). The additional positive effect of $DCA2^2$ indicated that probability of caterpillar presence along DCA2 had an optimum for lower values of DCA2. Succession towards heathland had a stronger effect on caterpillar presence in Pisserotte compared to Libin as shown by the interaction effect. A single model was selected among the models with lowest AIC values according to the parsimony principle.

Parameter	Modality	Estimate	Standard error	Wald 95% Confidence Limits	
Intercept		1.781	0.517	0.769	2.794
DCA1		-3.147	0.669	-4.457	-1.837
DCA2		-1.051	0.696	-2.416	0.314
$DCA2^2$		1.716	1.196	-0.629	4.060
DCA2 x Site	Libin	4.465	1.685	1.162	7.767
	Pisserotte	0			

Caterpillar behaviour and thermal profiles of hummocks

Caterpillars were observed basking on old stems or feeding on young leaves and stems of the host plant *V. oxycoccos* that grows on the *Sphagnum* hummock surface. However, this was only during periods of the day with cooler ambient temperature and lower solar radiation (i.e. early in the morning or late in the evening under sunny conditions, or all along the day under cloudy conditions). Under unsuitable temperature conditions or higher solar radiation (i.e. midday under sunny conditions or when clouds disappeared), they left the host plant and entered inside the *Sphagnum* hummocks, at different depth of the acrotelm layer.

Surface temperature of *Sphagnum* and *Polytrichum* hummocks varied considerably, ranging from 5°C at night to 30°C at noon. Besides, temperature inside the hummocks differed strongly between *Sphagnum* and *Polytrichum* hummocks. *Sphagnum* hummocks provided a very stable thermal environment of 12°C at 30 cm depth, whereas temperature inside *Polytrichum* hummocks at the same depth fluctuated between 8°C and 18°C (**Figure II.2A and B**).

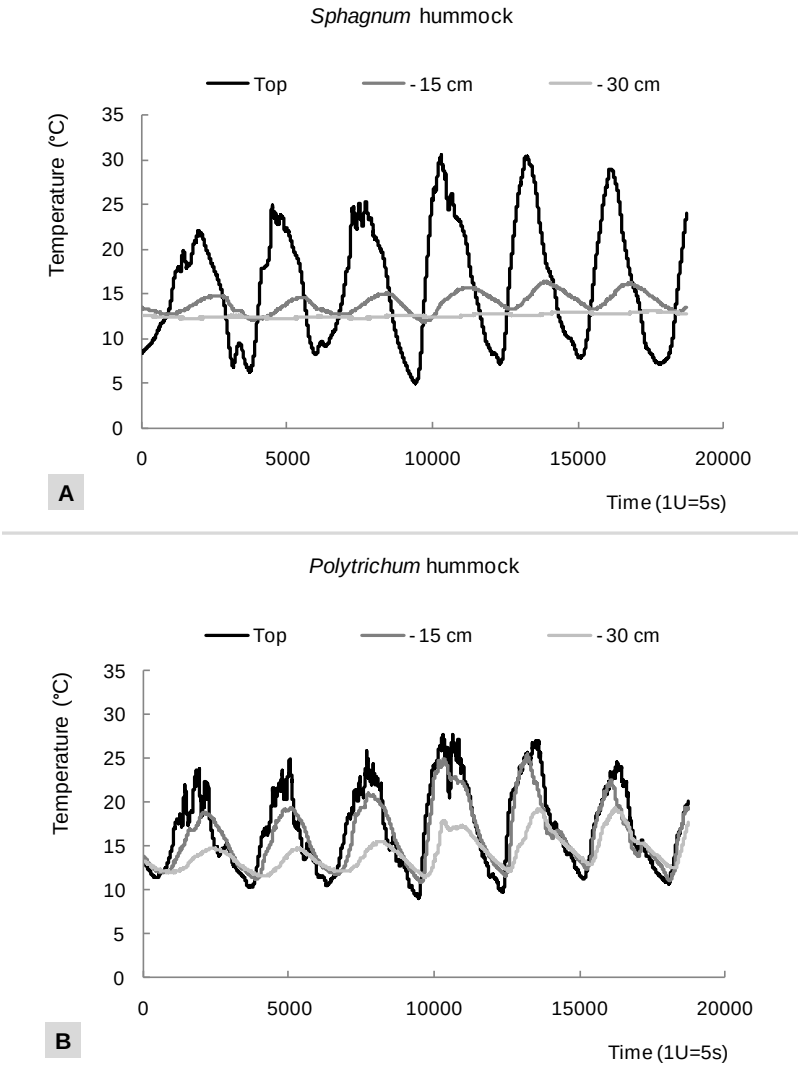


Figure II.2. Variation of temperature in three different depths (at the surface, at 15 cm and at 30 cm depth) in a *Sphagnum* hummock (**A**) and a *Polytrichum* hummock (**B**). Surface temperature of both types of hummock varied considerably between 5°C to 30°C. Temperature inside *Sphagnum* hummocks was much more buffered (at 30 cm depth stable at 12°C) than inside *Polytrichum* hummocks.

Caterpillar density

The gradients in vegetation composition as shown by DCA in the different caterpillar transects in the Libin nature reserve (**Figure II.3A**) were very similar to those presented above on the larger data set of vegetation plots. The first axis (DCA1) was correlated to Ellenberg indicator values of humidity (Pearson correlation tests; humidity: P = 0.007, R = -0.82; temperature: P = 0.44, R = 0.29). Hence, it represented a gradient of humidity, from aquatic plant species growing in open pools and peat bog hollows (higher values of DCA1) to plant species growing on wet soil of fens (lower values of DCA1) and near spruce plantations. The second axis (DCA2) was not correlated to humidity and temperature conditions; its only classified successional stages, from pioneer stages (higher values of DCA2) to rushes, fens and local colonization by *Calluna vulgaris* (lower values of DCA2). Abundances of *Sphagnum sp*. and *V. oxycoccos* were similar across all caterpillar transects (**Figure II.3A**).

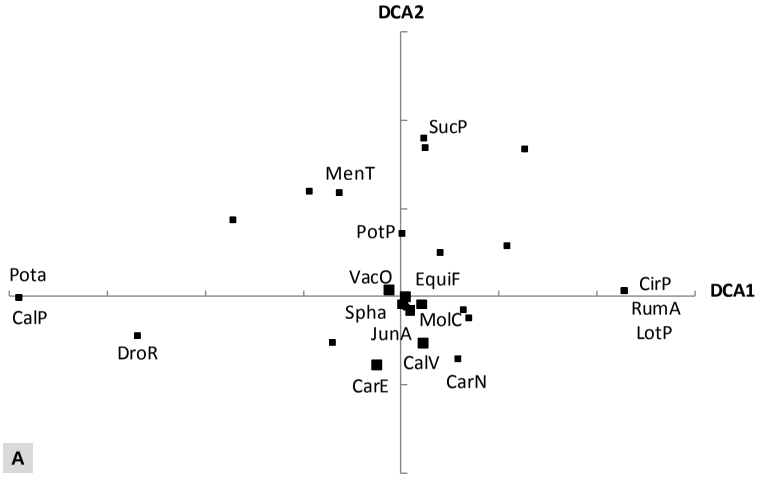
Mean temperature on the hummock surface ranged from 14.5 °C to 16.9°C. This surface temperature was somewhat higher in transects where *Sphagnum* occurred under wetter conditions (16.1°C on average) compared to transects where *Sphagnum* occurred under drier conditions (15.1°C on average). Buffering ability between caterpillar transects was markedly different; temperature differences between the top and the center of the hummocks ranged from 8.8 to 12.3°C in drier transects and from 14.4 to 23.6°C in more humid transects. Buffering ability was then higher under more humid conditions and lower under drier conditions (i.e. near spruce plantations).

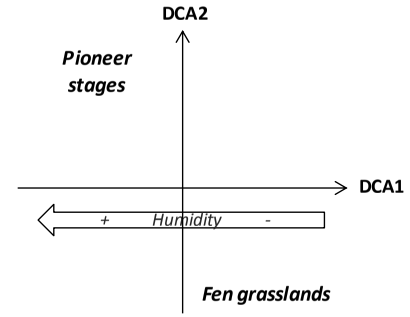
We counted 268 *B. aquilonaris* caterpillars. Numbers decreased from 74 under wetter conditions to only 1 under drier conditions. **Figure II.3B** shows caterpillar density along the environmental gradients. The best model selected according to AIC criterion (**Table II.2**) showed that caterpillar density was higher under more humid conditions (lower values of DCA1) and in pioneer stages (higher values of DCA2). Additionally, caterpillar density was higher under greater thermal buffering ability of the *Sphagnum* hummocks (with higher values of the variance of the difference between temperature at the top and inside *Sphagnum* hummock.

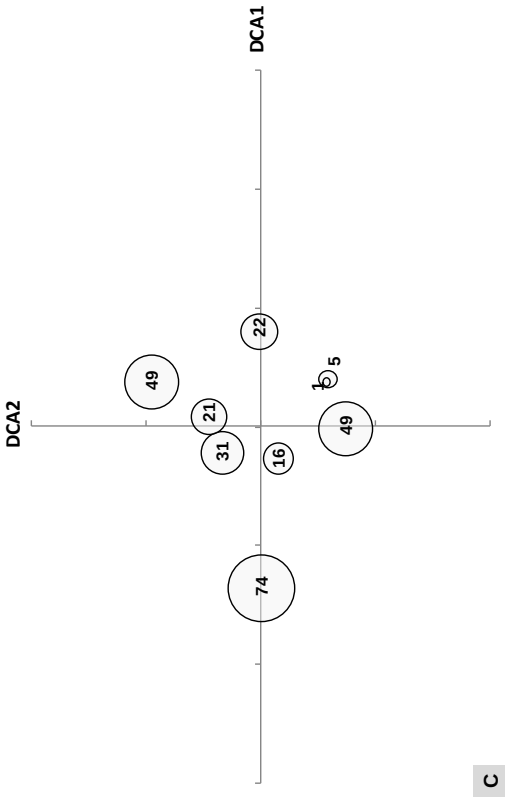
Table II.2. Results of the linear regression in Libin showed that (1) density of caterpillars was higher under more humid conditions (lower values of DCA1) and in floating mats compared to rushes and fens (higher values of DCA2). Caterpillar density increased with thermal buffering ability of the *Sphagnum* hummocks (Temp_Var). Total area of available *Sphagnum sp*. hummocks and mean temperature on hummock surface in each caterpillar transects had no effect on caterpillar density. Based on AIC, a single model was better and, hence, selected.

Parameter	Estimate	Standard error	Wald 95% Confidence Limits	
Intercept	0.648	0.373	-0.082	1.378
DCA1	-0.538	0.094	0.354	0.721
DCA2	1.626	0.208	1.219	2.033
Temp_Var	0.187	0.024	0.139	0.234

Figure II.3. A) Graphical representation of DCA using the plant species abundance from the 45 plots in the nine transects in Libin. Black squares represented position of each plant species; bigger squares represented plant species that contributed the most to the axis formation. CalP = *Calla palustris*; CalV = *Calluna vulgaris*; CarE = *Carex echinata*; CarN = *Carex nigra*; CirP = *Cirsium palustris*; DroR = *Drosera rotundifolia*; EquiF = *Equisetum fluviatile*; JunA = *Juncus acutiflorus*; LotP = *Lotus pedunculatus*; MenT = *Menyantes trifoliata*; MolC = *Molinia caerulea*; Pota = *Potamogeton sp*.; PotP = *Potentilla palustris*; RumA = *Rumex acetosa*; Spha = *Sphagnum sp*.; SucP = *Succisa pratensis*; VacO = *Vaccinium oxycoccos*. **B)** Horizontal axis (DCA1) represents a gradient of humidity and vertical axis (DCA2) represents natural succession of the peat bog, from pioneer stages to fen grasslands. **c)** Circles size represented the number of caterpillar found (noted in the centre of each circles) in the nine caterpillar transects according to the vegetation composition (DCA1 and DCA2). Caterpillar number was greater under more humid conditions (lower values of DCA1) and in pioneer stages (higher values of DCA2).


DCA2
SucP
MenT
PotP
Pota
VacO
EquiF
CirP
DCA1
CalP
Spha
MolC
RumA
LotP
JunA
DroR
CalV
CarN
CarE
A


DCA2
Pioneer stages
DCA1
+
Humidity
-
Fen grasslands
B


DCA1
DCA2
22
49
21
31
16
5
49
74
C

Temperature and caterpillar survival

Across all laboratory treatments, caterpillar survival rate was high and ranged from 60% to 94%. Logistic regression models showed a significant effect of temperature conditions on survival rate ($P = 0.0012$), but there was no effect of humidity ($P = 0.15$) and also no effect of the interaction between temperature and humidity ($P = 0.56$). Independent of humidity, caterpillar survival rate was higher under low temperature conditions than under high temperature conditions (**Figure II.4**).

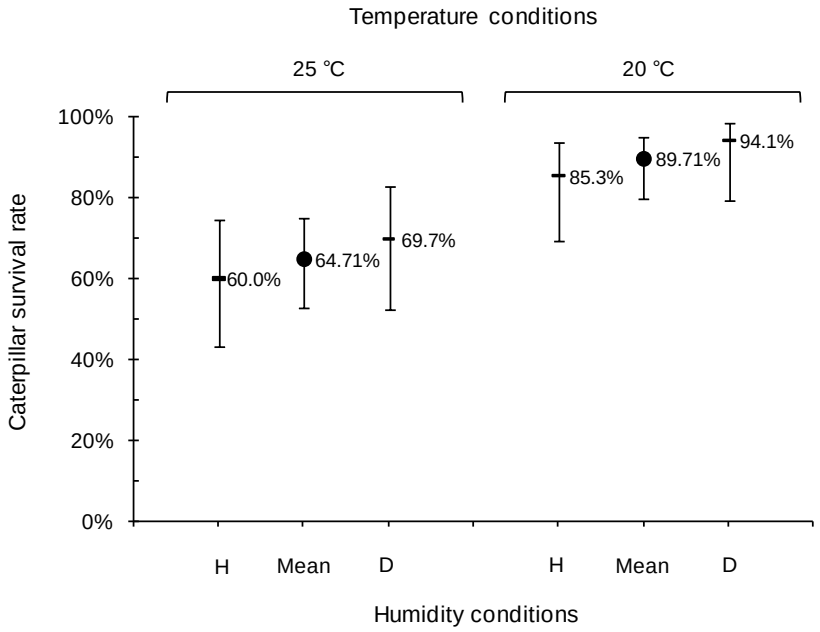


Figure II.4. Caterpillar survival rate (and 95 % confidence interval) relative to rearing treatment in the laboratory (humidity: D for low humidity treatment and H for high humidity treatment; temperature: daily temperature of either 20°C or 25°C). Survival of caterpillars was significantly higher under lower temperature conditions. No significant effect of humidity was found.

II.4 DISCUSSION

It has been recognized that several thermophilous ectotherms like butterflies use exceptionally warm microclimates in early successional vegetation stages for their larval stages in the cool climate of NW-Europe compared to the central and southern parts of their distribution where they also occupy cooler later successional stages (Thomas 1993; Warren *et al.* 2001). For glacial relict species, the situation may be similar but reversed, making them more vulnerable under climate warming.

Our field study on *B. aquilonaris* caterpillar presence and density relative to thermally-relevant differences in vegetation structure showed specific larval environmental requirements of this glacial relict butterfly at both the ecosystem and micro-environment scale. Firstly, caterpillars were largely confined to early successional stages of the peat bog ecosystem. Secondly, caterpillars were observed to exploit suitable micro-habitat provided by *Sphagnum* hummocks (but not other hummocks) within these early stages. Thirdly, a decline in the thermal quality of this micro-habitat through a reduction of its ability to buffer temperature against daily fluctuations is likely to affect caterpillar survival. We discuss the significance of these findings in relation to the larval ecology and conservation of this regionally threatened peat bog species in an era of climate change.

The host plant *V. oxycoccos* was widely distributed and typically occurred in high densities at both study sites. It either grew on *Polytrichum* hummocks, *Sphagnum* carpets or *Sphagnum* hummocks, but the vast majority of caterpillars (>90%) was found on *Sphagnum* hummocks only. Additionally, caterpillar density increased with thermal buffering ability of the *Sphagnum* hummocks in Libin. In line with van der Molen and Wijmstra (1994), our detailed temperature recordings suggest that *Sphagnum* hummocks function as thermal buffers for daily temperature fluctuations. Their interior part offered a stable environment at relatively low temperature. Caterpillars were observed to commute between the host plant just above the surface layer of the *Sphagnum* hummock and this relatively cool and stable environment inside the hummock according to surface temperature during the day. This behaviour enables caterpillars escaping from unsuitable, warm environmental conditions. Moreover, higher temperatures affected larval survival as shown by our lab experiment. Hence, we conclude that *Sphagnum* hummocks represent a key resource for the survival of this glacial relict species *B. aquilonaris* as they function as larval thermal refuge. The functional significance of this aspect of habitat-use is likely to increase with climate change. A comparative analysis of this thermal habitat aspect between southern and northern populations would be an interesting next step.

The thermal properties of *Sphagnum* hummocks do not exclude additional functions that can be important for caterpillar survival. During our lab experiment, we frequently observed caterpillars touching the

Sphagnum leaves with their mouth parts. This probably involves absorbing water and/or nutrients, which could help caterpillars avoiding desiccation stress after periods of host plant feeding under insolated conditions (Kührt, Samietz and Dorn 2005). It could improve caterpillar growth and survival (Rodrigues and Moreira 2004). *Sphagnum* hummocks may also help avoiding frost (as freezing depth rarely exceeds 20 cm depth) and flooding during earlier instars of the caterpillars during winter. The significance of hummocks to avoid attack by parasitoids requires further testing, but interestingly, there was not a single caterpillar parasitized in our study populations, as well as in five other populations (J. Choutt, unpublished data). This seems to be an unusually low parasitoid load for a butterfly (Thomas *et al.* 2002).

The total area of suitable caterpillar habitat (i.e. area with *Sphagnum* hummocks within host plant patches) was larger in Libin compared to Pisserotte (nearly 9000 m^2 in Libin VS less than 1500 m^2 in Pisserotte) and adult density was six times higher in Libin compared to Pisserotte. Since population density is likely to reflect the differences in quality and quantity of adult and larval resources between the sites (Dennis, Shreeve and Van Dyck 2006a; Turlure *et al.* 2009b), we argue, in our situation where parasitoids are absent, that (1) the lack of appropriate larval thermal environment principally reduces the carrying capacity (especially in the Pisserotte peat bog), and that (2) a decrease of thermal buffering ability of *Sphagnum* hummocks (as observed in the drier part of the Libin) represents a decline in habitat quality. As we focused on post-hibernation caterpillars only, our data could show the combined effect of oviposition choice and caterpillar survival. Further experiments are needed to disentangle the relative role of both

components in explaining the observed pattern of caterpillar distribution. Since oviposition behaviours can be under selection (e.g. Thompson and Pellmyr 1991), it would be interesting for a comparative analysis to include several populations with different resource settings and environmental conditions (including different vegetation management regimes).

Climate change will influence habitat quality through changes in vegetation composition

The combined effect of autogenic processes (i.e. natural succession from floating mats to heathlands, Mauquoy and Yeloff 2007) and human disturbance (i.e. spruce plantation and associated drainage, Hendon and Charman 2004) induces hydrologic changes in peat bog ecosystems. Lower water tables will lead to a reduction of *Sphagnum* hummocks and an expansion of shrubs (e.g. *C. vulgaris* and *Vaccinium* sp.). The successional gradient was clearly present at both study sites. The Libin peat bog had more humid conditions and a lower degree of shrub colonization. However, the close proximity of spruce plantations in the northern part of the peat bog locally reduced humidity. This is likely to affect the buffering ability of the *Sphagnum* hummocks in this zone. In the Pisserotte peat bog, succession towards heathland was clearly more advanced. The small areas of early successional stages with *Sphagnum* hummocks were sparse and surrounded by fens, wet meadows, shrubs and trees. Using data of both sites, we showed that caterpillar presence decreased with peat bog succession towards heathland and less humid conditions, even if the host plant is still widely distributed among the

later successional stages. Hence, this result confirms that the larval stage of *B. aquilonaris* is, at least in our region, strictly confined to early successional peat bog stages.

According to van Breemen (1995), *Sphagnum* mosses can be viewed as ecosystem engineers; they regulate the entire peat bog ecosystem, and support life under cold, wet and relatively acid conditions (Nungesser 2003). Moreover, the microstructure of peat bogs (i.e. hummock-hollows complex) results from the equilibrium of mean climate conditions, plant species growth and peat accumulation. Therefore, it is likely that the ongoing climate change will influence peat bog functioning, and as a consequence it is likely to impact on habitat suitability of glacial relict species like *B. aquilonaris*. Regional warming will exacerbate and accelerate the process of natural succession to drier, heathland-type of peat bog (Hendon and Charman 2004). As *Sphagnum* species are highly sensitive to changes in water level and temperature, drought is predicted to have deleterious effects (Heijmans *et al.* 2008). So based on our work combined with the peat bog literature, climate warming is predicted to reduce the availability and suitability of functional larval habitat of *B. aquilonaris*. Under warmer, drier conditions on the short term, caterpillars have to go deeper in the hummocks as the buffering ability will become less efficient, and it remains to be tested how such a change in activity budget may affect their survival. On the longer term, when the surface of *Sphagnum* hummocks shrinks, there will be a clear negative population response.

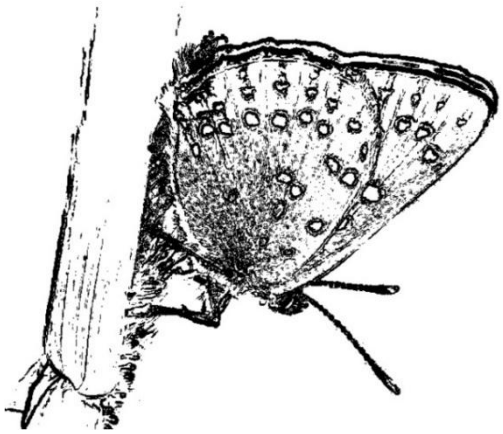
Mitigation effects of climate change for glacial relict species by peat bog management

Adapted management based on the general aspects of butterfly ecology including the conservation of abundant nectar and host plant resources (New *et al.* 1995) may not be enough, or even inappropriate, to conserve habitat of glacial relict species like *B. aquilonaris*. Our study clearly supports the idea that the thermal environment exploited by caterpillars should be considered as a functional resource (Magnuson, Croder and Medvick 1979; Tracy and Christian 1986), and hence, it should be taken into account together with the other larval and adult resources (Dennis, Shreeve and Van Dyck 2006a). So, thermal conditions and tolerances need to be explicitly included in habitat definition of ectotherm species of conservation concern in general, and glacial relict species in particular. Hence, an appropriate management of peatbog systems with an explicit goal to conserve a population of *B. aquilonaris* (or other glacial relicts) needs to maintain (or create) a sufficiently large surface of early successional stages. And from our study, we now know that only host plants on top of well developed *Sphagnum* hummocks are of functional significance. This thermal dimension, or in other words the thermally suitable subsample of hostplants, need to be considered for (meta)population viability analyses and conservation plans, actions and monitoring (Grundel and Pavlovic 2007). Restoration of degraded peat bogs requires a careful consideration of the hydrology of the system. Cutting surrounding spruce plantation and blocking the drainage effect will, for example, improve the hydrological self-regulating capacity of the local peat bog system via *Sphagnum* moss functioning (Smolders *et al.* 2003). Based on our results, it would be now warranted to monitor

how different restoration management methods affect the surface and configuration of functional larval habitat for *B. aquilonaris*. Although this conclusion has a wider validity, it appears to be essential for glacial relict species, especially to anticipate additional effect of global warming. Management to maintain or restore *Sphagnum* hummocks is likely to benefit also other species of the peat bog ecosystems. Several studies have demonstrated that *Sphagnum* hummocks were also important habitats for many invertebrate predators of peat bogs (Henrikson 2006; Spitzer and Danks 2006), including ants (Desrochers and van Duinen 2006) and spiders (Norgaard 1951; Biteniekyte and Relys 2006). But for most species we are lacking detailed ecological knowledge on their thermal environmental relationships, and what it would mean for conservation strategies under climate change.

Chapter III

On the consequences of aggressive male mate locating behaviour and microclimate for female host plant use in the butterfly *Lycaena hippothoe.*



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Chapter II: illustration cover by Camille Turlure

ABSTRACT.

The distribution of ecological resources and their significance for males and females may vary considerably. Intersexual behavioural interactions may lead, combined with particular resource configurations, to sexual spatial segregation. We investigated this issue relative to host plant use in females of the purple-edged copper butterfly, *Lycaena hippothoe*. Males exhibited nectar resource-based territoriality, which is an uncommon mate-locating system in butterflies. They perched and patrolled in large territories harassing every passing female.

In our study system, the percentage of spatial dimension shared for adult and larval resources was estimated at 50 % and males monopolised 28% of the nectar-rich zones. Under these conditions of harassment, females travelled between nectar rich zones for feeding and zones with suitable host plants for egg laying, but often without nectar and hence with low male density. This is likely to limit their time budget and, potentially, their realised fecundity as suggested by the low number of eggs found relative to population size.

Females were also highly specialised in selecting host plants under particular environmental conditions. Using test choice in experimental cages, we showed that, in the absence of males, only micro-climatic conditions may significantly influencing egg-laying decisions. Moreover, results of egg-rearing experiments under different temperature treatments suggested that eggs were laid in thermally

suitable micro-environments. The highly selective egg-laying behaviour can be viewed as a preference-performance choice.

Knowledge of individuals' behaviour, including sexual interactions, can be highly significant for our understanding of habitat use, which in turn can be essential for conservation. We discuss this for *L. hippothoe*, a species of regional conservation concern.

III.1 INTRODUCTION

Knowledge of individuals' behaviour has the potential to improve and even alter our understanding of how populations fare in systems of conservation concern that are under anthropogenic pressure (Caro 1999). Behaviour can affect key demographic parameters like the effective population size in different ways (Anthony and Blumstein 2000; Shuster and Wade 2003). Understanding the habitat needs of a species is a basic requirement of any conservation action, but the study of habitat selection has been complicated by difficulties and debate about operational definitions of habitat and habitat use (Hall, Krausman and Morrison 1997; Caro and Eadle 2005). Resource-based approaches to define a species' habitat as the spatial projection of the ecological niche that recognises the fundamental requirements of organisms (Dennis, Shreeve and Van Dyck 2003b; Shreeve, Dennis and Van Dyck 2004) have recently regained much attention, particularly for insects like butterflies (e.g. Fred, O'Hara and Brommer 2006; Vanreusel and Van Dyck 2007; Turlure *et al.* 2009b). Opposite to more coarse-scale approaches at general vegetation-type or land-use level, more detailed estimates of resource abundance suggest that butterfly population size is strongly associated with resource availability (Schultz and Dlugosch 1999). Restoring degraded habitat by increasing adult and larval resources will play an important role in managing populations of rare species in human-dominated landscapes (Schultz 2001). However, the impact of changes in resource quality, quantity and configuration is likely to depend on the behavioural repertoire of the species considered and its evolutionary potential under altered conditions. Historic resource availability has

shaped breeding systems, including mating systems and mate-locating behaviour (Rutowski 1991), but these behaviours may no longer represent adaptive peaks under altered environmental conditions with changed resource distributions (Foster et al. 2003).

The distribution of different ecological resources and their significance for males and females may vary considerably (Croft et al. 2006). Several hypotheses have been proposed to account for sexual spatial segregation, including relationships with predation risk, nutritional needs, weather sensitivity, indirect competition and sexual harassment (e.g. Wolf, Kauermann and Trillmich 2005; Croft *et al.* 2006; Loe *et al.* 2006). In response to increasing male harassment, female water striders reduced, for example, their activity on the water and hence increased their time out of the water during which they are unable to forage (Krupa and Sih 1993). Adult dragonfly populations often have highly male-biased sex ratios at the breeding areas. This bias has been attributed to significant differences in habitat use between males and females since females use alternative areas to avoid male harassment. Foster and Soluk (2006) showed that, in the dragonfly *Somatochlora hineana*, areas dominated by males were more productive foraging areas for adults than the vegetation types where females were usually observed. Hence, sexual interactions can have relevance for our understanding of habitat use, which in turn can be significant for conservation (Foster and Soluk 2006).

Here, we address the issue of male and female resource use relative to intersexual behavioural interactions and oviposition in a butterfly of regional conservation interest, with a resource defense

polygyny system (Emlen and Oring 1977), *Lycaena hippothoe*. To locate mates, *L. hippothoe* males show perching behaviour in an aggressive territorial way by defending patches of nectar sources, which is an uncommon territorial system in butterflies (Fischer and Fiedler 2001c). Several butterfly species show non-territorial patrolling behaviour as a searching tactic to locate mates (Scott 1974), while (territorial or non-territorial) perching behaviour is usually associated with landmarks (e.g. Lederhouse 1982; Wickman and Wiklund 1983) or in some cases with host plants (e.g. Dennis and Shreeve 1988; Lederhouse *et al.* 1992).

Like other temperate-zone butterflies, *L. hippothoe* females strongly depend on suitable weather conditions in order to be active (Clench 1966). Moreover, females are highly specialised in selecting host plants under particular environmental (micro-)conditions to lay their eggs singly. Therefore, females fit the notion of time-limited organisms (Doak, Kareiva and Kingsolver 2006; Talsma *et al.* 2008); they mate only once soon after eclosion (Ehrlich and Ehrlich 1978) and they avoid additional copulations that would reduce their time budget for host plant selection, oviposition and nectar feeding. These activities are assumed to have a strong correlation with reproductive success and, hence, with fitness. Although most butterflies are capital breeders for nitrogenous components, they depend in the adult stage on the income of other components like sugars from nectar as fuel for energy-demanding flight behaviour (e.g., Boggs and Freeman 2005). Consequently, several studies have found higher probabilities of egg laying in zones with high nectar abundance (e.g., Murphy, Menninger and Ehrlich 1984; Janz, Bergstrom and Sjogren 2005). However, in *L. hippothoe* the aggressive defense of patches of nectar plants by males (Fischer and Fiedler 2001c)

results into significant sexual harassment of gravid females that entered nectar-rich territories. Therefore, we predict lower probabilities of egg laying in nectar-rich zones, and particularly in such zones with high male density. In order to test these hypotheses, we collected field data on male and female activities and in particular on egg distribution patterns in the field relative to key ecological resources and the presence of males. Moreover, as zones with and without males may also differ in other traits, we also included vegetation structure and particularly micro-climate at egg-laying site level in the different zones into our study site. Micro-climatic conditions, temperature in particular, has been shown to affect oviposition in several butterfly species (e.g. Shreeve 1986; Davies *et al.* 2006). Therefore, we measured temperatures in different vegetation types and we also did two experiments. The first experiment tested whether females were equally likely to lay eggs in zones with or without nectar plants when there are no males available. We did the experiment under standardised conditions in the laboratory and also on the field. The second experiment, in the laboratory, tested the effect of temperature on egg hatching, larval growth, survival and size before entering diapauses. We discuss the results relative to sexual differences in habitat-use and mate-locating system and also its significance for conservation.

III.2 METHODS

Study species

The purple-edged copper butterfly, *L. hippothoe* (Linnaeus 1761) is widespread in northern Europe, but much more localised in central Europe (Lafranchis 2004). In Belgium, it occurs in the Ardenne and Lorraine regions and is declining (Fichefet et al. 2008). *L. hippothoe* is ecologically confined to damp meadows, clearings and peat bogs. Adults fly in early summer (June-July) and they are rather opportunistic in their nectar plant use (Turlure C, unpubl. data). Females lay eggs singly on the unique host plant, the sorrel *Rumex acetosa*. *L. hippothoe* has one generation a year and hibernates as caterpillar.

Study area and quantifying resources

Field data were collected in the Fange de Pisserotte nature reserve, which is a peat bog (56 ha) located on the south side of the Plateau des Tailles (S-Belgium: 50°13'N, 5°47'E). Based on their general vegetation aspect, we selected 40 zones in the peat bog covering in total 17 ha. In each zone, ten randomly placed vegetation samples were recorded with a 1 m² grid (five in mid-June and five in mid-July) to measure the abundance of the host plant and of each nectar plant on a 0 to 25 scale. To assess the distribution and degree of segregation of adult and larval resources, we calculated niche breadth and niche overlap in space of host

plant and nectar plants. Niche breadth *B* (Edwards, Heckel and Guynn 1998) was calculated using Ricklefs' equation:

$$B = \frac{1}{\sum P_i^2}$$

where P_i is the proportion of individuals (host plant or nectar plant) in the *i*th zone. Hence, *B* can range from 1 to 40. Niche breadth was rather narrow but equal for host plant abundance and nectar resources (B_h = 15.03 and B_n = 15.44). The niche overlap *O* was calculated using Schoener's index:

$$O_{hn} = 1 - 0.5 \sum \left| P_{ih} - P_{in} \right|$$

where P_{ih} and P_{in} represent the proportion of the host plant and the nectar resources in the *i*th zone, respectively. Percentage of niche space shared by the host plant and the nectar resources was medium as O_{hn} = 52.04%. Then, zones were classified in four categories according to resource availability: (1) nectar resources only, (2) both nectar and host plant resources, (3) host plant only, and (4) no resources at all. Moreover, host plant and nectar abundances within the zones were positively correlated (Spearman correlation test, R = 0.54, n = 40, P = 0.00003).

Distribution and density of males and females

During the flight period of 2005 and 2006, we did a mark-release-recapture study by marking all encountered adults individually with a non-toxic permanent pen and by releasing them at the spot of capture. At each (re)capture, we recorded the zone (out of the 40 predefined zones), the unique marking code and the sex. Based on these data, we inferred

four demographic parameters: survival rate, recapture rate, total population size and sex ratio using Mark program (White and Burnham 1999; Schtickzelle, Le Boulengé and Baguette 2002). Additionally, we also determined local frequency of each sex in each of the 40 zones. χ^2 tests were used to assess the degree of matching between the frequency of adults (for males and females) and the relative area of each class of resource availability. Based on repeated surveys across the study area, we mapped male territories. During the flight season, the same territories were typically used by a sequence of different individual males. We compared the total percentage of the area used as male territories in each of the four vegetation categories reflecting the different levels of resource availability.

Adult behaviour

In 2006, we tracked a random sample of males and females individually to record in detail their behaviours per unit of time ($n_{females}$ = 20, total duration = 5900 s; n_{males} = 16, total duration = 2997 s). Behavioural tracking was only done under suitable weather conditions (i.e. no wind, no clouds, air temperature > 28°C). We recorded thermoregulation behaviour (i.e. dorsal basking, sensu Clench 1966), nectar feeding (and the flower species used), flight (i.e. direct flight and patrolling flight), interaction with other organisms during flights and oviposition behaviour of females, including pre-alightment and egg-laying behaviour (e.g., Jones 1977; Stanton 1982). From the observations of feeding activities, we inferred the set of nectar resources used by *L. hippothoe*. Abundances of seven flowering plants were then used as a measure of nectar

availability: *Angelica sylvestris*, *Cirsium palustre*, *Lotus pedonculatus*, *Valeriana repens*, *Succisa pratensis*, *Polygonum bistorta* and *Potentilla palustris*. We compared between males and females: (1) the proportion of time spent to each behaviour and (2) the mean duration of each behaviour in every tracked individual with ANOVAs.

Egg laying in the field

At the end of the flying period of 2005, we searched for eggs in all the zones on all located *R. acetosa* plants (total time spent searching was 37h30 by one to three persons simultaneously). We inspected more than 2000 *R. acetosa* plants and located 181 eggs on 98 different plants (**Figure III.1**). Since eggs are highly visible and egg shells remain on the host plant after larval hatching for about two weeks, there was a very low probability of missing an oviposition event on an inspected host plant (Turlure C, unpubl. data). For each of the 181 eggs, we recorded: (1) the position on the host plant (i.e. on the stem or on a leaf or on the flower and at which distance from the closer stem or leaf) and (2) the height of the *R. acetosa* plant and of the surrounding vegetation. For each of the 98 laying sites, we assessed the abundance of each plant species within a 1 m² plot (0 to 25 scale). We also estimated the abundance of plant species in 105 control plots within zones where the host plant was present, but where no eggs were found.

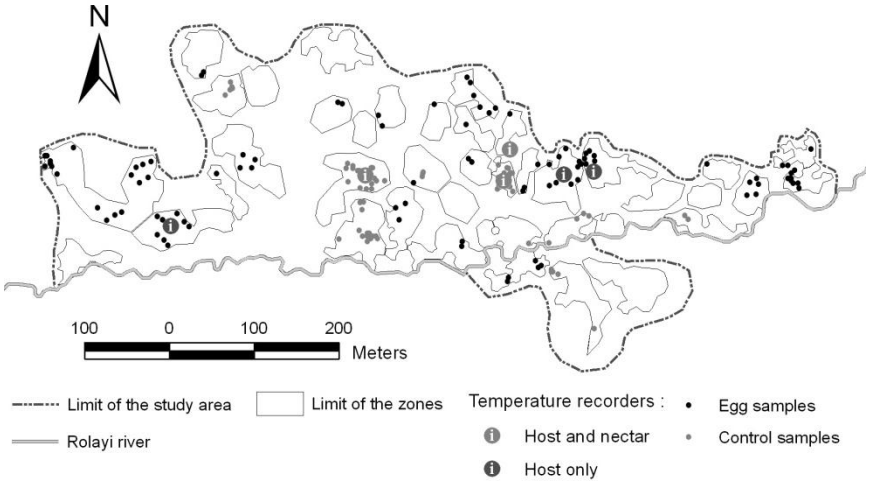


Figure III.1. Map of the study area ("Fange de Pisserotte" nature reserve). The dotted line represents the limit of the study area and the black lines delineate each of the 40 vegetation zones. Black dots: egg samples, *i.e.* samples in which *L. hippothoe* eggs were found on *R. acetosa* plant. Grey dots: control samples, *i.e.* samples in which no egg of *L. hippothoe* were found on *R. acetosa* plant. Black marker symbols: spots where temperature was recorded in zones with the host plant *R. acetosa* with eggs. Grey marker symbols: spots where temperature was recorded in zones with the host plant *R. acetosa* but without eggs.

Local conditions of soil moisture, light intensity and temperature were inferred for each of the 203 plots based on the abundance-weighted means of Ellenberg indicator values of the plant species (Ellenberg 1974). A Principal Components Analysis was used to create independent micro-climatic variables (CLIM1 and CLIM2, cumulative eigenvalues = 71.75%). CLIM1 was positively correlated with light intensity and negatively correlated with temperature; CLIM2 was positively correlated with moisture.

Egg presence was analysed by logistic regression (PROC GENMOD in SAS, with binomial distribution and logit link function) relative to (1) three characteristics of the zones: male density, female density and the resource availability (four classes as described previously); and (2) to three characteristics of the egg-laying site: host plant abundance (RUMA) and two micro-climatic conditions (CLIM1 and CLIM2).

Egg number on the host plant was analysed by generalised linear regression (PROC GENMOD in SAS, with Poisson distribution and log link function) relative to (1) the resource availability classes (see above) and (2) three characteristics of the egg-laying sites: the host plant abundance (RUMA), the host apparency and the connectivity between egg-laying sites. Host apparency was estimated by the ratio of vegetation height by *R. acetosa* plant height: the bigger the value of this ratio, the less apparent the host plant was. Egg-laying site connectivity was calculated as follow:

$$CONN_i = \Sigma e^{-D_{i,j}}$$

where $D_{i,j}$ is the distance between the laying site *i* and another laying site *j*. The bigger the value of CONN, the more connected the egg-laying site was.

We computed all the possible combinations of explanatory variables to explain egg presence and egg number, and we used multi-model inference to capture the substantial amount of information provided by the models in the set (Anderson 2008). Hence, we reported the AIC-weighted of each explanatory variable, expressing the probability that the variable influences the response (i.e. egg presence or

egg number), and also model-averaged parameter estimates and confidence intervals (see calculation methods in Burnham and Anderson 2002a).

We used χ^2 test to assess the degree of matching between the frequency of eggs and the relative area of each class of resource availability (as it was tested in adults).

Indoor and outdoor egg-laying experiment

In July 2006, we used two identical cages made of green nylon meshing (3x1x1.5 m) to test oviposition performance on host plants only versus a mixture of host plants and nectar plants in the absence of males. The first cage was installed under standardised conditions (under sodium light) in the laboratory on a floor covered by dry turf. The cage had a central part of 0.5 m² and at each side a compartment of 1.25 m² to provide two treatment conditions. In one compartment of the cage, we placed host plants only (i.e. ten pots with one *R. acetosa* plant in each). In the other compartment, we placed a mixture of host plants and nectar plants (i.e. ten pots with one *R. acetosa* plant in each and ten with flowering plant species, *C. palustre* or *A. sylvestris*). To control for host plant quality, all *R. acetosa* plants had on average similar size and no sign of senescence; they came from the same site outside our study area.

We repeated the experiment also in a similar cage under outdoor field conditions. The cage was placed in a short sedge fen in the study area, where many eggs had been found the previous year. The central

part of the floor inside the cage (0.5 m^2) was mown. In both treatment compartments (2x1.25m^2), we cut all herbaceous plants species other than Purple moorgrass *Molinia caerulea*.

The experimental procedure was the same for both the indoor and the outdoor experiment. A single female (captured in the study area just before the experiment) was released in the central part of the cage. After half a day, we removed the female from the cage, and we counted the number of eggs laid in each compartment of the cage. Next, the female was marked and released. The 30 pots were removed and replaced by other ones when plants were senescent or used. We also alternated the treatment (host plants only and host plants with nectar plants) between the right and the left compartment to avoid any cage orientation bias. Depending on weather conditions, we used the cage inside (cloudy days) or the cage outside (sunny days; n_{females} = 10 and 12, respectively). Numbers of eggs laid in the two compartments were compared by Wilcoxon paired t-tests. Average number of eggs laid per female under indoor and outdoor conditions was compared by a t-test.

Egg development and temperature

In July 2007, we captured four females in the study area. They were allowed to lay eggs during one day under the same laboratory conditions. Next, they were released at the place of capture. Eggs were placed individually in Petri dishes and assigned to one of two temperature conditions in two climate rooms. Temperature treatment corresponded to the temperature profiles recorded in the field between zones with used

host plants (vegetation type: host plants only) and not used host plants (vegetation type: host plants + nectar plants). Between July 16 and July 24 2006, ambient temperature at the vegetation level (at 30 cm from the soil) was recorded every minute in both conditions with six data loggers (**Figure III.1**). Temperature fluctuated between 1°C and 44°C in zones with used host plants and between 1°C and 36°C in zones with not used host plants. Temperatures were very similar during the night, but during the middle of the day, zones with used host plants were 3-9°C warmer than the zones with unused host plants (**Figure III.2**). Therefore, both climate rooms had similar low temperatures during the night (3°C), similar raising temperatures during the following hours, different day temperatures during 4 hours around noon and finally similar decreasing temperatures during the next hours, to mimic at best field conditions. We adjusted different day temperatures in climate rooms to 40°C for the high-temperature treatment and 35°C for the low-temperature treatment. Eggs in each climate room were checked every day until hatching. Caterpillars had *ad libitum* access to fresh *R. acetosa* leaves. Every day, we recorded caterpillar survival. Caterpillar length was measured daily in the morning as a size estimate 10 days after hatching and until the diapause with callipers (precision: 0.05 cm). Between the two temperature treatments, we compared (1) the number of days before hatching (ANOVA), (2) survival rate (χ^2 test), (3) caterpillar growing rate (goodness of fit test for linear regression models with the factors time and treatment and with the factors time, treatment and the interaction between both factors) and (4) the final size of caterpillars before entering diapause (ANOVA).

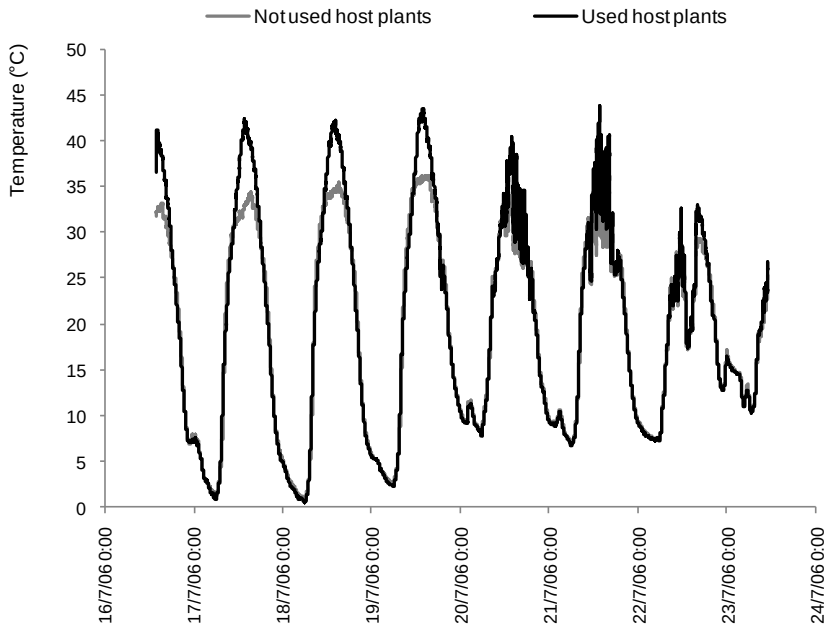


Figure III.2. Mean temperature recorded between July 16 and July 24 2006 in zones where host plants carried eggs and zones where host plants did not receive eggs.

III.3 RESULTS

Distribution and density of males and females

Adult activity was observed in a period of about 1 month (June 12 to July 16 in 2005 and June 28 to July 21 in 2006). Daily survival rate was constant (>90%) and recapture probability decreased over time for both years (details not shown here). For 2005 and 2006, total population size was estimated at 160 ± 27 and 197 ± 70 individuals, respectively. Males were more abundant than females in both years; sex ratio was 1.68 males per female in 2005 and 1.2 in 2006.

Male and female densities did not simply reflect relative area, but were related to resource availability (males: $\chi^2_3 = 155.01$, $P < 0.001$ and females: $\chi^2_3 = 23.82$, $P < 0.001$). Males mainly occurred in zones with host plant and nectar resources, whereas females were observed more frequently in zones with host plants only and in zones with host plant and nectar resources ($\chi^2_2 = 14.16$, $P = 0.002$, **Figure III.3**).

The study area counted ten different male territories that were used almost daily (**Figure III.4**). Together male territories covered 13.4% of the study area and 56.9% of the total area that contained resources used by the species (total area of territories = 10341 m^2; mean territory area =1034.0 ± 135.2 m^2). 96% of these territories were either in zones with host plants only (33%) or in zones with host plant and nectar resources (63%).

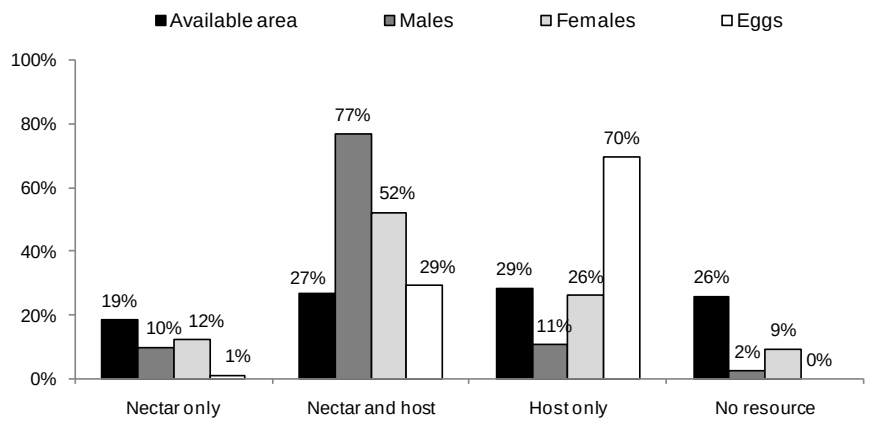


Figure III.3. Relative importance of the four different vegetation categories relative to resource availability (nectar only, nectar and host plants present, host plants only and no nectar or host plants present) for the presence of males (in dark grey), females (in light grey) and eggs (in white). Proportion of the total area studied for each category is indicated in black. Remark: two eggs were found on two completely isolated host plant present in the category "Nectar only".

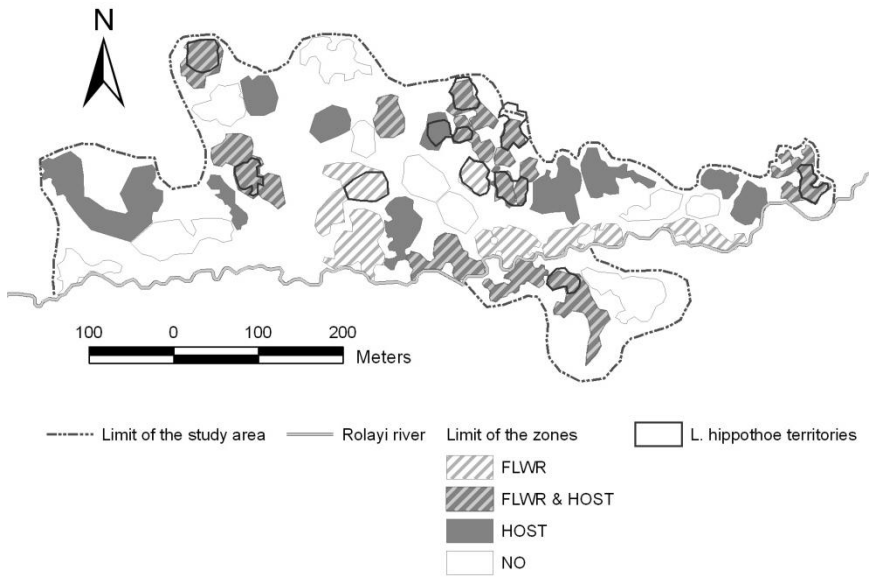


Figure III.4. Map of the study area ("Fange de Pisserotte" nature reserve). The dotted line represents the border of the study area. The bold black lines delineate *L. hippothoe* male territories. White areas: zones without resources for *L. hippothoe*. Grey areas: zones with host plants only. Hatched areas with white background: zones with nectar resources only. Hatched areas with grey background: zones with nectar resources and host plants.

Adult behaviour

Females never initiated interactions with conspecifics or other organisms, whereas males spent on average 4.7% of their active time budget in interactions. Half of the interactions were interspecific (mainly with males of the patrolling butterfly *Proclossiana eunomia*) and half were intraspecific with either females (30%) or males (20%). Oviposition behaviour, including both pre-alightment and egg-laying behaviours, covered on average 17.9% of the active time budget of females. In 88.5% of the cases, typical oviposition pre-alightment behaviour at a host plant was not followed by egg laying, but instead, the female decided to fly away. The duration of the pre-alightment behaviour followed or not by egg laying did not differ significantly (ANOVA: $F_{1,66} = 0.78$, $P = 0.38$).

Mean duration of feeding bouts and the proportion of time allocated to feeding were similar in both sexes (ANOVAs: $F_{1,35} = 2.34$, $P = 0.14$ and $F_{1,35} = 0.003$, $P = 0.96$, respectively). Females spent proportionally more time basking than males (ANOVA: $F_{1,35} = 4.26$, $P = 0.05$) and mean duration of basking bouts was longer than in males (ANOVA: $F_{1,35} = 4.04$, $P = 0.05$). The reverse was observed for flight behaviour: males spent proportionally more time flying than females (ANOVA: $F_{1,35} = 21.61$, $P < 0.001$) and mean duration of flight bouts were longer than in females (ANOVA: $F_{1,35} = 4.52$, $P = 0.04$; **Table III.1** and **Figure III.5**).

Table III.1. Mean duration (and confidence interval) of different behaviours in males (M) and females (F) of *L. hippothoe* as recorded during the flight season of 2006.

Behaviour	Sex	Samples	Mean (s)	CI
Flight	F	20	13.77	6.02
	M	16	23.23	6.73
Nectar feeding	F	20	61.11	32.65
	M	16	24.21	36.5
Basking	F	20	50.57	26.93
	M	16	10.6	30.11

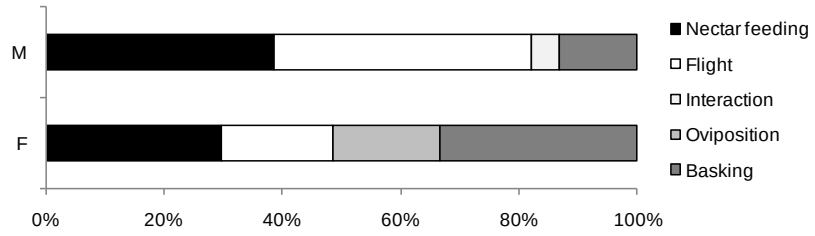


Figure III.5. Proportion of time spent to different behavioural activities for males (M) and females (F) of *L. hippothoe*.

Egg-laying sites

82% of the eggs were found on *R. acetosa* stems (16% on leaves and 2% on flowers). If an egg was found on the leaves or flowers, the host plant typically already carried an egg on the stem (79% of the cases).

Eggs were more likely to be present in zones with host plants, either alone or mixed with nectar plants. Egg presence was also significantly correlated with lower male density, higher female density, lower local host plant density and lower values of CLIM1, i.e. warmer and less light intensive micro-climatic conditions (**Table III.2**). Egg number was related to resource availability (i.e., no match between egg incidence and relative area: $\chi^2_3 = 184.01$, $P < 0.001$); there were more eggs in zones with host plant only (**Figure III.3**). More isolated egg-laying sites contained more eggs than more connected egg-laying sites. Host plant abundance and apparency had a very limited positive influence on egg number (**Table III.3**).

Table III.2. Multi-model inference gave for each variable the AIC weight, expressing the probability that the variable influences the response (here the presence of eggs) and model-averaged parameter estimates and confidence limits. For the categorical variable "Resource availability", the parameter estimate expresses the difference with the reference level fixed to zero (i.e., the class "No resource"). Results showed that (1) egg presence probability was greater in zones with host plant alone or mixed with nectar resources (variable weight = 100 % and higher parameter estimate for other categories than "No resource"), (2) egg presence was associated with lower male density and higher female density (variable weight > 97 %, negative parameter estimate for male density and positive parameter estimate for female density) and with (3) lower local host plant density (variable weight = 98.34 % and negative parameter estimate) and lower values of CLIM1 (i.e. higher micro-climatic condition of temperature and lower micro-climatic condition of light intensity; variable weight = 96.56 % and negative parameter estimate). AIC weight of CLIM2 did not reach high level. RUMA: host plant abundance around the egg-laying site (in 1 m²). CLIM2: moisture conditions.

		Resource availability			
	Intercept	**Flowers only**	**Host only**	**Flower and host**	**No resources**
Variable weight	100.00%	100.00%	100.00%	100.00%	100.00%
Parameter estimate	-28.015	25.619	30.568	30.177	0
Parameter st. e.	0.817	1.029	0.872	0.226	/

Adult density		Egg-laying site characteristics		
Males	**Females**	**RUMA**	**CLIM1**	**CLIM2**
97.03%	99.58%	98.34%	96.56%	33.21%
-0.241	0.844	-0.255	-0.903	-0.071
0.084	0.255	0.0856	0.341	0.105

Table III.3. Multi-model inference gave for each variable the AIC weight, expressing the probability that the variable influences the response (here the number of eggs) and model-averaged parameter estimates and confidence limits. For the categorical variable "Resource availability", the estimate expresses the difference with the reference level fixed to zero, here the class "Nectar and host". Results showed that number of *L. hippothoe* eggs on *R. acetosa* plant was higher (1) in zones with host plant only (variable weight = 99.3 % and higher parameter estimate for the category "Host only") and (2) on more isolated egg-laying sites (variable weight = 83.6 %, negative parameter estimate). AIC weight of RUMA and Apparency did not reach high level. RUMA: host plant abundance around the egg-laying site (in $1m^2$). Apparency: ratio of vegetation height by host plant height; the bigger the value, the less visible the host plant is. CONN: egg-laying site connectivity (the bigger the value, the more connected the egg-laying site is).

	Intercept	Egg-laying site characteristics		
		RUMA	Apparency	CONN
Variable weight	1	27.20%	46.35%	83.60%
Parameter estimate	2.773	0.001	0.004	-0.036
Parameter stde	1.577	0.009	0.177	0.017

Resource availability			
Nectar only	Host only	Nectar and host	No resources
99.30%	99.30%	99.30%	.
-0.061	0.548	0	.
0.728	0.167	/	.

Egg-laying experiment

In the indoor cage, individual females laid one to seven eggs. All eggs were laid in the compartment with both host and nectar plants (4.0 ± 0.6 eggs per female) and hence never in the compartment with host plants only (Wilcoxon paired t-test: $S = 39$, $df = 11$, $P = 0.0005$). In the outdoor cage, individual females laid four to 19 eggs, which was significantly more than under indoor conditions (t-test: $t = -4.62$, $df = 40.39$; $P < 0.001$). However, egg numbers did not differ with treatment in the outdoor cage (compartment with host plants only: 5.6 ± 0.9 eggs per female; compartment with both host plants and nectar plants: 5.3 ± 0.7 eggs per female; Wilcoxon paired t-test: $S = 4.5$, $df = 9$, $P = 0.707$).

Larval development, survival and temperature

We followed the development of 51 eggs. Egg hatching was faster in the high-temperature treatment compared to the low-temperature treatment (10.2 ± 0.6 days and 11.7 ± 0.6 days; ANOVA, $F_{1,50} = 13.36$, $P < 0.001$). 37% of the emerged caterpillars survived, and survival did not differ with temperature treatment ($\chi^2 = 0.579$; $P = 0.447$). Caterpillar growth rate did not differ with temperature treatment (models with and without interaction between time and treatment did not differ significantly; $\Delta AIC<2$). Caterpillars under the high-temperature treatment were bigger at diapause than caterpillars reared under the cooler treatment (mean caterpillar length: 7.44 ± 0.12 mm and 6.85 ± 0.10 mm; ANOVA, $F_{1,16} = 14.08$, $P = 0.0017$).

III.4 DISCUSSION

In our study population, *L. hippothoe* males defended large territories that contained in particular not only nectar sources but also host plants. Males made patrolling flights within their territory to search for females and to interact with other males. This territorial mate-locating system is assumed to be most profitable (i.e. maximising female encounter rate) under conditions of low population density and/or clear segregation of adult and larval resources (Emlen and Oring 1977; Alcock 1983; Cordero and Soberon 1990). The limited number of permanently used territories covered together about 28% of all nectar-rich zones of our study area. When females entered a nectar-rich zone, territorial males directly interacted with them by either spinning wheel flights or horizontal pursuits. Sometimes, females were even followed and chased beyond the boundaries of the large territories. Hence, this corresponds to the notion of female harassment.

Under conditions of female harassment, mated females should avoid entering male territories and losing time and energy, if possible. Males monopolised large surfaces of nectar plants. However, as demonstrated by Fischer and Fiedler (2001b), nectar is of key significance for female survival and realised fecundity in *L. hippothoe*. There was some spatial segregation of host plants and nectar plants, but resources were not completely separated as, for example, in Murphy, Launer and Ehrlich (1984); nectar and host plant resources overlapped for 52.04% in space, and host plant density was higher where nectar resources were present. This overlap may offer some opportunity for

females to lay eggs and feed in the same zone. However, there was a clear discrepancy between where females were most frequently observed (i.e. nectar-rich zones) and where we found most eggs (i.e. zones with host plants only and with low host plant density). Foraging females may have a higher detectability than egg-laying females, but the data on the behaviour of a series of individuals indicated that both nectar feeding and egg laying represented a significant part of a female's time budget, with the percentage of nectar feeding being on average somewhat larger. Thus, females have to move between nectar-rich zones and suitable low-density host plant zones, which reduces the time budget for both feeding and egg laying in time-limited organisms (Bernays 2001; Buchholz 2007). So, egg laying outside zones that contain both host and nectar resources is likely to be influenced at least partly by male harassment, as male density had a negative impact on egg presence.

Experiments with cages have been successfully used before to study host plant use (e.g. Janz and Nylin 1997; Talsma *et al.* 2008), but in our experiment, the indoor and outdoor variants of the experiment gave different and, at first sight, inconclusive results. However, environmental conditions in the two experiments were not identical. We argue that our indoor conditions represented sub-optimal environmental conditions for female activity. This explains why females laid significantly fewer eggs than under outdoor cage conditions and why they only used host plants close to feeding sources. The outdoor cage was constructed in a zone that was known to be a highly used area, at least in the year before the experiment. Under suitable environmental conditions and suitable weather conditions, females will equally use zones with or without nectar, at least at the spatial scale of the tested

cages (i.e. meters). In the absence of males like in our cage experiments, micro-climatic conditions may be the only really significant factor.

Despite our experience and intensive search effort for host plants and readily visible eggs, we found considerably fewer eggs than expected based on the estimated population size and expected average fecundity in this sedentary butterfly species. Fischer and Fiedler (2001a) showed an average fecundity of 464 ± 215 eggs for *L. hippothoe* females. Individuals were not likely to disappear from our population as daily survival remained high throughout the flight period. So, all this suggests that average realised fecundity and potentially also local recruitment were very low in this population. By far, the most of the pre-alightment behaviours (almost 90%) were indeed not followed by egg laying, suggesting that a large proportion of the host plants did not match the required needs for oviposition. An alternative interpretation could be that females were only inspecting plants but they had no mature eggs ready for laying at that moment. Thermal characteristics of the host plant probably are key features to the larval habitat. Influence of the oviposition site conditions on female behaviour relative to larval fitness expectation (Rausher 1979; Root and Kareiva 1984) may, hence, result into a preference-performance choice (Janz 2002). It could be argued that females in our population have to travel between nectar-rich zones and zones with suitable host plants and need to avoid harassing males, which all together limit their time budget for egg laying and, hence, their realised fecundity.

Because of the limited mobility of early stages, females are under selection to choose high-quality plants, and even parts of the plant

for egg deposition; offspring performance is better if larvae are able to find a good feeding place immediately after hatching (Janz 2005). As the host plant leaves wither rapidly, it is advantageous to lay the eggs on the stem of the host plant as eggs that have not yet been hatched may fall on the floor with the withered leaf (Wiklund 1984). Since feeding, assimilation and growth of the ecotherm caterpillars depend on the thermal characteristics of the micro-habitat, different host plant micro-sites may provide qualitatively different larval habitats. We experimentally showed that temperature had a significant impact on larval fitness. Higher larval growth rate and higher larval weight are assumed to be good fitness indicators in ectothermous herbivores (e.g. Nieminen, Nuorteva and Tulisalo 2001). With the applied low and high temperature, we did not find an effect on caterpillar survival nor on growth rate, but caterpillars reached a larger body size before diapause under the high-temperature treatment compared to the low-temperature treatment. Moreover, under higher temperature, larvae hatched earlier and reached faster their final pre-diapause size. Short development time, but reaching a sufficiently large size, is a clear advantage during the early stages of *L. hippothoe* on a host plant with a short growing season. This corresponds to our observed pattern of higher egg presence in warmer zones of the vegetation. Used and unused host plants differed in thermal profile (**Figure III.1**). Isolated host plants in zones with low host plant density have an increased probability to receive eggs in herbivorous insects like butterflies (e.g. Mackay and Singer 1982; Rausher 1983). However, in our system, zones with lower host plant density may also offer different thermal micro-habitats which confound the behavioural interpretation of egg spreading. It is now warranted to do a series of experiments in which we manipulate thermal characteristics

of host plants within and between different vegetation types and with and without intervening males.

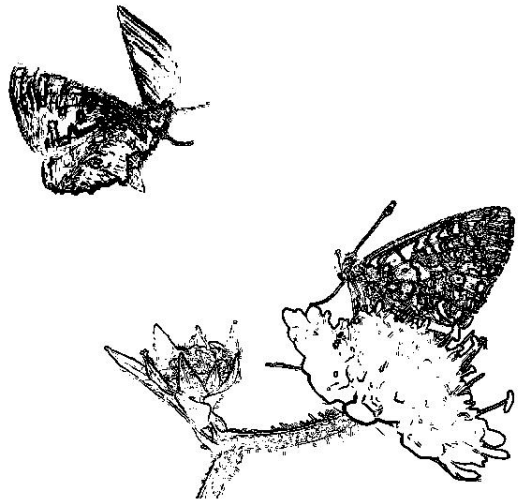
In this low-density population, males clearly showed territorial behaviour, but during a survey in another site with a threefold population density, larger resource abundance and also a larger spatial degree of overlap between nectar plants and host plants, all males were patrolling in an non-territorial way (Turlure C, unpubl. data). Fischer and Fiedler (2001c) also observed a flexible combination of territorial behaviour and non-territorial patrolling behaviour in male *L. hippothoe*, but this was correlated with ambient temperature. Male mate location behaviour has been considered as a fixed trait at the species level (Scott 1974), but in the meantime, several studies have shown evidence of physical and/or social environment-depended flexibility of male strategies (e.g. Alcock 1983; Wickman 1985). This is not exclusively the case for butterflies, but also for other insects with visually based mate location behaviour like, for instance, dragonflies (Corbet 1999; Alcock 1989).

Practical and conceptual issues in conservation biology could benefit from knowledge of individual behaviour (Buchholz 2007). Behavioural data on mating systems are fundamental to estimate effective population size Ne (Caro 2007). As behavioural traits can influence Ne by altering demographic parameters, it may also be incorporated in PVA (Anthony and Blumstein 2000). Behavioural differences between populations can be important, and generalising from single site studies should, hence, be done with much caution. However, several conservation studies have used general vegetation types as habitat units for species of conservation concern, which may not

necessarily represent the functional level of interaction between the organism and its environment. Dennis, Shreeve and Van Dyck (2003) argued for the use of a resource-based approach to define habitat; this approach takes into account the essential resources and environmental conditions for all life cycle stages. The approach has recently been used to generate functional habitat maps for species conservation (Vanreusel, Maes and Van Dyck 2007; Vanreusel and Van Dyck 2007) and also to detect subtle but essential differences in habitat use and, hence, for conservation management between species that seem to share the same habitat at first sight (Turlure et al. 2009b). Here, we illustrated that a resource-based approach of habitat is also important to examine how resource configurations (like degree of spatial overlap between larval and adult resources) may affect behavioural strategies and how the interaction between behaviour and resources, in turn, shows consequences for the demography of a species of conservation concern. It provides us with insight on how one could promote population productivity of a threatened species by managing from a functional point of view resource quantities, qualities and configuration.

Chapter IV

Morphology and mobility are affected by resources grain in butterflies.



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Chapter IV: illustration cover by Camille Turlure

ABSTRACT.

Sound demonstration of life history trait evolution requires high quality data that are extremely difficult to collect, restricting researchers to use surrogate data for life history traits.

We investigated the reliability of this approach by looking for relations between mobility and (1) resource grain and (2) morphological traits in butterflies. Results were used to assess the biological realism of morphological traits associated with flight as mobility proxies. We then investigated how biological, environmental and landscape variables affected these mobility proxies. We used a multi-species approach on two different sites. Morphological traits were measured on ca. 20 individuals per site, species and sex. Resource distribution was carefully monitored by investigating the spatial repartition and overlap of larval and adult feeding resources, together representing the resource grain. The spatial extent of individual station keeping movements was estimated from distances recorded between successive recaptures of individuals from mark-release-recapture experiments.

Morphological traits seemed reliable proxies of mobility, as both variables were strongly correlated. Morphological variations were related to flight type and spatial dimension of nectar resource. The most striking point was the clear relation between the index of relative investment in mobility vs fecundity in females with the spatial dimension of adult feeding resource. Given the generally accepted relation between abdomen volume and female fecundity, this suggests

that females might invest more in fecundity when nectar resources are widespread. No effect of landscape structure was underlined, indicating that functional grain of resources is more likely to influence mobility and evolution of morphology in butterflies.

IV.1 INTRODUCTION

How individuals map onto suitable resources has always been a central issue in ecology, but this topic has become of particular importance in the current era of global change when accurate predictions of changes in distribution areas are of overwhelming interest for modelling the modifications incurred by the biodiversity (e.g. Thomas *et al.* 2004; Wilson *et al.* 2007; Lenoir *et al.* 2008; Thuiller *et al.* 2008). If the presence of a given organism may be inferred from the reunion of all suitable resources required to complete its life-cycle (Southwood 1977; Dennis, Shreeve and Van Dyck 2003b; Guisan and Thuiller 2005; Hirzel and Le Lay 2008; Turlure *et al.* 2009b), the configuration of those resources in the landscape might be of prime importance by constraining the movements of mobile organisms (Dennis, Shreeve and Van Dyck 2003b; Baguette and Mennechez 2004; Revilla *et al.* 2004).

Individual movements between successive locations have classically been divided into two categories: those that are directed towards resources, to which an organism spends most of its time (also called station keeping, or routine movements), and those that are not (Dingle 1996; Nathan *et al.* 2008). Dispersal, i.e. movements having potential consequences of gene flow across space (Ronce 2007), mainly belongs to the latter category. Adaptive responses aiming at minimizing fitness costs entailed by dispersal have been both predicted theoretically (e.g. Heino and Hanski 2001 for a model, Ronce 2007 for a review) and documented empirically (e.g. Schtickzelle, Mennechez and Baguette 2006 for an example, Baguette and Van Dyck 2007 for a review).

Dispersal may also be traded off against other life-history traits, like fecundity (the oogenesis flight syndrome: Johnson 1969; Roff and Fairbairn 2001). However, the clear-cut distinction between special dispersal movements and routine movements has been challenged by Van Dyck and Baguette (2005), who also stressed that gene flow may occur as a by-product of routine movements in landscapes where resources are fine-grained (Baguette and Van Dyck 2007).

This raises the more general issue of the effect of resource grain (i.e. the spatial heterogeneity of resources) on the evolution of routine movements, which has been far less documented than the effect of landscape fragmentation on dispersal. Bell (1991) provided an extensive synthesis of how searching strategies changed according to various resource settings (see also Romero *et al.* 2009). However, other responses than such behavioural plastic changes are likely to occur if routine movements have even a small or moderate fitness cost because they occur with a high frequency during the whole life of organisms (Nathan *et al.* 2008). In this vein, Baguette and Van Dyck (2007) recently proposed that the grain of resources is a crucial factor shaping adaptive changes in mobility.

Populations of the same species are often confronted to a wide range of environmental conditions, including variation and variability in resource availability and location (e.g. Blondel *et al.* 2006). Organisms have the capability to adjust their phenotype to local environmental needs and changes (Dempster 1991; Singer, Thomas and Parmesan 1993). In particular, morphological traits in butterflies are often assumed to be good estimates of mobility (Singer and Thomas 1996) and hence,

accurate indicators of adaptation to those environmental factors that shape mobility. If morphological traits are reliable proxies of adaptation to local conditions, then they should have been influenced by biological variables (such as behavioural traits), by the landscape context, but also by environmental variables (such as resource abundance, quality and grain). Nevertheless, most studies on butterfly morphological traits have considered the responses of different populations of the same species (Wickman 1992; Berwaerts, Aerts and Van Dyck 2006) to habitat fragmentation, focusing on dispersal related movements (Thomas, Hill and Lewis 1998a; Van Dyck and Matthysen 1999; Hill, Thomas and Lewis 1999; Norberg and Leimar 2002; Schtickzelle, Mennechez and Baguette 2006) and neglecting smaller scales of variation such as resource grain within the habitat.

In this study, we investigated how mobility and morphology in butterflies can be affected by the spatial grain of adult and larval resources. For the sake of generality, we used a multi-species approach on four butterfly species in two different landscape contexts. Firstly, we examined the relations between mobility and 1) the range of movements made possible given the configuration of the study system and 2) the spatial dimension of two main resources required by adult butterflies (i.e. nectar resources to feed and larval host plant to lay eggs), inferred from indices of niche breadth and resource overlap. Secondly, we tested for the reliability of morphological traits as mobility proxies by testing for correlations between the observed movements of adult butterflies in the field and morphological traits classically associated with flight (i.e. thorax volume, wing area and wing loading). Next, we turned to the relation between these mobility proxies and behaviour (foraging and/or

mate locating), resource grain (spatial dimension and overlap of nectar and host resources) and population isolation in the landscape. Finally, we investigated how the grain of resources affected the relative investment in mobility (thorax volume) vs fecundity (abdomen volume) in females.

IV.2 METHODS

Study system

1. Species and sites

We studied four butterfly species that co-occur in Belgian peat bogs: the bog fritillary *Proclossiana eunomia*, the small pearl-bordered fritillary *Clossiana selene*, the cranberry fritillary *Boloria aquilonaris* and the purple-edged copper *Lycaena hippothoe*. Caterpillars of these four species are specialists and feed on a unique host plant: the bistort *Polygonum bistorta*, the violet *Viola palustris*, the cranberry *Vaccinium oxycoccos* and the sorrel *Rumex acetosa*, respectively.

Observations were carried out in two peat bogs in south-eastern Belgium: the "Fange de Pisserotte" in the "Plateau des Tailles" landscape and the "Troufferies de Libin" in the "Plateau de Recogne" landscape. Both sites were crossed by a river and surrounded by birch and willow forests and spruce plantations. The Fange de Pisserotte was a part of a large network of peat bogs areas, whereas the Troufferies de Libin was more isolated, with only two smaller peat bogs in its vicinity.

2. Population characteristics and nectar resources used

Previous data collected on both landscapes provided reliable dispersal kernels for each species (Baguette and Nève 1994; Baguette 2003; Baguette and Schtickzelle 2003; Schtickzelle, WallisDeVries and

Baguette 2005b; Schtickzelle, Mennechez and Baguette 2006; Turlure *et al*. 2009b; Turlure C., unpublished data). Accordingly, the eight studied populations were classified as isolated (no movement observed between populations or no population in the vicinity) or connected (movements observed between populations in the vicinity) (**Table IV.1**).

Table IV.1. Measures of the spatial dimension (using Ricklefs' formula) and overlap (using Schoener index) for host plant and nectar resources used by adults of each species in the two study sites. Each population was classified either as isolated (no movement observed between populations or no population in the vicinity) or connected (movements observed between populations in the vicinity).

Site	Species	Spatial dimension of		Overlap	Population
		Host plant	Nectar		
Libin	*B. aquilonaris*	2.93	5.63	41.36%	Isolated
	P. eunomia	4.82	4.82	100.00%	Isolated
	L. hippothoe	5.56	4.34	62.97%	Isolated
	C. selene	4.53	4.89	45.76%	Connected
Pisserotte	*B. aquilonaris*	2.18	2.01	27.60%	Connected
	P. eunomia	5.28	5.28	100.00%	Connected
	L. hippothoe	3.76	2.11	41.55%	Isolated
	C. selene	2.89	2.21	19.03%	Connected

In both study sites, we performed standard transect counts of adult butterflies (Pollard and Yates 1993) during the flight periods of the four species in the summer of 2006. Apart from the number of individuals encountered, we recorded the nectar resources used and the flight behaviour of each species and sex. From the observations of

feeding activities, we inferred the set of favourite nectar resources, i.e. plant species on which percentage of feeding observations was superior to 1/*n*, where *n* was the total number of plant species used by the butterfly species. From the observation of flight behaviour, we categorized males and females of the four species in three different classes: (1) patrolling flight (butterflies travel sinuously and regularly through the biotope), (2) glider flight (butterflies fly up to some height then glide) and (3) perching and chasing flight of territorial males.

3. Specific behaviour of females

To check for behavioural differences, a random sample of females of each butterfly species was individually tracked in Pisserotte in 2006. We recorded in detail their behaviours per unit of time (number of females and total duration: 83 and 22280 s for *P. eunomia*; 35 and 9724 s for *C. selene*; 7 and 2047 s for *B. aquilonaris*; 20 and 5900 s for *L. hippothoe*). We recorded the following behaviours: thermoregulation (i.e. dorsal basking and wing shivering), nectar feeding, flight (with and without interaction with other organisms) and oviposition behaviour of females, including pre-alightment and egg-laying behaviour (e.g., Jones 1977; Stanton 1982). As behavioural tracking was done under different weather conditions (which can greatly influence the duration of thermoregulation bouts) and as egg laying events were not recorded for each individual, we kept the comparison between species to the proportion of time spent flying and feeding. A three way Anova (with the following factors: species and behaviour crossed, female nested within species but crossed with behaviour) was used to test for existing differences in relative behaviour frequency between the species.

Measures of resource grain, species mobility and morphological traits

1. Resource grain

Among the two study sites, a series of zones were selected (40 zones, 17 ha in Pisserotte; 25 zones, 9 ha in Libin). In each of these zones, 10 randomly placed vegetation samples were recorded (five in mid-June and five in mid-July), on which a 1 m^2 grid was used to measure the abundance of each plant species on a 0 to 25 scale. The spatial dimension of larval (host plant) and adult (nectar) feeding resources was computed for each butterfly species in each site with Ricklefs' formula of niche breadth:

$$B = \frac{1}{\sum P_i^2}$$

where P_i was the proportion of plant species counted in the vegetation samples in the *i*th zone of the study site (Edwards, Heckel and Guynn 1998). For larval resources (B_l), the single host plant of the butterfly was considered; for adult resources (B_a), abundance of all the favourite nectar plants used by the butterfly (as defined in the previous part) were summed zone by zone before computing P_i and applying Ricklefs' formula. As zone numbers were not equal in each site, we standardized niche breadth to 10 zones; hence, B possibly ranged from 0 to 10. The percentage of spatial dimension shared by larval and adult feeding was estimated using Schoener's index of niche overlap:

$$O_{la} = 1 - 0.5\sum\left|P_{il} - P_{ia}\right|$$

where P_{il} and P_{ia} represented the proportion in the *i*th zone of the study site of either larval or adult resources (Linton, Davies and Wrona 1981).

2. Species mobility

Populations of the four species were studied by Mark-Release-Recapture (MRR) during the summers 2005 and 2006, in Pisserotte only because the regional conservation authority prohibited MRR in Libin. Every encountered adult was individually marked and immediately released at the location of capture. For each (re)capture, we recorded the location (i.e. one of the 40 zones), mark, species and sex. The successive captures of marked individuals allowed estimating mean amplitude of foraging movement of each species and sex. All distances were computed between centres of zones.

3. Morphological traits

During the flying period of the four species in summer 2006, around 20 individuals per species, sex and site (312 individuals in total) were captured. Each individual was measured alive with calipers to record thorax length *TL* along the centre line and width *TW* at widest part, abdomen length *AL* along the centre line and width *AW TW* at widest part, and lengths of the upper and lower edges of forewings and backwings (*FWU*, *FWL*, *BWU* and *BWL* respectively). All species being threatened and legally protected, detailed measures requiring killing individuals were no option. This was done at four different days during the flying period of each species, on newly emerged individuals, to limit differences in morphology due to individual age. To avoid pseudoreplication due to multiple measures of the same butterfly, each individual was marked with a black cross on the forewing with a non toxic permanent pen and released at the spot of capture.

From these measures, the following variables were estimated: volume of the abdomen *AV* (approximated as an ellipsoid volume with height equal to width), volume of the thorax *TV* (approximated as an ellipsoid volume with height equal to width), wing area *WA* (approximated as triangle), wing loading:, and index *IF* of relative investment in flight versus reproduction in females (Hanski, Saastamoinen and Ovaskainen 2006):

$$AV = \frac{4}{3}\Pi \times \left(\frac{AW}{2}\right)^2 \times \frac{AL}{2}$$

$$TV = \frac{4}{3}\Pi \times \left(\frac{TW}{2}\right)^2 \times \frac{TL}{2}$$

$$WA = \frac{WL \times \sqrt{WU^2 - WL^2}}{2}$$

$$WL = \frac{TV}{FWA + BWA}$$

$$IF = \frac{TV}{AV}$$

The expected existence of differences between species and sexes was tested looking for mean differences in morphometric measures using a three way crossed Anova with species, sex and site (random) factors (for *IF*, a two way crossed Anova with species and site factors only).

Are spatial resource repartition and morphological traits in relation with mobility?

Firstly, we used linear regressions to test relations between the mean amplitude of recorded movements and (1) the spatial dimension of larval and adult feeding resources (B_l and B_a), (2) the overlap between both feeding resources (O_{la}), and (3) the mean amplitude of possible foraging movements, estimated on the basis of the resource distribution as the average of the distance for all couples of two zones containing the resources used by the butterflies (Hoverstadt and Nowicki 2008); amplitude of possible movement therefore differed for the four butterfly species. Distances centre to centre ranged from 30 m to 870 m between zones in Pisserotte. To assess the relative importance of factors in explaining variations in amplitude of movement, we used a multimodel inference approach (Burnham and Anderson 2002a; Anderson 2008). We computed all the possible combinations of explanatory variables (i.e. 16 models) and reported the *AICc* weight of each explanatory variable (expressing the relative importance of this variable in explaining the response), and model-averaged parameter estimates and confidence intervals. Secondly, we tested relations between each morphological trait and the mean amplitude of movement observed using Pearson correlation.

Modelling morphological trait variations between sites

The differences between species and sexes in each morphological trait, obviously expected and observed, were removed by standardizing measures to get a mean of zero for each species and sex combination, leaving only differences between the two sites. Linear regression models were used to assess relations existing between morphometric features (*TV*, *WA* and *WL*) on the one hand and (1) resource distribution measures (B_l, B_a, and O_{la}), (2) population isolation and (3) flight type on the other hand (32 models computed); the latter variable was not used for *IF* morphometric variable (16 models computed). We followed the same multimodel inference approach to assess the relative impact of the explanatory variables on each response variable, reporting for each explanatory variable *AICc* weight, and model-averaged parameter estimates and confidence intervals (Burnham and Anderson 2002a; Anderson 2008).

IV.3 RESULTS

Nectar resources use, flight and feeding behaviour

Species used nectar resources differently (**Figure IV.1**). *P. eunomia* adults were narrow specialists, using almost only a single nectar resource (95.42% of the observations on *P. bistorta*, the host plant of caterpillars). *C. selene* mostly fed on *Cirsium palustris*, and to a lesser extent on *Lichnis flos-cuculi*. *B. aquilonaris* and *L. hippothoe* adults were rather opportunistic. *L. hippothoe* mainly fed on *Lotus pedunculatus*, *L. flos-cuculi*, and *C. palustris*, and less frequently on five other plant species. Spectrum of plant species used as nectar resources by *B. aquilonaris* was composed of 9 species.

Both sexes of *P. eunomia* and *B. aquilonaris*, and females of *C. selene* and *L. hippothoe* exclusively showed patrolling type of flight, in both sites. Males of *C. selene* showed in both sites the gliding type of flight, mainly above zones with high density of *C. palustris*. *L. hippothoe* males exhibited a territorial behaviour in Pisserotte only: they perched and engaged in pursuits against intruders using either spinning wheel flight or fast and short horizontal chases; on the contrary, they adopted patrolling behaviour in Libin (Turlure and Van Dyck 2009).

Female tracking showed that proportion of time spent flying and feeding were equal and did not differ among species (**Table IV.2**). 42 % of the egg laying behaviour observed were preceded and/or followed by feeding.

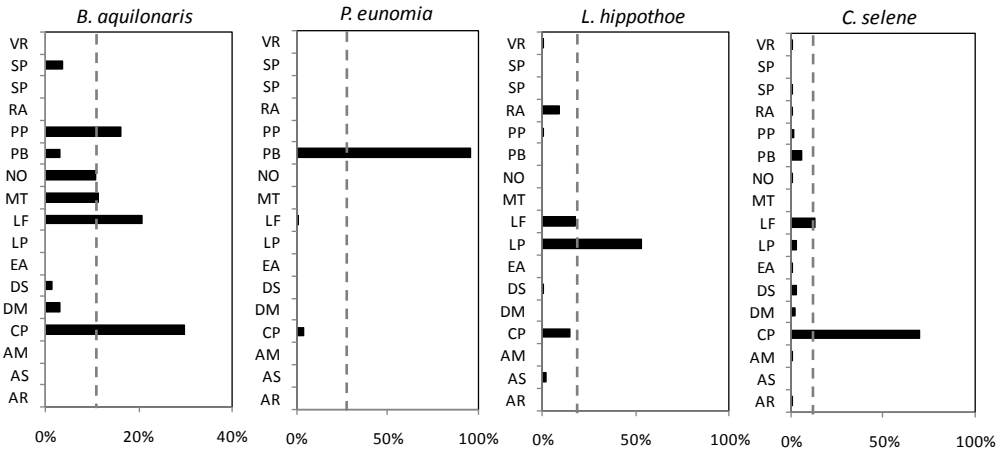


Figure IV.1. Spectrum of nectar resources used by the four butterfly species. Black bars represent the percentage of utilization of each plant species. Grey dotted lines separated favourite nectar resources from less used ones; threshold is not similar for all species as it equals 1/*n*, with *n* the number of plant species used by the butterfly species. AR = *Ajuga reptens*, AS = *Angelica sylvestris*, AM = *Arnica montana*, CP = *Cirsium palustre*, DM = *Dactylorisa maculata*, DS = *Dactylorisa sphagnicola*, EA = *Epilobium angustifolium*, LP = *Lotus pedonculatus*, LF = *Lychnis flos cuculi*, MT = *Menyanthes trifoliata*, NO = *Narthecium ossifragum*, PB = *Polygonum bistorta*, PP = *Potentilla palustris*, RA = *Rumex acetosa*, SP = *Stachys palustris*, SP = *Succisa pratensis*, VR = *Valeriana repens*

Table IV.2. No difference in the proportion of time spent flying and feeding was observed between species (three way ANOVA).

Effect	dF	Error terms	Sum of squares	Mean square	F	*P*
Species	3	Femelle (Species)	0.3611	0.1204	2.7569	0.3414
Behaviour	1	Femelle (Species) x Behaviour	0.0547	0.0547	0.8209	0.3874
Femelle (Species)	141	Residuals	7.6891	0.0545	0.7457	0.9587
Femelle (Species) x Behaviour	141	Residuals	10.311	0.0731	.	.
Species x Behaviour	3	Femelle (Species) x Behaviour	0.1868	0.0623	0.8513	0.4681

Resource spatial dimension and overlap

All measures of resource spatial dimension and overlap are represented in **Table IV.1**. Resource spatial dimensions ranged from 2.0 to 5.6; in other words, individual resources were distributed among 20 % to 56 % of the zones. They were smaller in Pisserotte than in Libin, except for the bistort (host plant and nectar resource used by *P. eunomia*). Overlap between spatial dimension of the host plant and nectar resources ranged from 19 % to 100 %; it was maximal (100 %) for *P. eunomia* as the species used the same plant species for larval and adult feeding. For the three other butterflies, the overlap was smaller in Pisserotte than in Libin: relatively high in both sites for *L. hippothoe* (> 40 %), really low

for *B. aquilonaris* and *C. selene* in Pisserotte (respectively 28 % and 19 %).

Relation between resource grain and mobility

For each species, the mean amplitude of recorded movements was smaller than the mean amplitude of possible movements. Linear regression analysis showed that the data strongly supported (*AICc* weight reached a high level) the hypothesis of wider average movements when spatial dimension of nectar was smaller and when the overlap between nectar and host plant resources was more pronounced (**Table IV.3**). Data did not support the existence of some effect of neither the mean of possible distances nor the spatial dimension of host plant.

Table IV.3. Generalised linear regressions on mean distances moved for each species indicated that foraging movements were linked to spatial dimension of nectar resource and the overlap between nectar resources and host plants. Variable weight is a multimodel estimate of the relative importance of this variable in explaining the response (see text for detail).

Variables	Variable weight	Parameter estimate	Parameter standard deviation
Intercept	100.00%	183.641	4.539
Mean possible distance	5.81%	-0.8496	1.0973
Spatial dimension of nectar	94.59%	-78.8979	21.701
Spatial dimension of host plant	8.58%	2.7431	3.0269
Overlap	83.30%	53.2054	20.3636

Relation between morphological traits and mobility

The mean amplitude of recorded movements was significantly correlated with all morphological traits, except for *IF* (Pearson correlation test: R = 0.73, n = 4, *P* = 0.27; **Figure IV.2**). The relation was positive with *TV* (Pearson correlation test: R = 0.78, n = 8, *P* = 0.022) and *WL* (Pearson correlation test: R = 0.8, n = 8, *P* = 0.017), and negative with *WA* (Pearson correlation test: R = -0.77, n = 8, *P* = 0.023).

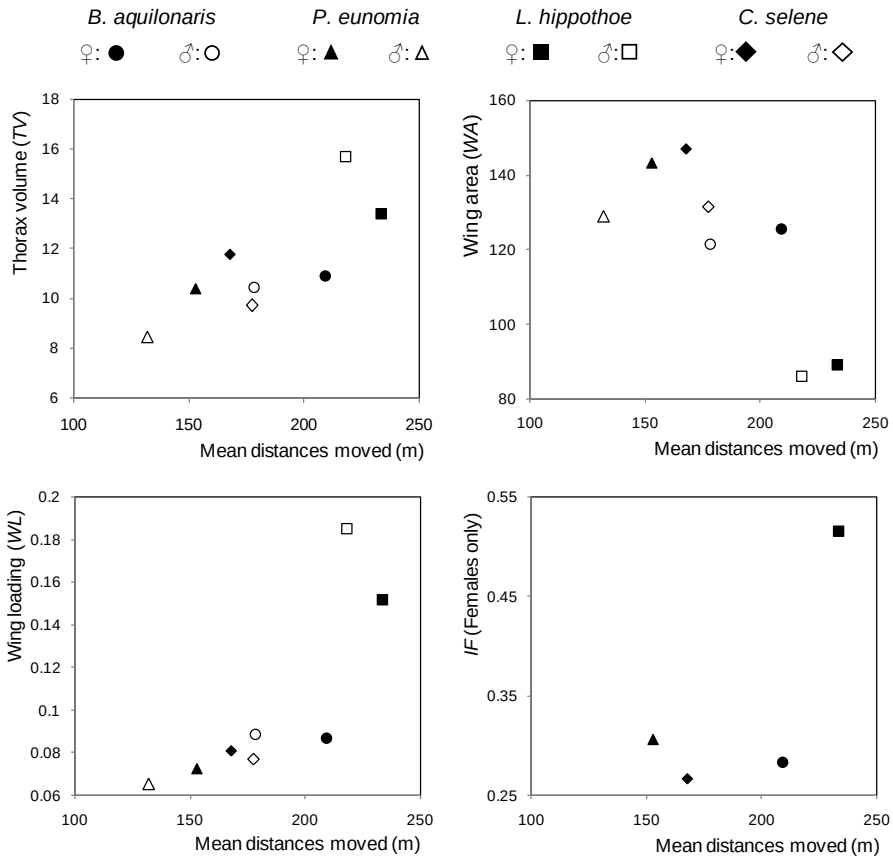


Figure IV.2. Relations between morphological traits and mean distance of recorded movements in Pisserotte were significant except for *IF*.

Modelling morphological trait variations between sites

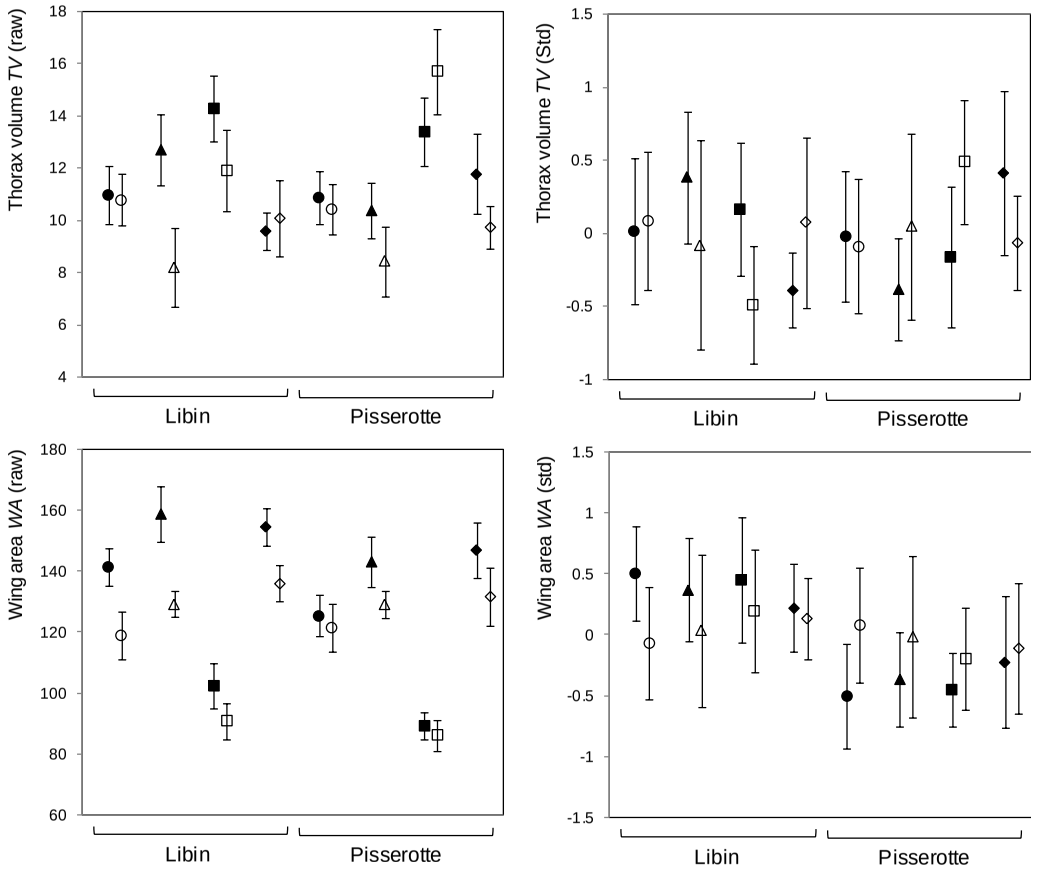
Some variations of morphological traits according to species and sexes were observed as obviously expected (**Table IV.4**, **Figure IV.3**), justifying that morphological data were standardized for each species-sex combination (**Figure IV.3**) before relating the variation between the two sites to explanatory variables via linear regression (**Table IV.5**).

TV was mainly related to flight type (variable weight = 58.40 %), with a larger thorax being associated with territorial behaviour and hence short and fast flight. *WA* was positively related to nectar resource spatial dimension (variable weight = 72.61 %). The best explanation of *WL* variation (wing loading decreasing with nectar resource spatial dimension and for glider and patrolling flight) were anyway limited (53.26 % and 49.63 % respectively). Data strongly supported a negative relation between *IF* and nectar resource spatial dimension (variable weight = 95.90 %). *AICc* weight of the other explanatory variables did not reach high levels.

Figure IV.3. Mean (and 95 % confidence interval) values recorded for four morphological traits (see text for detailed description of measurements). A) Raw measures. B) Measures standardized at the species-sex combination level to remove differences between species and sex dimorphism. Sample size ranged between 20 and 23 individuals per species, sex and site, except for *P. eunomia* males (8 individuals in Libin, 14 individuals in Pisserotte) because its flying period was drastically shorter than usually due to bad weather conditions.

B. aquilonaris ♀: ● ♂: ○ *P. eunomia* ♀: ▲ ♂: △ *L. hippothoe* ♀: ■ ♂: □ *C. selene* ♀: ◆ ♂: ◇

Figure panels are shown on the next pages…


Thorax volume TV (raw)
18
16
14
12
10
8
6
4
Libin
Pisserotte
Thorax volume TV (Std)
1.5
1
0.5
0
-0.5
-1
Libin
Pisserotte
Wing area WA (raw)
180
160
140
120
100
80
60
Libin
Pisserotte
Wing area WA (std)
1.5
1
0.5
0
-0.5
-1
-1.5
Libin
Pisserotte

Wing loading WL (raw)
0.25
0.2
0.15
0.1
0.05
0
Libin
Pisserotte
IF, for females only (raw)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Libin
Pisserotte
Wing loading WL (std)
1.5
1
0.5
0
-0.5
-1
Libin
Pisserotte
IF, for females only (std)
1.5
1
0.5
0
-0.5
-1
Libin
Pisserotte

Table IV.4. Measures of index *IF* of relative investment in flight versus reproduction in females were compared using a two way crossed Anova with site as random factor. Measures of thorax volume (*TV*), wing area (*WA*) and wing-loading (*W*L) were compared using a three way crossed Anova with site as random factor.

Index "mobility vs fecundity" *IF*	dF	Error terms	Sum squares	Mean square	F	*P*
Site	1	Residuals	0.13	0.13	11.89	0.0007
Species	3	Site x Species	1.53	0.51	46.18	<.0001
Site x Species	3	Residuals	0.04	0.01	1.17	0.3226

Thorax volume *TV*	dF	Error terms	Sum squares	Mean square	F	*P*
Species	3	Species x Sex	723.66	241.22	34.86	<.0001
Sex	1	Site x Sex	87.52	87.52	12.65	0.0004
Site	1	Residuals	5.71	5.71	0.83	0.3642
Species x Sex	3	Site x Species x Sex	99.8	33.27	4.81	0.0028
Site x Species	3	Residuals	63.89	21.3	3.08	0.0279
Site x Sex	1	Residuals	22.64	22.64	3.27	0.0715
Site x Species x Sex	3	Residuals	150.21	50.07	7.24	0.0001

Wing area *WA*	dF	Error terms	Sum squares	Mean square	F	*P*
Species	3	Species x Sex	124202	41400.8	169.08	<.0001
Sex	1	Site x Sex	16179.5	16179.5	66.08	<.0001
Site	1	Residuals	4004.25	4004.25	16.35	<.0001
Species x Sex	3	Site x Species x Sex	1971.3	657.1	2.68	0.0469
Site x Species	3	Residuals	105.71	35.24	0.14	0.9335
Site x Sex	1	Residuals	2341.21	2341.21	9.56	0.0022
Site x Species x Sex	3	Residuals	694.36	231.45	0.95	0.4191

Wing loading *WL*	dF	Error terms	Sum squares	Mean square	F	*P*
Species	3	Species x Sex	0.34	0.11	162.14	<.0001
Sex	1	Site x Sex	0	0	1.12	0.291
Site	1	Residuals	0.01	0.01	9.64	0.0021
Species x Sex	3	Site x Species x Sex	0.01	0	2.55	0.0558
Site x Species	3	Residuals	0.01	0	5.69	0.0008
Site x Sex	1	Residuals	0	0	0.78	0.3776
Site x Species x Sex	3	Residuals	0.01	0	5.31	0.0014

Table IV.5. Results of linear regressions on morphological traits according to six explanatory factors. The variable weight is a multimodel estimate of the relative importance of this variable in explaining the response (see text for detail). Conclusions are that (1) females invested more in fecundity (vs mobility) when spatial dimension of nectar was larger, (2) thorax volume was bigger in territorial butterflies, (3) wing area increased with spatial dimension of nectar, and (4) wing-loading decreased with niche spatial dimension of nectar and for non territorial butterflies.

Index "mobility vs fecundity" ***IF***		**variable weight**	**Parameter estimate**	**Parameter st. d.**
Intercept		100.00%	0.6991	0.1831
Niche breadth of nectar		95.90%	-0.1878	0.043
Niche breadth of host plant		8.49%	-0.0064	0.0086
Overlap		24.21%	0.1091	0.1015
Population	Connected	6.30%	0.0063	0.0095
	Isolated		0	/

Thorax volume ***TV***		**Variable weight**	**Parameter estimate**	**Parameter st. d.**
Intercept		100.00%	0.3752	0.3179
Niche breadth of nectar		19.89%	-0.0055	0.0112
Niche breadth of host plant		25.68%	-0.0162	0.0198
Overlap		18.41%	-0.001	0.0554
Flight type	Glider	58.40%	-0.2755	0.2091
	Patroller		-0.3011	0.1932
	Territorial		0	/
Population	Connected	20.98%	-0.0204	0.0327
	Isolated		0	/

Wing area *WA*		Variable weight	Parameter estimate	Parameter st. d.
Intercept		100.00%	-0.3472	0.2564
Niche breadth of nectar		72.61%	0.0848	0.0417
Niche breadth of host plant		21.34%	0.0113	0.0185
Overlap		22.22%	-0.0416	0.0837
Flight type	Glider	19.41%	0.0353	0.0751
	Patroller		0.0212	0.0614
	Territorial		0	/
Population	Connected	30.84%	-0.0542	0.0553
	Isolated		0	/

Wing loading *WL*		Variable weight	Parameter estimate	Parameter st. d.
Intercept		100.00%	0.5572	0.3144
Niche breadth of nectar		53.26%	-0.051	0.0347
Niche breadth of host plant		38.42%	-0.0393	0.0348
Overlap		22.26%	0.0414	0.0895
Flight type	Glider	49.63%	-0.2296	0.1857
	Patroller		-0.2371	0.1729
	Territorial		0	/
Population	Connected	16.76%	-0.0059	0.0236
	Isolated		0	/

IV.4 DISCUSSION

The grain of the adult and larval feeding resources and of their overlap was markedly different both among species and between sites for each species. Firstly, observed movements of adult butterflies, as inferred from MRR data, depended on the grain of both adult feeding resource and its overlap with larval host plant. Secondly, morphological traits related to adult flight were correlated to observed movements of adult butterflies, which confirms their interest as proxies for mobility. Thirdly, we related morphological parameters either to biological variable or resource grain: variation in thorax volume was only explained by expression of male territoriality, and the grain of adult feeding resource had a significant effect on wing area. Finally, the trade-off between investments in mobility vs fecundity in females was again related to the grain of adult feeding resource. The grain of host plant resource and the landscape context (population isolation) had an effect neither on mobility nor on morphology.

Understanding individual mobility and being able to predict it according to the landscape connectivity seems to be nowadays one of the most urgent issues in current conservation biology (e.g. Ruckelshaus, Hartway and Kareiva 1999; Baguette 2003; Van Dyck and Baguette 2005). Mobility is obviously difficult to measure; the value of dispersal kernels as realistic measures of mobility has clearly been shown to be far from realistic (e.g. Cook, Dennis and Hardy 2001; Bowne and Bowers 2004). Here we chose the simplest measure, i.e. the mean of distances observed between successive captures of the same individual, to map

adult movements onto resource grain. Because adult butterflies need to feed regularly, it makes intuitively sense that butterfly mobility is constrained by the location of their nectar plants. Moreover, as documented by Wiklund and Ahrberg (1978) and Brommer and Fred (2001), an important ecological factor affecting movement in butterflies might be the spatial segregation between the larval resource (host plants) and the adult resource (nectar plants). We showed here that both the spatial dimension of adult feeding resource and its overlap with larval feeding resource directly influenced the mean distance effectively moved by flying butterflies.

Movements were positively correlated with thorax volume and wing loading, and negatively correlated with wing area. This result suggests that small displacements are associated with rather larger wings and smaller thoraxes (i.e. a low wing loading), whereas long displacements are associated with smaller wings and larger thoraxes (i.e. a high wing loading) (e.g. Norberg and Leimar 2002; Berwaerts, Aerts and Van Dyck 2006; Benard and McCauley 2008). The study of mobility, which involved catching butterflies, was allowed by the regional conservation agency in only one site (Pisserotte), where the grain of resources was tighter for all species than for *P. eunomia* (**Table IV.1**). Accordingly, the data on *P. eunomia* should distort the negative relation between the observed movements and wing area measurements (Figure 2). Indeed, removing points corresponding to *P. eunomia* from the relation between movements and wing area sharply increased its explanatory power (R^2 increased from 0.61 to 0.77). Altogether, according to the observed relation and this post-hoc test, we are confident that morphological traits related to adult flight (i.e. thorax

volume, wing area and wing loading) are efficient proxies for studying how resource grain scales mobility in butterflies.

Morphological traits related to adult flight were different among species and sexes, which was not surprising given the wide inter-specific differences in size associated with a consistent sexual dimorphism, females being always larger than males. More interesting, we found a significant association between thorax volume and male territoriality. Dudley (1991) showed that fresh thorax mass contained 90% of flight muscle mass in butterfly. These contractile muscles are used to produce wing flapping, and hence thorax mass or volume reflects the flight muscle allocation of the individual (Dempster, King and Lakhani 1976). In this multi-species system, one would expect the thorax volume to vary with flight type (Betts and Wootton 1988). Indeed, more powerful flight with high levels of acceleration used by territorial males would require more muscles (i.e. a bigger thorax) compared to patrollers and gliders (Dudley 1991). Not surprisingly, thorax measures were strongly related to flight type: *L. hippothoe* territorial males had larger thorax than other males or females. This findings also connects to the well documented difference between perchers and patrollers, where perchers need a larger thorax with more muscle to furnish the power for rapid take off when a female or a competitor male appears in their territory (Wickman 1992; Peixoto and Benson 2008).

In several studies, butterfly distribution was shown to be constrained by the availability of adult feeding resource (e.g. Murphy, Menninger and Ehrlich 1984; Schultz and Dlugosch 1999; Brommer and Fred 2001; Dennis *et al.* 2005). Here, we detected an effect of resource

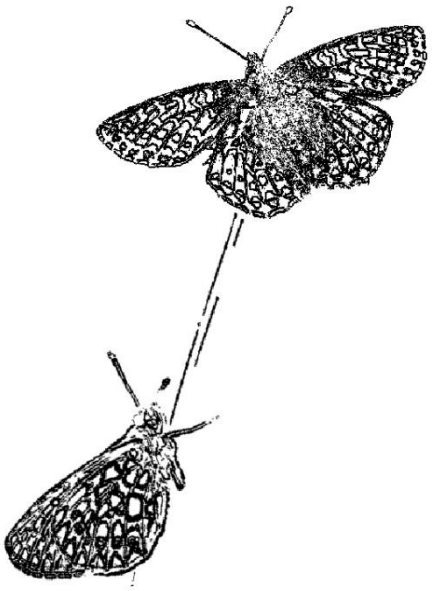
grain on morphological traits related to adult flight: wing area was larger and wing loading lower when nectar resources were widespread. As large wing area and low wing loading are associated with low range movements (e.g. Berwaerts, Aerts and Van Dyck 2006), this result suggests that butterflies restricted their foraging movement range when nectar resources were more widespread. Our correlative approach certainly deserves further confirmation. Anyway, if the relation between the loose grain of adult feeding resource and changes in morphological traits related to adult flight we observed here proves to be somewhat general, this effect might explain why many butterfly species decreased or disappeared even when their host plant was still present. As Van Dyck and Baguette (2005) pointed out, "it is an intriguing and yet unaddressed question to evaluate to what extent, and under what conditions, long-distance movements can evolve independently from movements associated with local resource use". If local resource settings negatively affect mobility by changing morphological traits associated with displacements, this should also decrease long-distance (dispersal) movements. This might explain why the connectedness of populations at the landscape scale has here no detectable effect on morphological traits associated with flight. Anyway, contrary to what was previously shown on several butterfly species (e.g. Thomas, Hill and Lewis 1998b; Hill, Thomas and Lewis 1999; Norberg and Leimar 2002; Hanski, Saastamoinen and Ovaskainen 2006), the impact of resource grain overruled here the potential impact of landscape configuration.

Finally, we tested for a potential effect of resource grain on the index of relative investment in mobility vs fecundity (i.e. the ratio thorax volume/abdomen volume) in females. The usual justification for this

latter assumption is that, as thorax weight reflects investment for flight (a larger thorax contains more flight muscles) and abdomen weight reflects fecundity (a larger abdomen contains more or bigger eggs), the ratio of the two represent a proper measure of the dispersal–fecundity trade-off (Zera and Denno 1997). In the four studied species, egg laying strategies of females are not much different, females laying one or a few eggs on multiple occasions (Turlure C. unpublished data); furthermore, individuals of different age have been sampled. Hence, we can assume that egg load will not affect flight capacity as it can be the case for females laying large amount of eggs at a time (such as *Euphydrias aurinia*). Moreover, the proportion of time devoted to the different behavioural registers was not different among species. The observed relation between fecundity and mobility is hence likely not much influenced by behavioural differences. However, several studies have also shown that highly mobile butterfly females have a large ratio thorax weight to abdomen weight (Dempster, King and Lakhani 1976; Hill, Thomas and Lewis 1999). According to the oogenesis flight syndrome (Johnson 1969), we found here that females had a larger abdomen and a larger investment in fecundity when the spatial dimension of adult feeding resource was large. The observed changes in morphological traits associated with flight might therefore be due to the fact that both time and potential opportunities for oviposition are lost during dispersal or foraging movement between highly fragmented resources in females ovipositing repeatedly (Hanski, Saastamoinen and Ovaskainen 2006; Baguette and Van Dyck 2007).

Chapter V

Estimating population size with a resource-based habitat approach: a test with butterflies.



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ABSTRACT.

1. Accurate estimates of population size are essential for effective conservation and restoration management of threatened species. Nevertheless, reliable methods to estimate population size, such as mark-release-recapture studies (MRR), are time and labour consuming and may generate negative impact(s) on both the habitats and organisms studied. Admittedly, this may complicate their use in nature reserves and for threatened species or also if one wants to study several sites at the time. Consequently, there is a strong interest to develop reliable proxies of population size that are less time consuming (e.g. the frequent use of habitat area in Population Viability Analysis).

2. Using two peat bog butterflies (*Proclossiana eunomia* and *Boloria aquilonaris*), we tested the reliability of habitat area as proxy for population size by (1) predicting population sizes based on the product of larval habitat area by adult emergence rate per spatial unit of habitat (by ground cover traps) for each species and (2) comparing these predictions to accurate population size estimates inferred from MRR studies. Habitat area was defined either as the total host plant area, or as the resource-based area (i.e. the area containing the different ecological resources and conditions needed by the caterpillars of each species).

3. Results on both species showed that: (1) adult population size was strongly related to larval habitat availability and quality when habitat was accurately defined according to functional resources, (2) resources other than the host plant have to be included in the habitat definition as

they play a role in the demographic response, (3) after careful control of its similarity, the resource-based habitat delineation can be reasonably well transferred among populations of the same species in a wider region.

V.1 INTRODUCTION

The number of alive individuals is the most fundamental demographic trait of a population and the primary target for many conservation plans (Williams, Nichols and Conroy 2002; Van Dyke 2008). The conservation status of a species (e.g. within European Natura 2000 policy framework) is typically expressed in terms of population size and population number (e.g. Joseph et al. 2006). Accurate estimates of the abundance (or census population size) are essential for effective conservation and restoration management (Sutherland 1996). Although several biological correlates have been evaluated for different taxonomic groups relative to extinction risk (e.g. Fischer, Blomberg and Owens 2003; Jones, Purvis and Gittleman 2003), population size and trend indeed appear to be one of the best correlates (Belovsky *et al.* 1999; O'Grady *et al.* 2004). But, a large part of population theory depends on case studies on fur-bearing animals, game or other birds and pests where logistical difficulties to study population size and dynamics have been overcome (Begon, Townsend and Harper 2006). Several species of conservation concern impose, however, important challenges to population biologists as estimating the number of individuals may be difficult with incomplete information.

In butterflies, two main methods have been established to assess species adult population size or at least adult population density: Mark-Release-Recapture studies (e.g., Schultz 1998; Fischer, Beinlich and Plachter 1999; Schtickzelle, Le Boulengé and Baguette 2002; Baguette 2003) and transects counts (e.g., Pollard 1977; Pollard 1988; Kitahara

2004; Dennis 2004b; Collier *et al.* 2006). There is ample evidence of reliable population size estimates in butterflies based on mark-recapture studies (Williams, Nichols and Conroy 2002; Haddad *et al.* 2007; Nowicki *et al.* 2008) as long as basic assumptions have not been violated (mainly unique and permanent markings, equal capture probability among individuals and absence of temporary emigration). But MRR studies are time- and labour-consuming and may have a non negligible impact on individuals due to handling and marking effects (Singer and Wedlake 1981; Gall 1984; Murphy 1988) and also on vulnerable vegetations due to trampling during repeated field visits. Hence, this method is sometimes questioned or even not allowed in nature reserves and particularly in the case of threatened species. Butterfly transect counts have became a popular study technique since the method (i.e. the Pollard walk) was established (Thomas 1983; Pollard and Yates 1993). This method is frequently used to assess trends in butterfly abundance for conservation (e.g. in national monitoring schemes; Thomas 2005) because (i) it is less time consuming and it has a lower impact on the butterflies and the vegetation than MRR methods (e.g., Gross *et al.* 2007; Nowicki *et al.* 2008) and (ii) the method can be used for a single species but also for the whole community (Collier, MacCay and Bekendorff 2008). However, this method allows estimating relative abundance, but not the absolute population size and its reliability has recently been criticized, mainly because imperfect species detection and adult longevity had not been taken into account (e.g., Zonneveld, Longcore and Mulder 2003; Kery and Schmid 2004; Haddad *et al.* 2007; Harker and Shreeve 2008). In case of extremely short life duration of adults (as in *Maculinea* species), estimation of population size can be based on egg counts (Maes *et al.* 2004; WallisDeVries 2004; Nowicki *et al.* 2007).

Such a method can be used only when eggs or egg shelters are visible. It consequently fits a smaller number of butterfly species. Nevertheless, there is a strong interest among conservation biologists to develop and use reliable proxies of population size, instead of relative abundance, that are less time consuming and generate no negative impacts.

As population size is conditioned among others by habitat availability (Jorge Soberon 1986; Boyce and MacDonald 1999; Fahrig 2001; Krauss, Steffan-Dewenter and Tscharntke 2004), habitat area is often used as a proxy of the carrying capacity and, hence of potential population size (e.g., in Population Viability Analysis; White 2000; Schtickzelle and Baguette 2009). In butterflies, host plant patches have often been used as blind surrogates for habitat. But other resources and the variation within host plant patches are also significant to recognize functional habitat (Vanreusel and Van Dyck 2007; Turlure *et al.* 2009b). The key role of food availability to understand butterfly populations dynamics, has been established since long (Singer 1972), but a resource-based habitat approach recently received again much more attention (Dennis, Shreeve and Van Dyck 2003b; Dennis, Shreeve and Van Dyck 2006a). Would the surface of such a resource-based functional habitat represent a better proxy of population size than simply using the host plant area, as it has been usually done?

In this study, we tackle this issue by estimating population size based on the combination of larval habitat area (i.e. the part of the population habitat that directly produced adult individuals) and adult emergence rate per spatial unit of habitat in two peat bog specialist butterflies. Larval habitat area was considered either as the total host

plant area (i.e. as defined in most study on butterflies) or as the resource based area (i.e. area containing the different ecological resources and conditions needed by caterpillars). In order to do so, we used ground cover traps to estimate the emergence rate of adult butterfly under different larval habitat quality conditions. The use of traps to estimate emergence pattern or phenology has been successful in many other organisms (e.g., cicadas: Callaham Jr et al. 2000, ticks: Cançado et al. 2008 or mosquitos: Service 1993), but neglected for butterflies (but see Goffart *et al.* 2001; Goffart, Schtickzelle and Turlure 2009). Reliable recognition and delineation of functional habitat and assessment of habitat quality for each species was based on results of previous studies (Turlure *et al.* 2009a; Turlure *et al.* 2009b). Higher rate of emergence (i.e. higher demographic response, Garshelis 2000) in high quality area was expected on the basis of larval habitat quality definition, which could furthermore strengthen this definition. Secondly, we compared the direct measure of population size inferred from MMR data for each species to indirect predictions of population size inferred from the product of habitat area by productivity (i.e. rate of emergence per m^2). We expected that the use of the resource-based area approach would allow a better prediction of the population size than the use of the total host plant area. Finally, we tested the transferability of our approach among different nature reserves by comparing the ratio of habitat availability to the ratio of observed adult density between sites located at close distance for the two species.

V.2 METHODS

Study species

The study species were two specialist butterfly species of conservation concern (listed as 'vulnerable' on the Red Data Book of European butterflies; van Swaay and Warren 2006). The bog fritillary *Proclossiana eunomia* is a specialist species of peat bogs and wet meadows. Adults fly in June and females lay egg clusters close to or under leaves of the host plant *Polygonum bistorta* (1987; Baguette and Nève 1994). The cranberry fritillary *Boloria aquilonaris* is a glacial relict species of acid peat bogs. Adults fly in July and females lay their eggs singly on the host plant *Vaccinium oxycoccos* (Bink 1992; Schtickzelle, WallisDeVries and Baguette 2005a). Both species have a boreo-alpine distribution with highly fragmented populations to the south. In Belgium, their populations are confined to the Ardenne and Lorraine region (Fichefet et al. 2008).

Study areas

We collected field data in two peat bogs: the Fange de Pisserotte nature reserve (50°13'N 5°47'E) in the "Plateau des Tailles" landscape and the Troufferies de Libin nature reserve (49°57'N 5°19'E) in the "Plateau de Recogne" landscape. Each of the nature reserves hosts one population of *P. eunomia* and one of *B. aquilonaris. P. bistorta* occurred in 21 patches (total area: 8888 m^2) in Pisserotte and in 16 patches (6113 m^2) in Libin.

V. oxycoccos occurred in 15 patches (9748 m²) in Pisserotte and in 9 patches (10643 m^2) in Libin. *V. oxycoccos* always occurred at a high density.

Resource-based definition of larval habitat quality

Our earlier work on the larval ecology of both species (Goffart, Schtickzelle and Turlure 2009; Turlure *et al.* 2009a; Turlure *et al.* 2009b), allowed (1) delineating suitable areas based on ecological resources within host plant patches (later called the "resource-based area") and (2) assigning a low (LQ) or high quality (HQ) to each delineated habitat zone depending on the availability/density of these resources. *P. eunomia* requirements consisted of a sufficiently dense cover of *P. bistorta*, with tussocks of mainly *Deschampsia cespitosa* (Turlure et al. 2009b). As tussock density did not vary strongly between delineated habitat areas (mean tussock number = 2.3 per m^2), the distinction between high and low quality was based on host plant density (mean host plant coverage: 62 % in high quality areas vs 27 % in low quality areas; ANOVA: $F_{1,26}$ = 15.73, P = 0.0005). *B. aquilonaris* requirements consisted of high density carpet of the host plant *V. oxycoccos* growing either on *Sphagnum* or *Polytrichum* hummocks (Turlure et al. 2009a). As *Sphagnum* hummocks provide a much more appropriate thermal larval environment than *Polytrichum* hummocks, the former represent high quality and the latter low quality habitat. (**Table V.1**).

Table V.1. Number and area of patches of the host plants *P. bistorta* and *V. oxycoccos* (of the butterflies *P. eunomia* and *B. aquilonaris*, respectively) in the two study areas in Belgium. Resource-based area was the suitable area within the host plant area that contained other resources needed by the caterpillars. Within the resource-based area, we distinguished between low (R-b area, low quality) and high (R-b area, high quality) quality according to the availability of the resources needed (see text for details).

Butterfly / Host plant	Study area	Type	Number of patches	Area (m^2)
P. eunomia / P. bistorta	Pisserotte	Host plant area	27	19630.48
		Resource-based area	21	8888.66
		R-b area, low quality	4	909.79
		R-b area, high quality	17	7978.86
	Libin	Host plant area	19	11671.48
		Resource-based area	13	6112.75
		R-b area, low quality	6	2012.59
		R-b area, high quality	7	4100.16
B. aquilonaris / V. oxycoccos	Pisserotte	Host plant area	15	8998.56
		Resource-based area	15	4417.54
		R-b area, low quality	8	2975.95
		R-b area, high quality	7	1441.59
	Libin	Host plant area	9	10643
		Resource-based area	9	9051.23
		R-b area, low quality	0	0
		R-b area, high quality	9	9051.23

Estimating population size and density

In 2006 (June to August), we studied the Pisserotte populations of both species by Mark-Release-Recapture (MRR) methods (Williams, Nichols and Conroy 2002). The study site was visited under suitable weather conditions allowing butterfly activity (i.e. no strong wind, few cloud and air temperature > 15°C). Adults were captured, individually marked and released on the spot of capture. At each (re)capture, we recorded date, species, marking code and sex. Demographic parameters (i.e. survival and recapture rates, daily and total population size) were inferred for each species from our MRR-data using Mark program (White and Burnham 1999). We followed the procedure as described in Schtickzelle, Le Boulengé and Baguette (2002).

During the same period, we also recorded in Libin and in Pisserotte the number of adults of both species flying within 10 m of transect lines (Pollard 1977). Two observers walked side by side along transects recording together the number of butterflies on one side of the transect line. Total transect length was 4200 m and 3400 m in Pisserotte and Libin, respectively. Transect counts were done under suitable weather conditions. Order of transects was altered at each visit. Following advises for optimal schemes in Zonneveld, Longcore and Mulder (2003), we performed more than five transects counts per species and site to obtain more reliable indexes of population density. We calculated an index of population density (*IP*) for each population from the transect count data by weighing the total number of individuals

recorded by the transect length and the number of visits made during the flight period (Thomas 1983; Williams, Nichols and Conroy 2002).

Adult emergence rate

To estimate the number of butterflies produced by a particular vegetation in Pisserotte, we placed emerging traps that covered each 1 m^2 over the vegetation in host plant patches (Goffart, Schtickzelle and Turlure 2009). This was done for both species. Each trap consisted of a cage in white fine netting (meshes of 2.25 mm^2). Before the end of the larval diapause period of *P. eunomia* (i.e., end of April 2006), we placed 34 traps in *P. bistorta* patches (19 in high quality areas, 15 in low quality areas). Before the end of the larval diapause period of *B. aquilonaris* caterpillars (i.e., beginning of June 2006), we placed 30 traps in *V. oxycoccos* patches (15 in high quality areas, 15 in low quality areas). In June 2008, 18 traps were additionally placed in high quality *V. oxycoccos* patches in Libin. The presence of emerged butterflies in the traps was checked daily during the flight period and each individual (butterflies or other insects) was released.

We used logistic regression models with appropriate contrasts to compare emergence rate relative to habitat quality and study area (for *B. aquilonaris* only). Using the number of presence and absence of emerged butterflies in the traps, we calculated for each species and site the probability of emergence and confidence interval per 1 m^2 (emergence rate) relative to habitat quality.

Larval parasitism

In May and June 2006, we searched for caterpillars of both species in all host plant patches in both study areas. Search time was proportional to host plant patch area to keep sampling effort constant. All caterpillars were collected and reared in the laboratory under the same conditions (natural temperature fluctuations; photoperiod L:D 12h:12h). They were kept in individual boxes with *ad libitum* access to fresh host plant leaves until pupation. This allowed estimating the rate of parasitism for each butterfly species and site. Emerging adults were released in their population of origin, whereas emerged parasitoïds were kept for further research. From this experimental breeding, we obtained an estimation of the rate of parasitism for each species and site.

Estimating population size from emerging trap data

We combined the data on larval habitat area, rate of emergence and rate of parasitism in order to get an indirect estimate of the population size of each species in Pisserotte. We used this combined information to predict the population size according to 6 alternatives (**Figure V.1**). These 6 predictions of population size were calculated as follows:

- *Population size I = Area1 * Er*, with *Area1* the total host plant area and *Er* the rate of emergence expressed as a unique measure from habitat of homogenous quality.

- *Population size II = Area1 * Er * (N_2/N_1)*, with N_2/N_1 the rate of survival to parasitism, which reduced the initial number of caterpillars collected within the population (N_1) to a lower number of caterpillars (N_2, i.e., the number of non parasitized caterpillars) and hence the number of adult butterflies.

- *Population size III = Area2 * Er*, with *Area2* the smaller area within host plant patches that contained the other resources required by the caterpillar species (i.e., the resource-based area).

- *Population size IV = Area2 * Er * (N_2/N_1)*.

- *Population size V = AreaLQ * ErLQ + AreaHQ * ErHQ*, where *AreaLQ* and *AreaHQ* (together summing to *Area 2*) took into account the variation in quality according to availability of other resources needed by the caterpillars (LQ for low quality areas and HQ for high quality areas). In this case, rate of emergence was expressed as differentiated measures according to habitat quality (*ErLQ* and *ErHQ* for rates of emergence in low quality and high quality areas respectively).

- *Population size VI* = [*AreaLQ* x *ErLQ* + *AreaHQ* x *ErHQ*] x (N_2/N_1).

  95 % confidence intervals for these 6 measures were straightly derived from the uncertainty in estimates of the rates of emergence. These 6 predictions of the population size were compared to the observed population size inferred from the detailed MRR data.

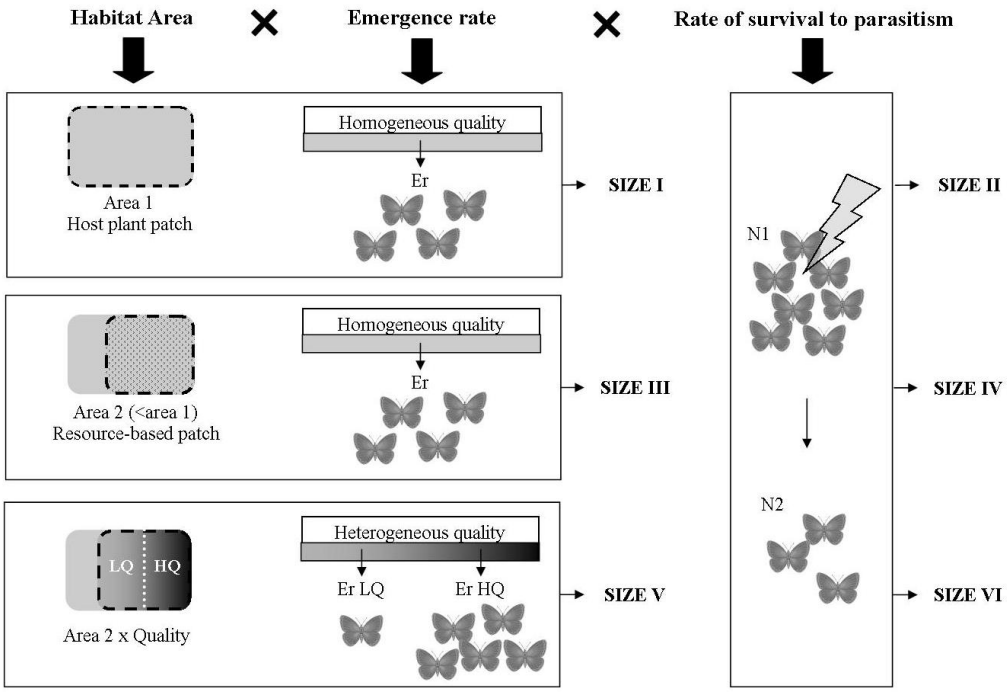


Figure V.1. Expected population size can be estimated by crossing caterpillar habitat area by emergence rate (per m^2), taking into account or not the pressure from the caterpillar parasitism, using alternatively each modality of the 3 factors. Caterpillar habitat area can be calculated either as the total area of host plant patches (*Area1*), or as the area containing host plant and other resources required by the caterpillar species (*Area2*), taking into account, or not, the variation in quality according to availability of the resources needed by caterpillars (LQ for low quality and HQ for high quality). Emergence rate can be expressed as a unique measure from habitat of homogenous quality (*Er*) or as differentiated measures according to habitat quality (*ErLQ* and *ErHQ*). If rate of caterpillar parasitism is considered, it can be view as a pressure reducing the initial number N_1 of caterpillars in the population to a lower number of caterpillars N_2. 6 indirect estimates of the population size can then be calculated.

Test of transferability

As described in Williams, Nichols and Conroy (2002), ratio of two indexes of population density can reflect a rate of change over time or relative to spatial differences in abundance. Assuming that detection probability did not differ between sites, we calculated two different ratios of population density for each species:

- *Ratio P-I* = $IP_{Pisserotte}$ / IP_{Libin}, with *IP* the index of population density.

- *Ratio P-II* = [$IP_{Pisserotte}$ / (1-$N_{2,Pisserotte}$ / $N_{1,Pisserotte}$)] / [IP_{Libin} / (1-$N_{2,Libin}$ / $N_{1,Libin}$)].

To estimate the rate of difference of habitat availability between sites, we calculated ratios of habitat areas, using either the total host plant area or the resource-based area, for both species:

- *Ratio H-I* = $Area1_{Pisserotte}$ / $Area1_{Libin}$.

- *Ratio H-II* = $Area2_{Pisserotte}$ / $Area2_{Libin}$.

To test which estimate of the caterpillar habitat area was the most appropriate (i.e. the total host plant area and/or the resource-based area), we compared ratios of population density and ratio of habitat area for the two species; a match between ratios indicating a possible transferability of the habitat definition from one site to the other.

V.3 RESULTS

Population size and density

Basic MRR statistics for *P. eunomia* and *B. aquilonaris* in Pisserotte are summarized in **Table V.2**. Daily survival rates were constant during the whole flight period in both species (> 90% for *P. eunomia* and > 79% for *B. aquilonaris*) and recapture rate decreased over time (details not shown here). Total population size (± 95 % confidence interval) was estimated from MMR data at 324 ± 73 and 546 ± 247 individuals for *P. eunomia* and *B. aquilonaris*, respectively. Population size of *B. aquilonaris* was estimated with a lower accuracy because of the low number of recaptures, which is directly linked to bad weather conditions during flight period. Adult densities of *P. eunomia* and *B. aquilonaris* adults, estimated from transect counts, were very similar in Pisserotte (*c.* 4.9 adults per 1000 m transect), but in Libin they were twice and six times higher (**Table V.3**).

Emergence rate and habitat quality

Traps typically hosted either none or a single adult butterfly. The emergence rate of both species was higher in higher quality areas (**Figure V.2**), significantly for *B. aquilonaris* (χ^2_2 = 9.83, *P* = 0.0017) but not for *P. eunomia g*iven the weak numbers of emerged individuals (χ^2_2 = 1.49, *P* = 0.22). Not a single *B. aquilonaris* individual emerged from low quality areas in Pisserotte. There was no statistical difference

in emergence rate of *B. aquilonaris* in the high quality zones of the two sites (χ^2_2 = 0.33, *P* = 0.56). No cocoon of parasitoids was found under the traps.

Table V.2. Basic statistics of the MMR studies on *P. eunomia* and *B. aquilonaris* in Pisserotte in 2006. Daily recapture and survival rates were similar in both sexes for each species; only the first one varied through the season. Estimated population sizes are shown with 95 % confidence interval. F: females, M: males.

Statistics of the MRR studies	*P. eunomia*			*B. aquilonaris*		
	F	M	Total	F	M	Total
Number of MMR sessions			12			9
Number of marked individuals	65	77	142	45	81	126
Number of recaptures	27	51	78	7	21	28
Daily recapture rate	11% - 55%			8% - 42%		
Daily survival rate	90.41%			79.13%		
Population size	166	158	324	206	340	546
± 95 % CI	± 46	± 42	± 73	± 56	± 85	± 247

Parasitism

75% (112/150) and 26% (31/128) of the *P. eunomia* caterpillars were parasitized in Pisserotte and Libin, respectively. The parasitoid was a braconid wasp of the genus *Cotesia* (J. Choutt, unpubl. data). Out of 40 and 35 *B. aquilonaris* caterpillars collected in Pisserotte and Libin, respectively, not a single individual was parasitized.

Table V.3. Estimated population density (per 1000 meter transect) based on transect counts for *P. eunomia* and *B. aquilonaris* in the a) Pisserotte and b) Libin nature reserves. F: females, M: males.

a)		Pisserotte (one transect is 4200m)			
Species	**Sex**	**Flight period**	**Number of transects**	**Number of individuals**	**Population density (1000m)**
P. eunomia	F	June 6 - July 10	9	87	2.3
	M		11	139	3.01
	Total		11	226	4.89
B. aquilonaris	F	June 28 - July 18	8	68	2.02
	M		9	119	3.15
	Total		9	187	4.95

b)		Libin (one transect is 3400m)			
Species	**Sex**	**Flight period**	**Number of transects**	**Number of individuals**	**Population density (1000m)**
P. eunomia	F	June 7 - July 10	8	151	5.55
	M		6	182	8.92
	Total		10	333	9.79
B. aquilonaris	F	June 21 - July 19	7	450	18.91
	M		7	435	18.28
	Total		8	885	32.54

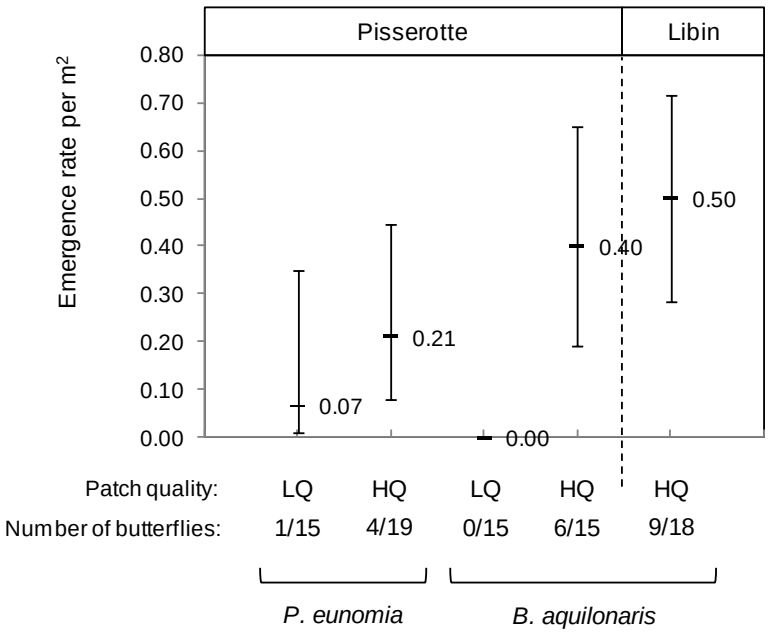


Figure V.2. Adult emergence rate per m^2 (and 95 % confidence interval) of the butterfly species *P. eunomia* and *B. aquilonaris* according to caterpillar habitat quality (LQ for low quality, HQ for high quality) and study area (Pisserotte and Libin).

Estimating population size from emergence trap data

For *P. eunomia* the predicted population sizes based on the trap data ranged from 331 to 2887 individuals according to the adopted method (i.e. to the six population size estimates; **Figure V.3A**). As the MRR-based population size was 324 ± 73 individuals, only the results of population size method IV and VI yielded realistic predictions. The other methods overestimated the population size by a factor 2.3 to 8.9.

For *B. aquilonaris* the predicted population sizes ranged from 577 to 1800 individuals according to the adopted method (**Figure V.3B**). Since we found no evidence of parasitism for this species in our study areas, only methods I, III and V were applied. Only method V (i.e. using suitable habitat area with variation in quality) gave a prediction in agreement with the population size obtained from MMR data (546 ± 247 individuals). The other two methods overestimated population size by a factor 1.6 to 3.3.

Transferability

For both species, there was a good match between the ratio of resource-based area and the index of population density (corrected for parasitism rate in *P. eunomia* only, because parasitism was absent for *B. aquilonaris* in these sites), whereas the ratio of total host plant area overestimated the ratio of index of population density (1.16 times for *P. eunomia*, 5.31 times for *B. aquilonaris*) (**Table V.4**). Hence, this suggests that the applied definition of suitable larval habitat (i.e., the resource-based definition of habitat) can be reasonably transferred between study areas.

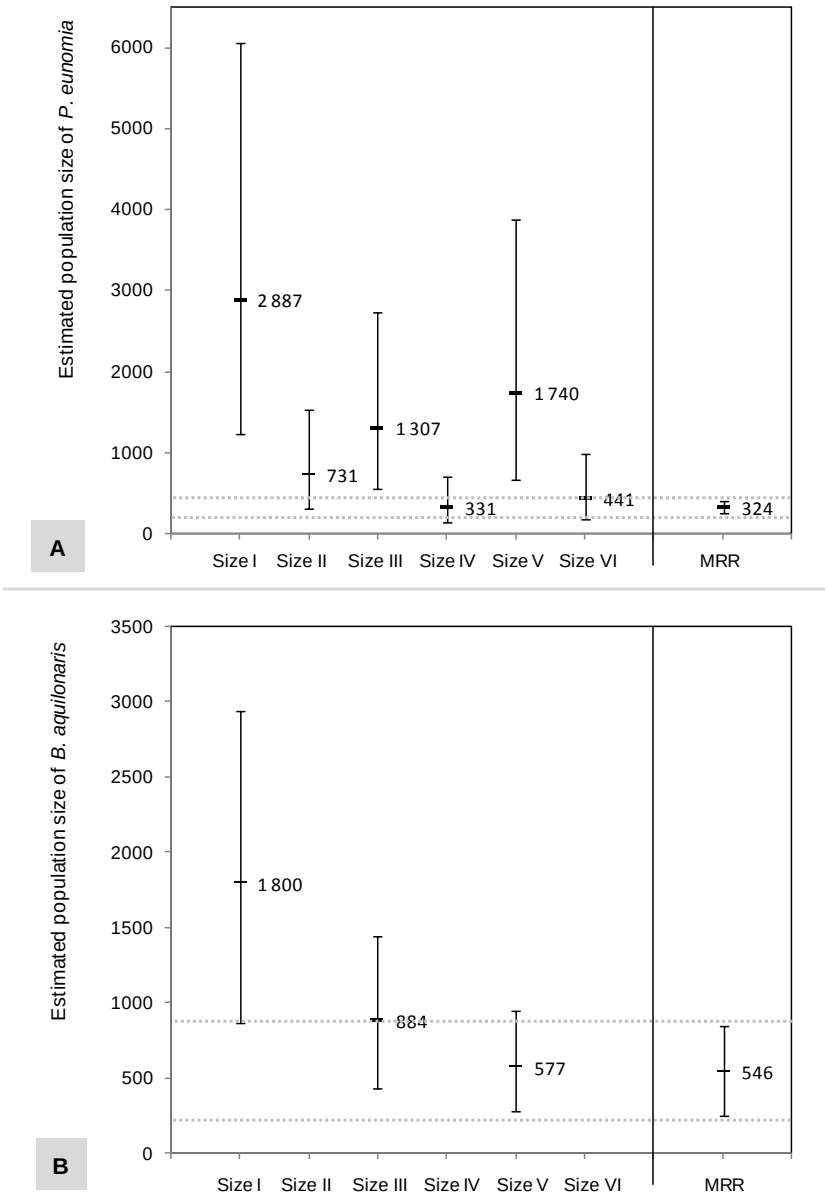


Figure V.3. Population sizes predicted with the six methods described (Figure V.1 and text), and observed population size from MRR data for *P. eunomia* (A) and *B. aquilonaris* (B).

Table V.4. Ratios of a) caterpillar habitat area (total host plant area or resource-based area) and b) population density index (estimated adult density with and without correction for parasitism rate) between sites calculated for both species. As no parasitism was observed in *B. aquilonaris* caterpillars, the ratio of initial expected density was not calculated.

a) Species and sites		Caterpillar habitat area		
		Total host plant area	Resource-based area	Ratio of total host plant area / resource-based area
P. eunomia	Pisserotte	19630	8889	2.21
	Libin	11671	6113	1.91
	Ratio	1.68	1.45	
B. aquilonaris	Pisserotte	8999	1442	6.24
	Libin	10643	9051	1.18
	Ratio	0.85	0.16	

b) Species and sites		Population density index		Rate of parasitism
		Estimated adult density	Initial expected density	
P. eunomia	Pisserotte	4.89	19.31	0.75
	Libin	9.79	13.2	0.26
	Ratio	0.5	1.46	2.89
B. aquilonaris	Pisserotte	4.95		
	Libin	32.54		
	Ratio	0.15		

V.4 DISCUSSION

Results on both butterfly species clearly showed that, firstly, adult population size was strongly related to larval habitat availability and quality when habitat was defined according to resources. Secondly, this indirectly confirmed that resources other than the host plant, such as functional resources, have to be included in the species habitat definition as they play a role in the demographic response of the species. Thirdly, we showed that the resource-based definition of the habitat can be reasonably transferred in space and used for several populations of the same species within a biogeographic region.

Adult population size was linked to availability and quality of larval habitat

Larval habitat quality was defined according to the host plant density and the availability of structural resources: higher quality corresponded to the presence of *Sphagnum* hummocks covered by the host plant for *B. aquilonaris* (Turlure et al. 2009a) and the presence of grass tussocks with high density of the host plant for *P. eunomia* (Schtickzelle, Turlure and Baguette 2007; Turlure *et al.* 2009b). The expected differences in larval habitat quality for each species were confirmed by the difference in rates of adult emergence. Definition of larval habitat quality for *B. aquilonaris* was highly reliable since no adult ever emerged in traps under low quality habitat. A comparable situation was observed for *P. eunomia*, with a lower emergence rate in low quality areas. Accordingly,

adding either the variation in host plant structure related to tussocks and hummocks, or the variation in host plant density clearly improved the definition of larval habitat quality definition for *B. aquilonaris* and *P. eunomia*, respectively.

The relation between larval habitat and adult population size resulted into a simpler model for *B. aquilonaris* as there was no larval parasitism detected. In this case, the prediction of population size from the resource-based area modulated by quality nicely matched with the population size as inferred from MMR data. This result supports the idea that resource-based area is a reliable proxy for the real habitat area, whereas host plant area resulted into a considerable overestimation. *P. eunomia* provided a more complex model since the rate of parasitism was important at the larval stage. No parasitoid cocoon was, however, found under the traps indicating that either the traps were placed, by chance, over unparasitized caterpillars, or traps prevented parasitism. Anyway, in both cases the correction for parasitism rate to the prediction of population size was justified. The prediction of population size from the resource-based area modulated by quality showed a far better match with population size inferred from MMR data than the prediction from the total host plant area. This prediction of population size could be even further improved by taking into account (1) a differentiated measure of parasitism rate according to habitat quality (parasitism rate may often be higher in high quality habitat) and (2) the rate of pupal parasitism. Indeed, not a single pupae from caterpillars collected in the field was parasitized; whereas ichneumonid wasps did emerge from pupae collected in the field (Choutt J. unpublished data). This suggests that female wasps laid their eggs directly in pre-pupal caterpillars (Shaw,

Stefanescu and van Nouhuys 2009), but pupae were not accessible under the traps. As mentioned before, we never found parasitism in *Boloria aquilonaris* pupae under free field conditions.

Results from both species clearly showed that adult population size was correlated with larval habitat availability and that the resource-based habitat definition and associated habitat quality measures improved the prediction of the population size. It is now warranted to test our approach for more species and ecosystems.

Transferability of the resource-based definition between populations

Defining resource-based habitat in different populations is also a time consuming procedure, but it becomes an interesting investment if the definition drawn from data collected in one population can be transferred to other populations (i.e. a species-specific definition of the habitat at least for a particular region). Testing spatial transferability is of prime importance to the use of the habitat area as a proxy for population size in non sampled sites (Randin et al. 2006). Here, by comparing the ratios of population density and habitat availability between sites, we checked whether an increase in habitat area induced a similar increase in population density. As the ratios of population density and resource-based habitat area were congruent, we argue that our resource-based definition of the larval habitat for the two species can be reasonably well transferred between populations. A test for spatial transferability of a resource-based habitat definition was also successful in an earlier study on heathland butterflies (Vanreusel, Maes and Van Dyck 2007).

Spatial transferability of the habitat definition could also be of high relevance, either at short time scale to confirm the reliability of the definition, either on longer scale to predict the effects of natural succession or management actions (Binzenhofer et al. 2005). This was not tested in our current study but data collected on the two populations of Pisserotte provide some indications for transferability at short time scale. Firstly, as changes in the vegetation structure of the studied peat bogs are very slow (Turlure C. & Choutt J., personal observations), and as within our study period there were no major perturbations, we can make the assumption that host plant area and functional habitat availability remained stable between 2004 and 2008. Secondly, estimation of population size from MMR data in Pisserotte ranged from 204 to 1436 individuals for *P. eunomia* and from 90 to 545 individuals for *B. aquilonaris* in this four year period. Even if emergence rate can change over time (according to, for example, weather conditions or parasitism rate), the prediction using the resource-based approach still gave a better estimation of the real population size compared to the prediction using the total host plant area, suggesting that the resource based definition of the habitat could also be transferred at a time scale of at least a few years.

Application of the resource-based habitat in Population Viability Analysis

Previous PVA on the two species in the Plateau des Tailles landscape used the total host plant area as a proxy for carrying capacity (Sawchik *et al.* 2002; Schtickzelle, WallisDeVries and Baguette 2005a). But, as total

host plant area overestimated three to ten times the population size in Pisserotte, it is also likely to overestimate the carrying capacity of the sites for both species. Host plant area was also used as a proxy of carrying capacity in most other butterfly PVA studies (Per Sjorgren-Gulve and Hanski 2000; Schtickzelle, Le Boulengé and Baguette 2002; Schultz and Hammond 2003). Knowing that host plant area may overestimate the amount of functional habitat, and that this may vary among sites (the ratio of host plant area and functional habitat area was not constant between sites in our case, **Table V.4**), one should be more careful when using such surrogate data in PVA as it may lead to an underestimation of the extinction risk. As stated by White (2000), Coulson et al. (2001) and Schtickzelle and Baguette (2009), PVA is a useful and powerful tool to predict probability of extinction and effect of management scenario, but it requires extensive and reliable data on the target species and populations. We argue that using the resource-based, functional habitat approach instead of the total host plant area as a proxy for the carrying capacity would give more reliable predictions of the metapopulation viability.

General discussion

General discussion : illustration cover by Camille Turlure

Both habitat network (i.e. habitat surfaces and connectivity of habitat zones) and habitat quality contribute to the occupancy and survival of a metapopulation within a landscape (Thomas *et al.* 2001b; Krauss, Steffan-Dewenter and Tscharntke 2004; Krauss *et al.* 2005; Bauerfeind, Theisen and Fischer 2008). The relative importance of both factors may depend both on the species and the landscape, or in other words, on the dispersal ability and the spatial scale of variation in habitat composition for the studied species (Gripenberg and Roslin 2005). In a context of species conservation, determining which aspects of habitat quality and spatial arrangement of resources best account for variation in species distribution can guide management actions (Schultz and Crone 2005). Hence, defining a habitat both in qualitative and quantitative terms is of particular concern for conservation.

In this general discussion, we first compile the results obtained from modelling the habitat of each species to test the appropriateness of three definitions of the habitat that are generally used for butterflies: (1) host plant, (2) vegetation types, and (3) resource-based definition of the habitat. Secondly, we discuss the implications of our results in combination with the literature, in order to draw a more complete picture of the habitat concept from a butterfly's point of view. Finally, we present both short and long term research perspectives.

Definition of the habitat of the five study species

1. Species-specific resources

In Chapter I, we showed the significance of tussock presence, high density of the host plant and cool micro-climatic conditions to define the caterpillar habitat of *P. eunomia*. Abundance of *P. bistorta* was also important for adults as it is the main feeding resource. Abundance of *L. helle* caterpillars were related to the presence of the host plant (*P. bistorta*) and warmer micro-climatic conditions compared to *P. eunomia*. Adults of *L. helle* were more often present when nectar resources were more abundant, and where there were woody edge structures.

In Chapter II, we showed the importance of particular peat bog structures (i.e. *Sphagnum* hummocks) covered by the host plant (i.e. *V. oxycoccos*) for caterpillars of *B. aquilonaris*. Adults of this species were observed feeding mainly on *P. palustris*, *N. ossifragum*, *M. trifoliata*, *L. flos-cuculi* and *C. palustris*.

In Chapter III, we showed that resources needed by *L. hippothoe* adults and eggs were overlapping in space in Pisserotte. But eggs were laid where the host plant occurred at lower abundance, whereas adults fed within nectar and host plant rich zones in Pisserotte. This was not the case in Libin as adults and eggs were both found in nectar and host plant rich zones.

In Chapter IV, we presented the list of most frequently used nectar resources of each species. For *C. selene,* it included *L. flos-cuculi* and *C. palustris*. We found a small number of *C. selene* caterpillars, always in very humid conditions characterised by the presence of the host plant, *V. palustris*. Based on these results, we are now able to draw a schematic picture of what composed the habitat for these five butterfly species (**Figure c.1**)

2. Habitat definitions based on host plant or vegetation type are suitable for specialist species only

To test for the appropriateness of the host plant, the vegetation type or the resource-based definition of the habitat of the five butterfly species, we used a Multiple Correspondence Analysis MCA (Benzecri 1992). This was done for each site separately. The aim of this analysis was to highlight the associations between resources, including host plant, and vegetation types, or the spatial cohesion of the different resources by graphic representation.

Variables used were the vegetation type (six classes: swamps, rushes, wet meadows, fen grasslands, short sedge fens and heathlands), the woody edge structure (three classes: no edge, some nearby trees, surrounded by trees), the tussock density (three classes: no, few, many), the presence of *Sphagnum* and *Polytrichum* hummocks, the host plant abundance (three classes: no, few, many) and the abundance of each nectar resource (three classes: no, few, many) for each zone (area of each

zone was considered as covariable). Abundances of adults and caterpillars (or eggs for *L. hippothoe*) of each butterfly species were added as illustrative continuous variables to the MCA.

Next, we evaluated the relations between (1) resources needed by the species relative to vegetation types, (2) caterpillar, egg or adult abundance relative to vegetation types, (3) caterpillar, egg or adult abundance relative to host plant abundance, and (4) caterpillar, egg or adult abundance relative to all their ecological resources. This can be done by interpreting the relative position of different variables on the MCA because a close position of two variables on a two-dimensional graph indicates a strong positive association between them. Below, we discuss in detail the results obtained for each species and site separately.

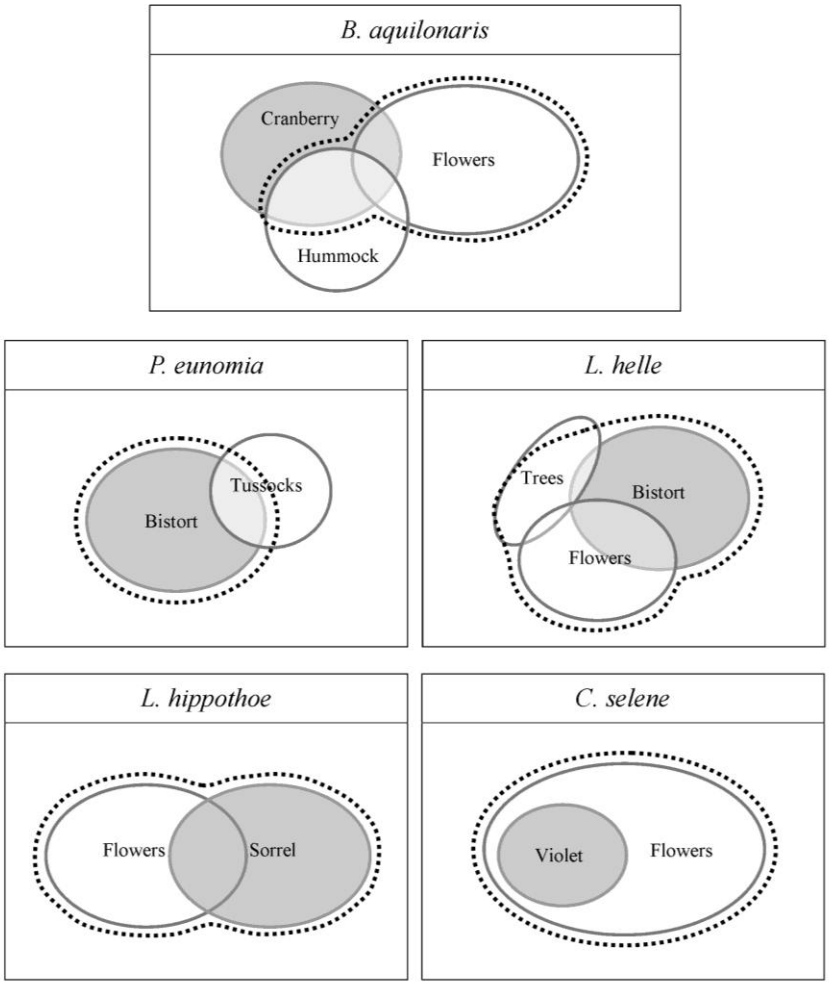
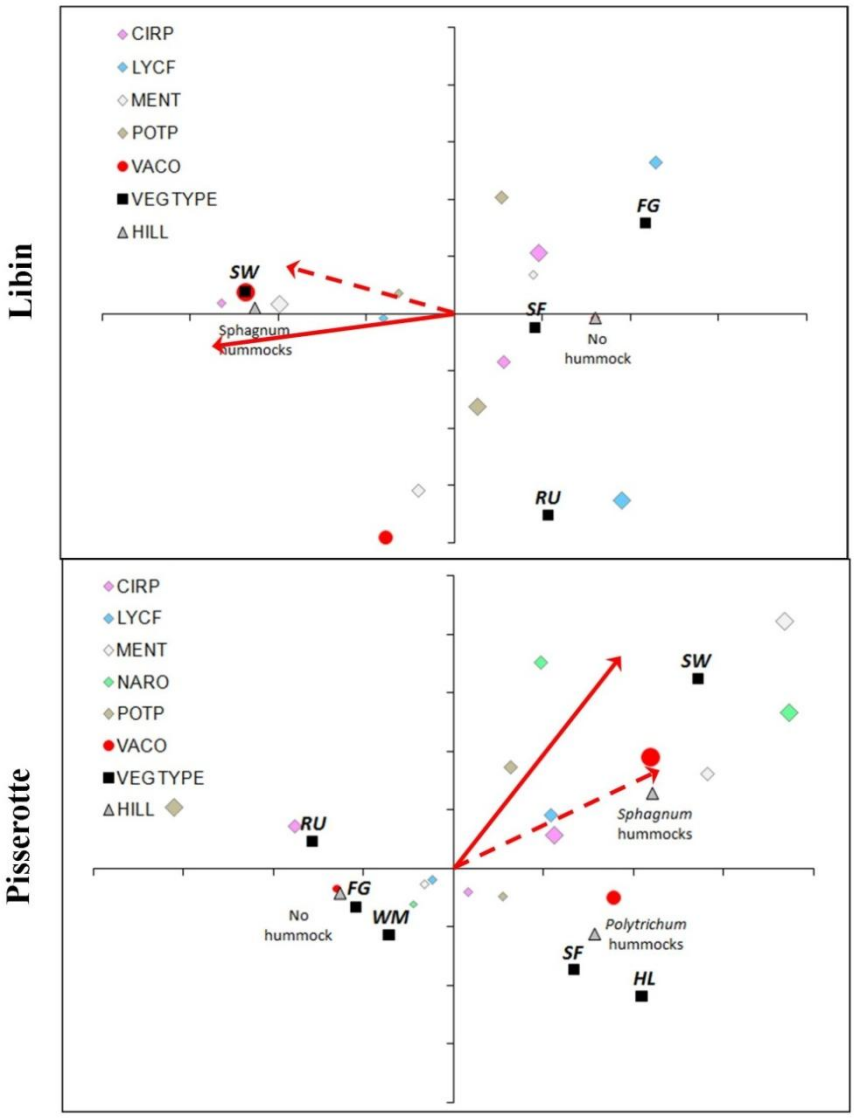


Figure c.1. Schematic representation of the habitat composition of the five butterfly species, according to adult and larval ecological resources, both consumables and utilities, that were empirically demonstrated. Each ellipse represents a resource. The dotted line represents the bound of the species habitat.

♂ *B. aquilonaris* (**Figure c.2**)

In the case of *B. aquilonaris*, resources needed by the caterpillars (i.e. high abundance of *V. oxycoccos* and *Sphagnum* hummocks) were aggregated in swamps in both sites. *Polytrichum* hummocks and lower abundance of the host plant occurred more often in short sedge fens and heathlands in Pisserotte and in rushes in Libin. Nectar feeding resources (i.e. *C. palustris*, *P. palustris*, *M. trifoliata*, *L. flos-cuculi* and *N. ossifragum*) were clearly more abundant in the proximity of swamps in Pisserotte, but were more widespread in Libin. Resources needed by both caterpillars and adults were then more or less aggregated in one vegetation type (i.e. in swamps). As a consequence, we observed increasing densities of both adults and caterpillars of this species in this vegetation type. Because of the strong positive correlation of all resources in space, the ***habitat definition based on vegetation type appears to be appropriate for this species***.

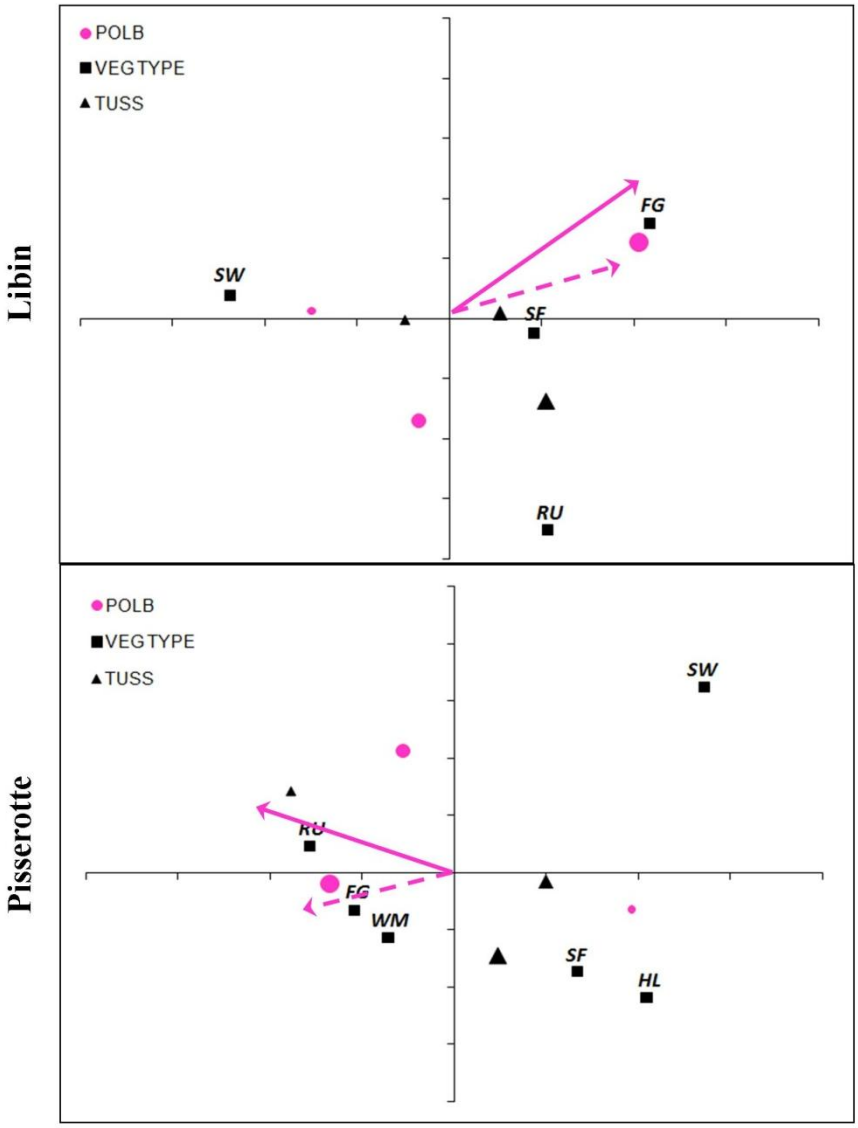
Figure c.2. Graphical representation of the MCA on resources for *B. aquilonaris* in both sites. Black squares represent the vegetation types (*SW*: swamps, *RU*: rushes, *WM*: wet meadows, *FG*: fen grasslands, *SF*: short sedge fens and *HL*: heathlands). Increasing size of the red dots represents the increasing abundance of the host plant (*VACO*: *V. oxycoccos*). Increasing size of the coloured diamonds represents the increasing abundance of each nectar resource (*CIRP*: *C. palustris*, *LYCF*: *L. flos-cuculi*, *MENT*: *M. trifoliata*, *NARO*: *N. ossifragum*, *POTP*: *P. palustris*). Grey triangles indicate the presence of *Sphagnum* hummocks, *Polytrichum* hummocks or no hummock. Plain red arrow represents the increasing abundance of *B. aquilonari adults. Dotted red arrow represents the increasing abundance of B. aquilonaris caterpillars.*


Libin
CIRP
LYCF
MENT
POTP
VACO
VEGTYPE
HILL
SW
Sphagnum hummocks
SF
No hummock
FG
RU
Pisserotte
CIRP
LYCF
MENT
NARO
POTP
VACO
VEGTYPE
HILL
RU
FG
No hummock
WM
SW
Sphagnum hummocks
Polytrichum hummocks
SF
HL

ଓ *P. eunomia* (**Figure c.3**)

Adults and caterpillars feed on the same plant species, *P. bistorta*. In Libin, a higher abundance of the host plant (*P. bistorta*) was observed in fen grasslands, whereas in Pisserotte, the host plant was more abundant in rushes, wet meadows and fen grasslands. Tussock density was equal in short sedge fens, fen grasslands and rushes in Libin, and lower in swamps in Pisserotte. Both adult and caterpillar abundances were increasing near higher *P. bistorta* abundance. For *P. eunomia*, habitat definition based on vegetation types was clearly inappropriate, as several vegetation types were used in one site, while only one was used in the other site. Nevertheless, there was a good match between both adult and caterpillar abundance and host plant abundance. Hence, ***habitat definition based on host plant (patches) appears to be suitable in this case***.

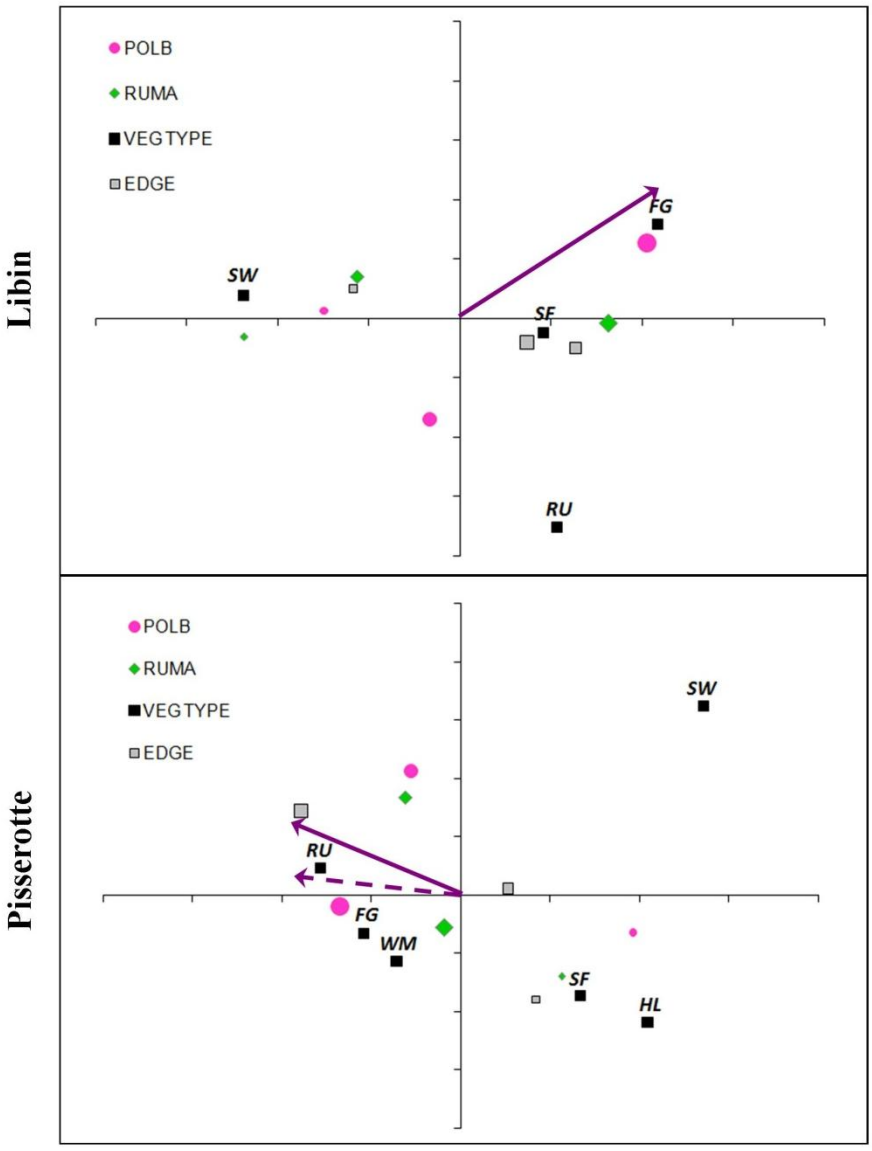
Figure c.3. Graphical representation of the MCA on resources for *P. eunomia* in both sites. Black squares represent the vegetation types (*SW*: swamps, *RU*: rushes, *WM*: wet meadows, *FG*: fen grasslands, *SF*: short sedge fens and *HL*: heathlands). Increasing size of the pink dots represents the increasing abundance of the host plant (*POLB*: *P. bistorta*). Increasing size of the black triangles represents the increasing density of tussocks. Plain pink arrow represents the increasing abundance of *P. eunomia* adults. Dotted pink arrow represents the increasing abundance of *P. eunomia* caterpillars.


Libin
POLB
VEGTYPE
TUSS
FG
SW
SF
RU
Pisserotte
POLB
VEGTYPE
TUSS
SW
RU
FG
WM
SF
HL

ↀ *L. helle* (**Figure c.4**)

Distributions of host plant and nectar resources were similar to those of *P. eunomia*. Woody edge structures were more pronounced in short sedge fens and fen grasslands in Libin and in rushes in Pisserotte. Given the very small population of *L. helle* in Libin (only 30 individuals counted during two years), caterpillar presence and abundance were investigated in Pisserotte only. Distribution of the abundance of caterpillars was very similar to the distribution of the abundance of adults, i.e. near high bistort abundance and near trees. As resources were aggregated in several vegetation types***, the habitat definition based on vegetation types appears to be inappropriate, while the habitat definition based on host plant could be more appropriate***.

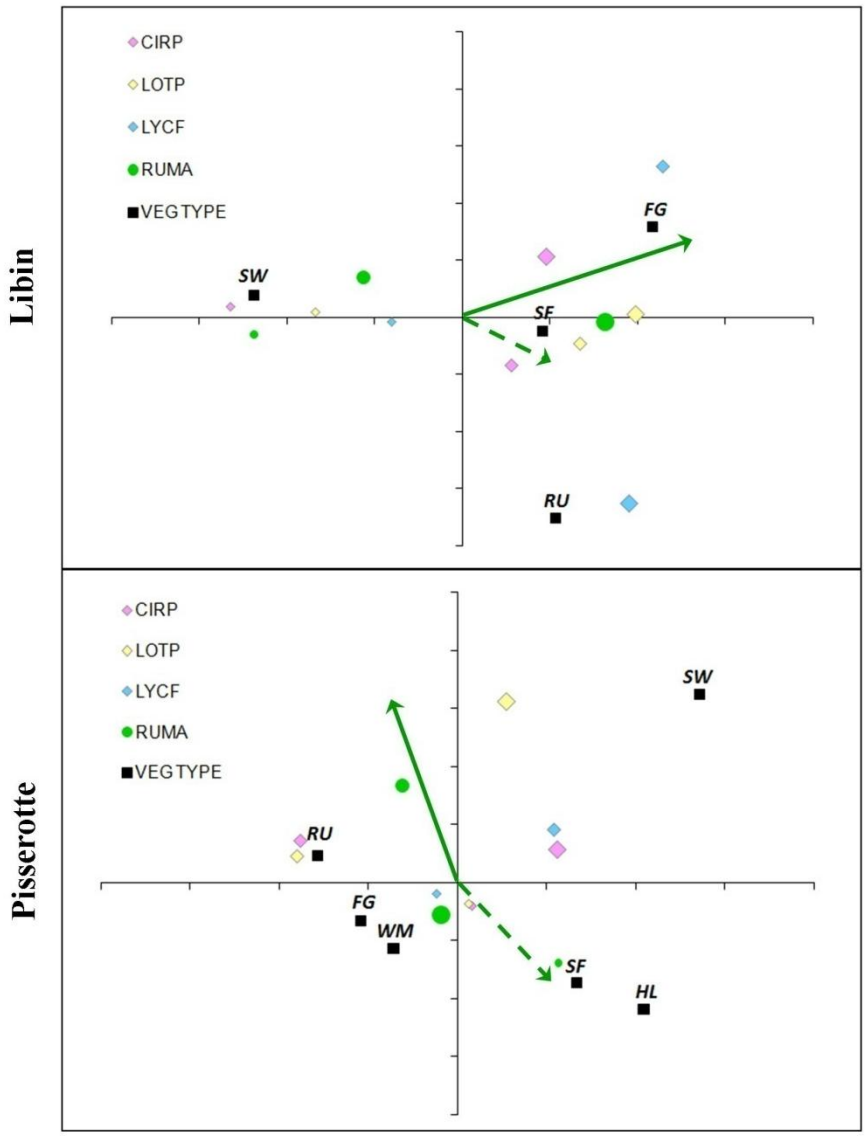
Figure c.4. Graphical representation of the MCA on resources for *L. helle* in both sites. Black squares represent the vegetation types (*SW*: swamps, *RU*: rushes, *WM*: wet meadows, *FG*: fen grasslands, *SF*: short sedge fens and *HL*: heathlands). Increasing size of the pink dots represents the increasing abundance of the host plant (*POLB*: *P. bistorta*). Increasing size of the green diamonds represents the increasing abundance of the other nectar resource (*RUMA*: *R. acetosa*). Increasing size of the grey squares represents the increasing density of woody edge structure. Plain violet arrow represents the increasing abundance of *L. helle* adults. Dotted violet arrow represents the increasing abundance of *L. helle* caterpillars.


Libin
POLB
RUMA
VEGTYPE
EDGE
FG
SW
SF
RU
Pisserotte
POLB
RUMA
VEGTYPE
EDGE
SW
RU
FG
WM
SF
HL

ଌ *L. hippothoe* (**Figure c.5**)

Abundance of the host plant (*R. acetosa*) was higher in fen grasslands and short sedge fens in Libin, and in wet meadows and fen grasslands in Pisserotte. Nectar resources used by adults were relatively widespread in the different vegetation types. Egg abundance increased in short sedge fens for both sites, independently of the host plant abundance. Adult abundance was clearly related to the abundance of the favourite nectar feeding resource (i.e. *L. pedunculatus*) in both sites. As the distribution of the complete sets of resources used by the species was uniform neither in Libin, nor in Pisserotte, ***the habitat definition based on host plant or vegetation type does not suit this species***.

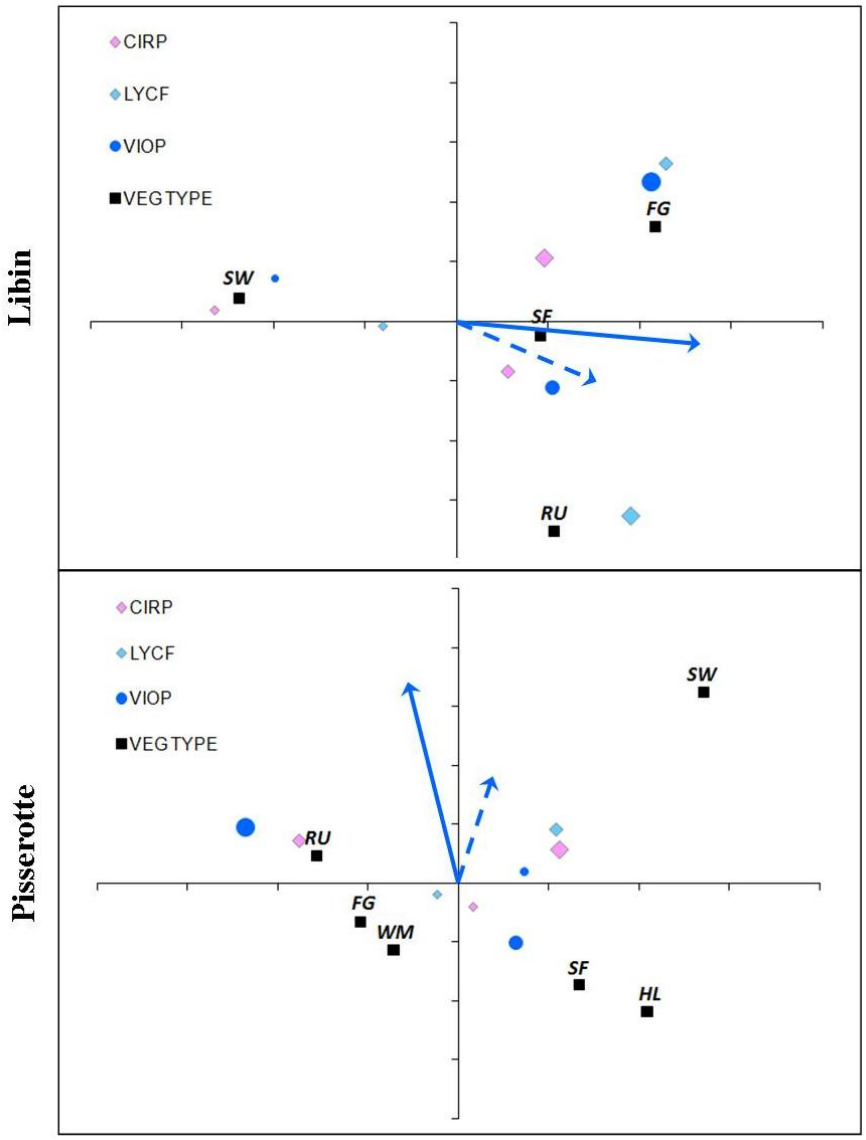
Figure c.5. Graphical representation of the MCA on resources for *L. hippothoe* in both sites. Black squares represent the vegetation types (*SW*: swamps, *RU*: rushes, *WM*: wet meadows, *FG*: fen grasslands, *SF*: short sedge fens and *HL*: heathlands). Increasing size of the green dots represents the increasing abundance of the host plant (*RUMA*: *R. acetosa*). Increasing size of the coloured diamonds represents the increasing abundance of each nectar resource (*CIRP*: *C. palustris*, *LOTP*: *L. pedunculatus*, *LYCF*: *L. flos-cuculi*). Plain green arrow represents the increasing abundance of *L. hippothoe* adults. Dotted green arrow represents the increasing abundance of *L. hippothoe* caterpillars.


Libin
CIRP
LOTP
LYCF
RUMA
VEGTYPE
FG
SW
SF
RU
Pisserotte
CIRP
LOTP
LYCF
RUMA
VEGTYPE
SW
RU
FG
WM
SF
HL

ᔓ *C. selene* (**Figure c.6**)

The host plant of *C. selene* was more abundant in fen grasslands and to a lesser extent in short sedge fens in Libin. In Pisserotte, higher abundance of the host plant was observed in rushes. Nectar resources used by adults (*C. palustris* and *L. flos-cuculi*) were relatively widespread in all vegetation types, except for swamps. Distribution of caterpillars and adults were closely connected, but not clearly associated to a particular vegetation type or to host plant abundance. This is the most generalist species among the study species, and ***neither definition of habitat based on the host plant nor based on vegetation type matched***.

Figure c.6. Graphical representation of the MCA on resources for *C. selene* in both sites. Black squares represent the vegetation types (*SW*: swamps, *RU*: rushes, *WM*: wet meadows, *FG*: fen grasslands, *SF*: short sedge fens and *HL*: heathlands). Increasing size of the blue dots represents the increasing abundance of the host plant (*VIOP*: *V. palustris*). Increasing size of the coloured diamonds represents the increasing abundance of each nectar resource (*CIRP*: *C. palustris*, *LYCF*: *L. flos-cuculi*). Plain blue arrow represents the increasing abundance of *C. selene* adults. Dotted blue arrow represents the increasing abundance of *C. selene* caterpillars.


Libin
CIRP
LYCF
VIOP
VEGTYPE
FG
SW
SF
RU
Pisserotte
CIRP
LYCF
VIOP
VEGTYPE
SW
RU
FG
WM
SF
HL

ᘓ Finally…

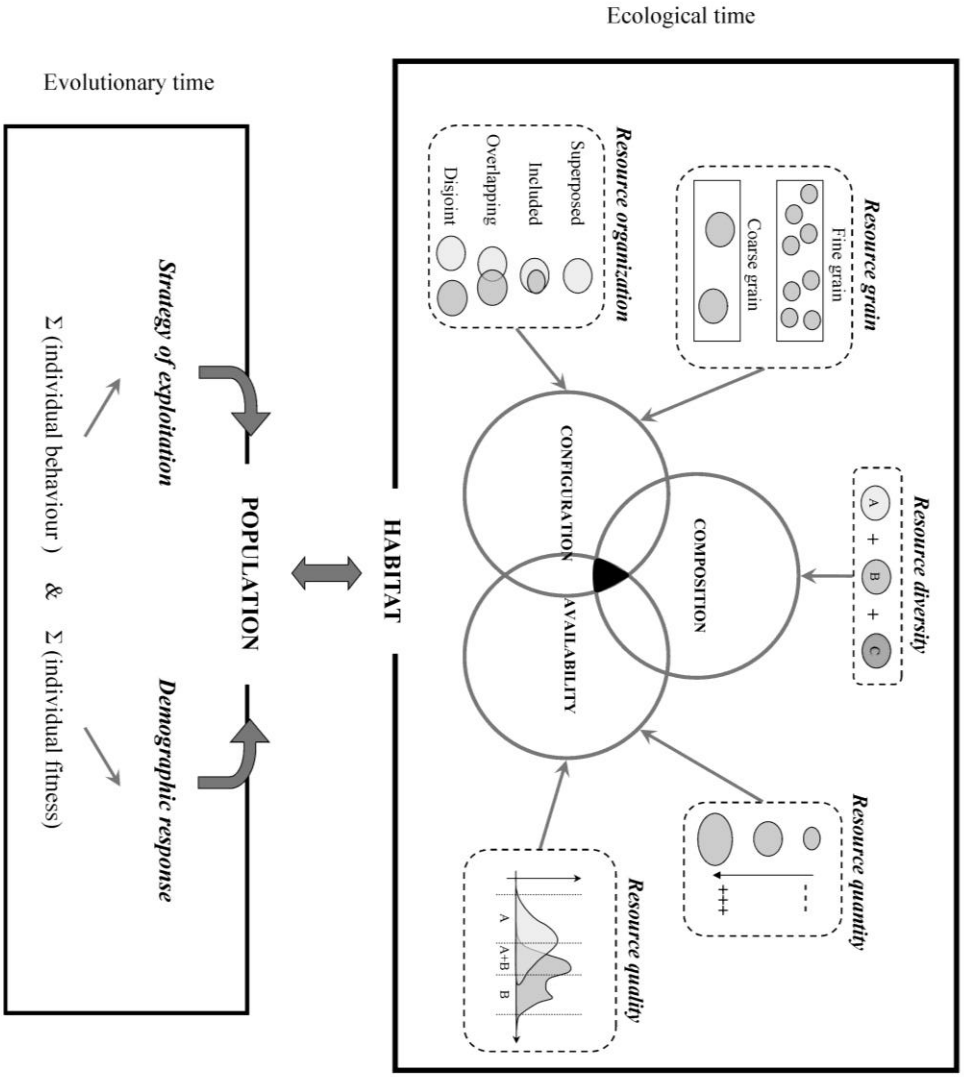
Given these five examples, it is clear that the definition of the habitat based on host plant abundance (or patches) or vegetal type is mostly weak. Such definitions may be only suitable for species for which all resources are aggregated within or near host plant patches or in a particular vegetation type. Hence, we can show based on this sample of butterfly species the significance of considering several resources when defining the habitat of a species. ***The resource-based approach is likely to be widely applicable***.

The resource based definition of the habitat from a butterfly's point of view

According to the results of this thesis on five butterfly species, and the literature, we can now draw a more complete, functional definition of the habitat concept from a butterfly's point of view. A functional definition of the habitat based on ecological resources incorporates three major parameters that are interconnected: (1) resource composition (i.e. the list of resources required by the organism), (2) the resource configuration (i.e. both the grain of each resource and the organization of all the resources) and (3) resources availability (in both time and space). Intersection of these three parameters represents the functional habitat of a given population or a given species within a landscape (**Figure c.7**). Variations in these parameters are likely to influence individual fitness, demographic response of the whole population, individual behaviour and the evolution of the strategies of resources or habitat exploitation.

Below we discuss in detail these three parameters and stress their importance on individual and population responses using both results obtained from the five study species and a non exhaustive list of examples from the literature. Additionally, we discuss (1) how habitat quality can be inferred from these three parameters of habitat, (2) if habitat can be bounded in all cases and (3) if the resource based definition is universal (i.e. applicable for all the populations of the same species).

Figure c.7. The resource-based definition of the habitat can be decomposed in three parameters, represented by the three circles: the resource composition (i.e. the list of resources required by the organism), the resource configuration (i.e. both the grain of each resource and the organization of all the resources) and the resource availability (in both time and space). The intersection of these three parameters (black area) represents the functional habitat of a given population or a given species within a landscape. Variations in these parameters are likely to influence population parameters: individual fitness, demographic response of the population, individual behaviour and the strategies of resources or habitat exploitation. Habitat parameters relate to ecological time, while population parameters relate to evolutionary time.


Ecological time
Evolutionary time
HABITAT
POPULATION
Resource grain
Fine grain
Coarse grain
Resource organization
Superposed
Included
Overlapping
Disjoint
Resource diversity
A + B + C
Resource quantity
+++

Resource quality
A
A+B
B
CONFIGURATION
COMPOSITION
AVAILABILITY
Strategy of exploitation
Demographic response
Σ (individual behaviour) & Σ (individual fitness)

1. Habitat composition

Habitat composition refers to the co-occurrence of the different resources required by each individual of the population to complete its life cycle. It includes both consumables (i.e. feeding resources) and utilities (i.e. physical sites and environmental conditions for various activities). According to the knowledge of butterfly's ecology, its habitat may be composed of (1) nectar feeding resource(s), mate location sites, roosting sites and egg-laying sites for adults, (2) support and appropriate microclimate for eggs, (3) host feeding resources, appropriate structure and microclimate for caterpillars and (4) appropriate structure and microclimate for pupae (see more details in Dennis, Shreeve and Van Dyck 2006a).

In butterflies, it is obvious that a certain amount of host plants is needed to host a population at a site. Host plant(s) used by butterfly species are generally well documented and their presence and abundance are often used to predict population occurrence within a landscape. For example, Sharp, Parks and Ehrlich (1974) found a positive relationship between *Plebejus saepiolus* adult presence and the presence of *Trifolium sp.*, its unique host plant (but also favourite nectar resource). More recently, in the 230 patches they prospected, Bauerfeind, Theisen and Fischer (2008) found that *L. helle* patch occupancy was strongly influenced by the abundance of the host plant.

Contrary to host plant needs, our knowledge is much less complete about nectar resources use and its significance for species distribution: butterflies were indeed often viewed as opportunistic nectar

feeders. Nevertheless, Tudor *et al.* (2004) observed that butterfly species clearly differed in the range of nectar resources they used, specialist flower users being often of conservation concern. In our case, *P. eunomia* was observed to feed mainly on one flower species, whereas the four other species tended to be more opportunistic, *B. aquilonaris* feeding on nine different plant species in two study sites (Chapter IV). Loertscher, Erhardt and Zettel (1995) found a positive relationship between the distributions of adults and their preferred nectar sources in several butterfly species (i.e. *Melanargia galathea*, *Lysandra coridon* and *Ochlodes venatus*).

Structural resources were often neglected although they are of high importance and generally relates to micro-climatic conditions. In Chapter I and II, we found a clear relation between structures provided by grass tussocks or *Sphagnum* hummocks and the presence of caterpillars of *P. eunomia* or *B. aquilonaris*, respectively. Grass tussocks entered also in the composition of *Coenonympha tullia* caterpillars habitat as they favoured caterpillar survival during periods of flooding (Joy and Pullin 1997; Dennis and Eales 1997). At the adult stage, trees and scrubs are often used as shelter for roosting and for mating (Dover, Sparks and Greatorex 1997; Pywell *et al.* 2004; Dennis 2004b; Binzenhofer *et al.* 2005). In *Plebejus argus*, the significance of these structural elements was observed to vary with local weather conditions: adults were more abundant near scrubs under wind exposed conditions (Dennis and Sparks 2006).

The number of resources involved in habitat composition may vary according to species. Generalist species are likely to use a wide range of

resources, while more exigent species are likely to need more specific resources. Hence, resources are probably less easily discernable for generalist species, for which individuals may exploit resources differently, in different locations.

2. Habitat configuration

Habitat configuration refers to the way resources are spatially distributed within the habitat. Each individual resource can be distributed either heterogeneously (i.e. fine grain) or homogeneously (i.e. coarse grain) in the habitat (Levins 1968; Pianka 1970). The way all the resources are distributed and arranged together relates to the original concept of resources complementation and supplementation (Dunning, Danielson and Pulliam 1992), which is simplified here to resource organization. From a lower to a higher degree of patchiness, these arrangements can be classified as superposed (i.e. all resources are present in the same location), inclusive (i.e. the distribution of at least one resource includes all the others), overlapping (resources share some space) or disjoint (i.e. all resources are completely separated). Both distribution of each resource and all resources together are likely to affect (1) habitat, through constitution and shape of patches, habitat boundaries, connectivity between patches, but also (2) population, through habitat exploitation, individuals distribution and movements.

Baguette and Van Dyck (2007) and Dennis and Hardy (2007) proposed that types of movements (i.e. “direct linear flight” or “searching flight”) depend on the grain of resources within the habitat or

within the landscape and are integrated in the process of resource finding. In Chapter IV, we used indexes of niche breadth and overlap to define the grain of nectar and host resources. We demonstrated that the grain of nectar resources constrained mobility in the five study species; larger movement ranges were associated with more widespread nectar resources use. More generally, butterfly with wider niche breadth (i.e. polyphagous species) or with high resource availability may be expected to be more mobile (Shreeve 1992). At the opposite situation, when resources availability is low or when resources are spatially separated, the associated cost of exploitation may lead to more sedentary individuals through a strong selection against high mobility (Komonen et al. 2004). For example, in the relatively sedentary *Coenonympha tullia* butterfly, most suitable conditions for population persistence were defined as overlapping or continuity between host and nectar (Dennis and Eales 1997).

A conflict of interest may occur for females when host and nectar resources do not overlap: they have to choose between meeting their own requirements and those of their offspring. Some species were observed to prefer staying at nectar rich zones (Grossmueller and Lederhouse 1987; Brommer and Fred 2001) while others avoid feeding at the cost of longevity (e.g., most moth species). These different behaviours may affect the distribution of the next generation (Murphy, Menninger and Ehrlich 1984; Boggs 2003). In their study, Fred, O'Hara and Brommer (2006) demonstrated that the configuration of host and nectar resources used by *Parnassius apollo* impacted on adult distribution. Females of this species were more abundant in host plant patches close to nectar resources, independently of the host plant abundance. Moreover, the

spatial configuration of nectar and host plant resources had consequences for population dynamics, as dispersal behaviour was resource oriented. In Chapter III, we observed that *L. hippothoe* females moved between nectar and host plant rich zones to feed and low density host plant zones for egg laying. This behaviour was explained as a consequence of male harassment behaviour and as a preference-performance choice of females. More generally, in Chapter IV, we found a strong positive relationship between the index of relative investment in flight versus fecundity according to the spatial distribution of nectar resources; females invested more in fecundity when nectar resources were widespread. Understanding behaviour relative to resource distribution can be of key significance to define species-specific habitat. This also states the importance of considering adults and larval needs in the same time when defining habitat of a species.

3. Resource availability

Resource availability refers to the accessibility and procurability of resources. It includes quality and amount of resources both in time and space, which can be closely linked.

ᔓ Resource availability in time

According to Southwood (1977), temporal variations of resources may be divided in three categories: predictable variations, unpredictable variations and ephemeral resources, which determine the length of favourable and unfavourable periods. Because of random environmental

fluctuations, there is no single pattern of resource distribution in both space and time. Accordingly, the length of each butterfly life stage may be in accordance with the availability of resource in time.

For example, caterpillar activity may be synchronised with host plant availability. In the study of Hellmann (2002), *Euphydryas editha bayensis* caterpillars were observed to change their host plant use according to host plant senescence and hence, availability. By changing host use over time, caterpillars of this butterfly species may track temporal declines in host quality and buffer the impacts of environmental variation. Larval diet choice may be viewed as an adaptive strategy for foraging on declining food resources. In *B. aquilonaris* caterpillars (Chapter II), we observed an adaptation of organisation of behavioural sequences according to weather conditions. Caterpillars were observed feeding on host plant under cool or cloudy weather conditions, while hiding and resting under hot and sunny weather conditions.

The flight period of adults may be in synchrony with the availability of nectar resources. This can arise with the timing of hatching and hatching asynchrony. Monophagous species such as *P. eunomia* showed a clear synchrony of their flight period with the flowering period of their nectar resource, *P. bistorta* (Chapter I), which was also observed in *Hypochrysops epicurus* by Hill (1992). Polyphagous adults tend to have longer flight periods (Garcìa-Barros 2000) than specialist species and exploit subsequent flowering plants according to their availability.

Temperature can also be considered as a resource with temporal fluctuations, leading to adaptations of adult behaviours or activities in time. For example, *Plebejus argus* adults were observed resting under cooler conditions, while actively flying under hotter or sunny conditions (Dennis and Sparks 2006). The mixture of solar insolation and shading provided by a medium canopy cover benefits for both sexes of *Lycaeides melissa samuelis* adults: females lay on larger host plant available in the shade, while males performed all their activities in the sunny part (Grundel, Pavlovic and Sulzman 1998).

Resource availability can be measured at the ecological time, while response of the populations to the variations of resources availability can be interpreted and measured at the evolutionary time.

ᔓ Resource quality and quantity

At the individual level, variations in availability and quality of larval food resources (stored nutrients) and nectar resources (incoming nutrients) was shown to affect adult morphology, longevity, reproduction and, hence, fitness in butterflies (Hill 1992; Jervis and Boggs 2005; Boggs and Freeman 2005). This is also true at the population level. Population size has been suggested to be strongly linked with abundance of host plant and nectar resources (Schultz and Dlugosch 1999). Several studies on different butterfly species have illustrated this: at the population level, (1) Krauss *et al.* (2005) showed that population density of *Polyommatus coridon* was largely determined by its larval food plant quantity, (2) James, Gilbert and Zalat (2003) pointed out that population size of *Pseudophilotes sinaicus* was affected by resource area and the

quality of habitat and (3) at the metapopulation level, Leon-Cortes, Lennon and Thomas (2003) showed that the probability of regional extinction of *Hamaeris lucina* was linked to the reduction of habitat quantity (and increasing isolation of habitat). In Chapter V, we also demonstrated that the availability of larval functional habitat clearly influenced the adult population size in two species (i.e. *P. eunomia* and *B. aquilonaris*). At the community level, habitat quantity and quality affected the overall species richness and the abundance of moth communities (Summerville and Crist 2004; Summerville, Steichen and Lewis 2005).

4. The combination of resource composition, configuration and availability determines habitat quality

Habitat quality refers to the ability of the habitat to provide conditions that favoured population growth and persistence. Availability of food resources have been invoked as the main determinant of population size (Pianka 1974; Pollard 1981) and has lead to the concept of carrying capacity (i.e. the maximum population size an organism can reach in absence of enemies and catastrophes). But the sole availability of resources does not necessarily imply quality. The examples quoted in the previous parts, among others, indicate the importance of resources (both consumables and utilities) co-occurrence, composition, quality and configuration to determine the quality of any given location or habitat for supporting population of a given species (Maes, Shreeve and Dennis 2006; Dennis and Hardy 2007).

To measure habitat quality, we may focus on the pattern of habitat use, as suggested by Jorge Soberon (1986). As there is an explicit link between demographic response and habitat quality, the population response (i.e. the sum of individual fitness, survival and fecundity that would influence population size, growth and persistence) can be used to define habitat quality in a first given location. As stated by Thomas *et al.* (1998), populations of target organisms are expected to be larger with the increase of all complementary resources and supplementary resources, denser resources, more compact resources and decreased variance in resources. Once the relation between habitat parameters and population parameters are defined, with assumption that the resource-based definition of the habitat is transferable between populations, rules of habitat quality can be designed. For example, in chapter V, larval habitat quality for two species (*P. eunomia* and *B. aquilonaris*) was defined according to the presence of abundance of host plant and structural resources. This definition of quality was reasonably transferable between the two study populations. Dennis and Eales (1997) proposed a quantitative assessment of habitat quality based on binary score according to 23 parameters, including the availability and configuration of all the resources needed by *C. tullia*. Occurrence of the species was tested on 166 sites and highly correlated with this index of habitat quality, meaning that habitat quality can be transferred between populations for this species also.

Deterioration of habitat quality plays an important role in the extinction risk faced by local populations (Thomas 1984; Thomas, Thomas and Warren 1992). Inferring habitat quality based on quantitative and reliable parameters, rather than on the binary view of

habitat versus matrix or defining habitat quality on arbitrary criteria, is then of utmost interest. Such habitat quality estimates can be integrated in metapopulation models (Hanski and Gilpin 1991; Hanski and Simberloff 1997; Schtickzelle and Baguette 2009), and will make it possible to identify where resources are lacking in specific regions resulting in clear guidelines for landscape restoration and identifying potential locations for species to occur (e.g. Vanreusel and Van Dyck 2007).

5. Habitat scale and boundaries

Habitat scale has to be defined according to the relevant scale for the organisms rather than to the scale of convenience for the observers (Mitchell 2005). As separated resources can be exploited by mobile organisms, habitat scale can then be defined according to the extent of individual movements (Baguette and Mennechez 2004).

Dennis and Sparks (2006) stated that identification of the habitat bounds and essential resources within them are a key to conserve organisms. Defining habitat boundaries will be more or less feasible according to the different levels of resource configuration and availability (Baguette and Mennechez 2004). Habitat bounds can be easily discernable when spatial distribution of resources is coarse-grained or when resource organization is of the "included" type. This was the case in Chapter V when delineating the larval habitat of *P. eunomia* and *B. aquilonaris*: the few resources needed were clearly coarse grained and aggregated. Nevertheless, when resources are fine

grained and widespread, defining bounds of habitat are far from obvious. Moreover, the more resources are used (or taken into account), the greater the probability to find resources in what is called the matrix (Dennis, Shreeve and Van Dyck 2006a) and the less discernable the habitat bounds are. For example, Sharp, Parks and Ehrlich (1974) did not find any association between host or nectar species distribution and the adults in several species, because plants species were too widespread. The butterfly species they observed wandered nearly randomly in large area, making the delineation of their habitat impossible.

Habitat is an attribute of the population (Blondel 1995), which means that habitat and population could be two sides of the same concept (from two different points of view, the environment and the organism, respectively), or that defining habitat and defining population are the two sides of the same problem! Indeed, even if population is « the core of evolutionary understanding and biological conservation" (Hey *et al.* 2003), it is also defined in various ways, and we need a synthetic definition of the population concept. The main difficulty lies also in the spatial and temporal determination of bounds (Thomas and Kunin 1999; Berryman 2002; Baguette and Stevens 2003; Schaefer 2006; Waple and Gaggiotti 2006).

6. Is the resource-based definition universal?

Given the number of parameters included in the resource-based definition such as previously described, it is not a restrictive definition, and it might be applicable to a wide range of butterfly species and under

a wide array of circumstances. In theory, resource composition should be the same in habitat of different populations of the same species. Variations in resources availability and distribution should occur more frequently and lead to local adaptation of populations, through behavioural and demographic adaptations. Results from chapter V and previous studies (Dennis and Eales 1999; Dennis, Shreeve and Van Dyck 2003b; Vanreusel, Maes and Van Dyck 2007) suggested that the resource-based definition of the habitat can be spatially transferred between populations, at least within a landscape or a given geographic region. Nevertheless, "it is questionable whether a habitat model applies to all" the populations of a species (Dennis, Shreeve and Van Dyck 2006a). Hence, transferability of habitat definitions has to be treated cautiously and surely needs further investigation. Moreover, as changes in current climate are likely to lead to changes in biotope suitability, transferability in time is also questionable. Although most of these issues emerged from butterfly studies, the resource-based definition of the habitat can be relevant and theoretically used for many other organisms (Maes, Shreeve and Dennis 2006).

Perspectives

1. Short term perspectives

Given the amount of data collected during this phD, there are still some open questions that require further research (which is already scheduled). Three main topics are developed below.

- As *P. eunomia* and *B. aquilonaris* caterpillars were mainly observed on grass tussocks and *Sphagnum* hummocks respectively, we made the assumption that these structures provided different micro-climatic conditions. Caterpillars could use the variation of temperature either by moving among or around these structures (i.e. thermoregulation behaviour). We recorded the body temperature of several caterpillars for both species under different conditions: different positions on the tussocks for *P. eunomia* and different depths inside the *Sphagnum* hummocks for *B. aquilonaris*. We will search for relations between the variations of body temperature and caterpillar position, ambient temperature, light intensity and period of the day.

- The amount of carbon and nitrogen contained in host plants can greatly influence the growth and survival of caterpillars. By collecting *V. oxycoccos* plants at different locations (i.e. different conditions of humidity and different stages of evolution of the peat bog), we would like to test to what extent host plant quality is influenced by environmental conditions. Results will be available in May 2009. Moreover, caterpillars will be collected and reared this summer on host plant of different quality (with and without nitrogen-addition) to see how host plant quality can influence growth rate and survival of caterpillars of this species. This experiment will be carried out in collaboration with Gert-Jan van Duinen (University of Nijmegen, The Nederlands) and Michiel WallisdeVries (Dutch Butterfly Conservation, University of Wageningen, The Nederlands).

- During transect counts performed in 2006 and 2007 to assess the abundance of adults of the five study species, we also recorded the abundance of all the butterfly species in the communities of Pisserotte and Libin. These data will be analysed to underline factors (such as the vegetation type, the host plant and nectar diversity) that influenced (1) butterfly diversity as a whole, (2) butterfly abundance and (3) occurrence and abundance of each species independently. Preliminary analysis already showed that diversity of generalist species can be related to nectar abundance and richness, while diversity of specialist species was more explained by the diversity of host plants.

2. Long term perspectives

The significance of the resource-based definition has been tested and demonstrated here on five butterfly species in two different populations. Nevertheless, additional experiments would be useful to further explore this field:

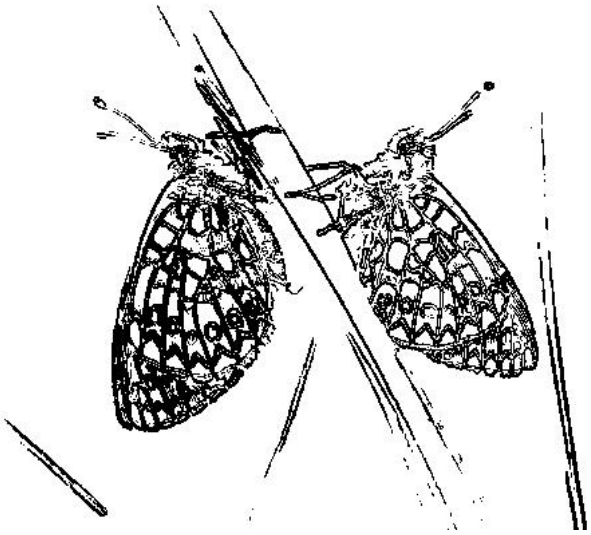
- Knowledge of resources required by non mobile stages (i.e. eggs and pupae) has not been explored yet (except the few data collected on *L. hippothoe* eggs). It would be interesting to underline factors affecting survival and growth of both stages, and hence integrating resources required by eggs and pupae in the current definition of habitat of our five species.

- Determining species habitat based on resources is a time consuming procedure that has been done here for two populations only. For the sake of generality, it would be interesting to test the validity of the definitions established for these five butterfly species on more than two populations. Additionally, long time surveys of habitat availability and use would provide assessment of habitat stability or evolution through time. In other words, large-scale and long-term studies are necessary in order to test the spatio-temporal transferability of such a definition.

- We could also go a step further by using the resource-based approach to estimate the matrix quality and testing its influence on individual dispersal propensity. Both habitat quality and matrix quality approaches are two parts of the same story and should be integrated for better understanding of metapopulation functioning.

- As stated by Bolnick *et al.* (2003), "most ecological and theoretical studies of resource use and population dynamics treat conspecific individuals as ecologically equivalent". But there is now clear evidence that variation of ecological traits among individuals of the same population or species occurs in a broad array of taxa (Skúlason and Smith 1995; Smith and Skúlason 1996; Bolnick *et al.* 2007). Hence, variations among individuals should be investigated, measured and integrated to generate a truly integrative approach to evolutionary ecology through individual-based models. Individual specialization might indeed have important ecological, evolutionary, and conservation implications.

Epilogue



Epilogue: illustration cover by Camille Turlure

A short questionnaire…

At the end of this thesis, I also wondered how different groups of people perceive the concept of an organism's habitat. The groups of interest included other ecologists, but also reserve managers and citizens (further referred to as "naives"). Therefore, we created a short questionnaire that was sent to 12 persons of the three groups (36 persons in total). Firstly; they were asked to answer the following two questions (**Annex e.1**):

1. Which of the following definitions of an organism's habitat seems the most appropriate to you? Is it a) the place where an organism lives, b) an ecosystem or a vegetation type that is well known and defined (further referred to as "vegetation-based definition") or c) a set of particular conditions and resources (further referred to as "resource-based definition").
2. Which of the three schemes best represents the habitat of a butterfly? (cf. **Annex e.1**)

Secondly, they were also asked to read a brief and vulgarized summary of the comparison of the habitat of two butterfly species based on Chapter I (**Annex e.2**) and next they had to answer the two questions again. The main objective was testing to what extent our scientific demonstration of the significance of a resource-based definition of an organism's habitat was convincing to the different groups. In order to test this, we compared the two responses before and after reading the summary of the results.

Was our demonstration convincing?

For each group of 12 persons, we counted the scores obtained by each possible answer to the two questions. We used Multiple Correspondence Analysis (MCA) to search for relations between answers to the two questions about habitat definition and the three groups of respondents. This was done independently for the two series of answers (before and after reading the summary of results). A close position of two points on the bidimensional graph of a MCA indicated a strong correlation between them.

Figure e.1a illustrates the results of the first series of answers to the two questions and indicated that: 1) Because points representing each habitat definition (Question 1) and its associated scheme (Question 2) were grouped together, we can consider that answers given by each person were coherent. 2) the group of naive people was in the centre of the three possible answers, meaning that, as expected, there was no clear preference for a habitat definition among citizens. 3) Ecologists thought that habitat can be best viewed as a set of conditions and resources. 4) Reserve managers viewed the habitat as a particular vegetation type.

Figure e.2b illustrated results of the second series of answers to the two questions and indicated that: 1) ecologists obviously had not changed their answers and kept their view as a set of conditions and resources. 2) Naive persons shifted their answers to the resource-based

definition of the habitat and its associated scheme. 3) Answers of the reserve managers became divided between the resource-based and vegetation-based definitions of the habitat. 4) After reading the short summary of Chapter I, none of the groups answered anymore that habitat is the place where an organism lives.

Although based on small sample sizes, these results tend to suggest that we could convince non-scientists to adopt non-intuitive views and concepts, once the concept was clearly explained …

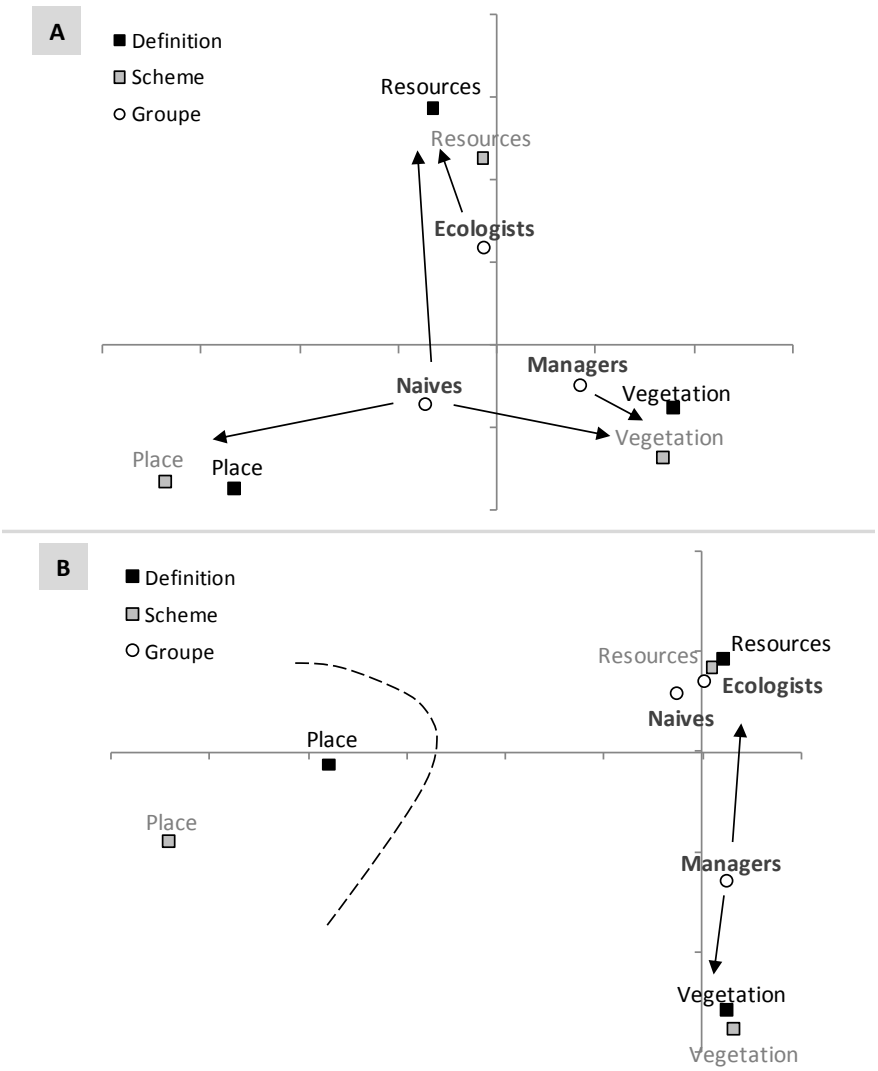
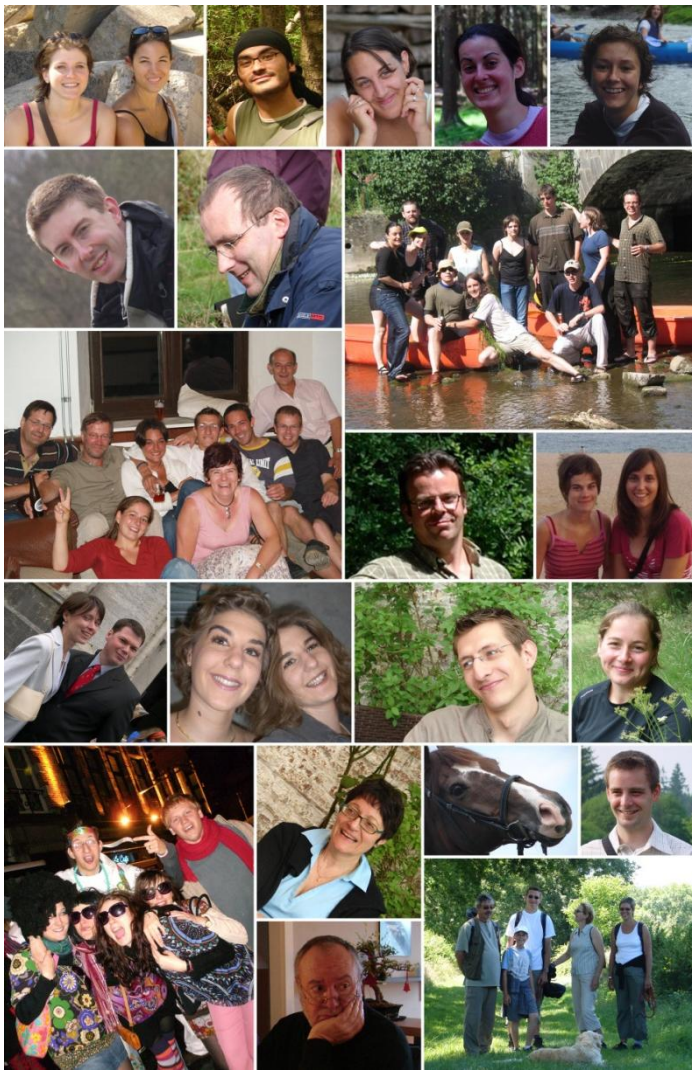
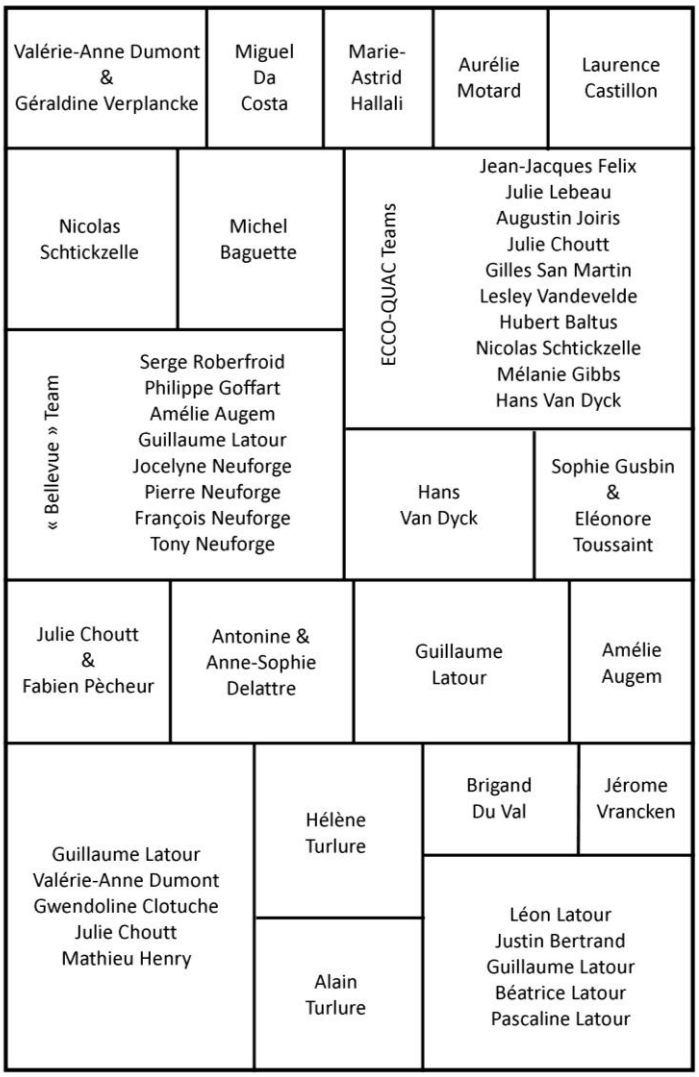


Figure e.1. Graphical representation of the two MCA using scores from answers to the two questions. Black squares = possible responses to the first question. Grey squares = Possible responses to the second question. White dots = group of persons. a) First series of answers to the two questions of the questionnaire. b) Second series of answers to the same questions.

Remerciements





Pictures: Camille Turlure & Friends ...

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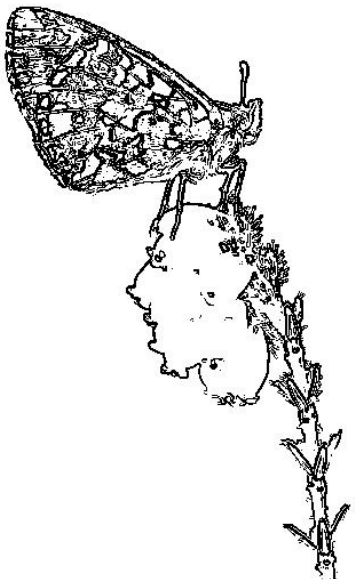
Annexes



Annexes: illustration cover by Camille Turlure

Annex i.1. Sum in the 10 vegetation samples of the abundances of each plant species per zone (i.e. ranging from 0 to 250). Site: *P* = Pisserotte, *L*=Libin. Vegetation type: *WM* = wet meadows, *SW* = floating mats and swamps, *HL* = heathlands, *RU* = rushes, *FG* = fen grasslands, *SF* = short sedge fens. Abundances of the host plants are underlined in grey. Abundances of the main plant species that determined the vegetation types are surrounded together.

Species	Site	P	P	P	P	P	P	P	L	L	L	L	L	L	L	P	P	P	P	P	P	P
	Zone	T01	T03	T12	T16	T29	T33	T38	L02	L08	L09	L10	L11	L12	L20	L21	T26	T31	T32	T37	T13	T14	T27
	Vegetation type	WM	WM	WM	WM	WM	WM	WM	SW	SW	SW	SW	SW	SW	SW	SW	SW	SW	SW	SW	HL	HL	HL
Deschampsia cespitosa	DESC	**142**	**81**	**139**	**102**	**64**	**72**	**212**	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0
Anemone nemorosa	ANEN	**96**	**10**	**82**	**68**	**8**	**66**	**65**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polygonum bistorta	**POLB**	**172**	**205**	**198**	**201**	**44**	**99**	**219**	0	2	28	0	0	0	**58**	10	0	0	6	22	0	0	0
Carex echinata	CARE	0	0	0	0	0	0	0	**2**	**18**	**0**	**74**	**24**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	2	0	0
Carex rostrata	CARR	0	0	0	0	0	0	0	**64**	**0**	**106**	**4**	**0**	**20**	**0**	**16**	**0**	**0**	**0**	**0**	0	0	0
Empetrum nigrum	EMPN	0	0	0	0	0	0	0	**64**	**0**	**0**	**0**	**14**	**0**	**32**	**0**	**0**	**0**	**0**	**0**	0	0	0
Eriophorum polystachion	ERIP	0	0	0	0	0	0	0	**64**	**32**	**70**	**144**	**198**	**112**	**80**	**114**	**0**	**0**	**0**	**0**	25	0	0
Drosera rotundifolia	DROR	0	0	0	0	0	0	0	**0**	**26**	**0**	**50**	**36**	**40**	**0**	**0**	**0**	**0**	**0**	**0**	0	0	0
Equisetum fluviatile	EQUI	0	0	0	0	0	2	0	**4**	**12**	**8**	**48**	**48**	**12**	**2**	**0**	**0**	**3**	**21**	**19**	0	0	0
Menyanthes trifoliata	MENT	0	0	0	0	0	0	0	**0**	**178**	**14**	**36**	**54**	**98**	**34**	**0**	**0**	**18**	**134**	**0**	0	0	0
Narthessium ossifragum	NARO	0	0	0	0	0	0	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**125**	**87**	**8**	0	0	0
Potentilla palustris	POTP	0	0	0	0	0	22	0	**0**	**0**	**0**	**42**	**50**	**12**	**16**	**0**	**0**	**0**	**26**	**0**	0	0	0
Succisa pratensis	SUCP	0	0	4	0	0	0	0	**0**	**8**	**22**	**32**	**16**	**0**	**0**	**0**	**0**	**4**	**1**	**0**	0	0	0
Vaccinium oxycoccos	**VACO**	0	0	7	0	0	0	0	**200**	**162**	**140**	**242**	**104**	**182**	**64**	**152**	**108**	**38**	**131**	**163**	**123**	**68**	**47**
Calluna vulgaris	CALV	0	0	14	0	0	8	0	62	24	38	54	22	42	10	128	24	75	35	43	**70**	**122**	**61**
Polytrichum sp.	POLY	0	40	14	28	0	5	0	54	20	60	14	48	10	44	34	101	8	28	39	**112**	**156**	**128**
Vaccinium myrtillus	VACM	2	0	3	0	5	8	0	0	0	0	0	0	0	0	0	0	0	0	1	**0**	**19**	**13**
Vaccinium uliginosum	VACU	0	0	0	2	9	0	16	0	0	0	0	0	0	0	0	0	0	0	0	**44**	**23**	**7**
Vaccinium vitis-idaea	VACV	25	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**62**	**144**	**0**
Eriophorum vaginatum	ERIV	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	62	21	0	**41**	**9**	**0**
Juncus acutiflorus	JUNC	52	180	2	181	171	85	37	176	168	68	42	76	90	110	144	166	26	50	68	42	28	111
Viola palustris	**VIOP**	1	0	0	6	**54**	0	0	0	0	0	0	14	0	0	0	32	0	0	1	0	0	25
Sphagnum sp.	SPHA	71	83	85	141	23	29	0	176	220	218	242	220	246	154	224	192	111	144	233	142	110	72
Carex nigra	CARN	14	9	21	14	6	11	0	6	4	0	0	6	2	30	0	10	43	62	4	32	9	48
Angelica sylvestris	ANGS	0	0	0	0	9	4	0	8	0	0	0	0	0	0	0	0	0	6	3	0	0	0
Cirsium palustris	CIRP	0	2	0	0	22	10	0	8	16	0	0	4	0	0	0	0	0	0	14	0	0	0
Lotus pedunculatus	LOTP	5	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0	0
Rumex acetosa	**RUMA**	11	13	0	0	**147**	29	0	16	18	0	0	0	0	0	0	11	0	10	5	0	0	0
Ranunculus acris	RANA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Molinia caerulea	MOLC	74	7	85	18	12	55	0	92	116	56	28	62	68	28	58	8	46	23	22	101	124	83
Trientalis europaea	TRIE	0	0	0	12	26	2	0	0	0	0	0	0	0	0	0	3	14	15	2	0	0	0
Caltha palustris	CALP	0	0	0	0	0	15	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
Cardamines pratensis	CARP	0	0	0	0	0	0	0	0	0	0	4	0	0	8	0	0	5	4	0	0	0	0
Deschampsia flexuosa	DESF	0	2	1	0	0	3	55	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Dryopteris sp.	DRYC	1	11	22	0	8	10	0	0	0	28	0	0	0	2	24	0	0	4	7	0	0	9
Epilobium palustris	EPIP	0	0	0	0	4	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Filipendula ulmaria	FILU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium molugo	GALM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustris	GALP	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium saxatile	GALS	67	34	50	46	85	43	24	0	0	0	0	0	0	0	0	5	0	0	28	0	1	0
Holcus lanatus	HOLL	0	24	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holcus mollis	HOLM	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	20
Luzula multiflora	LUZM	0	0	0	0	0	0	0	14	8	6	0	0	0	0	0	0	0	0	0	0	0	0
Lychnis flos-cuculi	LYCF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Lysimachia thyrsiflora	LYSI	6	9	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myosotis scorpioides	MYOS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla erecta	POTE	0	0	0	1	8	0	0	0	0	0	0	0	0	4	0	0	0	2	0	0	0	0
Valeriana repens	VALR	0	0	0	0	13	2	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0

Species	Site	L	L	L	L	P	P	P	P	P	P	P	P	P	P	P	P	P	P
	Zone	L01	L07	L14	L22	T02	T04	T05	T07	T09	T10	T17	T18	T21	T24	T25	T28	T34	T35	T40
	Vegetation type	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU	RU
Deschampsia cespitosa	DESC	0	8	22	0	17	0	0	0	0	0	0	0	19	0	0	8	12	0	0
Anemone nemorosa	ANEN	0	0	0	0	12	0	0	0	0	0	63	82	0	0	0	0	0	11	0
Polygonum bistorta	**POLB**	**46**	**166**	**50**	0	**169**	**135**	**181**	**76**	**215**	**154**	**54**	**97**	31	0	**139**	12	11	**137**	**170**
Carex echinata	CARE	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex rostrata	CARR	0	0	0	12	0	13	0	0	0	0	0	0	0	0	0	0	1	2	0
Empetrum nigrum	EMPN	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriophorum polystachion	ERIP	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drosera rotundifolia	DROR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum fluviatile	EQUI	186	0	0	28	0	0	0	0	0	0	0	0	0	0	5	0	0	0	20
Menyanthes trifoliata	MENT	6	0	0	16	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Narthessium ossifragum	NARO	0	0	0	0	0	0	0	0	0	0	23	0	0	0	21	0	0	0	0
Potentilla palustris	POTP	44	0	30	78	15	51	31	0	0	0	26	24	0	0	0	0	36	33	0
Succisa pratensis	SUCP	0	0	0	0	0	5	1	0	4	0	7	13	3	0	0	0	0	0	0
Vaccinium oxycoccos	**VACO**	0	0	0	10	0	0	0	0	0	0	0	7	16	**41**	17	0	0	0	0
Calluna vulgaris	CALV	8	0	0	8	0	0	4	0	0	0	0	0	15	25	19	0	0	0	0
Polytrichum sp.	POLY	0	6	0	0	0	27	27	96	50	49	39	21	79	25	12	20	24	21	0
Vaccinium myrtillus	VACM	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0
Vaccinium uliginosum	VACU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0
Vaccinium vitis-idaea	VACV	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Eriophorum vaginatum	ERIV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus acutiflorus	JUNC	**250**	**236**	**218**	**234**	**202**	**200**	**210**	**179**	**181**	**222**	**205**	**195**	**165**	**195**	**193**	**190**	**243**	**241**	**208**
Viola palustris	**VIOP**	**16**	**20**	**18**	**8**	**136**	**88**	**69**	**0**	**17**	**6**	**90**	**21**	**0**	**154**	**25**	**0**	**115**	**111**	**0**
Sphagnum sp.	SPHA	**0**	**132**	**0**	**176**	**123**	**194**	**105**	**96**	**42**	**78**	**118**	**103**	**102**	**198**	**61**	**44**	**170**	**122**	**40**
Carex nigra	CARN	**0**	**22**	**10**	**2**	**30**	**0**	**15**	**40**	**51**	**40**	**25**	**13**	**60**	**2**	**24**	**44**	**0**	**0**	**0**
Angelica sylvestris	ANGS	18	8	12	6	0	0	0	0	0	0	0	9	6	0	0	0	0	0	0
Cirsium palustris	CIRP	8	4	8	14	1	0	0	0	0	0	4	23	0	0	0	0	1	0	9
Lotus pedunculatus	LOTP	82	12	86	0	0	0	0	0	0	0	0	24	15	0	0	0	1	0	0
Rumex acetosa	**RUMA**	**52**	**42**	12	0	8	37	22	0	5	0	32	29	12	35	61	8	20	**45**	2
Ranunculus acris	RANA	8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Molinia caerulea	MOLC	0	106	12	66	23	10	22	35	15	4	41	83	7	0	23	32	46	34	47
Trientalis europaea	TRIE	0	0	0	0	0	1	0	0	0	6	0	4	0	18	0	0	0	32	4
Caltha palustris	CALP	18	0	66	0	0	0	0	0	0	0	12	27	0	0	0	0	0	0	0
Cardamines pratensis	CARP	0	0	54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	DESF	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0
Dryopteris sp.	DRYC	0	8	0	0	0	0	0	0	6	2	0	3	7	0	13	9	7	6	0
Epilobium palustris	EPIP	68	6	12	16	0	3	0	1	0	0	0	3	3	0	0	0	2	9	0
Filipendula ulmaria	FILU	0	0	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium molugo	GALM	12	0	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustris	GALP	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0
Galium saxatile	GALS	0	0	0	0	15	12	6	103	38	87	57	12	66	0	85	113	54	0	26
Holcus lanatus	HOLL	26	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Holcus mollis	HOLM	0	0	44	0	12	0	6	0	0	34	0	5	49	0	0	82	0	0	5
Luzula multiflora	LUZM	0	12	0	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0
Lychnis flos-cuculi	LYCF	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Lysimachia thyrsiflora	LYSI	0	26	24	0	22	2	0	0	0	0	0	15	0	13	3	0	0	24	0
Myosotis scorpioides	MYOS	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla erecta	POTE	0	14	0	0	0	0	0	0	0	0	10	14	0	0	0	0	5	0	0
Valeriana repens	VALR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	Site	L	L	L	L	L	L	L	L	P	P	P	P	P	L	L	L	L	L	P	P	P	P	P	P
	Zone	L05	L13	L15	L16	L17	L18	L19	L25	T06	T08	T19	T20	T22	L03	L04	L06	L23	L24	T11	T15	T23	T30	T36	T39
	Vegetation type	FG	FG	FG	FG	FG	FG	FG	FG	FG	FG	FG	FG	FG	SF	SF	SF	SF	SF	SF	SF	SF	SF	SF	SF
Deschampsia cespitosa	DESC	0	26	16	0	56	10	20	38	21	12	24	14	0	0	0	0	0	0	0	0	0	0	0	0
Anemone nemorosa	ANEN	0	0	0	0	0	0	0	0	38	0	0	86	0	0	0	18	0	0	2	43	0	24	0	0
Polygonum bistorta	**POLB**	**132**	**208**	**86**	**178**	**66**	**78**	**68**	**64**	**76**	**181**	**108**	**133**	0	0	**48**	**98**	**40**	0	0	39	0	0	0	21
Carex echinata	CARE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carex rostrata	CARR	8	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	28	14	0	0	0	0	0	0
Empetrum nigrum	EMPN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriophorum polystachion	ERIP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0
Drosera rotundifolia	DROR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum fluviatile	EQUI	16	0	0	0	4	0	0	0	0	0	0	0	0	0	0	2	28	6	0	0	0	0	0	0
Menyanthes trifoliata	MENT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	0
Narthessium ossifragum	NARO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potentilla palustris	POTP	12	0	66	16	34	10	34	0	0	0	0	0	0	20	0	0	38	40	0	0	0	0	0	24
Succisa pratensis	SUCP	0	0	4	0	0	6	12	0	0	4	0	9	0	0	12	0	0	8	0	7	6	11	0	0
Vaccinium oxycoccos	**VACO**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	29	0
Calluna vulgaris	CALV	0	0	0	0	0	46	0	16	0	0	0	0	11	0	0	0	0	0	35	12	32	0	10	0
Polytrichum sp.	POLY	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	222	167	75	6	8	0
Vaccinium myrtillus	VACM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	8	0	0
Vaccinium uliginosum	VACU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	4	18	1	5	8
Vaccinium vitis-idaea	VACV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	44	14	0	16
Eriophorum vaginatum	ERIV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
Juncus acutiflorus	JUNC	250	240	244	198	220	98	240	216	181	215	168	197	211	224	232	192	122	150	80	121	66	205	37	93
Viola palustris	**VIOP**	**42**	14	6	0	8	32	4	**64**	**63**	10	9	6	28	10	30	**52**	30	26	0	0	0	0	3	2
Sphagnum sp.	SPHA	16	0	10	0	0	0	0	14	0	0	0	0	20	70	158	100	0	24	66	107	43	91	46	50
Carex nigra	CARN	0	20	0	18	14	50	0	0	34	5	18	29	8	8	18	0	20	0	22	15	46	13	8	17
Angelica sylvestris	ANGS	**22**	**8**	**2**	**8**	**10**	**0**	**0**	**30**	**15**	**7**	**8**	**23**	**0**	12	12	4	20	8	0	0	0	0	0	0
Cirsium palustris	CIRP	**10**	**4**	**2**	**18**	**4**	**18**	**18**	**6**	**28**	**4**	**2**	**19**	**0**	10	6	2	16	8	0	0	0	0	30	5
Lotus pedunculatus	LOTP	**36**	**80**	**74**	**46**	**24**	**24**	**72**	**2**	**21**	**0**	**0**	**46**	**0**	0	12	2	0	10	0	0	0	0	0	0
Rumex acetosa	**RUMA**	**42**	**100**	**82**	**70**	**52**	**14**	**74**	**124**	**142**	**94**	**102**	**76**	**133**	**88**	**40**	**58**	**50**	**60**	0	0	1	**80**	**69**	**55**
Ranunculus acris	RANA	**24**	**14**	**32**	**6**	**108**	**8**	**48**	**6**	**0**	**0**	**0**	**0**	**0**	0	0	0	0	0	0	0	0	0	0	0
Molinia caerulea	MOLC	18	0	50	0	0	60	18	134	9	12	33	2	25	**112**	**144**	**126**	**150**	**186**	**131**	**139**	**81**	**145**	**213**	**210**
Trientalis europaea	TRIE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	3	0	42	2	7
Caltha palustris	CALP	4	36	44	50	50	0	0	0	0	0	0	0	0	0	0	24	2	14	0	0	0	0	0	0
Cardamines pratensis	CARP	0	0	8	30	12	2	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	DESF	0	68	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	2	4	0
Dryopteris sp.	DRYC	0	0	12	8	6	4	0	14	0	1	32	2	7	46	34	24	26	16	0	0	4	4	9	3
Epilobium palustris	EPIP	20	16	4	14	0	0	20	20	1	0	0	5	0	30	6	10	14	0	0	0	0	3	0	2
Filipendula ulmaria	FILU	64	0	34	0	66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium mollugo	GALM	0	34	0	36	12	0	10	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium palustris	GALP	4	0	0	0	0	0	0	6	0	0	0	0	0	14	0	6	0	20	0	0	0	0	0	0
Galium saxatile	GALS	0	0	0	0	0	20	20	0	106	29	107	47	60	0	0	0	0	0	4	12	81	113	30	40
Holcus lanatus	HOLL	0	36	0	0	0	0	0	0	6	12	0	0	0	0	0	0	0	0	0	5	0	0	0	0
Holcus mollis	HOLM	0	0	0	0	0	0	0	10	2	0	0	0	25	0	0	0	8	2	0	0	35	4	0	4
Luzula multiflora	LUZM	0	0	0	0	0	4	26	0	0	0	0	0	0	0	14	0	0	0	0	1	2	0	0	0
Lychnis flos-cuculi	LYCF	4	10	38	10	24	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Lysimachia thyrsiflora	LYSI	52	0	26	4	36	0	2	0	0	0	0	1	0	2	22	0	0	0	0	2	0	4	0	0
Myosotis scorpioides	MYOS	0	0	0	0	0	0	4	26	0	0	0	0	0	24	0	0	20	26	0	0	0	0	0	0
Potentilla erecta	POTE	0	0	0	0	0	0	6	0	0	3	0	0	0	4	16	0	0	0	2	7	0	6	0	0
Valeriana repens	VALR	0	0	0	0	26	0	0	0	0	4	2	12	0	0	0	0	0	0	0	0	0	0	0	0

Merci de bien vouloir répondre à ce très court questionnaire en numérotant dans les cases prévues à cet effet: 1, 2 ou 3 par ordre décroissant de pertinence ou d'importance.

(1= réponse la plus importante et 3 = réponse la moins importante)

Question 1

Numéroter ces définitions de l'habitat d'une espèce selon leur pertinence, de la plus pertinente à la moins pertinente :

- ☐ C'est l'endroit ou l'espèce vit
- ☐ C'est un écosystème (type de milieu) bien précis
- ☐ C'est un ensemble de conditions ou ressources

Question 2

Numéroter ces trois schémas (ci-contre) représentant l'habitat d'une espèce de papillon, du plus pertinent au moins pertinent:

- ☐ Schéma A
- ☐ Schéma B
- ☐ Schéma C

Schéma A

Habitat = L'intégralité du lieu dit de la Fagne Pisserotte

Schéma B

Habitat = Uniquement la partie « tourbière » de la Fagne Pisserotte

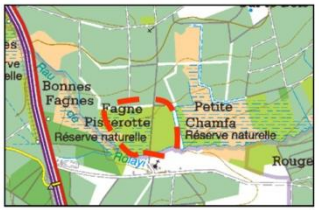
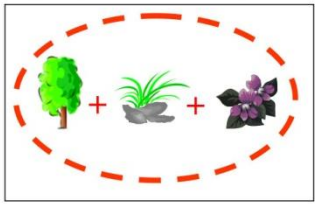


Schéma C

Habitat = Ensemble de conditions présentes à la Fagne Pisserotte



Annex e.2. Brief and vulgarized summary of the comparison of the habitat of two butterfly species (i.e. Chapter I).

Merci de bien vouloir lire ce petit résumé d'une étude menée sur deux espèces de papillons, Et de répondre à nouveau aux questions du questionnaire précédent.

Notre étude porte sur deux espèces de papillons: le cuivré de la bistorte (*Lycaena helle*) et le nacré de la bistorte (*Proclossiana eunomia*). En Belgique, ces deux espèces de papillons se rencontrent dans les fonds de vallée humides et dans les tourbières. Leurs chenilles se nourrissent des feuilles de la même plante: la bistorte (*Polygonum bistorta*).

Pendant l'été 2005, nous avons compté les papillons qui volaient dans une réserve naturelle de l'Ardenne belge: la Fagne de Pisserotte. Dans cette tourbière, les deux espèces étaient présentes en grand nombre, à raison de plus de 10 papillons comptés tous les 100m. Cependant, elles n'occupent pas les mêmes endroits de cette tourbière. En effet, le cuivré vole à proximité des arbres où ils passent la nuit, alors que le nacré ne se préoccupe pas de la présence des arbres.

Nous avons aussi recensés les chenilles de ces deux espèces de papillons. Toutes deux ont été trouvées à proximité de la plante dont elles se nourrissent, mais de nouveau, comme pour les papillons adultes, elles n'occupent pas les mêmes endroits de cette tourbière. Les chenilles du nacré se trouvaient à proximité de petits monticules appelés touradons, sur lesquels elles peuvent se mettre à l'abri des fluctuations du lit de la rivière, ce qui n'est pas le cas des chenilles du cuivré.

Les besoins de ces deux espèces sont donc différents: on les retrouvent, tant pour les adultes que pour les chenilles, à différents endroits de la tourbière. De plus, la présence de ces deux papillons varie au cours du temps: elle suit l'évolution de la répartition géographique de leur plante nourricière.