<u>Systematic Review</u>

Title:

Is the Matrix Important to Butterflies in Fragmented Landscapes?

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Abstract

The quality and extent of the ‘matrix’ in terrestrial fragmented landscapes may influence the persistence and behaviour of patch-associated fauna. Butterflies are a popular target group for fragmentation studies and represent an ideal assemblage to explore the impact and role of the matrix in patchy landscapes. To date, there has been no attempt to synthesise available research and assess the extent to which the matrix is included in studies of fragmented butterfly populations. Addressing this issue is important for improved understanding of habitat use in fragmented landscapes, and for the successful management and conservation of butterfly biodiversity.

Our systematic review of 100 empirical research papers spans 50 years, and identifies how (and indeed if) the matrix is recognised in studies of butterfly populations in fragmented landscapes. We found that it was significantly more likely for studies **not** to include the matrix in their experimental design. This is of particular concern given 60% of papers that excluded the matrix in their research did so in systems where the matrix was expected to contain resources of value for patch-associated species (as it was either a heterogeneous landscape or had similar structure to patches). Of the papers that *did* consider the matrix, 80% (n=24) reported a negative effect of the matrix on butterfly species and/or communities.

Matrix effects may influence the survival and persistence of faunal groups in a world increasingly dominated by fragmented habitats. Our review suggests that future research should clearly define the matrix, and incorporate it in appropriate experimental designs.

Introduction

Habitat fragmentation and habitat loss pose major threats to global biodiversity (Gray 1997; Harrisson et al. 2012; Foley et al. 2005; Saunders et al. 1991). Therefore, efforts to understand the spatial and ecological dynamics that underpin responses of populations to fragmentation have been a key focus for ecologists and conservationists worldwide (i.e. reviewed in Turner 2005; Collinge 2009). Recently, there has been growing recognition of the importance of the areas between habitat patches (termed the 'matrix') in mitigating species responses to, and behaviour within, fragmented landscapes (Vandermeer and Carvajal 2001; Jules and Shahani 2003; Lindenmayer and Fischer 2006; Franklin and Lindenmayer 2009). Here, we define the matrix as the dominant (usually non-native) vegetation cover in which other land-cover types (i.e. habitat patches) are embedded (Driscoll et al. 2013). Patch-associated species cannot establish self-sustaining populations in the matrix. Because the matrix and habitat patches are defined according to species resource requirements (Dennis 2012; Dennis et al. 2013), what the matrix is for some species or was the matrix at one point in time, may not be at other times or for different species (Driscoll et al. 2013).

In terrestrial landscapes, the matrix often consists of a complex mosaic of different land cover types (Ricketts 2001). This complexity may influence the degree of permeability, ease of dispersal, and rates of migration for patch-associated flora and fauna (Krauss et al. 2003; Dennis 2012; Ricketts 2001). Some matrix types may successfully contribute to the persistence and survival of populations within patches by: 1) providing food resources to fauna inside patches (Kennedy et al. 2010; Brady et al. 2011; Dennis 2004), 2) influencing conditions experienced at the edges of patches which in turn favours certain species over others (Ries and Sisk 2010; Lindenmayer et al. 2009; Driscoll and Donovan 2004), and/or 3) facilitating the dispersal of species between patches (Gascon et al. 1999; Jauker et al. 2009; Kuefler et al. 2010) and influencing the outcome of movement into patches (Schwab and Zandbergen 2011).

Despite the pivotal role the matrix can play in patchy landscapes, there are many studies of fragmented landscapes that do not include the matrix in their experimental design or discussion of their findings (Baguette et al. 2003; Brueckmann et al. 2010; Krauss et al. 2004; Summerville and Crist 2001). The common use of Island Biogeography and metapopulation theories for understanding spatial dynamics in fragmented landscapes (Simberloff and Abele 1976; Jorge 1992; Baguette 2004) often results in the matrix being treated as an 'ocean' that is, uniform in nature and unsuitable for populations associated with patches of native vegetation (Lindenmayer and Fischer 2006; Franklin and Lindenmayer 2009; Ricketts 2001). This conceptual simplification of fragmented landscapes and lack of attention to the matrix is often unjustified. For example, in landscapes where the matrix is similar in structure to patches or consists of variable (heterogeneous) habitats, it is possible that the matrix offers resources of value to patch-associated species and communities (Jules and Shahani 2003; Baum et al. 2004; Bender and Fahrig 2005; Goodwin and Fahrig 2002; Revilla et al. 2004; Dennis 2004). Therefore, the exclusion of the matrix in so many studies represents a potentially large knowledge gap in modern conservation ecology.

Butterflies have been a very popular study group within fragmented landscapes (reviewed in Warren and Bourn 2011). They represent an ideal group to explore the impacts and role of the matrix. This is because most species are easy to identify, catch, mark and observe (Kremen 1994; Franzén and Ranius 2004; Lomov et al. 2006). In addition, many have very specific resource requirements (e.g. Dennis et al. 2004; Prudic et al. 2007), therefore making the distinction between patch and matrix obvious. However, the extent to which the matrix is included in the experimental design of fragmentation studies (i.e. surveys conducted in the matrix as well as within fragments) seems highly variable. While some studies show that matrix type can have a strong influence on the movement of butterflies between patches (Stasek et al. 2008; Ries and Debinski 2001; Ross et al. 2005a; Dover 1996; Ricketts 2001), many others completely exclude the matrix and focus solely on the characteristics of patches (such as patch size, shape, isolation etc.; e.g. Dover and Settele 2009; Debinski and Holt 2000; Steffan-Dewenter and Tscharntke 2002).

Here, we review a sample of empirical papers that have been published in major journals in an effort to summarise how (and indeed even if) the matrix is being incorporated into butterfly studies, and, where the matrix has been considered, the response of butterflies to the matrix. While other reviews have examined the effects of patch attributes such as size, shape, distance from other patches and dispersal between patches (e.g. Fahrig 2003; Debinski and Holt 2000; Dover and Settele 2009), none have yet quantified when and how the matrix is sampled in fragmentation studies on butterflies. This is a pivotal area to address as the response of butterflies to the matrix may have profound implications for the survival and persistence of many species in fragmented landscapes (e.g. Ricketts 2001).

The key aims of this paper were to identify: 1) how often fragmentation studies mention the matrix (on any level); 2) how common it was for such studies to include the matrix in the experimental design (and how this was done); 3) whether these papers showed a negative or positive impact of the matrix, and; 4) whether there was adequate justification for studies that did *not* include the matrix.

By asking these questions, we identified the knowledge gaps that currently exist in our understanding of the role the matrix plays for butterflies in fragmented landscapes. The information gained from our review is especially relevant for a world increasingly dominated by patchy landscapes (Gray 1997; Harrisson et al. 2012; Foley et al. 2005; Saunders et al. 1991).

Methods

Review Process

Using the key elements of our review topic to guide the development of a suitable search term, we identified relevant studies through an electronic search of Web of Science using the terms "(butterfl* OR Lepidoptera) AND fragmentation". The search terms we used for our systematic review were chosen as they returned both the greatest number of total papers, and the highest number of relevant papers. We acknowledge that other search terms may have returned different papers that were missed in our review, although other search terms were not as comprehensive as the string we used (Appendix A). Further, while we acknowledge that other search engines may have returned different or additional relevant literature, we chose to use Web of Science as it is one of the most widely used, reliable and comprehensive search databases of scientific literature (Falagas et al. 2008).

The literature returned in our search was then subject to a three-stage process before being accepted into the final systematic review. First, any article with a title that was irrelevant to butterfly species/communities and landscape fragmentation was removed. The abstract of each remaining article was then read. Any article that appeared to address landscape fragmentation and butterfly biodiversity (or individual species) was accepted. The full text of all remaining articles was read, and either rejected or accepted into the final review (criteria for rejections are mentioned below).

Research questions asked of each paper were aimed at gathering information on where the study was performed, the experimental design, as well as key findings of each paper. As our main questions referred to the matrix, we specifically collected data on whether a paper mentioned the word matrix, if the authors defined the matrix, if/how the matrix was included in the experimental design, and any key results or management recommendations made which related to the matrix. A full list of the information extracted from each paper is given in Table 1.

Table 1 Description of all data collected from each paper included in this systematic review (n=100)

Area	Data Collected/Question Asked	Possible Responses	Conditions (if applicable)
Matrix Related	Was Matrix Defined?	Yes/No	-
	Matrix Definition	As stated in journal	-
	Type of matrix	Farmland, Grasslands, Plantations, Forest, Grasslands, Urban Areas, Mixed Matrix Types, Did Not Specify or Other (as stated in journal)	-
	Was the Matrix Included in the Experimental Design?	Yes/No	-
	If Included, how was the Matrix Incorporated into Experimental Design?	As stated in journal - includes things like surveys in the matrix, looking at differences between patches surrounded by different matrix types, vegetation surveys in matrix etc.	-
	Was there an Effect of the Matrix on Results?	Yes/No	-
	What was Causing the Effects of the Matrix?	Summary of main mechanisms driving effects as stated in journal	-
	Were Management Recommendations made for the Matrix?	Yes/No	-
	What were the Recommendations for the Matrix?	Summary of recommendations as stated in journal	-
Fragmentation Related	Fragment type	Bogs/Peats/Wetlands, Forest, Grasslands/Meadows, Patches of Specific Plant Species, Woodlands, Other	-
	Was Fragmentation Defined?	Yes/No	-
	Definition	As stated in journal	-
	Cause of Fragmentation	Agricultural Intensification, Naturally Fragmented, Experiments, Abandonment of Management Practices, Habitat Loss, Increasing Vegetation Cover, Plantations, Urbanisation, Habitat Destruction, Other (or didn't specify)	-
	Type of Survey	Trapping/baiting, transects, mark/recapture, live samples, monitoring plants, whole sites, still observations, tracking, other	-
	Area Covered		-
	Number of Fragment Sites	As stated in journal	-
	Number of Different Fragment Types	As stated in journal (number)	-
	Types of Fragments	As stated in journal - fall into categories stated above in 'Study Sites'	-
	Was there Butterfly Manipulation?	Yes/No	Manipulation identified as studies where butterflies were handled, raised in labs, where tissues samples were taken etc.
	Manipulation Type	As stated in journal	-
	Was There a Significant Impact of Fragmentation?	Yes/No	-
	What was Causing these Effects?	Summary of main mechanisms driving results as stated in journal	-
	Was the Effect Reported as Negative?	Yes/No	-
	Were Management Recommendations Made?	Yes/No	-
	What were these Recommendations?	Summary of recommendations as stated in journal	-
Summary Statistics	Author, Title, Year Published	As stated in journal	-
	Reference Type	Journal Article, Opinion, Book	Only looked at journal articles
	Volume, Issue, Pages	As stated in journal	-
	Title Appropriate	Yes/No	See methods for exclusions
	Abstract Appropriate	Yes/No	See methods for exclusions
	Focus of Research	Biodiversity, Dispersal, Distribution, Edge Effects, Extinction Debt, Flight, Genetics, Life-History Traits, Mate-finding, Population Dynamics, Resource Requirements	-
	Hemisphere	Northern/Southern	-
	Country	As stated in journal	-
	Region	Africa, Asian, Australasia, Europe, North America, Central America, South America	-
	Location	As stated in journal	-
	Organisational Level	Species, Community, Assemblage	-
	Species Number	>1 or 1	-
	Species Name	If applicable, as stated in journal	-
	Study Length	Cross-Sectional or Longitudinal	-

We applied a range of specific criteria to select appropriate papers. Non-English language searches were not conducted as part of our review. However, our literature search did identify work from across the globe, and all relevant papers were included regardless of geographic origin. As the aims of our review related to the assessment of research-based, scientific studies, only empirical studies in peer-reviewed journals were included. Further, only quantitative research was included as it was important to be able to assess methodologies used to evaluate if, and how, the matrix was included in the experimental design. We concentrated our review efforts on studies conducted in terrestrial systems as opposed to studies conducted on island systems (such as ocean archipelagos). If our literature search returned a paper that referred to data previously published which had already been reviewed, the article was rejected to avoid over-representation of any one set of results.

We assessed only those papers that focussed on adult butterflies. Papers that dealt solely with larvae, caterpillars, eggs or only moth species were not considered. Adult butterflies can be quite mobile, and their perception of, and interaction with the matrix is different to that of larvae or caterpillars (Weiss et al. 1988; Bergerot et al. 2010). Many moth species are nocturnal and therefore there may also be marked differences in how they perceive the matrix compared to diurnal butterfly species (Öckinger and Van Dyck 2012; Öckinger et al. 2010).

Use of the Terms 'Matrix' and 'Habitat'

For papers reviewed which explicitly mentioned the term 'matrix', we scored them as including the matrix and recorded the definition of the matrix that they used (Table 2). For the remaining papers that did not use the term, it was still important that we discovered if the matrix had been considered in their experimental design. While we recognise that the matrix may be defined in various ways (e.g. from conservation biology viewpoint, an individual species or human perspective etc. Crow and Gustafson 1997; Lindenmayer et al. 2009; Lindenmayer and Franklin 2002; Fischer et al. 2004; Bunnell 1999), we marked a paper as including the matrix if they studied butterflies or surveyed for species-specific resources in the land-cover types surrounding native vegetation patches. This remained the case even if those land-cover types were found to offer suitable habitat to butterflies, and therefore may not be considered a matrix from the butterfly's point of view.

We also acknowledge that there are different definitions for 'habitat' (Fahrig 2003; Hall et al. 1997; Franklin et al. 2002; Dennis 2012). To both complement our definition of the matrix, and make comparisons across multiple species and systems possible; throughout this paper we use the term 'native vegetation' when referring to patches of native vegetation and spare the use of the word 'habitat' to refer to the particular places occupied by a given species.

Statistical Analysis

We performed a one-sample t-test to assess whether papers returned in our search, were significantly ($P \leq 0.05$) more likely to have included the matrix in their experimental design compared to excluding it (i.e. null hypothesis that papers did include the matrix). We performed this test using all 100 papers sampled. Statistical tests were performed using GenStat 14 (Payne et al. 2011).

Results

Our literature search was completed in September 2011. Our search terms returned 460 papers spanning 50 years. After reading their titles and discarding those papers that did not address the research area of interest, 190 papers remained. The abstracts of all 190 papers were read to assess for suitability for inclusion in our final review. After this evaluation, the final review incorporated a total of 100 papers, from 36 different journals.

Analysis of our summary statistics and fragment-related questions is presented in Appendix B. The following section focuses on our results from matrix-related data analysis.

The Matrix

Acknowledgement of the Matrix

Of the 100 papers we reviewed, almost half (n=48) mentioned the word 'matrix' in the text. However, of these, we found that only 8 papers actually defined the matrix (Table 2). Most of these papers (n=6) loosely referred to the matrix as areas outside of remnant patches, with only three (Krauss et al. 2005; Muriel and Kattan 2009; Chardon et al. 2003) acknowledging that the matrix may be used by study species (Table 2).

Table 2 Of the 100 papers reviewed, only 8 defined the word matrix. Definitions used by each of these papers are given below

Article	**Definition of Matrix**
Batary et al. (2009) *Journal of Insect Conservation*	Area of lower biomass and different structural complexity around the fragments
Krauss et al. (2005) *Ecography*	Area between habitats including barriers, corridors and stepping stones
van Halder et al. (2008) *Biodiversity and Conservation*	The areas of uniformly unsuitable habitat that surround habitats - does point out that landscape matrices are not entirely hostile
Muriel and Kattan (2009)	High-quality matrices are defined as structurally complex habitats that

Conservation Biology	offer microclimatic environments, refuges, or food resources similar to those in the forest
Fowles and Smith (2006) *Journal of Insect Conservation*	Landscape between habitat patches (point out that it is not homogenous)
Chardon et al. (2003) *Landscape Ecology*	The matrix is areas that are not source patches for species - so matrix could include habitat and non-habitat
Ricketts (2001) *American Naturalist*	The non-habitat surrounding the native habitat patches of interest
Bergerot et al. (2010) *Plos One*	The spaces in which landscape patches are embedded

The Matrix in Experimental Design

We found that it was significantly more likely for studies **not** to include the matrix in their experimental design (n=70, $t_{1,99} = 6.51$, $P < 0.001$). Of the thirty papers that did include the matrix, only twenty explicitly mentioned the word 'matrix' (Table 1, 2).

For papers that included the matrix in the experimental design, 40% (n=12) either did not specify the matrix type, or the matrix included several different landscape cover types and so could not be classified (mixed/other category Fig. 1). Of the matrix types that could be identified, the most common land cover types in the studies we reviewed were forest (n=8), farmland (n=7) and plantations (n=6; 1 coffee plantation, 4 pine plantations, 1 *Eucalyptus* plantation, Fig. 1).

Only nine (30%) of the thirty papers that included the (potential) matrix in the experimental design actually surveyed butterflies in the areas between recognised habitat patches (Table 3). The remaining studies examined how the presumed matrix influences within-patch mechanisms (such as movement or dispersal, n=13, Table 3), or simply surveyed areas within the land-cover surrounding habitat patches to look for suitable vegetation or resources for species associated with patches (n=8, Table 3).

Table 3 Of all 100 papers reviewed, 30 included the matrix in their experimental design. Description of how the matrix was included in the experimental design of these papers is outlined below

Article	**The Matrix in Experimental Design**
Bukovinszky et al. (2005) *Oikos*	Examined differences in species abundance/richness in patches surrounded by grass versus barley
Collinge et al. (2003) *Conservation Biology*	Examined differences in species abundance/richness in patches surrounded by differing percentages of urbanization
Cozzi et al. (2008) *Landscape Ecology*	Examined barrier effects of the matrix on butterflies within patches
Davis et al. (2007) *Landscape Ecology*	Surveyed for suitable butterfly resources up to 2km into the matrix surrounding patches
Fowles and Smith (2006) *Journal of Insect Conservation*	Surveyed for suitable butterfly habitat in the matrix surrounding patches

Guitierrez et al. (1999) *Oecologia*	Surveyed for butterfly food plants in areas outside of the 'optimal habitat'
Krauss et al. (2003) *Journal of Biogeography*	Noted the landscape context of matrix surrounding patches
Kumar et al. (2009) *Biodiversity & Conservation*	Mapped topographic variables and landscape metrics at radii of 300, 600 to 2,400 m around patches
Leidner and Haddad (2010) *Conservation Genetics*	Noted the matrix type (urban areas, forest or sand dunes) surrounding patches
Ribeiro (2008) *Diversity & Distributions*	Examined differences in species abundance/richness in patches surrounded by different matrix types
Ricketts (2001) *The American Naturalist*	Examined differences in the dispersal rates in and out of patches surrounded by willow thickets versus conifer forest
Rickman and Connor (2003) *Ecography*	Examined differences in species abundance/richness in patches surrounded by 5 different landscape uses
Ries and Debinski (2001) *Journal of Animal Ecology*	Examined different in edge behaviour of butterflies within patches surrounded by different matrix types (crops, road, field and tree-line)
Ries and Sisk (2008) *Oecologia*	Examined edge response of butterflies within patches to 12 different edge (matrix) types
Roland et al. (2000) *Ecology*	Examined differences in the dispersal rates in and out of patches surrounded by different matrix types
Rosin et al. (2011) *European Journal of Entomology*	Recorded % grass cover and % forest cover in matrix surrounding patches and used this to infer matrix permeability/quality
Schtickzelle and Baguette (2003) *Journal of Animal Ecology*	Examined differences in the likelihood of butterflies from continuous habitat and fragmented habitat to cross patch edges into the matrix
Schtickzelleet al. (2006) *Ecology*	Examined differences in the dispersal rates in and out of patches surrounded by different matrix types
Tscharntke et al. (2002) *Ecological Applications*	Landscape structure was estimated in 15 sectors (diameter of 1.5 km) around fragmented landscape
van Halder (2011) *Journal of Insect Conservation*	Measured variables in the matrix surrounding patches
Wettstein and Schmid (1999) *Journal of Applied Ecology*	Noted the habitat type surrounding patches and also measured some variables in the matrix

Effect of the Matrix and Management Recommendations

We found that 80% (n=24) of the papers that included the matrix in the experimental design reported a negative effect of the matrix on butterfly species and/or communities (only Bukovinszky et al. 2005; Muriel and Kattan 2009; Gutierrez et al. 1999; Collinge et al. 2003; Rickman and Connor 2003; and Ribeiro et al. 2008 did not). Of these papers, less than half (n=8) made management recommendations for the matrix (Table 4). A further three papers, which did not include the matrix in the experimental design, also made management recommendations specific to the matrix (Table 4). Management recommendations varied from open ended suggestions to consider the matrix in management plans, to more specific recommendations focussed on improving access to species-specific resource requirements in the matrix, such as; host-plant abundance, habitat resources for ant-mutualists, and altering vegetation structure to encourage and increase matrix permeability (Table 4).

Table 4 Of all 100 papers reviewed, 8 made management recommendations for the matrix.

Article	Management Recommendations
Wood and Samways (1991) *Biological Conservation*	Maintain landscape elements (within the matrix) that aid dispersal, particularly nectar sources for adult butterflies
Davis et al. (2007) *Landscape Ecology*	Ensure resources (particularly floral) are available in spaces around patches, in order to aid connectivity between patches
Barbaro and van Halder (2009) *Ecography*	Conserve landscape heterogeneity
van Halder et al. (2008) *Biodiversity and Conservation*	Manage stand structure so as to allow for understorey growth, which potentially provides resources to butterflies
Fowles and Smith (2006) *Journal of Insect Conservation*	Improve the condition of the matrix to improve amount of breeding grounds available
Ricketts (2001) *American Naturalist*	Change the management of the matrix to improve dispersal between patches
Ries and Debinski (2001) *Journal of Animal Ecology*	Modify the edge structure (i.e. the matrix), in an attempt to influence emigration rates between patches
Marin et al. (2009) *Biodiversity and Conservation*	Maintain the current matrix (as it contains patchy resources) rather than intensify agricultural practices
Nowicki et al. (2007) *Biological Conservation*	Matrix should not be concreted, best if it consists of habitat that is useful for ants (because of symbiotic relationship with the focal butterfly species)
Bergman et al. (2004) *Ecography*	Acknowledged that butterflies in patches are affected by the matrix, so management should consider the matrix
Zschokke et al. (2000) *Oecologia*	Acknowledged that unsuitable matrix may be a barrier to dispersal - so management should consider the matrix

<u>*Studies that Did Not Include the Matrix*</u>

We found that 60% (n=42) of the 70 studies that did not include the matrix in any way in their experimental design were investigating butterflies in systems where the matrix type was either similar in structure to patches or consisted of various land cover types and thus were highly variable (heterogeneous). All other studies (n=28) investigated butterflies in patches that were embedded in homogenous matrix landscapes that clearly contrasted with the patches of native vegetation (i.e. open vegetation within a pine plantation matrix, or rainforest patches within a farmland matrix).

Discussion

We present the first systematic review quantifying the extent of matrix inclusion in studies of butterflies occupying fragmented landscapes. Despite recognition of the importance of the matrix in a world increasingly dominated by patchy habitat networks (i.e. Jules and Shahani 2003; Franklin and Lindenmayer 2009), our results show that only 30% of the quantitative studies reviewed explicitly included the matrix in the experimental design. In cases where the matrix was included in experimental design, only a limited number of studies actually surveyed butterflies within the matrix. Further, only eight papers developed their results concerning the matrix into management recommendations. Of particular concern is the number of papers that studied landscapes where the matrix was similar to patches, but it was nevertheless not explicitly included in the experimental design, despite literature suggesting the matrix may offer resources of value to patch-associated species in such landscapes (Jules and Shahani 2003; Baum et al. 2004; Bender and Fahrig 2005; Goodwin and Fahrig 2002; Revilla et al. 2004).

Recognition of the Matrix and Definitions

We found that less than half the papers reviewed mentioned the word ‘matrix’, and that of these, only eight made some attempt to define what the matrix was in the context of their study (Table 2). While a lack of explanation of the matrix may not be an issue if it is clear that the matrix is a land-cover type completely unsuitable for patch-associated species, we found that many of the papers reviewed which failed to define the matrix, also failed to describe the vegetation or landscape characteristics of the matrix. This meant that determining if the areas between patches might be suitable for focal species was impossible. Further, we also found that when papers *did* define the matrix, this definition varied widely; from more species-specific resource-based approaches, to ones based on landscape-level vegetation structure (Table 2). Without the use of consistent definitions associated with consistent theory (Driscoll and Lindenmayer 2012), it becomes impossible to assess whether the assumptions made about the matrix, and its exclusion from experimental design, were valid. Further, it also makes reviewing the literature difficult, as papers that fail to use the term matrix may be missed in literature searches even if these papers contribute to the field of knowledge.

Butterfly response to fragmentation and individual's ability to use the matrix is significantly impacted by the quality of the matrix (e.g Krauss et al. 2003; Ricketts 2001). Therefore, it is important for studies to examine matrix quality and possible variations that exist within the matrix, rather than treat it as a uniform area (Krauss et al. 2003; Stasek et al. 2008; Vandermeer and Carvajal 2001; Prevedello and Vieira 2010; Dennis 2012). When studies fail to identify or describe characteristics of the matrix, there is a risk that differences within areas of the matrix will be overlooked (Prevedello and Vieira 2010). Such oversights may lead to over-simplified or misinterpreted conclusions about the effects of fragmentation on butterflies, which in-turn has negative impacts on the development of successful management and biodiversity conservation (Kupfer et al. 2006; Jules and Shahani 2003; Pearson et al. 1996). At the very least, it makes it impossible for readers and reviewers to assess whether the exclusion of the matrix was reasonable. Our review therefore highlights the need for studies of butterflies in fragmented landscapes to ensure clear descriptions and definitions of the matrix are provided. These definitions should use a functional resource-based approach (Dennis et al. 2003) to define what areas within the landscape really are unsuitable and hostile matrix and what land-cover elements constitute habitat for the particular species under question (Fischer et al. 2004; Dennis et al. 2006; Dennis 2012). In using such an approach, research will avoid over-simplifying the landscape (e.g. defining cleared land between native vegetation patches as a matrix despite the focal species occurring throughout both land-cover types), or identifying patches and matrix based purely on the human perspective (Lindenmayer et al. 2009; Bunnell 1999).

Inclusion/Exclusion in Experimental Design

Despite the recognition of the importance of the matrix in the broader fragmentation literature (Vandermeer and Carvajal 2001; Jules and Shahani 2003; Lindenmayer and Fischer 2006; Franklin and Lindenmayer 2009; Dover 1996; Dennis 2004), we found that 70% of studies reviewed *did not* include the matrix in their experimental design. This exclusion is of serious concern, especially as 60% of these studies were conducted in landscapes where the matrix was either similar in structure to patches or consisted of various vegetation/land-cover types and thus were highly variable. For example, Öckinger and Smith (2006), Yamaura et al. (2008) and van Halder et al. (2008) all performed research on butterflies in areas where the matrix was likely to have some features in common with habitat patches (as they were similar in structure; such as grassland patches with farmland matrix, or young pine embedded in older pine stands), but failed to include the matrix in their experimental design. Prevedello and Vieira (2010) found that in 88% of studies which examined the influence of different matrices on a range of taxa, matrices more similar to habitat patches displayed higher levels of functional connectivity for patch-associated species. Hence, it is likely that the matrix in those aforementioned studies was of higher quality for patch-associated species than studies where the matrix clearly contrasts with habitat patches (reviewed in Prevedello and Vieira 2010). Therefore, interpretations of the effects of fragmentation from such studies may be misleading, as they fail to determine whether or not the matrix may aid in the dispersal or survival of patch-associated butterflies (perhaps by providing food resources, or conversely increasing mortality rates during dispersal; e.g. Hudgens and Haddad 2003; Bender and Fahrig 2005). Failure to identify whether land-cover types surrounding native vegetation patches function as a matrix from so many of the studies presents a concerning knowledge gap. The opportunity to assess the effects and impact of the matrix on patch-associated butterfly species and communities has been overlooked.

We also found that, of those papers that did include the matrix in the experimental design, only 30% actually surveyed butterflies *within* the matrix. These papers found that matrix quality affected the ability of butterflies to disperse through, and use the spaces between, habitat fragments. The rest of the studies (70% of those that did include the matrix) only inferred conclusions about effects on butterflies from analysis of physical conditions or vegetation in the matrix. Most of these studies in fact only examined barrier effects posed by the matrix at the edges of native vegetation patches (Bukovinszky et al. 2005; Collinge et al. 2003; Cozzi et al. 2008; Krauss et al. 2005; Leidner and Haddad 2010; Ribeiro et al. 2008; Ricketts 2001; Rickman and Connor 2003; Ries and Debinski 2001; Ries and Sisk 2010; Roland et al. 2000; Schtickzelle and Baguette 2003; Schtickzelle et al. 2006; Wettstein and Schmid 1999). Such studies can therefore make conclusions only about the impact of the matrix immediately surrounding patches. Recent research has shown that within-patch dynamics are effected by the surrounding landscape on quite large spatial scales (tens of square kilometres; Bergman et al. 2004), and are not just limited to the area immediately surrounding a patch edge (e.g. Ross et al. 2005b; Didham and Ewers 2012; Kennedy et al. 2010). As such, these aforementioned experiments provide limited insight into landscape use and do little to extend our knowledge of how the matrix is used by patch-associated species (Prevedello and Vieira 2010; Kennedy et al. 2010).

Papers that included the matrix almost always found some effect of the matrix on butterfly species or communities (Table 3), predominantly related to dispersal ability and behaviour. Our findings support observations of other reviews concerned with quantitative matrix studies, which have shown that the matrix influences study parameters up to 95% of the time (Prevedello and Vieira 2010). Our results reaffirm the importance of considering the matrix in fragmentation studies to increase our understanding of populations in patchy landscapes. Further, our findings suggest that the inclusion of the matrix is important for a wider range of fragmentation studies than it is currently considered in, including those papers that we reviewed that did not consider the matrix.

Management and Future

We found that less than half of the already small number of papers that included the matrix in their study went on to provide recommendations about the management of the matrix. Most studies acknowledged that matrix heterogeneity and landscape elements that aid dispersal (presumably elements similar to those within habitat patches) should be maintained or increased (Table 4). While increasing habitat heterogeneity may inadvertently improve matrix quality for butterfly species, we suggest that management may need a more tailored approach to specifically target and successfully conserve butterfly species of interest. This is because butterflies have complex life cycles, and thus their resource requirements may change several times during their lifespan (Boggs 1992; Moran 1994; Kingsolver et al. 2011). Further, many species require the presence of specific plant species and/or ant species for survival (e.g. Fiedler and Maschwitz 1989; Dennis et al. 2004; Rodrigues et al. 2010; Forister et al. 2011).Therefore, we urge that future research should place more consideration on species-specific requirements (Dennis et al. 2006; Dennis et al. 2003) such as host-plant availability, habitat structure and the support of ant-mutualism so that butterflies are more likely to use or successfully traverse the matrix.

As landscapes become more fragmented (Gray 1997; Harrisson et al. 2012; Foley et al. 2005; Saunders et al. 1991), we need a sound understanding of how species interact with the land-cover types that dominate the patchy landscape, not just quantifications of patterns of occurrence within native fragments (Ricketts 2001; Brady et al. 2011; Prevedello and Vieira 2010). This is especially true given that the surrounding landscape can significantly influence the behaviour and, ultimately, persistence of individuals and communities in patches (Vandermeer and Carvajal 2001; Jules and Shahani 2003; Lindenmayer and Fischer 2006; Franklin and Lindenmayer 2009).

Future research in terrestrial fragmented landscapes should make concerted efforts to incorporate the matrix into experimental design, not only at patch-matrix boundaries, but to also consider responses to the matrix at larger scales. This will provide a more comprehensive understanding of the matrix, and therefore allow researchers to identify if and how areas of the matrix are used by focal species. Improving research in fragmented landscapes in these ways will allow research to better assess both the use of the matrix by patch-associated species and the role the matrix may play in mitigating the survival and behaviour of species within patches.

References

Baguette M (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. Basic Appl Ecol 5 (3):213-224. doi:10.1016/j.baae.2004.03.001

Baguette M, Mennechez G, Petit S, Schtickzelle N (2003) Effect of habitat fragmentation on dispersal in the butterfly Proclossiana eunomia. C R Biol 326, Supplement 1 (0):200-209. doi:10.1016/s1631-0691(03)00058-1

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT (2004) The Matrix Enhances The Effectiveness of Corridors and Stepping Stones Ecol 85 (10):2671-2676. doi:10.1890/04-0500

Bender DJ, Fahrig L (2005) Matrix Structure Obscures the Relationship Between Interpatch Movement and Patch Size and Isolation. Ecol 86 (4):1023-1033

Bergerot B, Julliard R, Baguette M (2010) Metacommunity Dynamics: Decline of Functional Relationship along a Habitat Fragmentation Gradient. PloS one 5 (6):e11294. doi:10.1371/journal.pone.0011294

Bergman KO, Askling J, Ekberg O, Ignell H, Wahlman H, Milberg P (2004) Landscape effects on butterfly assemblages in an agricultural region. Ecography 27 (5):619-628. doi:10.1111/j.0906-7590.2004.03906.x

Boggs CL (1992) Resource Allocation: Exploring Connections between Foraging and Life History. Funct Ecol 6 (5):508-518. doi:10.2307/2390047

Brady M, McAlpine C, Possingham H, Miller C, Baxter G (2011) Matrix is important for mammals in landscapes with small amounts of native forest habitat. Landsc Ecol 26 (5):617-628. doi:10.1007/s10980-011-9602-6

Brueckmann SV, Krauss J, van Achterberg C, Steffan-Dewenter I (2010) The impact of habitat fragmentation on trophic interactions of the monophagous butterfly Polyommatus coridon. J Insect Conserv 15 (5):707-714. doi:10.1007/s10841-010-9370-7

Bukovinszky T, Potting RPJ, Clough Y, van Lenteren JC, Vet LEM (2005) The role of pre- and post-alighting detection mechanisms in the responses to patch size by specialist herbivores. Oikos 109 (3):435-446. doi:10.1111/j.0030-1299.2005.13707.x

Bunnell FL (1999) What Habitat is an Island? In: Rochelle JA, Lehmann LA, Wisniewski j (eds) Forest Wildlife and Fragmentation Management Implications. Koninklijike Brill NV, Leiden, The Netherlands,

Chardon JP, Adriaensen F, Matthysen E (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (Pararge aegeria L.). Landsc Ecol 18 (6):561-573. doi:10.1023/a:1026062530600

Collinge SK (2009) Ecology of Fragmented Landscapes. John Hopkins University Press, Maryland

Collinge SK, Prudic KL, Oliver JC (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. Conserv Biol 17 (1):178-187. doi:10.1046/j.1523-1739.2003.01315.x

Cozzi G, Mueller CB, Krauss J (2008) How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? Landsc Ecol 23 (3):269-283. doi:10.1007/s10980-007-9178-3

Crow TR, Gustafson EG (1997) Ecosystem Management: managing natural resources in space and time. In: Kohm KA, Franklin JF (eds) Creating a forestry for the 21st century. Island Press, Covelo, pp 215-228

Debinski DM, Holt RD (2000) A Survey and Overview of Habitat Fragmentation Experiments (Sondeo y Revisión de Experimentos de Fragmentación de Hábitat). Conserv Biol 14 (2):342-355. doi:10.1046/j.1523-1739.2000.98081.x

Dennis RH, Dapporto L, Dover J, Shreeve T (2013) Corridors and barriers in biodiversity conservation: a novel resource-based habitat perspective for butterflies. Biodivers Conserv 22 (12):2709-2734. doi:10.1007/s10531-013-0540-2

Dennis RH, Shreeve T, Dyck H (2006) Habitats and Resources: The Need for a Resource-based Definition to Conserve Butterflies. Biodivers Conserv 15 (6):1943-1966. doi:10.1007/s10531-005-4314-3

Dennis RL (2012) A resource-based habitat view for conservation: butterflies in the British landscape. John Wiley & Sons,

Dennis RLH (2004) Butterfly habitats, broad-scale biotope affiliations, and structural exploitation of vegetation at finer scales: the matrix revisited. Ecol Entomol 29 (6):744-752. doi:10.1111/j.0307-6946.2004.00646.x

Dennis RLH, Hodgson JG, Grenyer R, Shreeve TG, Roy DB (2004) Host plants and butterfly biology. Do host-plant strategies drive butterfly status? Ecol Entomol 29 (1):12-26. doi:10.1111/j.1365-2311.2004.00572.x

Dennis RLH, Shreeve TG, Dyck HV (2003) Towards a Functional Resource-Based Concept for Habitat: A Butterfly Biology Viewpoint. Oikos 102 (2):417-426. doi:10.2307/3548046

Didham RK, Ewers RM (2012) Predicting the impacts of edge effects in fragmented habitats: Laurance and Yensen's core area model revisited. Biol Conserv 155 (0):104-110. doi:http://dx.doi.org/10.1016/j.biocon.2012.06.019

Dover J, Settele J (2009) The influences of landscape structure on butterfly distribution and movement: a review. J Insect Conserv 13 (1):3-27. doi:10.1007/s10841-008-9135-8

Dover JW (1996) Factors affecting the distribution of satyrid butterflies on arable farmland. J Appl Ecol 33 (4):723-734

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL (2013) Conceptual domain of the matrix in fragmented landscapes. Trends Ecol Evol 28 (10):605-613

Driscoll DA, Lindenmayer DB (2012) Framework to improve the application of theory in ecology and conservation. Ecol Monogr 82 (1):129-147. doi:10.1890/11-0916.1

Driscoll MJL, Donovan TM (2004) landscape context moderates edge effects: nesting success of Wood Thrushes in central New York. Conserv Biol 18:1330-1338

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515

Falagas ME, Pitsouni EI, Malietzis GA, Pappas G (2008) Comparison of PubMed, Scopus, web of science, and Google scholar: strengths and weaknesses. The FASEB Journal 22 (2):338-342

Fiedler K, Maschwitz U (1989) The symbiosis between the weaver ant, Oecophylla smaragdina, and Anthene emolus, an obligate myrmecophilous lycaenid butterfly. J Nat Hist 23 (4):833-846. doi:10.1080/00222938900770441

Fischer J, Lindenmayer DB, Fazey I (2004) Appreciating Ecological Complexity: Habitat Contours as a Conceptual Landscape Model. Conserv Biol 18 (5):1245-1253. doi:10.1111/j.1523-1739.2004.00263.x

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global Consequences of Land Use. Science 309 (5734):570-574. doi:10.1126/science.1111772

Forister ML, Gompert Z, Nice CC, Forister GW, Fordyce JA (2011) Ant association facilitates the evolution of diet breadth in a lycaenid butterfly. Proceedings of the Royal Society B: Biological Sciences 278 (1711):1539-1547. doi:10.1098/rspb.2010.1959

Franklin AB, Noon BR, George LT (2002) What is Habitat Fragmentation? Stud Avian Biol (25):20-29

Franklin JF, Lindenmayer DB (2009) Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Sciences 106 (2):349-350. doi:10.1073/pnas.0812016105

Franzén M, Ranius T (2004) Occurrence patterns of butterflies (Rhopalocera) in semi-natural pastures in southeastern Sweden. Journal for Nature Conservation 12 (2):121-135. doi:http://dx.doi.org/10.1016/j.jnc.2004.06.001

Gascon C, Lovejoy TE, Bierregaard Jr RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species richness in tropical forest remnants. Biol Conserv 91 (2–3):223-229. doi:10.1016/s0006-3207(99)00080-4

Goodwin BJ, Fahrig L (2002) How does landscape structure influence landscape connectivity? Oikos 99 (3):552-570. doi:10.1034/j.1600-0706.2002.11824.x

Gray JS (1997) Marine biodiversity: patterns, threats and conservation needs. Biodiversity and Conservation 6 (1):153-175. doi:10.1023/a:1018335901847

Gutierrez D, Thomas CD, Leon-Cortes JL (1999) Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (Erynnis tages). Oecologia 121 (4):506-517. doi:10.1007/s004420050957

Hall LS, Krausman PR, Morrison ML (1997) The Habitat Concept and a Plea for Standard Terminology. Wildl Soc Bull 25 (1):173-182. doi:10.2307/3783301

Harrisson K, Pavlova A, Amos J, Takeuchi N, Lill A, Radford J, Sunnucks P (2012) Fine-scale effects of habitat loss and fragmentation despite large-scale gene flow for some regionally declining woodland bird species. Landsc Ecol 27 (6):813-827. doi:10.1007/s10980-012-9743-2

Hudgens Brian R, Haddad Nick M (2003) Predicting Which Species Will Benefit from Corridors in Fragmented Landscapes from Population Growth Models. The American Naturalist 161 (5):808-820. doi:10.1086/374343

Jauker F, Diekötter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landsc Ecol 24 (4):547-555. doi:10.1007/s10980-009-9331-2

Jorge SM (1992) Island Biogeography and Conservation Practice. Conserv Biol 6 (2):161-161. doi:10.1046/j.1523-1739.1992.620161.x

Jules ES, Shahani P (2003) A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. Journal of Vegetation Science 14 (3):459-464. doi:10.1111/j.1654-1103.2003.tb02172.x

Kennedy CM, Marra PP, Fagan WF, Neel MC (2010) Landscape matrix and species traits mediate reponses of Neotropical resident birds to forest fragmentation in Jamaica. Ecol Monogr 80 (4):651-669

Kingsolver JG, Arthur Woods H, Buckley LB, Potter KA, MacLean HJ, Higgins JK (2011) Complex Life Cycles and the Responses of Insects to Climate Change. Integrative and Comparative Biology 51 (5):719-732. doi:10.1093/icb/icr015

Krauss J, Schmitt T, Seitz A, Steffan-Dewenter I, Tscharntke T (2004) Effects of habitat fragmentation on the genetic structure of the monophagous butterfly Polyommatus coridon along its northern range margin. Mol Ecol 13 (2):311-320. doi:10.1046/j.1365-294X.2003.02072.x

Krauss J, Steffan-Dewenter I, Muller CB, Tscharntke T (2005) Relative importance of resource quantity, isolation and habitat quality for landscape distribution of a monophagous butterfly. Ecography 28 (4):465-474. doi:10.1111/j.0906-7590.2005.04201.x

Krauss J, Steffan-Dewenter I, Tscharntke T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J Biogeogr 30 (6):889-900. doi:10.1046/j.1365-2699.2003.00878.x

Kremen C (1994) Biological Inventory Using Target Taxa: A Case Study of the Butterflies of Madagascar. Ecol Appl 4 (3):407-422

Kuefler D, Hudgens B, Haddad NM, Morris WF, Thurgate N (2010) The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecol 91 (4):944-950. doi:10.1890/09-0614.1

Kupfer JA, Malanson GP, Franklin SB (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Glob Ecol Biogeogr 15 (1):8-20. doi:10.1111/j.1466-822X.2006.00204.x

Leidner AK, Haddad NM (2010) Natural, not urban, barriers define population structure for a coastal endemic butterfly. Conserv Genet 11 (6):2311-2320. doi:10.1007/s10592-010-0117-5

Lindenmayer DB, Fischer J (2006) Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis. CSIRO Publishing, Canberra, Australia

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington

Lindenmayer DB, Wood JT, Cunningham RB, Crane M, Macgregor C, Michael D, Montague-Drake R (2009) Experimental evidence of the effects of a changed matrix on conserving biodiversity within patches of native forest in an industrial plantation landscape. Landsc Ecol 24 (8):1091-1103. doi:10.1007/s10980-008-9244-5

Lomov B, Keith DA, Britton DR, Hochuli DF (2006) Are butterflies and moths useful indicators for restoration monitoring? A pilot study in Sydney's Cumberland Plain Woodland. Ecol Manag Restor 7 (3):204-210. doi:10.1111/j.1442-8903.2006.00310.x

Moran NA (1994) Adaptation and Constraint in the Complex Life Cycles of Animals. Annu Rev Ecol Syst 25 (ArticleType: research-article / Full publication date: 1994 / Copyright © 1994 Annual Reviews):573-600. doi:10.2307/2097325

Muriel SB, Kattan GH (2009) Effects of Patch Size and Type of Coffee Matrix on Ithomiine Butterfly Diversity and Dispersal in Cloud-Forest Fragments. Conserv Biol 23 (4):948-956. doi:10.1111/j.1523-1739.2009.01213.x

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol Lett 13 (8):969-979. doi:10.1111/j.1461-0248.2010.01487.x

Ockinger E, Smith HG (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. Oecologia 149 (3):526-534. doi:10.1007/s00442-006-0464-6

Öckinger E, Van Dyck H (2012) Landscape Structure Shapes Habitat Finding Ability in a Butterfly. PloS one 7 (8):e41517. doi:10.1371/journal.pone.0041517

Payne RW, Harding SA, Murray DA, Soutar DM, Baird DB, Glaser AI, Welham SJ, Gilmour AR, Thompson R, Webster R (2011) GenStat Release 14. VSN International, Hemel Hempstead, Hertfordshire HP1 1ES, UK

Pearson SM, Turner MG, Gardner RH, O'Neill RV (1996) An Organism-Based Perspective of Habitat Fragmentation. In: Szaro RC, johnston DW (eds) Principles of Biodiversity. Oxford University Press, New York, pp 77-95

Prevedello J, Vieira M (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodiversity & Conservation 19 (5):1205-1223. doi:10.1007/s10531-009-9750-z

Prudic KL, Khera S, Solyom A, Timmermann BN (2007) Isolation, identification, and quantification of potential defensive compounds in the viceroy butterfly and its larval host-plant, Carolina willow. J Chem Ecol 33 (6):1149-1159. doi:10.1007/s10886-007-9282-5

Revilla E, Wiegand T, Palomares F, Ferreras P, Delibes M (2004) Effects of Matrix Heterogeneity on Animal Dispersal: From Individual Behavior to Metapopulation-Level Parameters. The American Naturalist 164 (5):E130-E153. doi:10.1086/424767

Ribeiro DB, Prado PI, Brown KS, Jr., Freitas AVL (2008) Additive partitioning of butterfly diversity in a fragmented landscape: importance of scale and implications for conservation. Divers Distrib 14 (6):961-968. doi:10.1111/j.1472-4642.2008.00505.x

Ricketts TH (2001) The Matrix Matters: Effective Isolation in Fragmented Landscapes. The American Naturalist 158 (1):87-99

Rickman JK, Connor EF (2003) The effect of urbanization on the quality of remnant habitats for leaf-mining lepidoptera on Quercus agrifolia. Ecography 26 (6):777-787

Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology 70 (5):840-852. doi:10.1046/j.0021-8790.2001.00546.x

Ries L, Sisk TD (2010) What is an edge species? The implications of sensitivity to habitat edges. Oikos 119 (10):1636-1642. doi:10.1111/j.1600-0706.2010.18414.x

Rodrigues D, Kaminski L, Freitas AL, Oliveira P (2010) Trade-offs underlying polyphagy in a facultative ant-tended florivorous butterfly: the role of host plant quality and enemy-free space. Oecologia 163 (3):719-728. doi:10.1007/s00442-010-1626-0

Roland J, Keyghobadi N, Fownes S (2000) Alpine *Parnassius* Butterfly Dispersal: Effects of Landscape and Population Size. Ecol 81 (6):1642-1653

Ross JA, Matter SF, Roland J (2005a) Edge avoidance and movement of the butterfly <i>Parnassius smintheus</i> in matrix and non-matrix habitat. Landsc Ecol 20 (2):127-135. doi:10.1007/s10980-004-1010-8

Ross JA, Matter SF, Roland J (2005b) Edge avoidance and movement of the butterfly *Parnassius smintheus* in matrix and non-matrix habitat. Landsc Ecol 20 (2):127-135. doi:10.1007/s10980-004-1010-8

Saunders DA, Hobbs RJ, Margules CR (1991) Biological Consequences of Ecosystem Fragmentation: A Review. Conserv Biol 5 (1):18-32. doi:10.1111/j.1523-1739.1991.tb00384.x

Schtickzelle N, Baguette M (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. J Anim Ecol 72 (4):533-545. doi:10.1046/j.1365-2656.2003.00723.x

Schtickzelle N, Mennechez G, Baguette M (2006) Dispersal depression with habitat fragmentation in the bog fritillary butterfly. Ecol 87 (4):1057-1065

Schwab AC, Zandbergen PA (2011) Vehicle-related mortality and road crossing behavior of the Florida panther. Applied Geography 31 (2):859-870. doi:http://dx.doi.org/10.1016/j.apgeog.2010.10.015

Simberloff DS, Abele LG (1976) Island Biogeography Theory and Conservation Practice. Science 191 (4224):285-286

Stasek DJ, Bean C, Crist TO (2008) Butterfly Abundance and Movements Among Prairie Patches: The Roles of Habitat Quality, Edge, and Forest Matrix Permeability. Environmental Entomology 37 (4):897-906. doi:10.1603/0046-225x(2008)37[897:baamap]2.0.co;2

Steffan-Dewenter I, Tscharntke T (2002) Insect communities and biotic interactions on fragmented calcareous grasslands,Äîa mini review. Biol Conserv 104 (3):275-284. doi:10.1016/s0006-3207(01)00192-6

Summerville KS, Crist TO (2001) Effects of Experimental Habitat Fragmentation on Patch Use by Butterflies and Skippers (Lepidoptera) Ecol 82 (5):1360-1370. doi:doi:10.1890/0012-9658(2001)082[1360:EOEHFO]2.0.CO;2

Turner MG (2005) Landscape Ecology: What Is the State of the Science? Annual Review of Ecology, Evolution, and Systematics 36 (ArticleType: research-article / Full publication date: 2005 / Copyright © 2005 Annual Reviews):319-344. doi:10.2307/30033807

van Halder I, Barbaro L, Corcket E, Jactel H (2008) Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. Biodiversity & Conservation 17 (5):1149-1169. doi:10.1007/s10531-007-9264-5

Vandermeer J, Carvajal R (2001) Metapopulation Dynamics and the Quality of the Matrix. The American Naturalist 158 (3): 211-220

Warren M, Bourn N (2011) Ten challenges for 2010 and beyond to conserve Lepidoptera in Europe. J Insect Conserv 15 (1):321-326. doi:10.1007/s10841-010-9356-5

Weiss SB, Murphy DD, White RR (1988) Sun, Slope, and Butterflies: Topographic Determinants of Habitat Quality for Euphydryas Editha. Ecol 69 (5):1486-1496. doi:10.2307/1941646

Wettstein W, Schmid B (1999) Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J Appl Ecol 36 (3):363-373. doi:10.1046/j.1365-2664.1999.00404.x

Yamaura Y, Kawahara T, Iida S, Ozaki K (2008) Relative Importance of the Area and Shape of Patches to the Diversity of Multiple Taxa. Conserv Biol 22 (6):1513-1522. doi:10.1111/j.1523-1739.2008.01024.x