

# Corridors and barriers in biodiversity conservation: a novel resource-based habitat perspective for butterflies

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**Abstract** Habitat loss and fragmentation, exacerbated by projected climate change, present the greatest threats to preservation of global biodiversity. As increasing habitat fragmentation and isolation of residual fragments exceeds the dispersal capacity of species, there is the growing need to address connectivity to maintain diversity. Traditionally, habitat corridors have been proposed as a solution. But, the concept of corridors (barriers) is poorly understood; typically they are defined as linear habitats linking up habitat patchwork, and are advocated without a detailed understanding of the elements making up species' habitats and the cost-effectiveness of alternative solutions. Yet, landscapes comprise an enormous range of 'linear' structures that can function in different ways to promote species' persistence and diversity. In this review, a functional definition of corridor (barrier) is developed to give prominence to connectivity as opposed to ad hoc structures *purported* to advance connectivity. In developing the concept, urgency to accommodate environmental changes compels a growing emphasis on organism diversity rather than a preoccupation with single species conservation. The review, in focusing on butterflies to address the issue of corridors for patchwork connectivity, draws attention to fundamental divisions among organisms in any taxon: generalists and specialists. Both groups benefit from large patches as these necessarily house species with specialist resources as well as generalists with very different resource types. But, generalists and specialists require very different solutions for connectivity, from short-range habitat corridors and gateways for specialists to habitat and resource stepping stones (nodes, surfaces) for generalists. Connectivity over extensive areas is most critical for moderate generalists

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and their conservation requires emphasis being placed on space–time resource heterogeneity; landscape features, of whatever dimensionality and structure, provide a vital framework for developing the variety of suitable conditions and resources for enhancing their diversity.

**Keywords** Connectivity · Generalism · Habitat · Landscape management · Matrix · Specialism

## Introduction

To conserve global biodiversity, there is a growing awareness of the importance of connectivity in landscape models (e.g., Walters 2007; Wang et al. 2008; Pullinger and Johnson 2010; Pinto et al. 2012). The imperative is driven by current and projected climate changes (McLaughlin et al. 2002) and the increasing exploitation and fragmentation of natural and semi-natural biotopes, processes which simultaneously shift, degrade and isolate habitats of species (Fahrig 2003; Scheffer et al. 2001; Opdam and Wascher 2004; Pimm 2008; Mantyka-Pringle et al. 2012). Habitat fragmentation and degradation are universally accepted as the main current threats to biodiversity (Travis 2003); as a potential counter, with changing climate, new ‘habitat’ space is emerging beyond current range margins (Hodgson et al. 2011). Much of this new space is unoccupied and inaccessible, but provides opportunities for translocating species (Willis et al. 2009; Thomas 2011; Devictor et al. 2012). As a key counter measure, enhancing connectivity has become a basic ingredient within landscape models (Crooks and Sanjayan 2006); the idea is to link isolated population units, and populated units to vacant patches (habitats), so as to redress local extinctions, reduce regional extinction probability and facilitate range adjustments with climate change.

However, despite our ability to measure connectivity (Zollner and Lima 1999; Calabrese and Fagan 2004; Bélisle 2005; Vogt et al. 2009; Lookingbill et al. 2010; Zetterberg et al. 2010), we are still far from having a clear understanding how the intervening space (matrix) between habitat patches affects movements. One review of 104 studies mainly on animals (Prevedello and Vieira 2010) attempted to clarify the confounding effects of matrix on patch isolation and area (Bender and Fahrig 2005). It concluded that matrix structure was less important than overall patch size and isolation but that in 88 % of studies, matrix types more similar in structure to the patch improved functional connectivity. This vital issue is highlighted by two recent evidence-based meta-analyses on movements related to matrix structures and corridors (Eycott et al. 2012; Gilbert-Norton et al. 2010). The basic conclusion is that matrix structures (or corridors) which simulate ‘habitats’ (viz., biotopes) allow increased movement, both emigration from patches and transfers, than structures that differ from them. In the case of connected habitat patches, ‘habitat’ corridors increase movements between patches by 48 % compared to unconnected patches. Such composite analyses are essential for determining landscape effects, but there are limitations to what they can currently reveal. In the matrix review (Eycott et al. 2012), only 20 studies across a variety of organisms and contexts were found to conform to the initial criteria of the study; the study is then limited as to numbers of species, replicates of studies for individual species, types of matrix transfer that can be compared (emigration, actual transfers, movement behaviour such as speed, direction and

linearity, immigration), and types of matrix contexts (land use). The corridor review (Gilbert-Norton et al. 2010) is based on 78 experiments (35 studies); almost a quarter (18 experiments, 23 %) of these showed that corridors were less effective in facilitating movements than the matrix, 10 of the 18 conducted with insects. In the case of both meta-analyses, habitat–matrix structures were defined purely on a binary (structural) contrast in vegetation (biotope) and not on organism resources (viz., habitat defined in terms of resources and conditions; Dennis et al. 2003, 2006, 2007; Turlure et al. 2009; Dennis 2010). As such, some fundamental problems are immediately evident in these studies. First, it is not clear exactly what, in detail, comprises a habitat for each organism in the study. Second, it follows, that the status of essential resources for species in both the demarcated habitat patches and matrix is also unknown: their number, quantity, quality, distribution, relative disposition, etc. These two issues expose a potential flaw in meta-analyses of complex concepts such as landscape, habitat and matrix, and may explain why ‘habitat’ in matrix fails to benefit some organisms (Goodwin and Fahrig 2002). Propositions from such analyses depend crucially on what is being compared; the greater the variability contained in the key concepts (definitions) determining inclusion criteria for any study, the greater is the uncertainty of any distinctions. The general conclusion from both the above studies is that ‘habitat’ like matrix or corridors should benefit connectivity. But how far is this true for any one group of organisms and why are there so many exceptions?

To enhance landscape permeability, the focus of attention is on the creation of habitat networks, ideally with physical links. In their absence, conservation falls back on the metapopulation model; this visualises landscapes largely in binary terms of a patchwork of habitat amidst a matrix of non-habitat (Hanski and Gilpin 1997). The habitat patches, deemed to be universally suitable for an organism, are typically identified from a single (and uniform) resource or vegetation type, whereas the matrix is understood to be uniformly hostile. In such situations movements of individuals between patches are modelled as functions of source population sizes (patch area is a notable surrogate) and distances between patches. This view of landscape conservation has been criticised on several counts, all related to a resource-based view of habitat (Dennis et al. 2003, 2006, 2007; Dennis 2010). Primarily, it is recognised that changes in type, abundance, quality and integration of resources for species, both in patch and matrix, affect survival, reproduction and development, as well as movements through a landscape (Dennis and Eales 1997, 1999; Dennis and Sparks 2006; Dennis 2010). A clear example that areas included in mainland matrix are not separated by completely hostile barriers belongs to the common observation that the species-area relationship tends to show different  $c$  and  $z$  coefficients between mainland and offshore island areas, thus suggesting that dispersal capabilities over mainland differ from those over completely hostile sea straits (Rosenzweig 1995). Despite the fact that landscapes comprise highly variable resources for any species, the binary patch/matrix view of landscape prevails and environmental scientists persist in referring to vegetation units as ‘habitat’; inevitably, this binary view of landscape is likely to pervade the incorporation of ‘habitat’ corridors into landscape restoration schemes (Donald and Evans 2006; Yu et al. 2012). Specific structures (see below for examples) are generally held to function in this polarised manner (movement or obstruction) (Forman and Godron 1981; Forman 1983; Dawson 1994; Zeller et al. 2012). The concept of corridors (barriers) has grown with the urgency to increase landscape permeability (Alagador et al. 2012). Corridors and barriers are generally distinguished as physical entities (homogeneous structures) inferred from their overall *perceived* impact (enhancing or deterring movements) on particular species, as in the meta-analysis of Gilbert-Norton et al. (2010). In this

way, the concepts describe a ‘black-and-white’ landscape lacking grade and variety, thus any notion of what resources actually constitute the habitat.

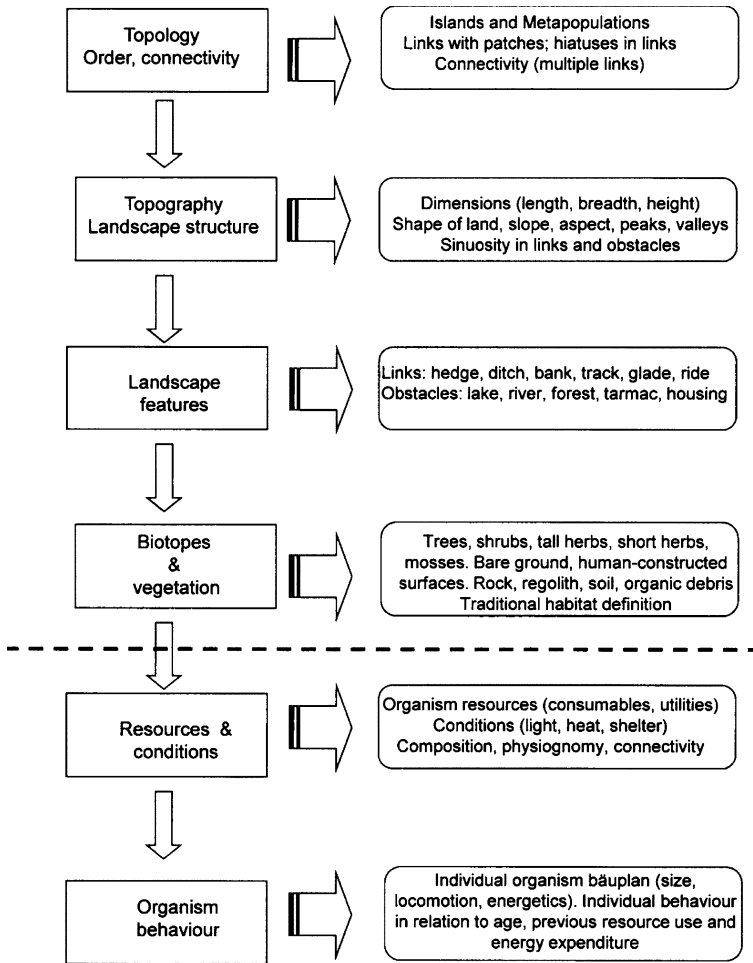
Herein, we examine the concept of corridor (barrier) through research findings on one group of intensively studied organisms to assess the wider utility of these landscape structures for establishing physical links between habitats. Specifically, we consider the effectiveness of connecting landscape structures for UK butterfly species (corridors/conduits, barriers/obstacles) which have been subject to severe losses in recent decades (Thomas et al. 2004a, b; Thomas 2005); butterflies are widely considered to benefit from physical (‘habitat’) links (Haddad 1999; Haddad et al. 2003). Three clear interconnected strands emerge as prominent in the corridor/barrier landscape debate. First, there is need to clarify what is actually meant by the terms ‘corridor’ and ‘barrier’; the binary treatment (habitat versus matrix) of landscape has led to a typological definition based on form (homogenous structures) rather than one on function, whereas corridor effectiveness clearly depends on factors influencing relative movements. Here, we develop a functional definition of corridor and barrier. Second, evidence is accumulating to show that ability to cross landscape depends both on individual capacity for movement and the environment (resources, non-resources, conditions); the outcome depends on the *interaction* between individual and environment and a close examination is made of this relationship: the factors influencing components of dispersal (emigration, transfer, immigration). In doing so we stress the importance of the resource-based habitat concept specifically for corridors and barriers and species-specific foraging behaviour in relationship to resources and conditions; only by so doing can it be appreciated how movements are affected and how conjunction of some organism resources may result, counter-intuitively, in formidable barriers (ecological traps). Third, with increasing landscape fragmentation, there is the overriding need to know how whole communities of organisms respond to different structures, purportedly corridors or barriers; individual potential for movement through, and persistence in, landscapes is extremely varied and, for this reason alone, no organism or structure should be viewed in isolation. Here, we develop a novel approach for assessing the need for connecting landscape structures based on life history attributes for mobility and resource use; combined they distinguish generalists from specialists in resource exploitation. The driver for this review is that a basic question in landscape management still remains: do we need corridors and to remove barriers? Investigating the issues noted above suggests a graduated approach in management for organisms on the specialist-generalist continuum; it indicates clearly that the matrix should be treated as a resource zone and built up as such; we argue that corridors and barriers be viewed within the resource-based habitat paradigm affecting, as they always do, more than just movements, and different species in contrasting ways.

### **What makes for corridors and barriers? A functional versus typological definition for corridors**

Corridors and barriers are traditionally described as properties of specific (pseudo-) linear features (Spellerberg and Gaywood 1993) which respectively facilitate or prevent movements. At the core is the relationship between movements and distance; typically movements (migration) across matrix are described by a negative exponential (or inverse power) function of distance (e.g., stochastic patch occupancy models, Ovaskainen and Hanski 2004; Ben-Zion and Shnerb 2012) though movements over the entire landscape, for the majority of species, are severely truncated at habitat margins (Olson and Van Horne 1998);

the basic landscape tenet is that specific features will function as corridors (or barriers) and enhance (or reduce) such movements. Rides, glades, stream banks, hedgerows, road verges, green lanes, and many other structures, are assumed to enhance movements of species (e.g., arthropods, Spellerberg and Gaywood 1993; Haddad 1999; mammals, Pereboom et al. 2008; birds, Ibarra-Macias et al. 2011); others, such as motorways, railways, urban zones, conifer forests, ley and cereal fields are similarly regarded as barriers to movement (Dawson 1994; Klar et al. 2009). But, apart from a few well-studied organisms (e.g., invertebrates and plants, Haddad et al. 2003), the extent to which this is true for any group of species is unknown and findings often conflict for the same organism (e.g., mice, Orrock and Danielson 2005). In fact, many of the landscape features described as corridor or barrier invoke a hierarchy in landscape organisation (Fig. 1) and tend to be composites of different structures. Even envisaged in basic topology, they can vary enormously (Fig. 2) with potential far-reaching consequences for connectivity and landscape management (see “[Conservation: the place of corridors and barriers in resourcing the landscape](#)” section); in detail, to organisms in transit, if not cursorily to human observers, they are infinitely heterogeneous in fine structure (i.e., slopes, aspect, vegetation), ‘force field’ contexts (i.e., moisture (humidity), light, heat, sound, air currents) and resources (habitat components), potentially having a number of distinct impacts on individuals, populations and species.

To understand the role(s) of corridors (barriers), the concept of heterogeneity for landscape structures is a vital starting point: heterogeneity for residual patch components (i.e., area, isolation, shape, edge effects, matrix quality) is an integral feature of habitat fragmentation (Didham et al. 2012). Heterogeneity in structure and resource in any feature is likely to have unpredictable consequences for the movement of different organisms. The more similar a corridor is to a habitat structurally (i.e., substrate, topography, biotope), the greater the likelihood that it may contain similar resource requirements for a species. However, this superficial level of assumed homogeneity can conceal disparity (heterogeneity) for resources and conditions and even in situations where corridors do indeed have full sets of habitat resources they are unlikely to be distributed in the same way along linear structures. Corridors and barriers arise if only because surfaces *are* heterogeneous, that is, landscapes of which they form a part are not uniform to force field influences. Even so, in any given landscape, expectations regarding transfers of organisms can be formulated in terms of adjacent surfaces, in themselves heterogeneous, intervening ones between exchanging sources (patches), and neighbouring ones. For instance, a ‘corridor’ will be relatively less effective the more permeable is the surrounding matrix. Thus, a corridor can be usefully defined as any structure, distinct from neighbouring ones, that facilitates relatively more transfers per unit area and unit time between contributing habitat units than predicted from the surrounding matrix. Expectation is based on size of source populations (source area and contexts of termini), distance and adjoining contexts (their surface resistance). This definition recognises that numerically more individuals may pass over the adjoining matrix, compared to a structure identified as a corridor, but significantly less in relative terms (per unit area). Corridors should also enhance the intrinsic rate of population growth and genetic diversity in recipient sources (destination habitats). Barriers are the reverse of corridors. They cause a relative decrease in transits per unit distance relative to neighbouring structures. These concepts of corridor and barrier are relative ones, sensitive to variation in space (scale, direction) and time, and corridors and barriers can be ranked in importance on the comparative numbers of individuals undergoing successful transmission. Theoretically, corridors may ‘release’ more individuals than enter the structure from a specific source. In this case, they may have an intrinsic rate of population increase greater than unity ( $r > 1$ ), act as sources in their own right, thereby functioning as ‘corridor

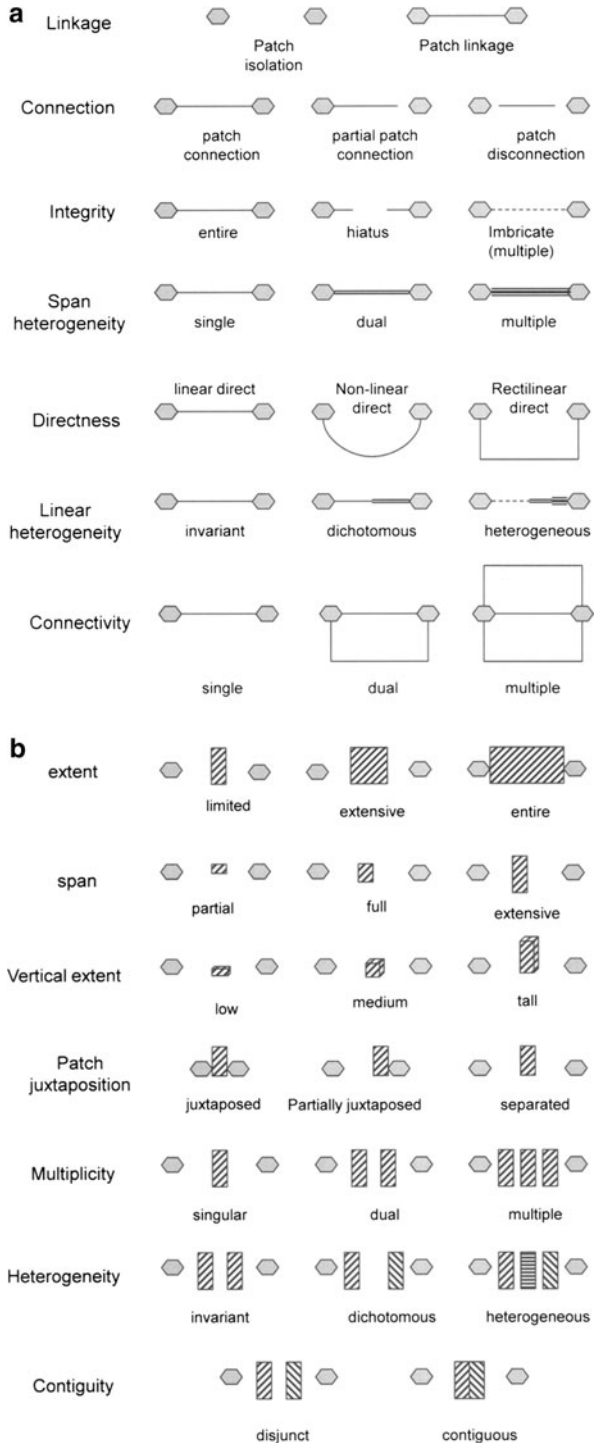


**Fig. 1** Layers of factors and approaches considered in organism transmission between habitat units across matrix. The lowest two layers from the resource-based habitat paradigm add new dimensions to complexity in individual organism transmission across the matrix

habitats'. In such situations the transit times of individuals through such corridors exceeds generation time. Alternatively they may function as drift nets capturing and redirecting individuals following other vectors (Dover and Settele 2009; Dennis 2010).

A functional focus to corridors (barriers), with its emphasis on movement-affecting processes, is very different from the traditional (typological) landform emphasis on specific landscape features with their too often assumed, polarised impacts on movements (conduit or obstacle; e.g., glades and rides versus conifer plantations) (Dawson 1994). To the extent that corridors can vary widely in structure, composition and context, it is a non-trivial question whether specific features should be regarded as synonymous with movement and its prevention. Yet, still, specific structures are considered to function as corridors (barriers), a concept advanced from studies on particular species to wildlife generally. To treat a feature in this way suggests that it is invariable in its influence, and that we understand

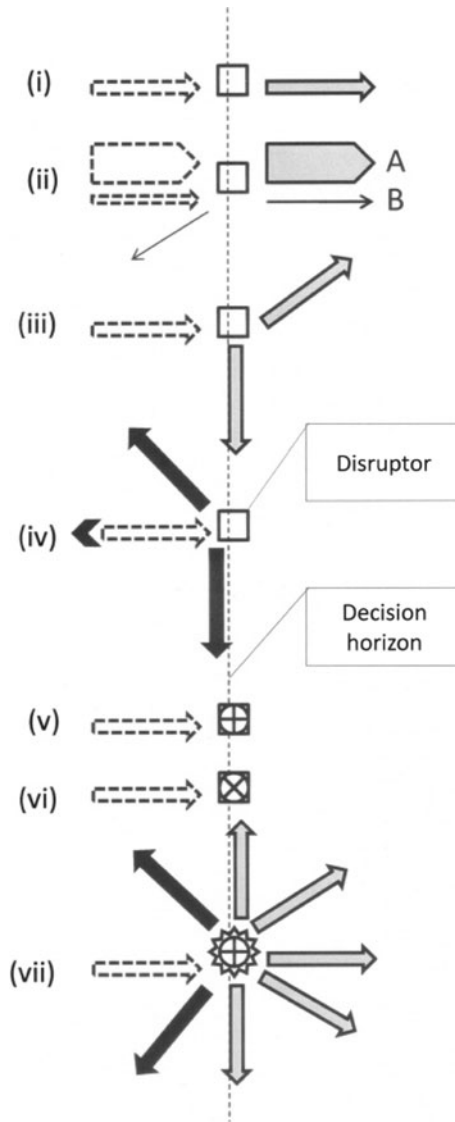
**Fig. 2** Basic topological and topographic components of landscape structures functioning as **a** corridors and **b** barriers for a pair of habitat patches. Landscape structures operating as corridors and barriers can take on a variety of basic topologies, on which more complex (vegetation, management, resource) structures develop and can be managed. *Hexagons* habitat patches, *lines* corridor links, *shaded blocks* barriers, heterogeneity indicates two or more physically distinct structures (e.g., bank, ditch)



**Fig. 3** Terminology and variability for responses by an individual organism to a matrix component (*grid square, cell, pixel, disruptor*) functioning as a potential gateway. *Box* disruptor, *pecked arrow* individual approaching disruptor, *entire arrows* path of individual following contact with disruptor (*grey transmitted, black reflected*). *Cross* resource use, *diagonal cross* death, *multi-pointed star* reproduction. (i) Unhindered transmission (no effect) (ii) increased or decreased speed of transmission (A Fast, high energy, large individual or individual in dispersive mode; B Slow, low energy, small individual or individual in non-dispersive mode); (iii) transmission with refraction or deflection; (iv) non-transmission (reflection) with or without deflection; (v) single or multiple resource use, including resting; (vi) mortality from agent at disruptor if only exhaustion in attempt to transmit; (vii) delayed (generation) multiple transmission/reflection following reproduction. Responses can be multiple, especially following resource use (v) involving (i) (transmission), (ii) (speed), (iii) (direction), (iv) (reflection), (vi) (death) or (vii) (reproduction for females followed by multiple outcomes). (i), (ii) and (iii) have corridor functions for individual  $n_i$  at time  $t$ ; (iv) is a barrier for an individual  $n_i$  and time  $t$ . (ii), (iii) and (iv) imply an influence of a disruptor but this may not be evident as resource use. The diagram illustrates how corridors and barriers link-up based on transmission of individuals. Corridors and barriers present multiple locations depending on the scale of mapping and resource descriptions (resource units as vector polygons or for raster cells, with specified quantities, qualities etc.) for multiple individuals. Basically any defined structure (resource) or spatial unit functions as a corridor when there is a high percentage of transference of individuals passing through the structure (disruptor, decision horizon or structural space) (most individuals keep on moving). A barrier is the opposite, when organisms have largely ‘reflected’ or died at the structure

how the particular feature affects the movements in organisms occupying the landscape, when we generally do not know at all. Even without any substantial knowledge of species’ behaviour or of the conditions presented by a set of so-called landscape ‘corridor’ features, clear variability in function can be ascribed to heterogeneity of form and diversity of organism. First, as landscape features and their surrounds vary in fine structure (Fig. 1) (topography, vegetation structure, management), which affect paths of individual movement, inevitably each path taken through the structure uniquely influences the fraction of individuals successfully passing through it; as not all individuals pass or fail to pass the structure, it is a corridor or barrier on the basis of the degree of permeability relative to adjoining structures and individuals migrating. It follows that the same structure may be more or less of a corridor (barrier) depending on its location at the core or margin of an organism’s geographical range or simply because of differences in land management (Shreeve et al. 1996a); furthermore, with rapid changes occurring in the force field of reference (i.e., for heat, light, moisture or air movement), a structure may be a corridor in one direction and a barrier in the other, and switches may occur depending on direction and intensity of field influences. Physical structures are known to vary in their impact over time, during the course of a day, season, a year, or over a longer period, depending on changing conditions (Dennis 1992, 2010). Second, barriers and corridors are unlikely ever to be uniform in their impact on organisms (Revilla et al. 2004; Lamberts et al. 2010; Turlure et al. 2011). Observation has demonstrated that individuals of the same species may respond quite differently to the same structure (Schoonhoven 1977), for instance a gateway through a structure (i.e., minimal corridor) under the same conditions, much as individuals vary in their capacity for manoeuvrability, speed of movement, lifespan and therefore transit distance (Fig. 3; e.g., *Anthocharis cardamines* at a motorway Bridge, Dennis 1986). As conditions impinge on individual capacity for movement, this means that a corridor for one population, species or individual may well present a barrier for another (Schreiber and Graves 1977; Krewenka et al. 2011; Shreeve and Dennis 2011). The importance of these two points to the corridor/barrier/matrix debate is highlighted in an examination immediately below of two related issues which are often confounded in movement studies (Zeller et al. 2012): (i) species’ capacity (life history attributes) for movements, and (ii) landscape (habitat) resources and conditions and their impact on butterfly movement behaviour.





**Species attributes: life history factors affecting capacity for movement**

Butterfly species vary substantially in their innate capacity for movement (Dennis and Shreeve 1996; Cook et al. 2001). But what, in detail, do we know of butterfly behaviour in relation to life history attributes that helps us to predict lifetime movements? The best evidence for response to matrix and corridor (barrier) function, or lack of it, comes from studies of individual movements (Shreeve 1992, 1995; Vandavelde et al. 2012). There are strict limits to successful dispersal; butterfly adult life spans are usually relatively short compared to many other organisms but vary considerably (a few days to several months), and migration distance is restricted by speed of transit, distance covered, and the negative

effects of intervening surfaces and conditions (e.g., weather). These studies have led to some useful generalisations on the effects of habitat fragmentation (e.g., *Pararge aegeria*, Bergerot et al. 2012). The impact of potential barriers and conduits for movement is now known to vary in relation to species, age, previous experience, requirements for resources, and to external factors such as weather (field influences; especially light, heat and air movement) which may influence capacity to move and forage for resources (Shreeve 1992; Dover and Fry 2001; Dover and Settele 2009; Dennis 2010). Different organisms respond to the same structures in different ways related to their modes of locomotion, lifespan and thus individual condition; butterflies are no different: flight mode differs markedly in relation to wing span and shape, wing loading, thoracic musculature and wing beat frequency (i.e., thoracic musculature) (Berwaerts et al. 2002). These various differences among individuals alone account for why responses to the same structures within the habitat and ‘matrix’ differ within and between species (Dennis 2004, 2010; Dennis and Hardy 2007).

Movements are also importantly affected by the stochastics of individual contacts with structures and timing in conditions. The issue here is a key life history variable: size. Organisms have finite size and the smaller they are compared to landscape structures, the greater the potential for passing through those structures at different points and along different tracks and therefore of experiencing different resources and obstacles. Landscape structures are approached and passed through at a point, in effect at a series of successive points (each the perceptual span of an animal) (Dover and Fry 2001). Corridor and barrier micro-structures, whatever they are, interact with age, sex and condition-driven individual behaviour in response to the fine structure (Shreeve and Dennis 2011) and therefore influence the type and speed of movement (Fig. 3). Timing is everything with movements, for as time changes (daytime, season) individuals are subject to changing conditions: a linear structure one moment in sun and shelter can soon be in shade and exposed to high winds; suitable resources present during one day may be depleted the next (Dover 1996, 1997; Dover et al. 1997; Dover and Sparks 2000; Dennis and Sparks 2006). Thus, it is possible to have different combinations of transfer for number and speed at the same location, such that at extremes an observer may experience few fast transfers or many slow ones, and in any direction. Consequently, it becomes evident, that as conduit dimensions through an obstacle need be no larger than to allow passage, there is no reason why a corridor or barrier may be envisaged as having any specific minimum criteria for length, width or depth (Fig. 3). This gives us a new perspective on landscape where each ‘pixel’ (small grid cell) is a momentary, fluctuating point of influence (imposed by landscape elements and conditions) (Fry 1995); it is a perspective inherent in the resource-based landscape view for conservation, as explained briefly below, and should be a prominent principle in landscape management.

### **Habitat and matrix: the resource-based view of corridors and barriers**

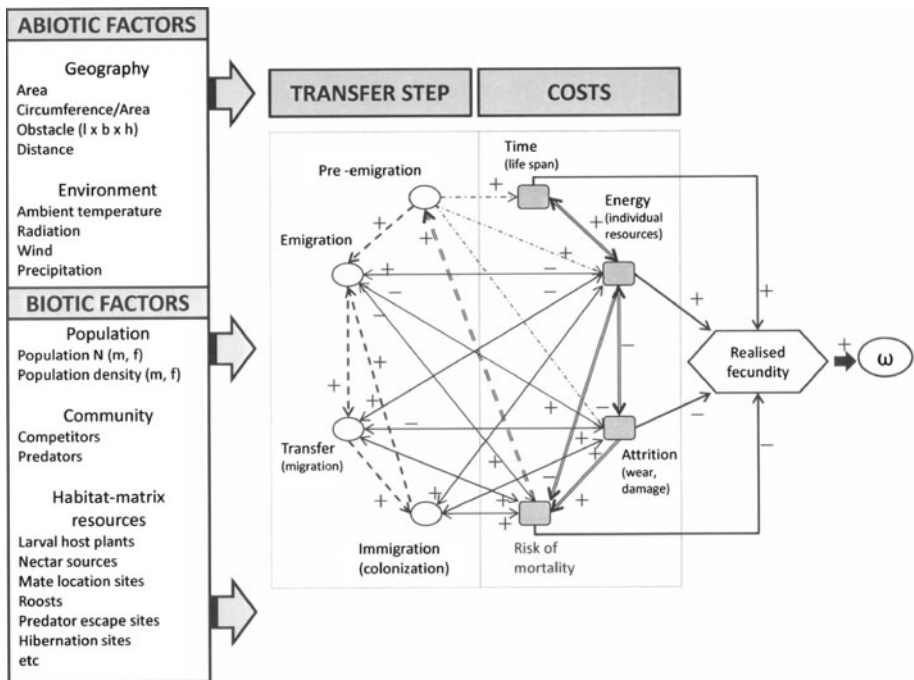
The contrast for structures (potential corridors or barriers) between the view of human observers and the perception of organisms in transit questions the exclusiveness and integrity of the traditional distinction of ‘habitat’ and matrix for organisms; cognitive approaches based on an organism-centred view become the most relevant (Farina and Belgrano 2006). In the resource-based definition of habitat, a vegetation zone or structure (viz., biotope) is unlikely to equate with habitat for most organisms (Dennis et al. 2003,

2006; Dennis 2010); many butterfly species, especially generalists, extend over a variety of distinct vegetation zones, increasing in number the more narrowly such vegetation zones are distinguished by human observers (Dennis 2010). Habitat is not simply an undifferentiated patch of vegetation occupied by an organism (Dennis and Shreeve 1996; Dennis 2010). The resource-based definition of habitat recognises that, within and across vegetation patchworks, individuals require and use a variety of resources and environmental conditions through their life cycles (Dennis and Hardy 2007). For instance, butterfly species require suitable conditions for flight, egg laying sites, larval feeding sites, pupation sites, mate location sites, mating sites, nectar sources, predator-escape zones, roost sites, and aestivation/hibernation sites. Each resource must be of suitable quality and quantity (Dennis 2010). ‘Foraging range’, in the definition, points to the contrasting kernels of movement for distinct mobile stages, larvae and adults, and the need for some resources (e.g., egg laying sites and larval host plant; host plant and pupation sites) to be closer than others (e.g., mate location sites and nectar sources). Clearly, the more resources required by an organism, the greater the number of potential combinations are likely to be encountered in vegetation zones, within both habitat and matrix (Dennis 2010). The key point here is that as purported corridor and barrier structures are simply extensions of habitat and matrix, a mix of resources and non-resources, the resource-based habitat concept applies equally to them as generally to habitat and matrix.

### Transit from source to destination: matrix-influenced behaviour

Although measures on movements among butterfly species reveal large differences in their innate capacities for movement (Dennis and Shreeve 1996; Cook et al. 2001; Stevens et al. 2010), inter-species movements are also hugely affected by landscape components affecting species’ resource distributions (Dapporto and Dennis 2013). As such, the resource-based habitat concept has wide-ranging implications for the passage of organisms over landscape matrix structures and biotopes. A key starting point is to appreciate the sequence of successful inter-patch transfers. Dispersal of individuals from source to destination habitats involves three fundamental steps: emigration from the natal patch, transfer (migration) across matrix, and immigration into (colonisation of) the destination patch; not only can individual success be baulked at any stage but passage through each zone has consequences for individual fitness (realised fecundity) once an individual (or their progeny) attains a destination (reproduction) patch. A constellation of factors influence transfer through each of these stages, abiotic and biotic, each imposing four basic costs to individual fitness: in time expended, energy lost, attrition (wear) and risk of mortality (Bonte et al. 2012; Travis et al. 2012); each in turn impacts on realised fecundity and individual fitness through lifetime reproductive success (Fig. 4). Furthermore, past and current selection imposed by the landscape and its biotic and abiotic components configures basic emigration patterns and the success of subsequent generations of dispersing individuals (Hill et al. 1999; Merckx et al. 2003; Merckx and Van Dyck 2006; DeVries et al. 2010; Travis et al. 2012). For instance, although it has been shown that *P. aegeria* in Morocco show no genetic diversification between oases and source areas separated by completely hostile desert, nevertheless butterflies from oases have more elongated wings, suggesting that they comprise a highly dispersive subset of the original population (Habel et al. 2012). Landscape structure, itself, is a key driver of evolutionary changes in dispersal (Baguette and Van Dyck 2007; Bergerot et al. 2012).

What does this mean for a butterfly moving from a source to a destination patch? The picture gained from this vantage is a highly complex one, of decisions, gains and costs to individuals in each pixel of resource space entered and left in transit (Fry 1995). During passage outside a zone where these resources integrate to produce a habitat (viz., resources intersect, join, or are within diurnal foraging range), continuous uninterrupted flight or return flight are just two of the numerous responses made by adult butterflies, which may stop, physically inspect objects, rest, thermoregulate, roost or engage in a range of activities, including interactions with other organisms (conspecifics, non conspecifics), mate location, mating, egg laying, feeding, evading predators, search flights, and so on (Dennis 2010). Recognition of the plethora of responses to surfaces has received empirical support from surveys conducted in agricultural (i.e., matrix) settings (Dover 1989, 1990, 1996, 1997; Dover and Fry 2001; Dover et al. 1992; Dennis and Hardy 2007). Counter-intuitively, responses by butterflies do not follow the simple formula that might be expected from recent meta-analyses on matrix and corridors (Eycott et al. 2012; Gilbert-Norton et al. 2010): that is, the more similar the vegetation structures—thus, in



**Fig. 4** Factors, components and costs of inter-patch dispersal. Factors (external to organisms) are divided into abiotic and biotic, and affect each stage of dispersal (emigration, migration and immigration/colonisation), sometimes differently (i.e., the system’s response to high population density may be positive (encourage) for emigration but negative (deter) for immigration). Pre-emigration components denote evolutionary changes to populations driven by changes to demography and movements. The model illustrates the links between components of dispersal and costs, as well as the causal impacts (correlation signs  $-$ ,  $+$ ) between components of dispersal and costs. **Bold pecked lines** links between dispersal components, **double lines** links between cost components, **double pecked line** an evolutionary feedback, **fine pecked lines** changes induced by evolution that reduce costs, **fine continuous lines** links between dispersal and cost components, **bold continuous lines** impact of costs on realised fecundity and individual fitness ( $\omega$ ),  $l$  length,  $b$  breadth,  $h$  height,  $N$  numbers of individuals,  $m$  male,  $f$  female

interpretation, the greater the number and quality of shared resources—the greater the permeability of structures. In fact, the very opposite can occur. At one extreme, resource laden linear strips (nectar plant rich hedgerows), though seen as vital for refuelling dispersal and reproductive potential, can effectively freeze movements as well as present predator killing zones (ecological traps; Dover 1997); at the other, virtually resourceless features (e.g., a fence, hedge, wood edge) can function as flyways and rapidly assist direction and speed of movements (Dover 1996). In the wetland butterfly, *Satyrodes apalachia* (Carolina, USA) a strong negative relationship has been found between the probability of entering a habitat and the speed of moving through it (Kuefler et al. 2010). This observation points to various conflicts that may occur in the transfer process between source and destination patches, particularly where a resource abuts chemically-treated intensive land uses (ecological traps), as well as to different types of movement within and between habitat patches (Van Dyck and Baguette 2005; Fig. 4). Even simple survey tapes drawn across open fields can direct movements of adult butterflies (Dover and Fry 2001). The prominent finding is the lack of consistency; species (and individuals) respond in different, often contrasting, ways to the same structures (Dover and Fry 2001). Moreover, for any one species, owing to changing field influences (i.e., sunlight, air movement, management), what is a barrier at one moment can become a corridor at the next, vice versa, and the concepts depend on space–time conditions (i.e., time of day, weather, sun angle, management practices) (Dennis and Sparks 2006; Dennis 2010). Furthermore the way that individuals respond to elements within the matrix is complex and may also depend on their physiological state and past reproductive history (Shreeve and Dennis 2011). In a recent study, the sea straits separating islands of the Tuscan Archipelago from mainland (6–20 km wide) was shown to be more permeable to Satyrines flying throughout the year compared to those flying only in summer probably because north-eastern winds, uncommon in summer, can favour dispersal over this completely hostile matrix during spring and autumn (Dapporto et al. 2012).

The overwhelming finding, for responses to structures purported to be corridor or barrier, is one of complexity at different levels: individual, population, species and higher taxa. No neat equation is presented by landscape matrices that would imitate habitat. Furthermore, a key point from Tobler's first law of geography (Dennis 2010): as the distance over the matrix between sites (source and destination habitats) increases there is likely to be an increase in surface heterogeneity; so the likelihood increases that individuals will cumulatively adopt behaviours and activities other than smooth, linear continuous flight (Dennis and Hardy 2007). This observation also applies to any target structure under consideration as being a corridor or barrier. To reiterate, the critical point is: although these structures may be designated as being distinct from others as to perceived function, structural detail or composition—that is, they are homogeneous in some human-defined respect, and thus a distinct category of structure (e.g., a hedge, lane, ditch)—they are highly unlikely to be homogeneous in terms of resources and conditions for organisms in transit. The only exception to this is likely to be where the matrix between sites is truly empty, such as with extensive water barriers or large resource-free intensive agricultural monocultures. The simple fact is that to derive an understanding of movements in habitat and matrix, a great deal more research is needed on response (behaviour) of butterflies to structures and resources, in different conditions, within habitat and matrix. These details, important as they are, present a highly complex view of butterfly responses to landscape elements. An immediate solution is to seek pattern in movement behaviour and resource use to guide management decisions on the efficacy of landscape connectivity: which species actually need corridors and why?

## Quantifying colonisation potential and migration capacity in butterflies

Recent comparative studies of British butterflies show that they fall into two broad classes: resource specialists and generalists, the latter further dividing into moderate and extreme generalists (Dennis et al. 2000, 2004, 2012; Shreeve et al. 2001; Dapporto and Dennis 2013). For two of these groups, it is becoming clear that corridors between habitat patches may have little relevance. First, specialists (e.g., *Cupido minimus*; *Lysandra bellargus*; *Maculinea arion*) tend to be highly sedentary, bound by highly specific resource requirements, and their movements within patches are typically extremely limited (maximum lifetime movements  $\leq 50$  m) (Wilson and Thomas 2002; but see Dennis and Bardell 1996). Second, extreme generalists (e.g., *Pieris brassicae*, *P. rapae*, *Pararge aegeria*) and continental migrants (e.g., *Vanessa atalanta*, *V. cardui*, *Colias croceus*), a number of which have long-lived adults (several months), typically disperse over long distances, and are capable of crossing sea barriers and utilising widely-scattered, tiny resource patches (Baker 1984; Dennis and Shreeve 1996; Dennis et al. 2007; Dennis 2010; Stefanescu et al. 2012). The populations of these extreme groups are persisting and growing; the habitats of specialists are comparatively easily maintained given suitable biotopes (Fox et al. 2011; Habel and Schmitt 2012; Dapporto and Dennis 2013), and extreme generalists are dependent on biome-diverse resources which are widespread and easily located as the species have wide-ranging migration capacity (Stefanescu et al. 2012). However, many of the third group, moderate generalists, are fast declining in the face of habitat fragmentation. Their demography is typically of a metapopulation patchwork and, for many, despite their ability to cross open country (e.g., *Anthocharis cardamines*, *Lasiommata megera*, *Maniola jurtina*, Shreeve 1992; Shreeve et al. 1996b; Dennis 2010), inter-habitat distances are now considered to exceed dispersal capacity over extensive regions (Thomas 2000). For these, the question remains whether they are best served by corridors or resource stepping stones.

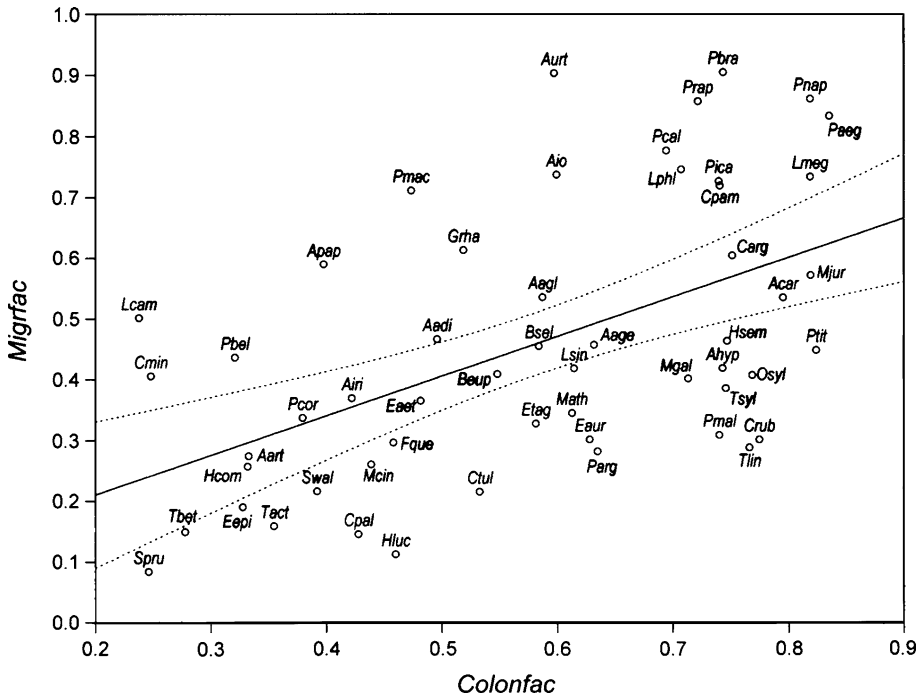
Further insights into the relationship of resource breadth and movement have arisen from studies in island biogeography (MacArthur and Wilson 1963). The occurrence of butterflies on British islands of different size and isolation is largely accounted for by two measures integral to the resource-based habitat model describing colonisation ability (generalism) and dispersal ability (migration) (Dennis et al. 2012). A more recent study has shown that these two measures also significantly influence butterfly distributions and distribution changes on the UK mainland (Dapporto and Dennis 2013). This suggests that these measures underlie the vulnerability of butterfly species to landscape fragmentation (i.e., shrinking and increasingly isolated habitat patches). Measures of generalism (*Colonfac*) and migration (*Migrfac*) for British butterflies are based on ten and four life history traits respectively (Table 1); data for the original variables are found in Dapporto and Dennis (2013). Continental migrant species that are not permanent residents are excluded: *Vanessa cardui*, *V. atalanta* and *Colias croceus*. *Colonfac* variables influence a species' ability to exploit a vacant patch (Dennis et al. 2012); increasing ability equates with increased generalism (resource breadth). *Migrfac* variables facilitate a species' capacity to access the patch and thus equate with migration ability (Dennis et al. 2012). *Colonfac* and *Migrfac* for species are computed as standardised means (between 0 and 1) for these variables (Dapporto and Dennis 2013). The two variables are significantly correlated (Pearson  $r = 0.53$ ,  $P < 0.0001$ ,  $n = 54$ ) but with  $R^2 = 28\%$ , they also have substantial independence of one another; their integrity and relationship is supported by a co-inertia analysis and Fourth Corner Analysis (RLQ and FCA, Dray and Legendre 2008) of the original variables (Dennis et al. 2012).

**Table 1** Colonisation and migration variables for British butterflies

Resource variables ( <i>Colonfac</i> , component based on 10 variables)	Symbol	Source
Number of biotopes exploited	BT	1
Number of larval host plants used	HP	1
Host plant abundance in natural vegetation classification categories	NVCab	2
Niche breadth (mean of Ellenberg ranges for all larval host plants based on all criteria but salinity)	Ellen	1
Larval host plant abundance taken over 8 biotopes	HPab	2
Larval host plant density (records/distribution cover)	HPdens	2
Nectar plant specialism (residuals of weighted regression of Nectar sources on nectaring records)	NEsp	2, 4
Number of nectar sources exploited	NEn	4
Symbiosis with ants (inverted scale: 1 to 4 with 1 highly dependent on ants)	Symb	3
Number of utility resources (outlets) used by pupae and adults (excluding nectar plants)	Utiln	1, 2
Migration variables ( <i>Migrfac</i> , component based on 4 variables)		
Mobility index	Mo	1
Flight period	FP	1
Wing span (mm)	WS	1
Voltinism (maximum number of broods per year in region)	Volt	1

Sources: 1, Dennis et al. (2000, 2004); 2, Dennis et al. (2005); 3, Dennis (2010); 4, Hardy et al. (2007); see Dapporto and Dennis (2013) for data relating to variables

The scatter of species, the variability in species' scores, within the two axes of *Migrfac* and *Colonfac* (Fig. 5) supports the notion of different approaches to the provision of resources within the landscape. The *Migrfac* index is based on empirical observations of movements in species (Dennis and Shreeve 1996; Cook et al. 2001; Dennis et al. 2004) supported by a recent meta-analysis on dispersal (Stevens et al. 2010). As such, the spread of species along the *Migrfac* axis suggests that whereas species at the high end are able to colonise habitat patches across wide expanses of open matrix, those at the lower end are increasingly challenged by isolation. Similarly, high values of the *Colonfac* index suggest the utility of substitutable resources in the landscape, while those at the lower end are likely to be dependent on singular, static, highly specific resources (Dennis 1992, 2010). As such, the species at either end of the regression line have highly contrasting habitat structures. In set notation for the resource-based habitat definition, the habitats of low mobility specialists are typified by resource intersection (overlapping resources), equivalence and equality (e.g., larval host plants used as nectar sources, mate location sites, etc.), whereas extreme generalists are characterised by substantial disjoint union (of complementary and supplementary isolated resources) linked by seasonal migration (Dennis and Shreeve 1996, p. 44; Dennis 2010). In effect, the regression line (Fig. 5) describes a joint axis of dispersal capacity and colonisation ability, and suggests a progression in minimal structures required for persistence in landscapes, providing a hypothetical model for future research work. Towards the top right (increasing generalism and mobility) stepping stone resources are likely to be of increasing utility; towards the lower left (increasing specialism and decreasing mobility) corridor habitats and large habitats become requisites for



**Fig. 5** The distribution of British butterfly species within axes of migration capacity (*Migrfac*) and colonisation ability (*Colonfac*); the indices are made up of standardised scores of four and ten variables respectively (see Table 1). Species: *Carterocephalus palaemon*, Cpal; *Thymelicus sylvestris*, Tsyl; *Thymelicus lineola*, Tlin; *Thymelicus acteon*, Tact; *Hesperia comma*, Hcom; *Ochlodes sylvanus*, Osyl; *Erynnis tages*, Etag; *Pyrgus malvae*, Pmal; *Papilio machaon britannicus*, Pmac; *Leptidea sinapis*, Lsin; *Gonepteryx rhamni*, Grha; *Pieris brassicae*, Pbra; *Pieris rapae*, Prap; *Pieris napi*, Pnap; *Anthocharis cardamines*, Acar; *Callophrys rubi*, Crub; *Thecla betulae*, Tbet; *Favonius quercus*, Fque; *Satyrrium w-album*, Swal; *Satyrrium pruni*, Spru; *Lycæna phlaeas*, Lphl; *Cupido minimus*, Cmin; *Plebejus argus*, Parg; *Aricia agestis*, Aage; *Aricia artaxerxes*, Aart; *Polyommatus icarus*, Pica; *Polyommatus coridon*, Pcor; *Polyommatus bellargus*, Pbel; *Celastrina argiolus*, Carg; *Hamearis lucina*, Hluc; *Limenitis camilla*, Lcam; *Apatura iris*, Airi; *Aglais urticae*, Aurt; *Aglais io*, Aio; *Polygonia c-album*, Pcal; *Boloria selene*, Bsel; *Boloria euphrosyne*, Beup; *Argynnis adippe*, Aadi; *Argynnis aglaja*, Aagl; *Argynnis paphia*, Apap; *Euphydryas aurinia*, Eaur; *Melitaea cinxia*, Mcin; *Melitaea athalia*, Math; *Pararge aegeria*, Paeg; *Lasiommata megera*, Lmeg; *Erebia epiphron*, Eepi; *Erebia aethiops*, Eaet; *Melanargia galathea*, Mgal; *Hipparchia semele*, Hsem; *Pyronia tithonus*, Ptit; *Maniola jurtina*, Mjur; *Aphantopus hyperantus*, Ahyp; *Coenonympha pamphilus*, Cpm; *Coenonympha tullia*; Ctul

persistence in landscapes. In a landscape envisaged as comprising habitat patches in completely empty matrix (an island archipelago), generalists and specialists have characteristic distributions; specialists tend to be restricted to the largest, closely connected patchworks, whereas generalists extend from these foundation zones to occupy smaller isolated patches, those generalist species with greatest dispersal ability to colonise, if only temporarily, the most isolated tiny nodes in the landscape (Dennis et al. 2010, 2012). A prominent feature, then, of generalist and specialist species is that they form nested distributions, with less diverse communities forming almost perfect subsets of more diverse ones, each dominated by extreme generalists (Ulrich et al. 2009; Dennis et al. 2012). This feature of communities is a crucial one for landscape management.



## Conservation: the place of corridors and barriers in resourcing the landscape

Faced with unprecedented losses to diversity from landscape fragmentation and climate change (Thomas et al. 2004a, b; Foden et al. 2013; Rybicki and Hanski 2013) maximizing habitat space and ensuring connectivity (conduits) are primary conservation targets, and habitat corridors would be thought to best enhance connectivity (Chetkiewicz et al. 2006; Alagador et al. 2012). Barriers, too, would be thought to have a place, inasmuch as they have potential for directing target species away from ‘killing zones’, so called ecological traps (e.g., motorways; polluted areas) (Klar et al. 2009). However, it is evident from the foregoing appraisal that habitat corridors are perhaps not the most appropriate matrix structures for arthropod conservation other than for highly sedentary, specialist organisms (e.g., stenotopic flightless beetles; Eggers et al. 2010; Kotze et al. 2011). First, they are not essential for ensuring inter-patch movements (dispersal) of all organisms, certainly not for free-flying insects such as butterflies. Even for specialist butterflies with the lowest migration and colonisation indices, inter-patch movements are sufficient to maintain integration between *closely* placed habitat patches (<1 km) (e.g., *Plebejus argus*, Lewis et al. 1997) and greater movements have been found for other specialists (e.g., *Hesperia comma*; Davies et al. 2005). Thus, as all butterfly species, even the most sedentary, are capable of crossing ‘empty’ matrix, dispersal of species falls on the extent of matrix and its composition in relation to a species’ perceptual range. Second, even when so-called corridors provision full habitat resources there is the counterintuitive finding that linear (so-called) habitat corridors can be deleterious to successful movement, inadvertently containing inappropriate structures, resource concentrations, and conditions that create killing grounds or ecological traps; a corridor of one biotope can function as a barrier for another (Eggers et al. 2010). Third, de novo habitat corridors in extent sufficient to link up distant habitats for generalists would be extremely expensive to develop and manage.

There is a further crucial issue in landscape management for species: target specific organisms or target communities. Although financial resources and data are available for the development of networks to conserve some species (e.g., *Icaricia icarioides fenderi* in Oregon’s Willamette Valley, USA; Schultz and Crone 2005; McIntire et al. 2007), sufficient knowledge is not currently adequate to do so for a community of organisms; the complexities for resource allocation are profound (Dennis 2010). Faced with currently projected massive environmental changes, conservation can ill afford to focus habitat and matrix resource structuring on single species and must necessarily adopt a programme to generate and maintain organism diversity. It would not be appropriate to give attention to a single butterfly, or butterfly species plural, and ignore bugs, beetles, birds, plants, mammals and reptiles, in effect, the entire community. However, provision for diversity creates complexity for corridor management. Recently, solutions to enhancing landscape for diversity have been sought in two formulae: (i) the ‘more, bigger, better and closer’ (MBBC) directive, emanating from landscape ecology, in making space for nature with its emphasis on habitat patchworks (Lawton et al. 2010); (ii) the landscape heterogeneity approach which encompasses both habitat patchworks and matrix (Benton et al. 2003) with its emphasis on resources and conditions (Shreeve and Dennis 2011). The function of corridors and barriers needs to be viewed in these contexts. Neither of these approaches is without its problems. The reality is that in the case of MBBC, there are usually many ‘more’ smaller, poor quality so-called habitat (=biotope) patches than there are ‘bigger better’ ones. Also, the fewer the habitat patches, the more isolated they are likely to be. In theory heterogeneity works very well, a ‘something for everyone’ approach, but too great a heterogeneity can result in resource patches that are smaller and worse, rather than bigger

and better for particular species; as evident in this review of British butterflies, specialists often require large zones of relatively homogenous biotope. The implication is that the heterogeneity has to be in the right place and structured for community needs.

Bearing in mind that diversity in patches is nested and includes both the rare and common, the specialist and generalist (Dennis et al. 2012), the distribution of species within axes for resource breadth (*Colonfac*) and migration capacity (*Migrfac*) provides firm guidelines for landscape prescription: (i) the importance of habitat heterogeneity for the main semi-natural patches (large sites with a variety of biotopes or finer vegetation units) for specialists and generalists underlying ‘better’ in the ‘more, bigger, better, closer’ directive; (ii) the importance of heterogeneity in resourcing the matrix for generalists. The first point takes us beyond the well known species–area relationship—that species benefit most from large sites (islands, biotope patches), that small patches can become sieves and have higher extinction debt (Cronin 2007)—to the firm observation of nested biodiversity (Ulrich et al. 2009; Dennis et al. 2012). Generalists occupy the same patches (islands, biotopes) as specialists but require different resources and conditions, thus vegetation units and structures. To cater for both in the patch (site) requires flexible management for heterogeneity over sites and especially high connectivity between resource units within sites (patches) for specialists. In this context, specialists with very limited mobility should benefit from corridors on a very small scale (i.e., gateways; see Fig. 3). As provision of suitable resource-based habitats for both generalist and specialist at sites necessarily reduces the space for both, maximizing dimensions of high quality (suitably resourced) space is at a premium. Second, moderate generalist species that frequently disperse beyond habitat bounds, and faced with critical inter-patch distances, should largely benefit from resource nodes in the matrix; the benefit will vary exponentially with the increase of distance between habitat patches and the quantity and quality of resources available. These need to be varied, to cater for different organisms, and widely distributed rather than sparse and condensed if only to avoid the impact of becoming predator (ecological) traps. Key resources for butterflies are larval host plants and nectar flowers but these are not the only ones, as indicated above. Management must necessarily be tailored to the range of specific requirements for species, as well as to the opportunities available in the landscape; as resource data are fully documented for most butterfly species, there cannot be any excuse from claims of ignorance.

Specialists tend to be site (biotope patch) bound. They are isolated by modest expanses of matrix (1–10 km matrix) and as indicated above need large habitat patches that relate to sustainable population numbers in such close proximity, if not connected, that gene flow is ensured (Habel and Schmitt 2012). Although broad short corridors would clearly enhance connectivity for some specialists, in effect this would be habitat enhancement (enlarging habitat patches) and best seen and treated as such. As even short habitat (fully resourced) corridors could also act as barriers to species that avoid such structures, there is sense in developing semi-open corridors for specialists occupying distinct, but intersecting biotopes on the same site (patch) (Eggers et al. 2010). Faced with the expense of corridors and logistical difficulties of creating and managing them, the fundamental issue is what best use to make of the matrix for generalists. Recall, for butterflies, that inter-patch distances are now argued to exceed dispersal range (Thomas 2000), so simply abandoning the land between habitat patches to whatever form the matrix will take from intervening land use is an option only for a state that can no longer invest in conservation. Unlike the situation in island biogeography where the matrix is a uniform immutable zone, terrestrial matrix comprises, or is capable of transformation into, a multitude of different spaces that can be occupied by resources and, though smaller, full habitats (topologically, structurally,

vegetation, resources etc.). As outlined above, landscape can be conceived of as a hierarchy of structure and surfaces (Fig. 1) and even at the simplest level (i.e., topology) a wide variety of structures exist that vary in different ways (e.g., connectivity, integrity, directness, linkage heterogeneity for etc., Fig. 2) and that can be managed for shape, connectivity and resource dimensions. For instance, such matrix structures provide a variety of edge situations (Ewers and Didham 2006) which provide essential resource distributions for many butterflies (e.g., egg laying sites, nectar sources, roosts, flyways in suitable conditions; Dennis 2010). Alternatives exist then for investing in a wide variety of structures (nodes, surfaces) which house smaller habitat patches and resource stepping stones for different species, as well as linear structures (arcs; open and imbricate corridors) which contain both habitats and resources (nodes and surfaces) for generalists, and which provide breaks in the natural force fields (i.e., sunlit edges, shade, wind breaks etc.) thereby catering for different needs of species (Dennis 2010). The alternative, developing corridor structures *de novo*, can be expensive as well as intrusive to other land uses. There are, however, situations which fully support corridor construction: (i) terrestrially-bound, conservation priority, species that urgently require physical links; (ii) landscapes already endowed with a framework of corridor structures. In the latter case longstanding structures may suitably act as templates for further development of nodes and surfaces for both species' resources and full habitats (i.e., wood edges, hedges, ditches, stream banks, green lanes, walls), the latter having the benefit of specifically enhancing between-generation connectivity for species.

Despite the manifold problems over potential corridor creation, on the whole, species of most organisms are likely to benefit from the presence of matrix resources amid wide expanses of intensive land use, specific resources that can be used in transit, and small, even tiny, habitat patches. For butterflies, nectar and roosts (resting places in inclement conditions) enhance and preserve energy, predator escapes minimise losses and damage, and mate location sites and host plant patches facilitate reproduction; all, can reduce the risk of mortality and contribute towards an increase in realised fecundity and individual fitness (Fig. 4). One great potential advantage of small isolated habitats in the matrix is that their colonisation and temporary population build-up is likely to be enhanced by lack of competition and enemies (i.e., parasitoids, predators), thus generating more propagules for the next generation (Holt 2010); also, increasing the number of resource stepping stones, thereby enhancing movements, counters evolutionary changes (reduced wing size and/or thorax musculature) to isolated marginal habitat 'islands' within the matrix. Furthermore, extinction of temporary populations on stepping stones subsequently provides vacant space for the next cycle of temporary colonisation (Dennis et al. 2010). As such, there is a question of whether occasional extinction on matrix habitat 'islets' may not actually work in favour of persistence in landscapes by allowing rapid growth of a founder population and generation of propagules in an empty site. These points are important in relation to the abundance of features and structures in landscapes (i.e., hedges, hollows, ditches, wood edges, stream banks, etc.) that could lend themselves usefully to varied management and heterogeneity in resource allocation for the wide variety of organisms. Such structures provide invaluable targets for resources that interfere minimally with the main thrust of human economy; they provide obvious nodes, zones and paths for resourcing and enhancing the landscape. Conservation may not be able to reverse the full devastation of industrial land use economies, but the current and projected losses to diversity place on conservation organisations and stakeholders the responsibility to enhance conditions and resources for wildlife over marginal land where loss to land production is minimal. In the matrix the emphasis is best directed towards generalists, and there being so many, towards

heterogeneity. Heterogeneity will benefit more species, and generalists are better able to exploit heterogeneity than specialists, primarily as they have greater potential for transferring between distinct (supplementary) outlets for the same resource type (i.e., larval host plants: Dennis et al. 2011, 2012).

## Conclusions

Extinction debt is likely to be particularly high in landscapes with fast declining natural vegetation cover, low landscape connectivity, degraded natural vegetation and intensive land use in modified areas. Generally, though, because landscapes are so varied, and habitat (biotope) fragmentation can have highly complex effects on species distributions (Ewers and Didham 2006), there is no simple landscape scenario to maintaining biodiversity, not within any region. Individuals and species respond very differently to structures purported to function as corridors and barriers; consequently, as the entirety of landscape diversity is threatened, broad solutions need to be sought to counter current losses. Here, we suggest a novel approach which caters for the known range of species' requirements (along the specialism–generalism gradient) and modes of locomotion, founded on the resource-based definition of habitat (Dennis et al. 2003, 2006, 2007). It is argued that corridors (and barriers) are still an important tool for ensuring connectivity between local populations within and between sites (patches) for specialists (Beier and Noss 1998). However, over the matrix outside sites (main habitat patches), the focus of attention should be on generalists, resourcing the matrix for them (Dennis et al. 2003; Dennis 2010). To cater for generalists and specialists, heterogeneity is a key concept for developing suitable zones of habitat within patches, where both are found and the specialists associated with distinct biotopes, and for creating a diversity of resources in the matrix, dominated by generalists.

Enhancement of resources in the matrix is most efficiently achieved by using available landscape features and structures, many of which have been described typologically as corridors (barriers) (Dennis et al. 2003, 2006, 2007; Fischer and Lindenmayer 2007; Davies and Pullin 2007). Other solutions, such as low resistance matrix may also have a key part to play in improving landscape permeability (Baum et al. 2004). All such approaches recreate biotope heterogeneity, the foundation for biodiversity (Benton et al. 2003). Where management has access to sufficient funding and open space, links and nodes can be cost effectively directed and constructed using mathematic algorithms (minimum spanning trees, Steiner trees; Prömel and Steger 2002; Chetkiewicz et al. 2006; Stanojević and Vujošević 2006) to create links and 'crow-fly lines' within the perception range of organisms for resource nodes (Pe'er et al. 2005; Pe'er and Kramer-Schadt 2008). An increasing number of spatial models are being developed to direct the location of movement 'corridors' (Pullinger and Johnson 2010; Landguth et al. 2012).

To move beyond such a broadcast prescription much additional research is needed. Although data are available on movements of specialists within and between habitat patches, less is known of their use of biotope (linear) corridors and gateways (Fig. 3). Knowledge of behaviour, movement, and resource use by generalists in the matrix—the impact on survival, reproduction, population persistence—is in its infancy; there is a large area of potential research based on direct observation and large scale, controlled, field experiments. In particular, there is a need to explore the behaviour of species within matrix contexts in relation to life history attributes and resource breadth, as well as the impact of matrix on the genetic and physical attributes of propagules and isolated populations within

the matrix, in turn, their impact on connectivity between populations occupying the main habitat patches.

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