Journal of Insect Biodiversity 2(8): 1-32, 2014 http://www.insectbiodiversity.org

JOURNAL OF INSECT BIODIVERSITY
ISSN: 2147-7612

REVIEW ARTICLE

Ten years of the resource-based habitat paradigm: the biotope-habitat issue and implications for conserving butterfly diversity

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Abstract: The widely used term 'habitat' underlies all aspects of a species' (and community's) population size, consequently population changes, distribution and range size and changes; ultimately, habitat parameters determine the status of species, whether thriving or threatened with extinction. Habitat parameters also lie at the root of species' evolution (speciation) involving cycles of resource specialism/generalism. A basic problem is that habitat has long been treated as synonymous with biotope. But, the two variable terms habitat and biotope describe very different phenomena and we make a case for clarity in the use of the term 'habitat', especially when the focus is conserving biodiversity. In this review, in reference to butterflies, we distinguish habitat from biotope as a real, grounded resources-based and conditions-based entity, and explain how usage of the terms greatly affects our perception of population status, and of population, distribution, range and speciation processes, central to conserving biodiversity.

Key words: Biodiversity, biotope, climate change, dispersal, ecotone, extinction, generalism-specialism, geographical range, habitat, migration, population, speciation.

"*There are known knowns. These are things we know that we know. There are known unknowns. That is to say, there are things that we know we don't know. But there are also unknown unknowns. There are things we don't know we don't know*." Donald Rumsfeld, not on butterfly ecology but it may as well have been.

Introduction

There is perhaps no more contentious issue in biodiversity conservation than a species' habitat; over recent years increasing attention has been given to this topic and the resources needed by arthropod species (New 2010, 2012a,b, 2014). The first of three papers on a resource-based definition for habitat (RBH) appeared just over 10 years ago (Dennis *et al.* 2003, 2006, 2007). It was followed up by a response to concerns over the implications of the concept to continued application of contemporary ecological models (e.g., metapopulations; Baguette & Mennechez 2004; Shreeve *et al.* 2004), expansions of the concept (Dennis *et al.* 2006, 2007) and a more extensive treatment for butterflies (Dennis 2010). Like many advances beforehand, it was a concept of its time, ripe for development. Faced with the conundrums of relating habitat to vegetation units, past researchers had come close to making this distinction between biotope and habitat (e.g., Webb 1993; Thomas & Morris 1994). Variants of the concept were independently proposed by several authors (Dunning *et al.* 1992; Caughley & Sinclair 1994; Hall *et al.* 1997; Weddell 2002) with the idea of habitat as a single definable physical entity (location) first being explicitly formulated and illustrated in a book on butterfly island biogeography (Dennis & Shreeve 1996). The resource-based habitat (RBH) definition was developed to highlight the deficiencies of applying the term habitat to biotopes (vegetation units) (Dennis 2010). Even so, in the scientific literature as well as in general use, habitat is still found to refer to vegetation units or biotopes, even though it is now apparent that such units usually fail to envelop all species' resources. In this paper, the reasons and implications for this continued usage are considered, as well as the relevance of the RBH for population status, especially for studies on population dynamics. All of these issues ultimately impact on biodiversity conservation (i.e., speciation, species' extinction). Suggestions are presented intended to avert problems caused by inappropriate application of the term habitat, that is, problems for research findings based on habitat comparisons and studies based on habitat structures, which ultimately become problems for conservation practice.

Habitat and biotope: insights and inferences

To understand why habitat is still used as a synonym for biotope, and the implications for conserving biodiversity, it is first useful to appreciate the basis for the RBH concept and the contexts in which habitat is still used to refer to biotopes.

Reasons for, and events leading to, the development of the RBH concept

The resource-based approach to habitat definition initially developed out of a need to provide a (then) more precise definition of migration (Dennis & Shreeve 1996), coined simply as movements between habitats (after Baker 1978). The question was: what exactly is a habitat? It is an old question that has invariably been sidestepped through simply referring to biotope as habitat; biotopes are for the most part easily recognised and a species' habitat is embedded in biotopes. However, the literature contains frequent pointers to the difficulties raised by the biotope concept of habitat; sins are basically twofold, of commission and omission. An organism's habitat can rarely be expected to fit neatly into a biotope patch: the dimensions of the biotope may exceed that of the habitat space (commission) or it may fail to embrace all of its resources and conditions (omission) (Fig. 1). The first error is less serious, inasmuch as designating a larger zone than the habitat will tend to overestimate resources necessary to support a population; an important exception is in cases of extinction debt where resources are actually insubstantial and the population is in decline (Pulliam 1988; Jackson & Sax 2009; Hylander & Ehrlen 2013). The second error is certainly critical for species' conservation – a habitat bulging beyond the biotope bounds – especially if the biotope patch fails to include vital resources, as will often be the case in ecotone species (e.g., *Satyrium ilicis*; Dirk Maes, personal communication). In this case resources and conditions are underestimated and management based on the biotope patch may well fail. Using biotope as a

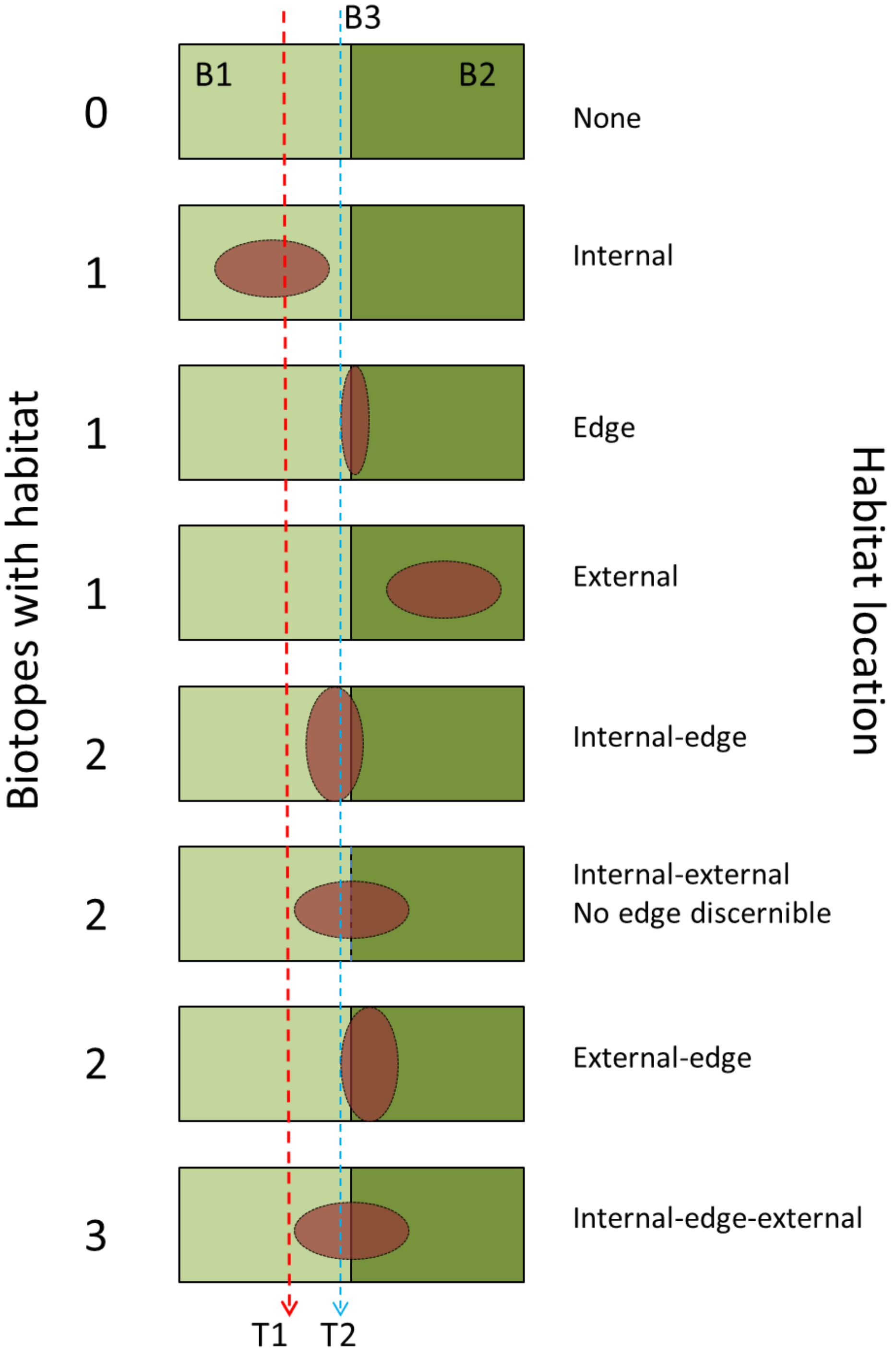


Figure 1. Habitat-biotope combinations for two biotopes. The habitat (brown) for a single species is shown as occupying none, one, two or three of two main biotopes (B1 light green, B2 dark green) separated by an intervening structural edge biotope (B3, continuous line), absent in one set (6th down, pecked line). Those species whose resource-based habitats incorporate edge biotopes can be referred to as ecotone species. The positions of two transect lines for population assessments (or other survey) are shown; these will pick up more or fewer individuals of the species in each case. Transect counts will also be affected by whether the habitat is represented by the full suite of resources for all life history stages and conditions for the species or, alternatively, just part of the habitat possibly including or excluding the habitat core (containing the larval host plant, thus egg, larval and pupal resources). Different designation of the resource-based habitat (full suite or early stage suite of resources) evidently affects the status of the biotopes if interpreted as habitat. As the RBH structure differs for species, especially specialists and generalists, a transect section will bisect varying fractions and types of habitat components for different species.

synonym for habitat fails to convey anything about the composition, condition and disposition of resources in a biotope. But, any mismatch of biotope with the RBH can cause further problems, some of which may be serious. For instance, using biotope as a substitute for habitat can lead to an assumption that patches of the same biotope form suitable habitat for a target species. However, a mismatch between biotope and habitat is increasingly likely where these patches are marginal in some respect, for instance geographically and/or environmentally (e.g., different soils, management history), or simply where biotopes have different contexts (i.e., different neighbouring biotopes) and management.

Thus, spatial variation in biotope content (i.e., composition, structures, management, etc.) frustrates the process of matching RBH with the biotope. Biotope, like habitat, is a variable, but they are actually different variables; biotope is distinctly hierarchical enclosing nested subsets of vegetation types and conditions. Heterogeneity can be easily overlooked when treating a particular biotope as a fixed category. Researchers thus find themselves in difficulties whether applying biotope as habitat to broad divisions (e.g., moorland) or to finer subsets (e.g., heather moorland, bilberry moorland etc.); in the former case the unit can only crudely describe the actual habitat, and as subsets lower in the hierarchy are selected they are more likely to underestimate the resources and conditions needed to support a species. The situation is not helped when the same researchers refer to several (a hierarchy of) distinct stages of a vegetation as a particular species' habitat; an example is moorland in Britain, divided into heather, bilberry and cotton grass, all variously referred to as habitat for birds such as waders and grouse (Grant & Pearce-Higgins 2012). The solution – where there is uncertainty concerning species' resources and conditions, thus habitat bounds – has sensibly been to refer to vegetation patches where species are located as biotope, not habitat.

Dual contexts in which habitat is used to describe biotope

Before considering the reasons biotope is referred to as habitat, it is first useful to describe the contexts in which habitat as biotope is applied. Habitat, as biotope, has been used explicitly in two distinct ways: (i) to identify a particular species' living space (Odum 1963; Lincoln *et al.* 1982); (ii) to describe particular vegetation types, each of which is regarded as unique living space (i.e., a habitat) for a collection of species or communities (Lawton *et al.* 2010; UK Natural England 'habitats' http://www.naturalengland.org.uk/Images/sone-section3.2_tcm6-4728.pdf). Thus, in the first case, the habitat of a speckled wood butterfly *Pararge aegeria*, is typically described as being a wood, and that of a meadow brown butterfly *Maniola jurtina* as a meadow or tall grassland. Such usage conveys the message that all resources and conditions suitable for the development and survival of the species through its life cycle are contained in a specific biotope, wood and meadow respectively. The second case often heralds a focus of attention on a distinctive vegetation/substrate target and its fauna (e.g. rainforest of New Guinea; Flow Country of Caithness) for priority conservation action, as in the case of the European Habitats Directive (habitat types [biotopes] under the European Habitat Directive 1992). This use of habitat to describe a biotope in a more general manner (i.e., woodland habitat, marshland habitat), ascribes a special status to a biotope, and in so doing extends the single species concept to multiple species; thus, wood, meadow, fen, moor, or finer divisions of these biotopes (e.g., bilberry moor, heather moor etc), are regarded as recognisable zones in which a collection of species live and thus, by implication, have all or most of their key resources.

It would not be possible for such links between organisms and habitat as biotope to be made unless there was some correspondence between the species' populations and distributions and the biotope; the primary evidence emanates from field survey and distribution mapping, but often this is not rigorous and associations are anecdotal. Some obvious problems emerge in more careful examination in biotope occupancy: (i) Associations between a broad biotope category and an organism are often loose ones, containing a variety of vegetation types and substrates; of crucial importance is the fine detail which is often glossed over. When finer categories are used, a species will be found to expand beyond the bounds. (ii) Surveys and observations are often focused on a single life history stage (e.g., adult in butterflies) or resource being exploited (e.g., larval host plant in phytophagous insects; nest sites in birds). (iii) Actual resource use by that and other life history stages is rarely audited. (iv) Associations between a broad biotope category and an organism are often made from observations over short time periods and fail to account for circadian (i.e., daily or seasonal) resource use. (v) The importance of surrounding substrates – used by an organism and key to population maintenance – is often not considered (i.e., ecotones such as hedgerows and woodland edges; adjacent biotopes such as scrub, bare ground etc.) (Fig. 1). Analysis of biotope (vegetation) associations for butterfly species has been rarely attempted – but, classic examples are the work of Balletto and colleagues in Italy (Balletto *et al.* 1987, 1988 with citations to earlier publications). When it has been done, distinctive associations are evident, but on close inspection are also found to be highly varied, even for specialists (e.g., *Plebejus argus*; Thomas 1985; Ravenscroft 1990). The fact is that it has become increasingly apparent that use of biotope labels fails to describe the habitat of most species at a scale useful for local management, for example most UK butterfly species (Dennis 2010: Appendix 7); even a casual observation of vertebrates, particularly birds, reveals that they exploit a wide range of biotopes, particularly for nesting and feeding, and how can one ignore the disseminated habitat components of migratory species?

Reasons why habitat is still used to refer to biotope

Thus, the question has to be asked why biotope continues to be used as a synonym, and not just a surrogate, for habitat. There are several reasons apparent: (i) It has long been in traditional usage and is a familiar term to convey ground-based findings on distributions and populations to the wider scientific community and public. (ii) It is simple to apply. Biotopes are generally easy to identify and to describe (e.g. UK National Vegetation Classification; Rodwell 1991-2000) and present ‘natural’ units for conveying species distributions. (iii) A resource-based habitat can be a complex physical construct, and a less simple (multidimensional) concept to grasp.

To describe a habitat for a species over a region, based on its resource use and suitable environmental conditions, requires an in depth knowledge of species not easily obtained. Even if a species’ resources and conditions are well known, tracking them down in the field often presents immense logistical difficulties. Faced with these observations, it seems entirely reasonable that biotopes (or vegetation units) act as surrogates for habitat. But, what are the dangers of such usage? Several emerge: (i) In treating biotope (vegetation unit) as the habitat, there is typically a failure to consider or to investigate the resources and conditions for species that occur in the biotope. (ii) There is the danger of assuming that resources and conditions for species, particularly their spatial disposition, in the biotope are homogeneous from place to place and unchanging over time. (iii) There is a danger of losing sight of how species respond to changes in biotopes (i.e., development and growth, plastic responses, interactions, behaviour, movements). The focus becomes one of broad changes to the biotope and environmental conditions rather than a wider and deeper focus incorporating responses by individuals – both stochastic and behavioural, and through adaptations to selection pressures – within populations occupying the biotope. From these observations more overarching dangers are associated with using habitat (= biotope) unreservedly for biodiversity conservation.

Despite these fundamental criticisms, the objective of this contribution is not to present arguments for the abandonment of the traditional habitat (meaning biotope) usage. Habitat applied in this manner clearly has advantages of simplicity in communication and is critical for conserving species under the European Habitats Directive (Maes *et al*. 2013). However, in this review, we attempt to draw sufficient distinctions between habitat as biotope and habitat as experienced by individual species (RBH) so as to direct attention where the former usage may best be used, when it is appropriate (and inappropriate) to apply, and how to use it successfully. The primary aim of science should always be to describe relationships accurately: fundamentally, biotope is a community term, habitat a species-specific one – the two should not be confused. If confounded, this can lead to aberrant reasoning, inadequate models and failed reconstructions of reality, and has consequences for biodiversity conservation. Here, we draw attention to the importance, always, of thinking in a resource-based mode when referring to species' habitats, particularly when attention is focused on management plans to conserve specific populations; the RBH view provides a tool for assessing the appropriateness of applying basic environmental units (vegetation divisions) for identifying and analysing species' habitats. The starting point is the individuation of habitat.

Resource-based habitat paradigm: Individuation or habitat from an individual's perspective

The term 'habitat' has, as its basis, the place where an organism lives (a habitation from the Latin habitātus, past participle of habitāre to dwell; Thompson 1995), thus where it finds requirements for living. Various forms of the RBH definition have been developed; at its simplest, 'a habitat is that collection of resources and conditions ensuring persistence of a population at a site' (Dennis 2010; Fig 2). A species' habitat forms part – fundamentally, the ground-based part – of the hyperdimensional space describing a species' niche (Q, species' characteristics, R, resource variables, S, space and T, time; Dennis 2010: 11). Habitat is, in effect, a set of mapped physical spaces, elements describing parameters of resources and conditions. The variation in resources and conditions – describing the *suitability* of components comprising a species' habitat – can be effectively collapsed within axes for resource composition, physiognomy and connectivity (Dennis *et al.* 2006; Fig. 3). The above RBH definition (Dennis 2010) is sufficient for species whose populations are compact (occurring at a site), their resources intersecting or contiguous (close union) linked by 'trivial' movements of individuals (Fig. 2a-e). It becomes increasing difficult to apply to species whose populations are not restricted to single sites (open rather than closed populations), whose resources become progressively more disjoint, ultimately linked by long-distance seasonal migrations (Fig. 2f-g). To cater fully for species with open populations a wider definition may be applied: 'A habitat is that collection [set] of ground-based resources and conditions sufficient to maintain a population or cohort of a species.' This definition is valid for all eukaryotic organisms, and ensures that the resource demands of two distinctive groups of arthropods are included, of critical importance for biodiversity assessments: (i) species that are multivoltine and exploit contrasting seasonal resources, and (ii) species whose individuals come together at some stage in their life cycle, but which travel immense distances for some seasonal resource(s). Inclusion of species that undergo long distance migration forces human observers to undertake the necessary, if discomforting, task of conceptualising habitats of organisms that extend beyond their own habitat dimensions and to the need for integrating resource planning at supra-state and supra-continental scales (Stefanescu *et al.* 2013). In entomology – compared to vertebrates, especially birds – there is a greater tendency to

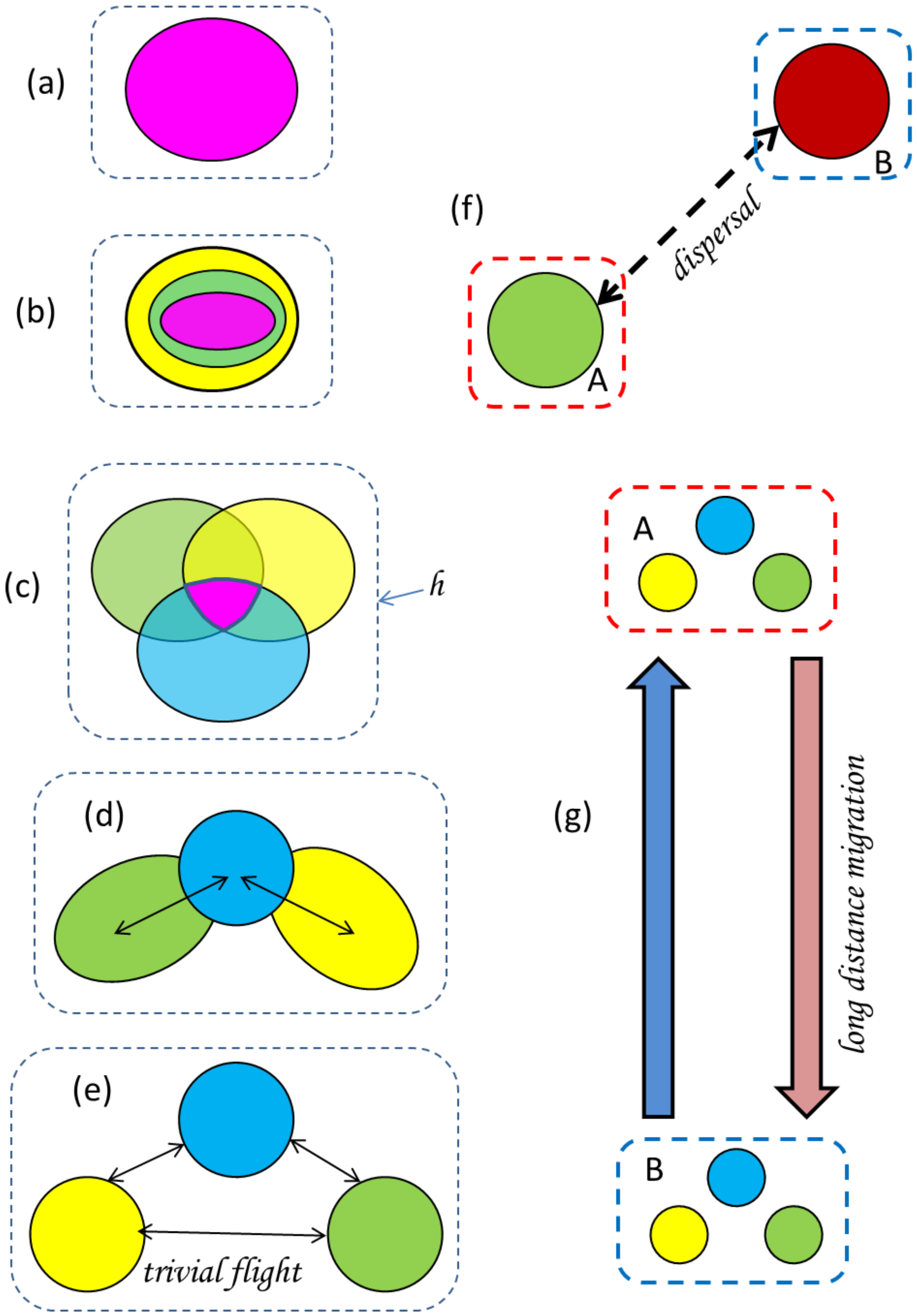


Figure 2. The resource-based habitat. Basic variants of resource disposition are illustrated, each diagram illustrating just one spatial relationship between resources: (a) Equivalence and equality of resources comprising a habitat. (b) Nested intersection (equivalence, intersection and union) of resources comprising a habitat (c) Intersection and union of resources comprising a habitat. (d) Contiguous union of resources making up a habitat. (e) Disjointed union of resources linked by ‘trivial’ (daily resource-seeking) flights making up a habitat. (f) Disjointed non-union (likelihood that resource spaces not used by same individuals in succeeding years) of resources linked by seasonal dispersal (movement across distinct biotopes), each part comprising a seasonal habitat. (g) Disjointed non-union of resources linked by seasonal long distance migration (movement between biomes and over large water bodies), each part comprising a seasonal habitat. Field examples of habitats will have combinations of multiple resource disposition. A maximum of three resources are illustrated in each diagram: nectar resource (blue), larval resource (green), roost sites (yellow); overwintering sites (brown); habitat boundary (*h*, pecked rounded squares, red summer and blue winter; habitat core purple).

exclude species from biodiversity assessments of sites and regions that are: (i) not permanent residents or (ii) do not overwinter or breed. It should be noted that all RBH definitions stretch the concept beyond habitat as a local dwelling place (a human analogy, often insubstantial as it fails to take in lifetime movements for resource acquisition), often far beyond, to the full set of conditions and resources required to maintain an interacting cohort of individuals over some fraction of Earth space for a minimum unit ≥1 organism generation time.

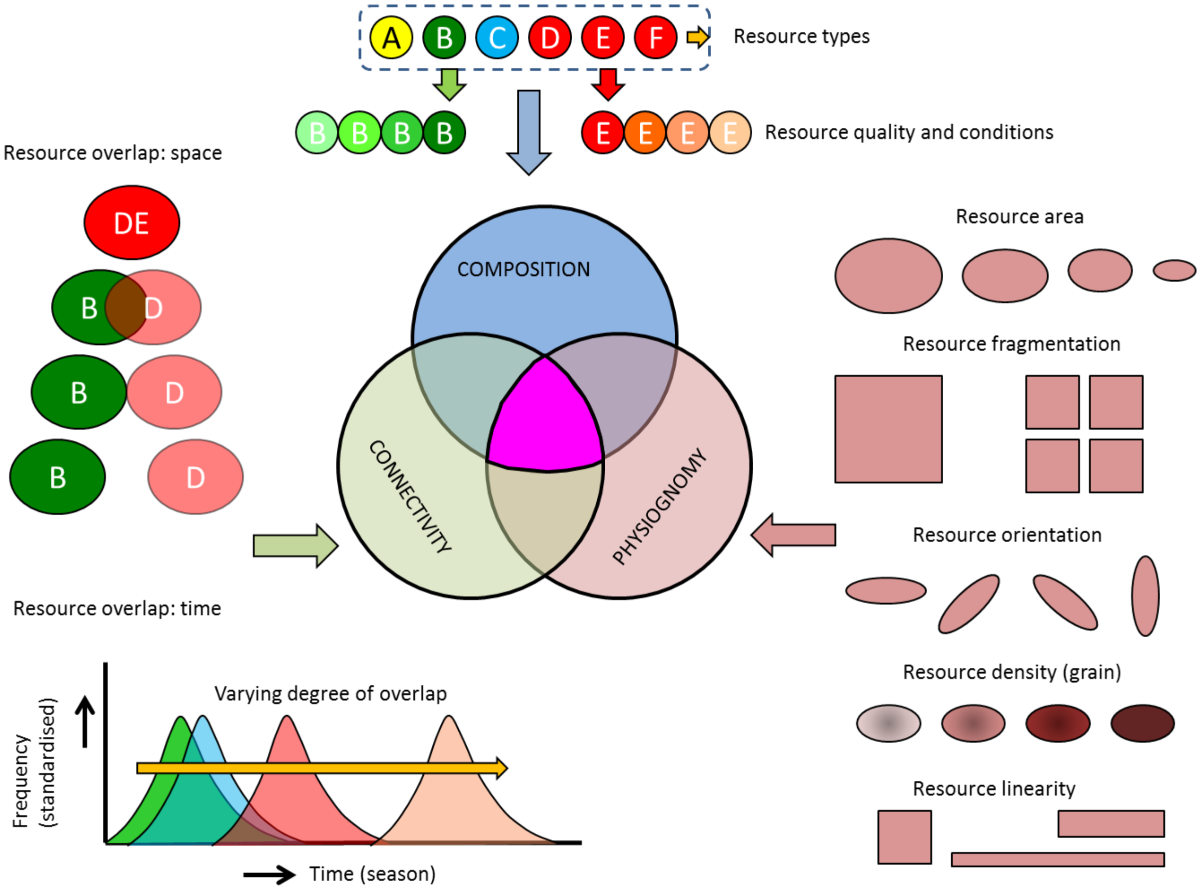


Figure 3. Basic dimensionless model for habitat *suitability* based on three variables: resource composition, physiognomy and connectivity (Dennis *et al.* 2006). Each of these variables is described by a number of parameters. The purple zone where the three intersect can be regarded as the collection of conditions for which the functional habitat becomes increasingly maximised, although in fact the intersection of maximum values for the basic variables could impair function if it also increases competition and exposure to enemies. The functional habitat (resources all accessible to most individuals) depends on individual mobility in each species. Turlure (2009: 239) used a similar set of variables describing suitability of habitats: composition, availability and configuration; availability depends on individual resource type composition (subsets), physiognomy and connectivity, and configuration is described by resource physiognomy and connectivity.

The RBH, or any other, habitat definition is most realistically visualised when considered from the vantage of single individuals. In fact, it becomes vital to consider habitat at the level of the individual, since only then does it become apparent that habitat is a variable, and how variable, and not a constant. It undermines the erroneous assertion that change over a landscape is not to varying species' habitat demands – treated by some as a constant – but variation in, and the condition of, resources. A habitat comprises two kinds of resources (consumables and utilities) and suitable conditions in which to exploit them, thus for individuals to reproduce, develop and survive. A habitat can then be traced through the lifetime track and resource use of individuals forming a local population (or cohort of interacting individuals if not confined to a compact site). For a phytophagous insect such as a butterfly, this track is determined by movements at two spatial scales, by the larva and adult, small steps from <1 cm to a few metres by the former, and distances potentially spanning centimetres to many kilometres (>1000 km at extremes) by the latter. This life time track of an individual is actually an intricate, complex web of reciprocal movements between resources outlets, where moves are made on a variety of different temporal and spatial scales (Fig. 4). As such, the consecutive movements of any one individual will bring it into contact with different resource items varying in size, density, age, structure, condition, taxonomy, and in other ways. This is certain for several reasons: for instance, (i) the variability (genetic and physical owing to sex, age and timing of appearance) in selectivity (electivity) of individuals (Wiklund 1975, 1981; Singer & Lee 2000); (ii) competition for resource items; and (iii) stochasticity, random contacts with different resource items, all of which vary in space-time (e.g., egg laying in *Anthocharis cardamines*; Dennis 1982, 1983) and whose condition and context impose pressures on the individual. From this vantage one thing is certain: no two individuals will adopt an identical life time track (Schoonhoven 1977) other than individuals of the same clutch laid on the same plant and whose life cycles are prematurely terminated. By simple observation, then, the resource exploitation of every individual will differ (vary) and thus habitat measured from a sample of individuals will be a variable, with each resource attribute being described by a measure of variation (or by frequencies of categorical variables) as well as one of central tendency (e.g. host plant use). When outlying populations of a species become extinct, some portion of that variability is lost.

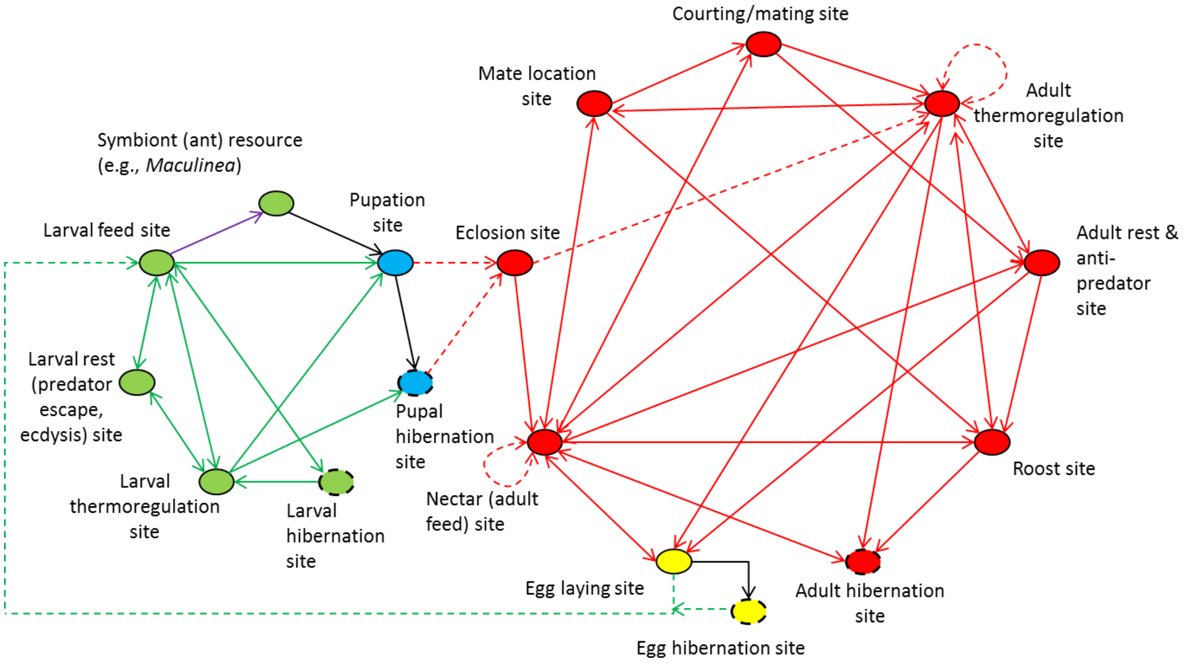


Figure 4. Life-time resource track between resource types for a single individual of a butterfly species. Movements are limited to the larval (green arrows) and adult (red arrows) stage, with one British species conveyed (transported) by a symbiont ant (purple arrow). Most adult movements are by flight, though some involve walking as well as/instead of flight (pecked line). Resource types distinguished for stages (egg, yellow; larva, green; pupa blue; adult red). Depending on species, hibernation stage could be any stage (pecked oval) with black arrow indicating no movement from previous site.

At the heart of the RBH concept is the web of interactions that each individual establishes with the ground environment showing resource use, paths adopted and conditions used and avoided. A local population of individuals would produce a highly complex nexus and this variation can be sampled as any other life history or ecological attribute by taking a random collection of individuals over space-time in the field. What should this sample contain? For a phytophagous insect such as a butterfly species, it would need to include a sufficiently large sample of resource use and conditions experienced and avoided for (i) both sexes, (ii) through different life history stages, (iii) including actual paths of movement, (iv) through environmental cycles (i.e., diurnal, seasonal, brood) impinging on the life cycle. Such complexity for habitat assessment is currently impossible to map for any one individual, let alone for an adequate sample of individuals. Even so, it may soon be feasible; accurate tracking of individual movements is fast advancing, especially for birds using transmitters and satellite telemetry (Fiedler 2009; Meyburg & Meyburg 2009; Strandberg *et al.* 2010; Klaassen *et al.* 2014); in butterflies, the best achieved to date is unique mark tags on wings of adults which give linear moves between release and recapture points, and individual surveys on the location and behaviour of different stages (Pollard & Yates 1993; Dennis 2004). But, techniques are likely to advance to provide continuous tracks of individual insects' movements; a start has been made (e.g., butterflies, Cant *et al.* 2005; Niitepold *et al.* 2009; bumblebees, Osborne *et al.* 1999; Hagen *et al.* 2011; wasps, Sumner *et al.* 2007).

What makes for habitat integration?

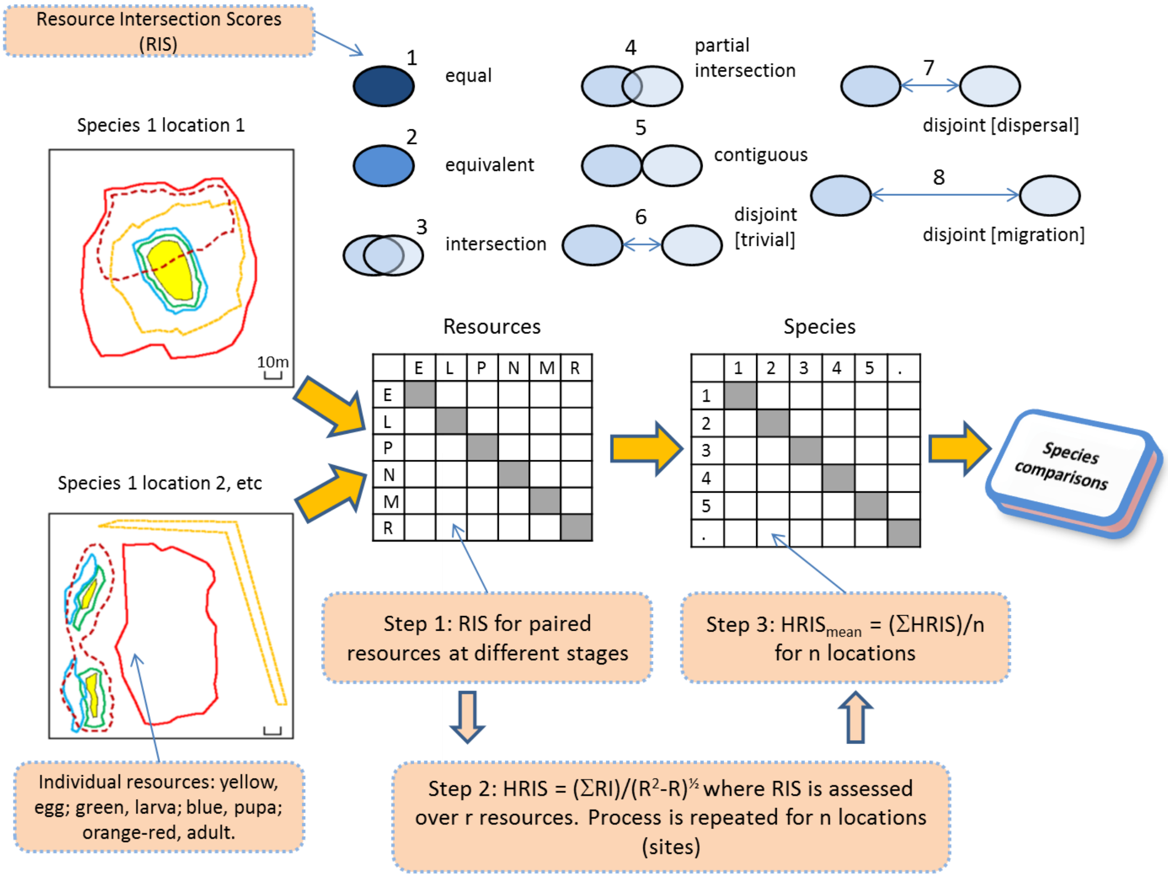
Although similar suites (types) of resources and conditions make up organisms' habitats there is clearly enormous variation in the manner in which they are integrated in different species (Dennis *et al.* 2003; Dennis 2010): at one extreme species may typically have all their resources on one site (e.g., concentrated habitat of lycaenid *Cupido minimus*) (Morton 1985); at the other extreme, resources required during different seasons and stages of the life cycle can be in different biotopes (e.g., dispersed habitat of pierid *Gonepteryx rhamni*, Pollard & Hall 1980; scrub and woodland aestivation in the Mediterranean of the grass feeding *Maniola jurtina*, Scali 1971) or in different biomes on different land masses (e.g., Nymphalidae such as *Danaus plexippus* and *Vanessa cardui*, Brower *et al.* 1977; Calvert & Brower 1986; Stefanescu *et al.* 2013); the latter example may be unusual among butterflies and other insects, but is common among birds which spend different seasons in different biomes, different biogeographical regions and/or on different continents (Berthold *et al.* 2001; Newton 2008; Ruth *et al.* 2012).

Two basic groups of factors determine integration of habitat components: (i) spatial arrangement of suitable conditions and resources, and (ii) individual mobility (Figs. 2 and 4). Integration is advanced by space-time intersection and contiguous union (overlap, coincidence, seriation) of suitable resources and living conditions, thus of parameters for resource composition and physiognomy, particularly by the intersection of consecutively used resources (Fig. 2; Dennis & Shreeve 1996). However, integration depends fundamentally on the capacity for individual movement. For phytophagous insects such as Lepidoptera, owing to the limitations of larval movements, resources from egg to pupal stage need to be in close proximity, typically intersecting or contiguous, especially where such resources are used reciprocally as between larval feeding bouts, rest and ecdysis. In contrast, movements at the adult stage vary enormously among species, from adult life time movements of <50m to >1000km (Fig. 4). The key factors in resource integration (RBH identity) differ for species contrasting for movement capacity. For species with limited adult movement (dispersal) capacity, the key factor to integration is the spatio-temporal disposition of resources affecting early stages within sites; such species are also specialists, highly vulnerable to the condition of those resources. On the other hand, for those species capable of migrating over hundreds of kilometres, environmental (weather, airstream) conditions during long flights are of critical importance for successful inter-resource transit; such species typically select favourable airstreams at particular altitudes and when baulked are dependent on suitable refuelling (nectar) stops during passage (e.g., *Vanessa atalanta* and *V. cardui*; Baker 1978, 1984; Dennis 1993a; Alerstam *et al.* 2007). They may also depend on the integrity (condition, dimensions, persistence and predictability, thus sequential coincidence) of any key resource at destinations (e.g., enemy-free larval feeding zones for *Vanessa cardui*, Stefanescu *et al.* 2012; condition of fall migration fuelling stations and overwintering sites for *Danaus plexippus*, Calvert & Brower 1986; Brower *et al.* 2006; Barve *et al.* 2012; Pleasants & Oberhauser 2013).

The distinction between resource integration and habitat compaction

The traditional usage of the term habitat envisages resources as being compact, co-occurring within a single biotope and found at a single site. However, from the foregoing discussion on resource integration, it will be seen that there is a vast difference between resources being integrated and a compact habitat. Mobility ultimately delimits integration whereas resource intersection underpins habitat compaction (Fig. 5). Increased resource intersection ensures greater potential for a correspondence between biotope and the RBH. But resource intersection is not sufficient, in itself, to ensure the existence of a compact habitat: for that, resources should share the same space (sets of different resources individuated to spatial units must be equal or nested subsets); then, degree of compaction increases directly with resource density (i.e., compaction increases as the so-called ‘trivial’ non-resource space between resource elements is eliminated). However, resource elements may be spread out widely so that even though substantial intersection occurs, RBH bounds may be expansive, resource density low and resources permeated with non-resource space (trivial spaces or internal matrix). Moreover, importantly, various resource types may be supplemented (same resource) or complemented (novel resource) by additional outlets (Dennis 2010) which, at one and the same time, may enhance resource integration but also may extend the habitat into a wide array of additional biotopes, rendering it less compact. In this way, an atom provides a useful analogy for habitat: the spaces between both resource items and resource types may be simulated by that between distinct atomic particles; thus, just as electrons remain in an uncertain, non-deterministic and probabilistic orbital around the nucleus so do resources and conditions around zones of primary consumer resources. Implications hold for habitat limits and the internal matrix among resource items. First, reference is often made to the habitat boundary, but this can be illusive to locate in practice. Second, much as atomic mass can be condensed by an escalating force of gravity, so too can resources in a habitat become progressively denser with increasing concentration (convergence and overlap) of favourable environmental parameters affecting resource distributions. But, one can get carried away with analogies and it is best not to press them too far!

From the above, it becomes evident that the relationships (degree of overlap, equality, nestedness) between a species’ resource items in a landscape provide a useful basis for developing an index of habitat compaction (Dennis & Shreeve 1996). For instance, resource items can be identified and mapped to real space compartments (i.e., grid or small vector land units) and their overlap quantified or categorised. However, not all resource outlets for a species may be easily mapped or for that matter measured and quantified. Even so, species’ biology is massively affected by relative resource dispositions, and that is something that can be assessed without sophisticated measurement or quantitative survey. For instance, in a simple classification of different species, the habitat may be described (qualified, scored) in broad terms of the physical relationship among resources typically found at most locations (i.e., a sample of sites; from existing autecological surveys). Different resource categories (consumables, utilities, conditions) may: (i) include the same or different items (equality or not), and (ii) may intersect, be contiguous or be disjoint, the space for each resource being described by an envelope (convex polygon) around each resource type. The degree of feasible intersection is perhaps most appropriately scaled by typical movements: whether by trivial moves (walk, short flight between resource items), dispersal (abandonment of production resource site) or migration (over water); a simple example is presented in Fig. 5.



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.						▨

Individual resources: yellow, egg; green, larva; blue, pupa; orange-red, adult.

Step 1: RIS for paired resources at different stages

Step 2: HRIS = (ΣRI)/(R^2-R)^{½} where RIS is assessed over r resources. Process is repeated for n locations (sites)

Step 3: $HRIS_{mean}$ = (ΣHRIS)/n for n locations

Figure 5. Assessment of species' habitat resource intersection based on the mean sum of resource intersection scores (RIS) over samples of sites. RISs obtained for pairs of consecutively used resources (8 point scale) can be summed over sites and the average taken across pairs of resources providing a matrix of mean habitat resource intersection scores (HRIS) for species. For RIS 8 and 9, there is little likelihood of an individual (or its progeny) visiting the same site in a following year. Letter codes for resource use in this simplified example: E egg, L larva, P pupa, N adult nectar, M adult mate location, R adult roosting.

Generalism-specialism, resource integration and habitat compaction

Resource integration and habitat compaction are likely to have a close relationship with species' resource breadth, the number of similar or distinct outlets used by species. This is evident from what was stated above concerning the impact of supplementary and complementary resources on resource integration. Resource breadth may be measured along a sliding scale of specialism-generalism (Dapporto & Dennis 2013); as different resources are involved, it is a complex multi-dimensional concept, though it can be simplified by focusing on key resources, such as larval host plants (Dennis 2010: 19).

The basic expectation is that specialists will tend to have all their resources contained within a single, broad biotope patch and have a recognisable, compact habitat. Generalists, on the other hand will tend to have their resources spread over numerous biotopes, and over different parts of the same biotope (e.g., damper versus wetter, lighter versus shadier) and to have indistinct habitat bounds; the resource-structural differences between such specialists and generalists are mirrored in terminology for populations, referred to as ‘closed’ and ‘open’ population structures respectively (Pollard & Yates 1993). These patterns clearly exist (Fagan *et al.* 1999; Dennis *et al.* 2013); some notable specialists recognise biotope margins as intrinsic boundaries to their habitats (e.g., *Euphydryas editha*, Ehrlich 1961; Brussard *et al.* 1974), whereas a number of extreme generalists opportunistically exploit resources as far apart as different continents (e.g., *Vanessa cardui*; Stefanescu *et al*. 2012, 2013). The contrast in habitat structure and population spatial dynamics between specialist and generalist is likely driven by the impact of resource distributions and environmental conditions on life histories and movement patterns. Widely scattered resources, especially if varied and abundant, will tend to select for more extensive movements that, in turn, successfully integrate disparate resources. On the other hand, scarce but closely intersecting resources will discourage (select against) dispersal and enhance specialisation and habitat compaction, including the use of visual and other cues for habitat bounds (Fig. 6). But there are exceptions, where aspects of specialism may not necessarily lead to habitat compaction and where an open habitat structure may not be associated with host plant generalism. For example, in the former case, specialism on host plant parts (i.e., young growth), rather than on a host species, may present access to a wide range of plant species; in *Pieris napi* this leads to open habitat structures (Dennis 1985), whereas in *Plebejus argus*, owing to ant associations it does not (Thomas 1985). In the latter case (where an open habitat structure may not be associated with host plant generalism), abundance, temporal availability and ubiquity of a single host plant can substitute for a wide range of host plant species to ensure population integration (e.g., *Aglais urticae* on *Urtica dioica*; Vandewoestijne *et al.* 2004). Thus, the relationship between specialism/generalism, resource integration and habitat compaction, depends on resource variation (e.g., host plant and nectar species used), but also on abundance, ubiquity, finer aspects of resource exploitation (i.e., use of buds, flowers, pods, leaves, shoots, roots), space-time availability, as well as other constraints (i.e., symbionts). The pattern of habitat, dispersed or compacted, depends on the selection for individual movement capacity, movements between different resources and resource items as well as movements between habitat patches, the latter driven by habitat lifespan (i.e., driven by vegetation succession). Although some species stick closely to confined overlapping resource bounds, most species recognise and respond to resource rather than to a human abstraction, habitat. There is a distinction in the view of habitat and resource by human observer and target organism. To adapt the Rumsfeldian logic to the two subject case, a species’ resource is a known known - we know that they know one when they sense it - compared to which a habitat is a known unknown, that is, we know it exists but it is a moot point whether our target species has that insight: some evidently do, but do all?

These observations suggest that there will be a significant relationship between a species’ position on the specialism-generalism resource gradient and its movement capacity; also, that species with compact habitats should occur towards one extreme (specialism/weak movement capacity) of the relationship and those with indistinct (highly disjoint) habitat structures towards the other (generalism/strong movement capacity). This is basically what is found to be the case (Dapporto & Dennis 2013); species are distributed along a regression line describing colonisation ability (describing specialism/generalism and resource availability; Colonfac) and movement capacity (Migrfac) (R^2 = 28%, n = 54 species; R^2 = 31%, n = 60 species including long distance migrants). Species with widely disseminated

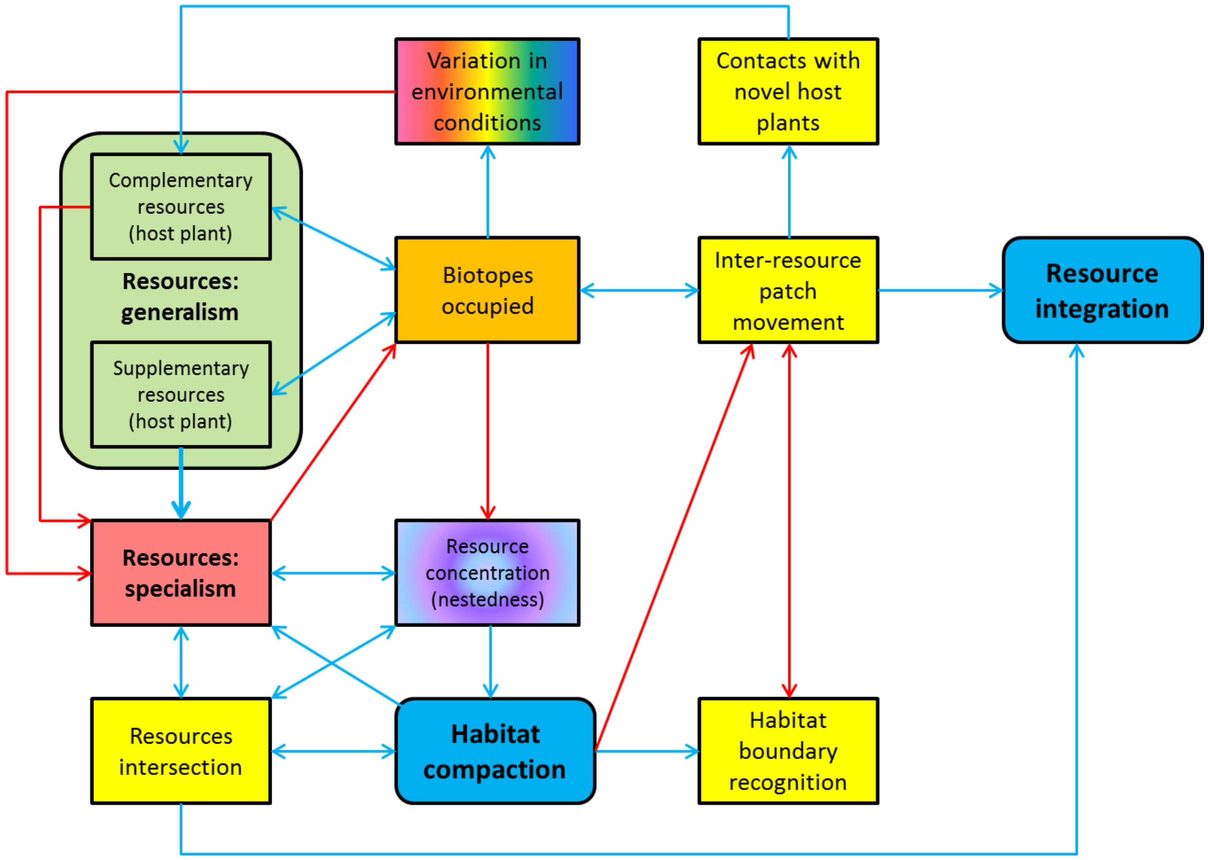

Figure 6. Basic factors leading to resource integration and compaction. Resource integration depends as much on inter-patch movements as on resource intersection, whereas resource (habitat) compaction is very much dependent on resource intersection and nestedness. Resource specialism and generalism, via resource supplementarity and complementarity, are key to driving these two outcomes. Blue arrows, positive relationships; red arrows, negative relationships.

resources (diffuse habitats) have both high migration capacity and colonisation ability (e.g., *Vanessa* species, *Pieris* species), whereas those with closely intersecting (compact) resources tend to have low migration capacity, particularly if colonisation ability is also low (e.g., *Maculinea arion*, *Polyommatus bellargus*); a faster turnover of resources through vegetation succession requires greater ability for movement (e.g., *Thymelicus sylvestris*, *Melanargia galathea*) (Fig. 7).

The resource-based habitat: implications for conservation biology

The relevance of the resource-based habitat concept to conservation biology (maintaining biodiversity) has three related aspects, namely: (i) relationships of species' populations (single and multiple species [communities]) to site (often called habitat) parameters (biotopes, vegetation types, substrates, topography etc); (ii) accounting for variation in population growth and shrinkage; and, (iii) accounting for variation in expansion and contraction of species' distributions and ranges. The latter engages processes that lift species out of threat (expansion) or drive them to extinction (contraction) respectively. The composition, physiognomy and integration of a species' resources can impact on all these aspects of conservation biology (Fig. 3; Dennis *et al.* 2007; Dennis 2010). In particular, substantial differences in species' resources are described by the degree of resource specialism/generalism; this has direct (i.e., resource-driven; e.g., degree of intersection) and indirect (i.e., individual response; e.g., movement capacity) consequences for resource availability and connectivity, thus for the degree of resource integration and habitat compaction, all of which can profoundly affect a species' status.

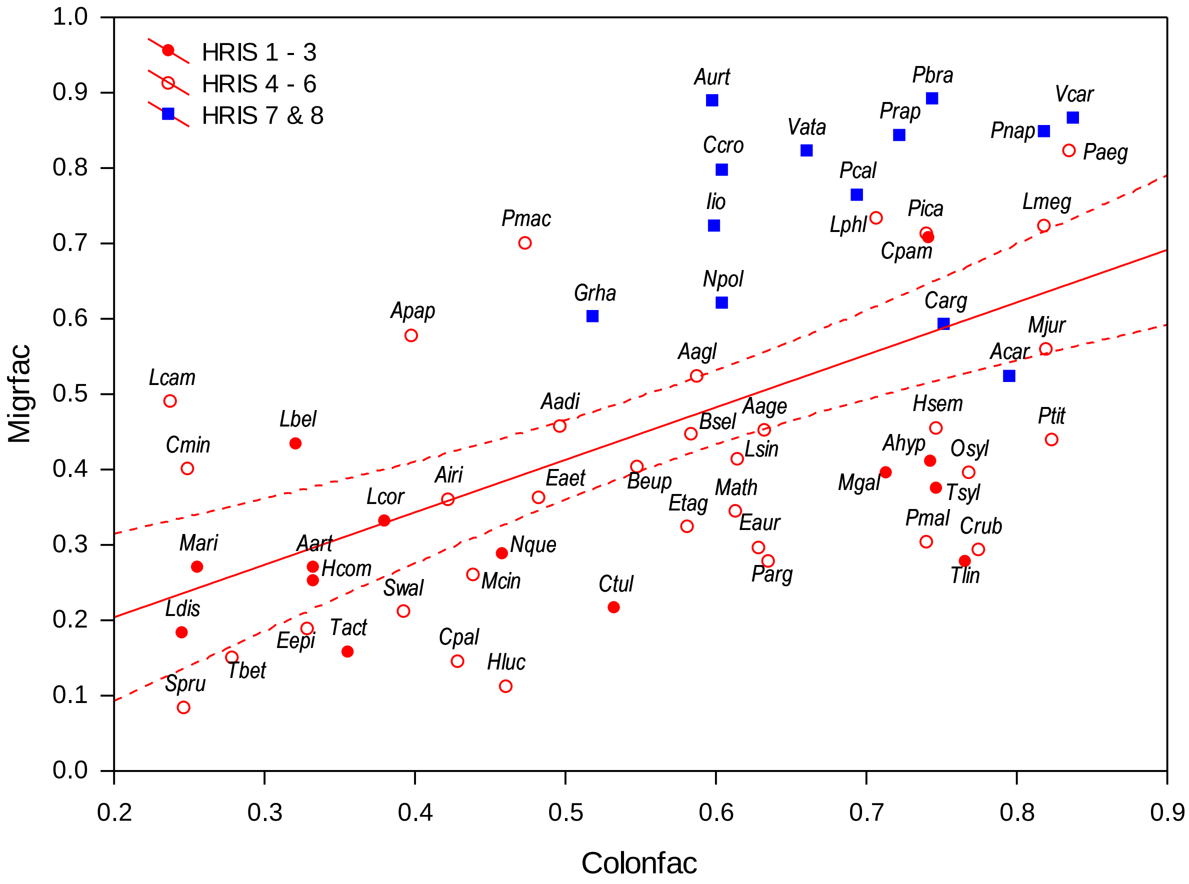

Figure 7. Relationship of colonisation ability and migration capacity in British butterflies. Colonfac (colonisation ability) is based on 10 variables and Migrfac (migration capacity) on four variables (see Dapporto & Dennis 2013 for original data and supplementary Table S1 and S2 for values and species codes). Points (species) are distinguished for habitat resource intersection scores (HRIS; see Fig. 5); those for which scores are uncertain are given intermediate codes (4 – 6).

Site biotopes and the resource-based habitat; inferences for populations and communities

The application of the term habitat for biotope in conservation, especially in insect conservation, largely occurs because of the tendency of insect conservationists to apply one or two basic conservation 'philosophies'. These two distinct paths for conservation strategy are: (i) a species-conservation oriented approach, and (ii) a biotope/habitat-conservation oriented approach (for full discussions of both approaches, the reader is directed to New (2012a). In the former case, as with many vertebrates, there is usually sufficient species-specific information to generate a species-specific action plan. On the other hand, invertebrate conservationists are usually confronted not only with inadequate species-specific data (particularly Hutchinsonian Shortfall [i.e., life history and resource data]; Cardoso *et al.* 2011), but a plethora of species all needing attention. Exceptions are a few flagship

Supplementary Table S1. Migration capacity (Migrfac) and Colonisation ability (Colonfac) scores for British butterfly species. See Table S2.

Species	**Code**	**Migrfac**	**Colonfac**
Carterocephalus palaemon	Cpal	0.1460	0.4276
Thymelicus sylvestris	Tsyl	0.3761	0.7457
Thymelicus lineola	Tlin	0.2790	0.7661
Thymelicus acteon	Tact	0.1590	0.3548
Hesperia comma	Hcom	0.2527	0.3320
Ochlodes sylvanus	Osyl	0.3962	0.7682
Erynnis tages	Etag	0.3238	0.5811
Pyrgus malvae	Pmal	0.3041	0.7400
Papilio machaon	Pmac	0.7012	0.4735
Leptidea sinapis	Lsin	0.4138	0.6145
Colias croceus	Ccro	0.7993	0.6039
Gonepteryx rhamni	Grha	0.6024	0.5186
Pieris brassicae	Pbra	0.8916	0.7432
Pieris rapae	Prap	0.8441	0.7215
Pieris napi	Pnap	0.8490	0.8183
Anthocharis cardamines	Acar	0.5248	0.7950
Callophrys rubi	Crub	0.2935	0.7745
Thecla betulae	Tbet	0.1504	0.2777
Neozephyrus quercus	Nque	0.2892	0.4579
Satyrium w-album	Swal	0.2113	0.3919
Satyrium pruni	Spru	0.0843	0.2462
Lycaena phlaeas	Lphl	0.7343	0.7071
Lycaena dispar	Ldis	0.1838	0.2449
Cupido minimus	Cmin	0.4013	0.2481
Plebejus argus	Parg	0.2784	0.6350
Aricia agestis	Aage	0.4529	0.6317
Aricia artaxerxes	Aart	0.2701	0.3327
Polyommatus icarus	Pica	0.7146	0.7395
Lysandra coridon	Lcor	0.3328	0.3793
Lysandra bellargus	Lbel	0.4357	0.3207
Celastrina argiolus	Carg	0.5924	0.7511
Maculinea arion	Mari	0.2711	0.2548
Hamearis lucina	Hluc	0.1134	0.4600
Limenitis camilla	Lcam	0.4907	0.2377
Aapatura iris	Airi	0.3611	0.4220
Vanessa atalanta	Vata	0.8228	0.6599
Vanessa cardui	Vcar	0.8670	0.8377
Aglais urticae	Aurt	0.8896	0.5969
Nymphalis polychloros	Npol	0.6215	0.6033
Inachis io	Iio	0.7243	0.5991
Polygonia c-album	Pcal	0.7655	0.6942
Boloria selene	Bsel	0.4477	0.5836
Boloria euphrosyne	Beup	0.4044	0.5479
Argynnis adippe	Aadi	0.4588	0.4957
Argynnis aglaja	Aagl	0.5247	0.5868
Argynnis paphia	Apap	0.5793	0.3978
Euphydryas aurinia	Eaur	0.2980	0.6282
Melitaea cinxia	Mcin	0.2616	0.4388
Mellicta athalia	Math	0.3444	0.6125
Pararge aegeria	Paeg	0.8233	0.8350
Lasiommata megera	Lmeg	0.7240	0.8184
Erebia epiphron	Eepi	0.1901	0.3276
Erebia aethiops	Eaet	0.3620	0.4815
Melanargia galathea	Mgal	0.3975	0.7131

Hipparchia semele	Hsem	0.4561	0.7467
Pyronia tithonus	Ptit	0.4394	0.8235
Maniola jurtina	Mjur	0.5605	0.8188
Aphantopus hyperanthus	Ahyp	0.4116	0.7427
Coenonympha pamphilus	Cpam	0.7093	0.7405
Coenonympha tullia	Ctul	0.2163	0.5326

Species names after Dennis 2010

Supplementary Table S2. Variables included in colonisation ability (Colonfac) and migration capacity (Migrfac).

Variables
A. Resource variables (Colonfac, component based on 10 variables)
Number of biotopes exploited
Number of larval host plants used
Host plant abundance in natural vegetation classification categories
Niche breadth (mean of Ellenberg ranges for all larval host plants based on all criteria but salinity)
Larval host plant abundance taken over 8 biotopes
Larval host plant density (records/distribution cover)
Nectar plant specialism (residuals of weighted regression of Nectar sources on nectaring records)
Number of nectar sources exploited
Symbiosis with ants (inverted scale: 1–4 with 1 highly dependent on ants)
Number of utility resources (outlets) used by pupae and adults (excluding nectar plants)
B. Migration variables (Migrfac, component based on four variables)
Mobility index
Flight period
Wing span (mm)
Voltinism (maximum number of broods per year in region)

See Dapporto & Dennis 2013 for details of references

(charismatic) species. Inevitably, conservation falls back on the latter (biotope-based) approach, the idea being that preservation of a given biotope (typically referred to as habitat) will preserve the associated invertebrate community. However, habitat (as biotope) prioritisation is often based on the species found to occupy it, which generates circular reasoning: to preserve species, for which we have no adequate data, we decide to preserve their biotopes, but to select the biotopes we use the species (Fattorini, personal communication).

Yet, quite clearly, a biotope is not a species' habitat and this has consequences for all biotope-based comparisons and management decisions. It does not mean that all biotope-based comparisons and decisions (across space and over time) are wrong or unproductive. It is of great interest to make such biotope-based comparisons, *but* only as long as differences for populations (species i) or species (species i-j, k) are related to differences and changes for resources (composition, dimensions, condition, disposition etc) and environmental conditions (i.e., light, temperatures, humidity etc.) within sites. The same qualification exists for management decisions. There is, of course, no need to refer to such biotope comparisons as habitat comparisons, apart from that of using a more familiar term with greater advertising power. Nevertheless, to treat different sites having the same biotopes (however delineated), without firm evidence, as equivalent in resources and conditions is certainly wrong. This was a major failing of early metapopulation work; admittedly, in accepting that resources differ in condition at sites, theoretical treatment becomes greatly more complicated, less like physics, with less capacity for reliance of modelling on stochastic functions; but, it also becomes more realistic when resource components are considered. Biotope studies, of one or more sites, and of one or more species, may be static (taken at time t_i) or dynamic (taken at intervals of time $t_{1,..\ i..m}$) (e.g., Özden *et al.* 2008, Özden & Hodgson 2011; Oliver *et al.* 2012). Whatever the dimensions of study (viz., species, space, time, resource variables), researchers should be aware that resources vary for more attributes than biomass or area. For instance, resources vary as to type (various consumer and utility resources), multiplicity (supplementation, complementation), location within sites, fragmentation (separate units and spacing), spatial relationships with one another (intersecting, disjoint), condition (age, previous use, growth, stage, light exposure, etc.), chemistry (nutrient levels, toxins), matrix contexts, and in many other ways (Dennis 2010).

From these common sense observations, a number of principles have been identified linking butterfly populations to biotopes (Dennis 2010). It is blatantly obvious that population sizes of *different* species occupying the same site will differ, if only because their resources/conditions differ in so many ways. Detailed autecological surveys, antedating the preoccupation with metapopulations, also clearly demonstrated how population sizes vary, between and within sites (biotopes), for a *single* species in relationship to changing resource conditions within sites (Thomas 1984; Warren 1992). An, admittedly, trivial expectation follows: population sizes will tend to be similar when dimensions of a key consumer resource are largely equivalent and will usually differ with contrasting resource dimensions. However, less thought has been given to variation around this relationship, to circumstances where populations – for a single species – differ significantly more or less than expected for dimensions of a key resource. If this point has been rarely considered, then the reason is likely to be found in: (i) a limited focus on a subset of resources and/or limited attributes of a resource (i.e., biomass), (ii) inattention to site resource attributes (composition, physiognomy [which also locates sites within environmental contexts], connectivity), particularly integration and compaction, and (iii) difficulties of identifying and measuring resource parameters (Dennis 2010). Nevertheless, it is well substantiated that varied resource attributes, other than biomass, within a site (biotope) can be critical for resource exploitation; clear examples are the placement of resources in different heat/shade environments (e.g., *Euphydryas editha*, Weiss *et al.* 1988; *Lycaeides melissa*, Grundel *et al.* 1998; *Hamearis lucina*, Anthes *et al.* 2008), and the degree and nature of resource integration and compaction (i.e., affecting competition and predation levels, as well as resource conditions) (*Maculinea arion*, Elmes & Thomas 1992; Patricelli *et al.* 2011).

Thus, mismatches of population status with habitat (= biotope) dimensions (or a surrogate measure such as biomass of a key resource) could well relate to a failure to consider a wider set of resource parameters at sites, as well as environmental agents affecting condition and exploitation of resources. A prominent danger is the assumption that site conditions vary only in resource area (resource biomass) and isolation, and that changes within and between sites relate largely to these two factors and to the response of individuals to changing conditions external to sites (i.e., weather, climate, fragmentation, broad scale changes in landscape exploitation). Thus when, for instance, species are found to occupy significantly fewer or more habitats (= biotopes) over time in relationship to site area and isolation, this is expected to be caused by external conditions imposed on an organism's capacity for exploiting habitat resources rather than changes to the resources in the biotopes themselves; yet, the greater the time interval, the larger such latter changes are likely to be, if only because of systematic changes to sites (vegetation succession) and changes in site management regimes in response to economic demands (Hodgson *et al.* 2014). Any comparison of population changes across biotopes over time which does not assess changes (i.e., composition, physiognomy, connectivity) of key resources within sites, could well fail to account for an important potential source of variation. If populations are not related directly to known suitable resource distributions, then associations are based on speculation about actual habitat influences of sites; for instance, numbers of individuals observed within such biotopes could simply represent overflow (increased dispersal) from source (or complementary) biotopes rather than effective colonisation of marginal (sink) biotopes. It follows that any multi-species collation or comparison of population status for a key resource (i.e., larval host plant for butterflies) for biotopes (vegetation units) is deficient if it fails to consider the degree of resource integration and compaction for the different species, as well as different species' dispersal capacities, within the surrounding so-called matrix (Dennis 2004). This is certain as species differ for specialism/generalism for every resource outlet – consumables and utilities (Dennis 2010). Thus, polyphagous species vary in fidelity to different larval hosts and consequently vary in their attachment to biotopes with different hosts; they also disperse more than monophagous specialists and have larger habitat bounds (Dapporto & Dennis 2013). Typically, species depend more or less on other consumer (nectar flowers) and utility resources, all of which may skew relationships founded on what initially appears to be a simple comparison of species for their habitats (biotopes) or area of larval host plants (Dennis 2004; Hardy *et al.* 2007).

These observations for population differences among biotopes for species have knock-on effects for species' communities. The degree of specialism/generalism (composition) for different resources, as well as different structures (physiognomy, connectivity) associated with different resources (utility and consumer resources), will influence the observed fidelity of species to particular biotopes, however they are delineated; inevitably, variation in biotope fidelity will be found over space and time (e.g., *Pieris napi* has dispersed resources and open population structures in England, but compact resources and closed population structures in north Scotland; Dennis 1993b).

Implications of resource based habitat for the size and changes of populations

According to Caughley (1994) the focus of conservation biology has two main threads: (i) the small population paradigm and (ii) the declining population paradigm. The former deals with the effect of smallness on the persistence of a population and has substantial theoretical support; the second has been the mainstay of much autecological research and the production of a large array of unique insights into decline, but of little theoretical or integrated development. In this view, large population size and a growing population present the clement, reversed viewpoint of the same set of processes, enhancing rather than depleting biodiversity.

Theory developed around the small population paradigm is widely appreciated and incorporates the extinction vortex, where smallness leads to inbreeding, reduced heterozygosity, exposure of semi-lethal recessive alleles, which reduces fecundity and increases mortality and further drives populations to lower numbers. The longer numbers are held down the more likely is this outcome. Caughley discusses population 'smallness' from one vantage, that of numbers. But, there is another aspect to smallness of populations, spatial dimensions. From what has been said above about habitats, the greater the area over which a population's various resources are distributed, the less likely it is that they overlap and the greater the mobility required for population integration: small populations distributed over a larger area have the disadvantage of numbers and the advantage of greater area; resources spread over a larger area may disadvantage individuals which need to spend additional time in individual movement, but this would depend on the balance between distances, speed of movement and adult lifespan. One expects that as populations increase in size, the areas they occupy increase in dimensions. But mismatches do occur where, in a single taxon, large populations are contained in very small areas and, conversely, very small populations are spread over a very wide region. Theory is preoccupied with population smallness but often does not build into its algorithms spatial smallness, or spatial extent associated with small numbers. Spatial smallness (i.e., a physical or ecological island) can place a finite limit on growth, whereas small populations per se are not necessarily doomed to be always small or be subject to the extinction vortex.

Here, the RBH plays its part, as a species' resource structure (composition, physiognomy, and connectivity) determines its potential spatial dimensions and population integration, as well as potential for growth (or decline). Key to this process is a species' place on the multidimensional resource specialism/generalism continuum. Consequently, there is an opposite danger to that advanced by Caughley (1994) – namely, the lack of general theory. A tendency to develop theory purely on numbers of individuals (usually some version of the effective population size) will tend to overlook habitat (resources and conditions) attributes which are instrumental in supporting the population. Limiting such considerations to a key production resource (area/biomass of food) may also omit other important resource attributes that force down population numbers.

The declining population paradigm is faced with the opposite problem. Here there are many facts, data, and case studies, all of which have yet to be cemented into theory. However, there is a basis for theory in the RBH, particularly in the generalism/specialism of organisms' resource base and conditions. Caughley (1994) draws attention to Diamond's (1984, 1989) evil quartet of agents of decline: (i) overkill (typically by humans); (ii) habitat destruction and fragmentation; (iii) impact of introduced species (new predators, parasites and competitors); (iv) chain of extinction (loss of symbionts, host species [food] and niche construction engineers). In fact all these agents undermine either the resources or conditions of a target organism. In the case of overkill – overkill of vertebrates is matched in butterflies by over-collecting and pesticide application – this reflects on the failure of anti-predator and anti-toxin resource space, such as places to hide or evade predation. Habitat destruction or fragmentation – again whether by humans or by some environmental agent (fire, flood, weather phenomenon, climate etc) – directly impacts on a target organism's resource base or the conditions for existence. Impact of introduced species includes not just predators or parasites (as for overkill) but also competitors, which again have the effect of narrowing the resource base and breadth of conditions accessible to individuals of the population belonging to the target species. Finally, chain of extinction includes such organisms (i.e., keystone species), which once lost, again undermine the resource base or conditions. As all Diamond's agents can be interpreted as an impact on resources and conditions, the basis for any theory of population decline is surely flexibility in response (resistance) of the target organism: generalism versus specialism for specific resources and eurytropism versus stenotropism for specific conditions. The argument goes that it is the breadth of resource use and life history associations that insure against population decline and not some central (mean, modal) value; with increased variance in resource use and conditions experienced (life history plasticity), the greater potential for population growth and less chance of population decline.

However, developing theory on flexibility or generalism/specialism is not a simple matter. Species are rarely generalists or specialists in all resource attributes, and may be flexible in response to some environmental agents but not to others. Furthermore, there will be species with narrow resources and conditions that will do better in specific circumstances. But, globally, organisms flexible in resource use and life history should have the greatest chance to combat agents of decline. Theory for population decline thus has a basis in elements of the RBH. Any algorithm will need to take into consideration the wide array of attributes of resources and conditions and weight them according to their significance in persisting at sites. How far do studies on population and distribution changes support notions of complexity in response to agents in inducing changes? For arthropods, a lengthy preoccupation on within site population dynamics (steady states, fluctuations) and potential causes (density dependence/independence), was followed by a focus on regional population studies, particularly spatio-temporal autocorrelation in population changes across sites for one or more species (Pollard 1991; Pollard *et al.* 1995). During the last two decades, as databases on organisms' distributions and populations have grown, and environmental threats have become prominent, interest has shifted to contrasting aspects (losses, gains) of populations and species. First, different aspects (population changes or species' distributions/ranges) were dealt with in separate studies (metapopulations, Thomas & Hanski 1997; distributions and ranges; Hill *et al.* 2003); then, composite studies have compared changes at contrasting range boundaries (northern and southern margins) in relationship to distinct phenomena and different processes (i.e., climate change, habitat fragmentation) (Parmesan *et al.* 1999; Warren *et al.* 2001). Subsequently, contrasting and counterintuitive findings have been disclosed for different range margins (cf., projections of climatic niches to future climatic scenarios in Europe [Settele *et al.* 2008] with direct observations [e.g., Catalonia versus Central and Northern Europe, Devictor *et al.* 2012]).

More recently, it has been shown that a mix of population changes (i.e., stability, decline and growth), and spatial changes (i.e., shifts in centroids, shrinkage and expansion), can occur simultaneously in the same region for the same species. The realisation is growing that the potential permutations of change across species can be numerous (Hardy *et al.* 2014) and the consequences for species' communities highly complex. The interest was on common response; now there is greater emphasis on distinct classes of responses or counterintuitive responses. The unique component for populations and their site resources is accounted for in the 'unexplained' variance ($1-R^2$) from assessments of spatio-temporal autocorrelation of changes at different sites (Devictor *et al.* 2012; Carvalheiro *et al.* 2013; Davey *et al.* 2013). It is clear that climate change can create new 'habitats' for butterflies in areas (biotopes) that were formerly unsuitable – as habitat is a variable, changes in habitat are to be expected. It is also clear that species can cope better than expected with global warming at southern margins (northern hemisphere), very likely through changes to the integration of different resources within distinct biotopes (i.e., profiting from shaded areas offered by shrubs and wooded areas, shifts in phenology and host plant preference etc.). For example, researches carried out by out of us (LD) have revealed that recent distributions of butterfly species in Tunisia and Sicily have remained substantially unchanged when compared to faunistic data available for the last 30-40 years.

From a RBH viewpoint such complex changes for different species at the same sites and different sites are not surprising. Even at small regional scales changes induced by different elements of climate, land use and land management, to species in different locations, are likely to impinge in contrasting ways on the individuals at those locations. Moreover, when a region (multi-species population patchwork) is subjected to the same changes in conditions, populations of the same or different species may respond very differently to changes experienced (Parmesan *et al.* 1999). This may occur because: (i) different populations of the same species, as of different species, have different local profiles (composition, physiognomy and connectivity) of resources and conditions (Dennis 2010); (ii) individuals in different populations differ in plasticity and variability in resource exploitation and sensitivity (life history tolerances) to conditions (Relyea 2002; Daza-Bustamante *et al.*

2002; Amarillo-Suarez & Fox 2006; Liefting & Ellers 2008, 2009; Daniels *et al.* 2012; Johansson & Richter-Boix 2013). As sites are never exactly equivalent for resources and conditions, though biotopes may appear to be so or treated as such, populations occupying them have potential to change differently in relationship to changing thresholds in resources and conditions, and in the ability of individuals in those local populations to contend with them. This is apparent in metapopulation studies when resource conditions of patches are accounted along with patch area and patch isolation, the usual parameters dictating population status (e.g., *Coenonympha tullia*; Dennis & Eales 1997, 1999; Thomas *et al.* 2001).

Resource-based habitat: speciation and species' extinction

It is but a small step from determining the part played by the RBH in declining and expanding populations to the impact on species' extinctions and speciation. The part played by habitat resources in both these processes has recently been reviewed (Dennis *et al.* 2011); it was argued that generalist species – compared to specialist species – are not only more likely to withstand population losses, ultimately extinction, but also have a higher probability of furnishing speciation through the eventual isolation of more widely spread populations based on distinct resources and adapted to different conditions. In this process, generalists have the greater opportunity of generating new species, than do specialists, if only because generalists present both a greater potential (number of spatial/adaptive outlets) for survival than specialists, greater plasticity to changes in populations than specialists (Magi *et al.* 2011; Svanback & Schluter 2012; Griffith & Sultan 2012), and ultimately of generating (establishing) new specialists which become distinct at species level. It was shown that a circular pathway could well be involved (Dennis *et al.* 2011; Fig. 8) in which generalism enables regional specialism. This process was first suggested by the shifting balance theory (Wright 1932, 1982) and can represent a basis for emergence of new species or changes in any natural history trait (Mallet 2010; Dennis *et al.* 2011). As a key part of this process, increasingly suitable conditions for colonising new biotopes (different resource contexts), such as climatic changes, could lead to adaptive radiation based on ecological fitting (via phenotypic plasticity and novel phenotypic responses, exaptations, resource use mistakes; Janzen 1985; Agosta *et al.* 2010; Nylin & Janz 2009) and host range use, thus increased variability in resources and conditions (variability in RBH), in effect another round of generalism (oscillation hypothesis: Janz & Nylin 2008; Nylin *et al.* 2014). Apart from true generalists occupying phylogenetically unrelated hosts, faux generalism (specialists specialised on a phylogenetically widespread resource) and faux specialism (generalists restricted to single/few resources by ecological conditions) would also enhance this process. A key feature of the process has been observed in morphological changes (novel variation) at expanding range margins (e.g., *Zizeeria maha*, Otaki *et al.* 2010; Buckley *et al.* 2010). It is likely that generalism – in the instance of phytophagous species, polyphagy (e.g. Nymphalidae) – is a transient phase overtaken rapidly by specialisation (Nylin & Janz 2009; Nylin *et al.* 2014).

Extinction has two routes, outright termination of a taxon (phylogenetic loss) and evolution into a new taxon (anagenesis and cladogenesis) (phylogenetic transformation). An interesting distinction between generalists and specialists is argued to prevail in their tendency to follow these pathways to extinction. Extinction of specialists will tend to involve the outright termination of a clade unless environmental changes and ecological fitting presents opportunities for ecological escape. On the other hand, in the case of generalists, 'extinction' is more likely to result in the production of daughter specialists (eventually new species) rather than outright extinction of the entire clade. In short, generalists – compared with specialists - have more opportunities to become extinct via evolution than outright termination.

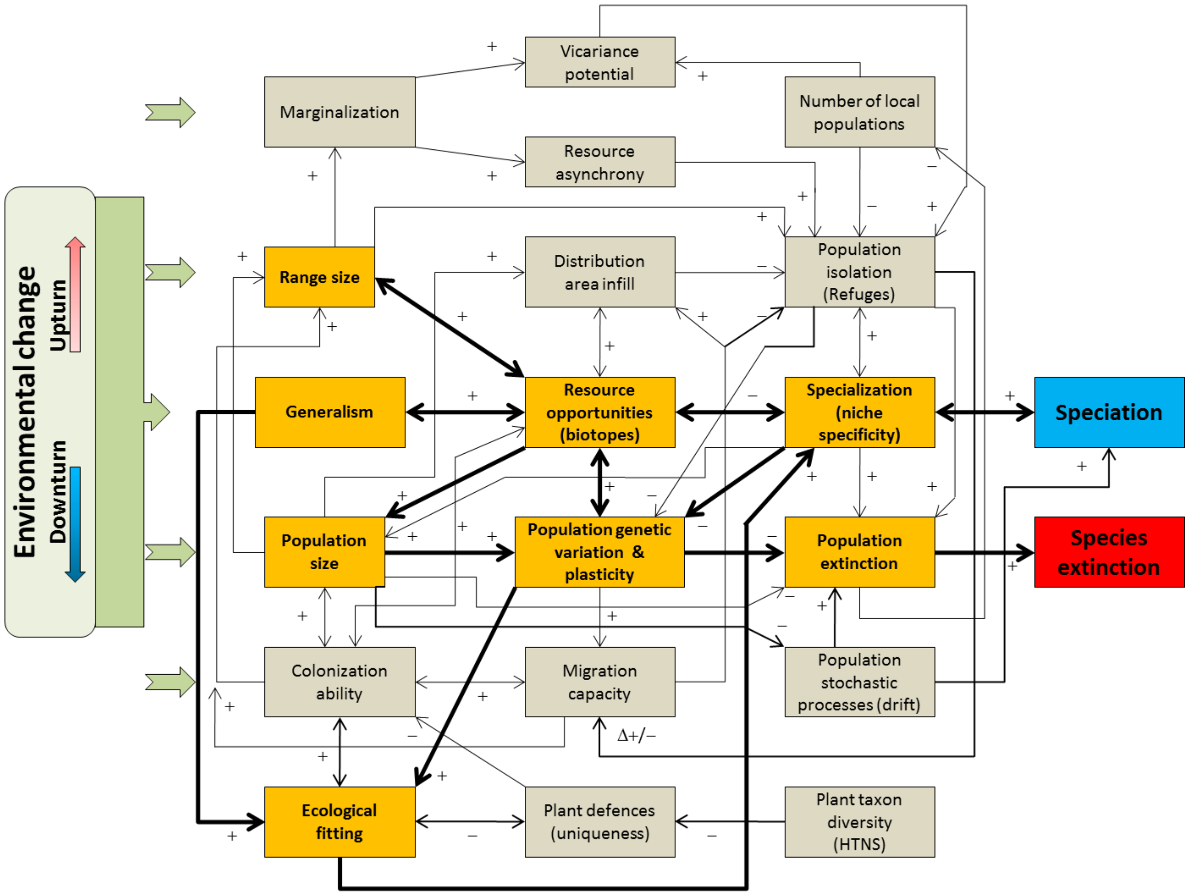

Figure 8. The influence of host specialism-generalism in phytophagous insects (butterflies) on speciation and extinction. Orange shaded boxes and bolder links highlight just two of the integrated effects of generalism in the model, resistance to extinction, and generation of inter-population variability, the path to speciation. The full model envisages a burgeoning of generalism followed by specialization, triggered by oscillations in environmental conditions (typically abiotic fluctuations/cycles, particularly climate; i.e. warmer/colder, wetter/drier) over millennia and geological time, with each cycle uniquely influencing range changes and abundances in different taxa. Upturns describe conditions that lead to higher population density, distribution infilling, and range expansion of any butterfly species; downturns, the reverse. See Dennis *et al.* 2011 for details of variables and effects. HTNS, host taxonomic neighbourhood size.

The advantage of generalists *sensu lato* over specialists in averting extinction and generating speciation is then simply one of numbers (resources) and opportunities (scale of occupancy generated by the link between generalism and movement capacity); on the other hand, for radiation from a strictly specialist base, the process is highly dependent on the dynamism and availability of resource phylogeny and geography (host plant relatedness and spatial disposition), expansion of the resource base increasing potential for evolutionary changes, and unleashing latent plasticity (exaptations) (Agosta *et al.* 2010). There are clearly specialists (monophagous butterfly species) with wide geographical ranges whose spatial expanse depends on the availability of their particular resources, their abundance and/or ubiquity; even in these situations, the fact that the organism is widely distributed ensures that it experiences a wide array of different resources and conditions and increases the likelihood of the geographical range eventually exceeding individual dispersal capacity, thus presenting the opportunity for regional/local adaptive shifts (cf., *Vanessa gonerilla* and *V. atalanta*; Patrick & Patrick 2012). As discussed above, the entire process is vulnerable to how resources and conditions are integrated in space/time – thus on intersection, degree of compaction and the mobility of individuals exploiting these resources and conditions – and the impact on population status; in all these aspects generalists have an advantage over specialists, at whatever level these are defined (Symons & Beccaloni 1999), in being on the right side of the low population and decreasing population paradigms. Ultimately, the differences reflect on their RBHs.

Conclusion

Species' habitats underpin community biotope occupancy, population status (closed versus open; small population paradigm; declining population paradigm) and species' dynamics (extinction threat; speciation) (see New 2012, 2014). With the recent renewed focus on biotope (= habitat) for securing biodiversity (European Habitats Directive 1992; Lawton *et al.* 2010), there is a greater need than ever to understand fully the relationship between true habitats of species (disposition of resource attributes and conditions) and readily identifiable units in the landscape used for recording and conserving (managing) biodiversity. Such units – typically vegetation categories – are often treated as uniform and homogeneous, or at least equivalent, in composition and structure, across patches. In this review, we have pointed out the dangers of treating them as such. It is a simple matter, essential for the outcome of site management, to know what is actually being compared. It is no different, in essence, from the process of establishing relationships between life history traits and external (environmental) factors across species, which now recognises the imperative of taking on board phylogeny.

The resource-based habitat approach is a sobering, even humbling track to follow in research; but, because of the difficulties presented, there will be a tendency to ignore its tenets. However, doing so will not assist in developing an effective dialogue, so urgently needed, between biodiversity science and policy to underpin the sustainable use and conservation of biodiversity (Young *et al.* 2014). For much of biodiversity, particularly for species with intersecting resources and limited movements, maintenance can be effectively managed by a focus on space-time heterogeneity (Settle *et al.* 2009; Shreeve & Dennis 2011; Dennis *et al.* 2013). However, there can be a decided sense of vertigo, loss of control, when habitats do not appear to conform neatly to compact units we so readily identify to notions of a site-based habitat, that is, units that are better referred to as biotopes. The greatest of challenges ahead is to cater for species with such unbounded habitats, disseminated resources, conserving them across state boundaries, vast expanses of hostile space – not a frictionless matrix at all, but one that gravely affects seasonal movements between seasonal resources; among butterflies, the current plight of the magnificent Monarch butterfly *Danaus plexippus*, makes this observation all too apparent (http://www.xerces.org/monarchs/).

Acknowledgements

Our grateful thanks to the referees, and the editor Dr Simone Fattorini, for their helpful suggestions on the manuscript, and to Dr Dirk Maes for permitting us to refer to his observations, and those of his colleagues, presented at the Butterfly Conservation UK

Symposium (Southampton) in April 2014, on the ecology of the Ilex Hairstsreak, *Satyrium ilicis* in Flanders, Belgium. We thank Peter Hardy for helping with proof corrections.

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Received: 18.03.2014 *Accepted*: 11.04.2014 *Published*: 18.04.2014
Cite paper: Dennis R. L. H., Dapporto L. & Dover J. W. 2014. Ten years of the resource-based habitat paradigm: the biotope-habitat issue and implications for conserving butterfly diversity. *Journal of Insect Biodiversity* 2(8): 1–32.
http://dx.doi.org/10.12976/jib/2014.2.8 http://www.insectbiodiversity.org