***Encyclopedia of Life Sciences* A21904**

The ecological consequences of habitat fragmentation

Raphael K. Didham[1,2,3]

[1]School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia

[2]CSIRO Entomology, Centre for Environment and Life Sciences, Underwood Ave, Floreat WA 6014, Australia

[3]School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

[*]**Correspondence:** Professor Raphael K. Didham, raphael.didham@uwa.edu.au, raphael.didham@csiro.au, Ph. +61 (0)8 9333 6762

Abstract

Habitat fragmentation is the process by which habitat loss results in the division of large, continuous habitats into smaller, more isolated habitat fragments. Habitat fragmentation is one of the most important processes contributing to population decline, biodiversity loss, and alteration of community structure and ecosystem functioning in anthropogenically-modified landscapes. Many thousands of individual scientific studies now show unequivocal evidence for the impacts of patch area, edge effects, patch shape complexity, isolation, and landscape matrix contrast on population and community dynamics in mosaic landscapes. However, striking disparities in the results of individual studies across differing taxa and differing ecosystems have raised considerable debate about the relative importance of the different mechanisms underlying fragmentation effects, and even debate about the utility of the ‘habitat fragmentation’ concept in general. Resolution of this debate lies in clear discrimination of the direct and indirect causal relationships among patch versus landscape variables. The most important recent advances in our understanding of the ecological effects of habitat fragmentation all stem from recognition of the strong context dependence of ecosystem responses, including spatial context dependence at multiple scales, time lags in population decline, trait dependence in species responses, and synergistic interactions between habitat fragmentation and other components of global environmental change.

Keywords: connectivity, context dependence, edge effects, extinction debt, habitat area, habitat fragmentation, habitat loss, isolation, landscape structure, matrix contrast, patch shape, species traits, synergistic interactions.

Introduction

All ecosystems are heterogeneous at some spatial scale. One of the greatest advances in theoretical ecology has been the realisation that spatial heterogeneity in environmental conditions can fundamentally alter the outcome of species interactions and community dynamics (Holt, 1984; Pickett & Cadenasso, 1995). Where patches of suitable versus unsuitable habitat occur in a heterogeneous mosaic at spatial scales that are relevant to resource acquisition, dispersal, reproduction, mortality, or other components of individual fitness, then heterogeneity will impose selective pressures on organisms to adapt to spatial patchiness in the landscape. In natural mosaic landscapes, organisms have been able to adapt to the patchiness of available habitat over evolutionary time scales (e.g., through traits that confer increased dispersal ability, or decreased resource specialisation), but this has not typically been the case in landscapes modified by recent human influence. In anthropogenically-modified landscapes, humans have been destroying habitat at rates that are without precedent in the Earth's evolutionary history (Skole & Tucker, 1993) – rates that far exceed the capacity for most species to adapt and respond to the decreasing availability and increasing patchiness of suitable habitat (Pimm *et al.*, 1995; Myers & Knoll, 2001). '*Habitat fragmentation*', then, is an expression of the impact that rapid human alteration of the spatial structure of the landscape has on ecological communities.

It is important to remember that habitat fragmentation represents just one subset of factors that are more broadly encompassed under the impacts of global land-use change (Foley *et al.*, 2005). Land-use change refers to all components of change in the quantity and quality of land cover types as habitat for organisms and productive land for humans. Although it would be tempting to portray fragmentation of natural land cover types as the 'quantity' component of land-use change (i.e. the amount and spatial arrangement of natural habitat remnants), and production intensity on modified land cover types as the ‘quality’ component (i.e. the increase or optimisation of inputs such as agrichemicals, fertilizer, water and energy to maximise production outputs such as food, materials or human living space), the reality is that there is no such simple dichotomy of effects in modified landscapes. Habitat fragmentation and land-use intensification are integrally intertwined (Figure 1). Patterns of habitat fragmentation have substantial effects on both internal habitat quality and external crop production by humans, while at the same time patterns of land-use intensification impose strong spatial structuring on communities in habitat remnants. Within the habitat fragmentation literature, these interaction effects are typically dealt with by ignoring the explicit mechanics of land management trade-offs that exist between maximisation of production and minimisation of biodiversity loss, and simply treating land-use intensification as one component of the external influences of the surrounding land-use matrix on processes occurring within habitat remnants. This is not to say that these effects are considered unimportant, but rather that emphasis is placed on the mechanistic details of patch dynamics within production landscapes (a conservation-centred approach), as opposed to the mechanistic details of how land-use productivity can be maximised while minimising biodiversity loss (a sustainable production-centred approach).

Defining habitat fragmentation

The fragmentation concept – pattern or process?

Most authors define habitat fragmentation as the *process* by which habitat loss results in the division of large, continuous habitats into a greater number of smaller patches of lower total area, isolated from each other by a matrix of dissimilar habitats (modified from Wilcove *et al.*, 1986; Ranta *et al.*, 1998; Franklin *et al.*, 2002; Ewers & Didham, 2006a). This integrates changes in the amount of remaining habitat as well as changes in the spatial arrangement of that habitat under the same ‘umbrella’ term (Figure 2A). However, other authors have argued that the term habitat fragmentation should be much more restricted in usage.

Some authors consider that fragmentation should be restricted to describing just one of five precise ways in which individual units of habitat are broken up (perforation, dissection, fragmentation, shrinkage or attrition; Forman, 1995; Collinge, 2009) because each process has a different ecological effect. While this may be true in some instances, there are serious limitations to any straight-forward separation of these small-scale processes, because perforation, for example, might be a transient precursor to dissection of habitat, which is itself a precursor to fragmentation, following which each subdivided piece of the dissected habitat might be subject to shrinkage and attrition. Clearly, a small-scale reductionist approach such as this is not helpful unless it is placed within a larger framework of spatial and temporal changes at the landscape scale.

Other authors have recognised fragmentation as a landscape-scale process, but have argued strongly for a dichotomy to be raised between habitat amount and habitat fragmentation as two separate, and independent, effects on biodiversity in fragmented landscapes (Fahrig, 2003). Because all quantitative measures of spatial dispersion of habitat increase strongly with decreasing habitat amount in the landscape, Fahrig (2003) and others have argued that the ‘independent’ effects of habitat fragmentation can only be determined after first taking into account the effects of habitat amount remaining in the landscape (Fahrig, 2003). Effectively, these studies are arguing that fragmentation is not the key process operating in fragmented landscapes – the key process is total habitat loss, irrespective of its dispersion in space – and fragmentation should instead be restricted to describing the *pattern* of spatial arrangement of remaining patches in the landscape following habitat loss (Figure 2B).

There is undoubtedly strong merit in explicitly considering the importance of habitat amount in the landscape. Many, if not most, earlier studies of ‘fragmentation’ simply sampled a few individual habitat patches and attributed all ecological effects to the spatial configuration of the patches, without considering that some or all of these effects might actually have been intercorrelated with other mechanisms related to the total amount of habitat remaining in the landscape (Fahrig, 2003). On the other hand, the key conclusion of Fahrig (2003) and others, that habitat fragmentation has a negligible effect on biodiversity after habitat amount is taken into account represents a striking paradox when placed alongside the many thousands of studies showing strong ecological effects of patch area, isolation, edge effects and other factors. Reconciling this paradox requires explicit consideration of the direct and indirect causal relationships between patch and landscape variables.

The underlying drivers of fragmentation - (pen)ultimate or proximate?

Consider a simple analogy for the debate about the ‘independent’ effects of habitat amount versus habitat fragmentation per se: if land-use change goes hand in hand with human population increase – that is, the two are completely intercorrelated with each other – can we better understand the mechanistic effects of land-use change by concluding that human population increase is the driver of change? The obvious answer is no. These drivers are interlinked in a chain of *ultimate* versus *proximate* causality, and mechanistic understanding only comes from identifying the proximate variables mediating the effect (Didham *et al.*, 2005). The same line of reasoning applies to the intercorrelation observed between decreasing habitat amount and increasing habitat fragmentation in modified landscapes (Figure 3A). Although habitat loss might ultimately (perhaps penultimately, if socioeconomic human drivers are also considered to) be responsible for ecological effects in modified landscapes, this does not improve mechanistic understanding without quantifying how these effects are indirectly mediated by the altered spatial arrangement of habitat remnants (Figure 3B). Habitat loss acts *via* the change in habitat arrangement, not *independently* of it. The direction of causality, and the temporal sequence of events, is clearly from habitat loss to the resulting change in spatial arrangement and not the other way around, although even some very influential publications have confused the direction of causality in some instances, suggesting that "habitat loss and isolation... may result from, rather than [equate to], fragmentation"; Forman, 1995, p.412). Of course, there can be very strong feedback effects between these processes, as in cases where linear features such as roads or powerline corridors initially create only a small amount of habitat loss, but result in increased edge effects and isolation effects (as well as increased human access) that might feedback on increased rates of habitat loss.

The relevance of fragmentation to conservation management – panchreston or paradigm?

Despite (or perhaps because of) the debate about how to properly define habitat fragmentation, and the vast and ever-growing literature on the separate effects of patch area, edge effects, patch shape complexity, isolation, and landscape matrix contrast, there is still a definite need within conservation management for a single umbrella term to fully encompass all of the patterns, processes and consequences of habitat change in modified landscapes. This umbrella term could either be 'habitat loss' or 'habitat fragmentation', and it would not matter which, as long as the underlying causal structure of variables is recognised (Figure 2b). Thus far habitat fragmentation has been the term that has resonated most widely across the literature, in both a colloquial and a scientific sense. Far from habitat fragmentation being a '*panchreston*' – an archaic term that Lindenmayer & Fischer (2007) used to denote fragmentation as a theory that is "made to fit all cases" and "used in such a variety of ways as to become meaningless" – habitat fragmentation remains the most useful *paradigm* in conservation management for describing the series of interlinked processes occurring in modified landscapes and for enhancing communication among disciplines and the public (Ewers & Didham, 2007b).

Patch dynamics in mosaic landscapes

Perhaps the greatest value of the seminal work by Fahrig (2003) is that she has cemented fragmentation as the landscape-level phenomenon that it truly is, not as a patch-level phenomenon. Much of what the study of habitat fragmentation is concerned with today is the ecological consequences of land-use change for organisms living in networks of remnant patches surrounded by a mosaic of modified or novel land use types. This was not always the case, though. The historical roots of habitat fragmentation are embedded in the stochastic spatial model of Island Biogeography Theory (IBT) (MacArthur & Wilson, 1967), which in its strictest form considers just patch area and isolation, incorporates no external influence beyond the probabilistic arrival of colonists across an inhospitable matrix and no internal patch dynamics beyond probabilistic extinction rates, and is 'neutral' to species identities or functional traits. Much has been made about the lack of relevance of habitat fragmentation to landscape ecology because this underlying basis of IBT does not fit the complexity of anthropogenically-modified landscapes, where strong external influences on patches are paramount, and there is a blurring of the boundaries between what constitutes the 'patch' and the 'matrix' from the niche perspective of an organism (Haila, 2002; Laurance, 2008). However, the reality is that this argument is a 'straw man' in many ways – a situation that never actually exists, but is set up simply to be falsified. There are no studies today that assume a strict IBT framework, and all researchers recognise the external influence of the surrounding matrix and the effects of variation in habitat quality and internal patch dynamics on remnant populations. Perhaps in this sense, the criticisms of early IBT approaches have been well heeded, and ‘mainstream’ habitat fragmentation studies are much more akin to studies in other branches of landscape ecology than ever before.

Within the wider discipline, the five key indirect drivers of fragmentation effects are ever more intensively studied, highlighting new aspects to the mechanistic basis for the effects of altered spatial arrangement of habitat on population and community dynamics (for more detailed discussion of these processes see reviews by Saunders *et al.*, 1991; Andrén, 1997; Didham, 1997; Tscharntke *et al.*, 2002; Henle *et al.*, 2004; Ries *et al.*, 2004; Ewers & Didham, 2006a; Kupfer *et al.*, 2006; Banks-Leite & Ewers, 2009; Collinge, 2009).

Reduced patch area

Reduction in the total amount of habitat in the landscape inevitably leads to a strongly skewed size distribution of remaining habitat patches, with many small patches and few large patches (Ranta *et al.*, 1998; Ewers & Didham, 2007a). The ecological effects of reduction in patch area are more widely studied than for any other variable, except perhaps edge effects, and this is largely attributable to the very long heritage of scientific interest in the underlying causes of the species-area relationship (Lomolino, 2000). Species-area relationships have been widely studied in the context of habitat fragmentation as well (Seabloom *et al.*, 2002; Ewers & Didham, 2006a), although this can be a contentious area of investigation (Simberloff, 1992). Conceptually, any changes in species richness at the patch level are best considered as an emergent property (or net outcome) of all the population-level and community-level changes that combine to alter species occupancy in fragmented landscapes.

First, at the population level, the effect of altered spatial arrangement of habitat on the distribution and abundance of individuals is the explicit theoretical domain of metapopulation ecology (Hanski, 1998). Reduced patch area limits resource availability, reduces colonisation rates, alters reproductive success, and imposes an intrinsic constraint on maximum population size. At the extreme, this exposes populations to an increased risk of local extinction (Hanski & Ovaskainen, 2000). The underlying mechanisms driving this relationship can be divided into four categories – environmental stochasticity, demographic stochasticity, natural catastrophes and reduced genetic diversity (Hanski & Gaggiotti, 2004) – but all four processes have the potential to interact, creating what have been described as "extinction vortices" (Gilpin & Soulé, 1986). These processes lie at the heart of population viability analysis (Beissinger & McCullough, 2002), which comprises a set of analytical and modelling techniques for predicting the probability of species extinction

Second, at the community level, there are typically large changes in species composition associated with reduction in patch area (Saunders *et al.*, 1991; Ewers & Didham, 2006a), as different species have widely varying resource and area requirements, and differing dispersal abilities. For instance, highly dispersive ground beetles are less affected by area reduction than less dispersive groups, because increased dispersal rates can lead to the 'rescue' of small populations that would otherwise have high extinction rates in small patches (de Vries et al. 1996). Because species with differing responses to patch area frequently interact with one another (e.g. via predator-prey or competitive interactions), there is no simple way to predict the community-level outcome of fragmentation from the sum of individual metapopulation models. The incorporation of species interactions into the spatial context of metapopulations is the theoretical domain of metacommunity ecology (Leibold *et al.*, 2004; Gonzalez, 2009). Metacommunity ecology has been responsible for the most significant re-invigoration of spatial ecology in recent years, and is increasingly seen as the theoretical underpinning to the study of habitat fragmentation (Gonzalez, 2009).

Finally, the net outcome of altered population and community dynamics is a characteristic reduction in species richness in small habitat patches (Figure 4A) (Ewers & Didham, 2006a). There are many potential explanations for a net positive species-area relationship such as this, including strong influences of reduced habitat heterogeneity, reduced resource concentration, increased disturbance, or altered colonisation-extinction dynamics (i.e. IBT) in small patches (or more likely a combination of these factors operating on different species). Unlike oceanic island systems, however, species-area relationships across habitat patches frequently show no net relationship, or even a negative relationship (Cook *et al.*, 2002; Ewers *et al.*, 2007) when there is an over-riding influence of external variables, such as context-dependence in the effects of the surrounding landscape matrix on the ability of species to invade and occupy small patches.

Increased edge effects

Habitat loss and reduction in patch area increase the proportion of habitat edge in the landscape, and expose fragment interiors to external influence (Didham, 1997). Edge effects describe the transition in abiotic and biotic variables that occurs across the boundary between adjacent land-use types (Cadenasso *et al.*, 2003). Edges are typically hotter, drier and windier than the interior of patches, with a higher light intensity and modified plant composition and habitat structure (Matlack, 1994; Williams-Linera *et al.*, 1998; Chen *et al.*, 1999; Harper *et al.*, 2005). These changes have pronounced effects on patterns of habitat use and the relative abundance of animals at patch edges as well (Ries *et al.*, 2004). Species richness typically increases at the edge, sometimes dramatically so for many invertebrate taxa (Didham, 1997;

Ewers *et al.*, 2007), and there can be substantial turnover in species composition (Ewers & Didham, 2008). Ultimately, changes in both species richness and composition are a composite of individual species responses, which are extremely varied both within and between studies (Didham *et al.*, 1998; Davies *et al.*, 2000). As a generality, though, high species richness at edges is typically a result of species influx from adjacent disturbed habitats, whereas patch specialists typically decline at edges (Figure 4B).

A continued problem in interpreting these types of ecological edge effects is that most studies have taken a 'one-sided' approach focusing on the internal dynamics of patch edges, without considering the 'two-sided' nature of edge dynamics (Fonseca & Joner, 2007; Ewers & Didham, 2008). This is particularly surprising as most drivers of edge effects originate external to the patch. Moreover, because of some curious properties of factors such as shading, wind turbulence, and spillover effects, the observed edge response for some variables may actually occur well outside the structural vegetation edge of the patch (Cadenasso *et al.*, 1997), and therefore be missed entirely if sampling only occurs within the patch. More generally speaking, the two-sided approach to edge studies places better emphasis on the fact that edges are three-dimensional zones of transition between habitats (Cadenasso *et al.*, 2003), and have no absolute quantifiable dimensions unless comparisons are made relative to both the adjacent patch and matrix interiors.

The other major recent advance in the study of edge effects is recognition that quantification of edge impact requires explicit discrimination of two quite distinct components of edge influence: edge extent (i.e. the distance over which a statistical difference in response can be detected between the matrix and the patch) and edge magnitude (i.e. the degree of difference in response between the patch interior and the matrix interior) (Harper *et al.*, 2005; Ewers &

Didham, 2006b). For example, a particular edge response with a large extent but a small magnitude of effect might not be considered to be as important, ecologically speaking, as an edge response with a small extent, but a very large magnitude. The majority of previous studies have focused on edge extent, rather than edge magnitude, even though it is the more difficult variable to quantify (Ewers & Didham, 2006b). There are probably as many rules of thumb about the distance of edge influence as there are edge studies (e.g., Skole & Tucker, 1993; Young & Mitchell, 1994; Chen *et al.*, 1999). However, it is worth pointing out that the reliability of these estimates is highly questionable, as most studies are limited in taking a one-sided approach to the measurement of edge effects (Fonseca & Joner, 2007), most lack the appropriate statistical rigour to determine edge extent reliably (Ewers & Didham, 2006b), and edge extent is notoriously variable between different response variables and different edge types (Laurance *et al.*, 2002). Edge extent can vary from a few metres up to a kilometre or more for different response variables (Ewers & Didham, 2008), and despite thousands of individual studies of edge effects there has been relatively little progress toward understanding the factors that determine edge extent (let alone appropriate integration of edge extent and edge magnitude).

Altered patch shape

Shape complexity is a patch attribute that has been extremely poorly studied in comparison to other components of habitat fragmentation (Ewers & Didham, 2006a). Fragments with complex shapes have a much higher proportion of total fragment area that is edge, rather than core habitat (Laurance & Yensen, 1991), and this has two important ecological consequences. First, patches with higher shape complexity may have correspondingly higher patch colonisation rates, and higher patch emigration rates, and this can cause greater variability in population size and a decreased probability of population persistence (Hamazaki, 1996;

Collinge & Palmer, 2002; Cumming, 2002). Second, shape complexity accentuates the extent to which edge effects permeate habitat patches (Collinge, 1996), reducing core area for patch specialists. These effects are likely to be particularly severe for linear patch features, such as strips of remnant vegetation along riparian zones. Surprisingly, these effects are also of special concern for the world's largest nature reserves. Recent studies suggest that a characteristic feature of fragmented landscapes is that shape complexity increases exponentially with increasing patch area (Ewers & Didham, 2007a), so that very large patches contain far less core area than might otherwise be expected. Furthermore, the highly convoluted nature of very large patches can result in the division of core habitat into multiple, disjunct core areas that are separated by regions of edge-affected habitat (Ewers & Didham, 2007a). Population estimates based on a literature review of the density-area relationship (Connor *et al.*, 2000) showed that disjunct cores in large fragments can reduce population size to one-fifth of that which could be supported if core habitat were continuous (Ewers & Didham, 2007a). Taken together, the assumption is that these processes will lead to increased species loss in patches with higher shape complexity (Figure 4C), but this has not been well studied.

Increased patch isolation

Patch isolation – and its converse, patch connectivity – are not absolute quantities, rather there are degrees of isolation in both time and space depending on the dispersal traits of the species in question and their ability to cross the intervening matrix between patches. As habitat loss increases in the landscape, both time since isolation and distance of isolation increase in concert, and this can make it difficult to distinguish their effects (Saunders *et al.*, 1991). Immediately after isolation, a patch will typically contain far more species than will be able to maintain viable populations in the long term, and species richness will decline through time in a process called ‘species relaxation’ (Brooks *et al.*, 1999). The time course of relaxation depends greatly on the initial population size in the patch and the average longevity of the organism, so can vary from months up to hundreds of years in the case of long-lived trees (Vellend *et al.*, 2006). Time of isolation can also be a significant factor confounding comparisons of species diversity or composition between different patches if some patches have been isolated for substantially longer than other patches.

The effects of time since isolation interact strongly with distance of isolation, as a narrow spatial separation between patches may represent only a limited barrier to some organisms, and allow populations to survive in the patch over the long term, when this might not otherwise be the case in a more spatially isolated patch. However, gap or matrix crossing abilities are highly variable between species. An extreme example of this was highlighted by Bhattacharya *et al.* (2003) who found that two species of *Bombus* bumblebees would rarely cross roads or railways despite the presence of suitable habitat that was within easy flying range. Because some matrix habitats inhibit dispersal more than others (see Roland *et al.*, 2000; Ricketts, 2001) and because species differ in their ability to disperse through matrix environments (Haddad & Baum, 1999; Collinge, 2000), the literature is full of seemingly disparate results regarding the effects of spatial isolation on species and communities (Ewers & Didham, 2006a). The most important conclusions from these studies are that spatial isolation effects can depend as strongly on the structure of edge habitats as on the permeability of the surrounding landscape, and the nature of species responses can depend as much on behavioural predisposition to disperse as on physical ability to traverse large distances.

Within conservation management, habitat corridors (either retained or restored) have been widely promoted as a means of maintaining species diversity (Hilty *et al.*, 2006) based on the general principle that more connected patches have lower species loss rates than more isolated patches (Figure 4D). Although there has been considerable debate over the potential disadvantages of corridors, such as facilitation of the spread of disease, invasive species, fire disturbance, and other threatening processes (Saunders & Hobbs, 1991), a wealth of studies ranging from small-scale moss microecosystems (Gilbert *et al.*, 1998) to large-scale forested landscapes (Damschen *et al.*, 2006) now show that corridors can increase population abundance and species diversity in habitat patches, and even have a significant effect on the outcome of species interactions and ecosystem functioning in fragmented landscapes (Tewksbury *et al.*, 2002; Levey *et al.*, 2005).

Altered matrix structure

The ‘matrix’ is a term broadly used to describe the human-modified land-use types surrounding remnant habitat patches, but variation in the structure and importance of the matrix for different species defies any simple dichotomy in attributes between ‘patch’ and ‘matrix’. For many species, human-modified land-use types provide supplementary or complementary resources that may compensate for limited resource availability in habitat patches (Ries *et al.*, 2004). Strictly speaking, then, there is no dividing line between what is a ‘patch’ and what is a ‘matrix’ in these cases, and some species may well perceive the whole landscape as ‘habitat’ and there would be no ‘matrix’ per se. However, it is likely that even in these cases habitat quality will still vary spatially in relation to the spatial distribution of dominant land-use types. For example, Perfecto & Vandermeer (2002) demonstrated that ants inhabiting forest patches in Mexican coffee plantations were actively foraging in the surrounding coffee ‘matrix’ and that some species were even able to survive in this land-use type in perpetuity. Furthermore, an increase in ‘matrix’ quality was associated with an increase in the number of species and individuals that occurred there (Perfecto & Vandermeer, 2002).

A growing body of evidence suggests that matrix quality is crucially important in determining the abundance and composition of species within habitat patches (Gascon *et al.*, 1999; Cook *et al.*, 2002). Matrix properties can affect the dispersal and movement of individuals between patches (Gascon *et al.*, 1999; Davies *et al.*, 2001), and the degree of structural contrast between patch and matrix determines the permeability of habitat edges to propagule movement (Collinge & Palmer, 2002), which taken together can be the prime determinants of colonisation-extinction dynamics (Brotons *et al.*, 2003; Kupfer *et al.*, 2006) and species loss (Figure 4E). For these reasons the study of matrix structure is frequently seen as the most important avenue for building a synthesis between patch and landscape perspectives on habitat fragmentation. At the same time, modification of matrix quality in order to facilitate dispersal, increase population size and increase the probability of population persistence at both patch and landscape scales is seen as a viable practical strategy for conservation management (Donald & Evans, 2006).

Confounding factors in the determination of species responses to habitat fragmentation

With the burgeoning fragmentation literature (Collinge, 2009) it is becoming ever more difficult to interpret the huge number of case-specific ‘exceptions’ to the typical patterns of response to fragmentation described above. In some cases the reason for this is that many supposedly well-accepted generalities were actually founded on relatively weak evidence in the first place. In other cases, the weight of evidence still supports perceived generalities, but disparate results point to the need for a fundamental reconsideration of what we understand about the mechanistic bases for fragmentation effects. In a recent review, Ewers & Didham (2006a) provide a structured framework for interpreting the very large number of factors that have been observed to confound straight-forward determination of the causal processes underlying species responses to fragmentation. These factors include the degree of context-dependence in the effects of individual components of fragmentation, the degree of temporal dependence in ecological responses, the degree of trait-dependence of observed species responses, and the degree to which fragmentation effects are dependent on, or interact with, other components of global environmental change. Most of these areas remain entirely unexplored, and represent the cutting edge of fragmentation research, and yet it is now clear that understanding context-dependence, in all its many forms, will be crucial to understanding the fragmentation process as a whole.

Interactions between multiple drivers of fragmentation

Recognition that "the matrix matters" (Ricketts, 2001) to our understanding of patch dynamics is tacit acknowledgement that patch processes are dependent on, or interact with, matrix context. Similar recognition of the interaction between matrix structure and the magnitude of edge influence has pervaded the contentious 'edge effects on nest predation' literature (e.g., Tewksbury *et al.*, 2006). Surprisingly, though, these examples of interactions between multiple drivers of fragmentation have not been taken more broadly as being indicative of the importance of spatial context-dependence among variables in general. For example, Ewers *et al.* (2007) showed the striking importance of synergistic interactions between patch area and edge effects on beetle communities in temperate forest remnants in New Zealand. Despite thousands of individual studies investigating the effects of patch area and thousands more studies separately investigating edge effects, only a handful of studies have tested for interactions between the two variables (Ewers *et al.*, 2007). In a similar vein, the importance of patch shape complexity is likely to be entirely dependent on the magnitude of edge effects, and similar arguments could be made for context-dependence among other variables. No-one has yet tested for higher-order interactions among suites of variables, but these almost certainly occur frequently, if not ubiquitously, as well.

Trait-dependence of species responses

A significant problem in interpreting the many seemingly contradictory species responses to fragmentation is that the life history and biology of most species is so poorly known that it is difficult to determine the mechanistic basis for population decline (or increase). In many cases ecologists and conservation managers are also seeking more generality to their conclusions about the effects of fragmentation than simply knowledge about how particular species respond. Consequently, considerable effort has been expended drawing generalisations about the traits of species that might confer susceptibility or resilience to fragmentation (Henle *et al.*, 2004). For example, a number of studies have found that habitat specialists, species with large body size, species at higher trophic levels, and those with poor dispersal abilities or a reliance on mutualist species are expected to go extinct first when habitat area decreases (see reviews by Tscharntke *et al.*, 2002; Henle *et al.*, 2004; Ewers & Didham, 2006a). In a similar vein, species at higher trophic levels (Zabel & Tscharntke, 1998) and species with ‘intermediate’ dispersal capabilities (Thomas, 2000) appear to be most sensitive to patch isolation. Recognising these trait-dependencies can explain many of the contrasting finds about the effects of patch area and isolation on species responses, and the same is true of the other drivers of fragmentation effects also. Overall, across all drivers of fragmentation effects, a very large number of traits have been proposed as being important in determining species responses, although Henle *et al.* (2004) suggested that just six ‘traits’ (defined in the broadest sense) have sufficient empirical support to justify being considered strong predictors of species' sensitivity to fragmentation: population size, population variability, competitive ability and sensitivity to disturbance, degree of habitat specialisation, rarity, and biogeographic location.

Time lags in ecological response

Given the inherent difficulties in measuring temporal responses to human disturbance, the issue of temporal context-dependence of fragmentation effects has been surprisingly widely considered, if not always well studied directly. A range of transient dynamics has been observed in habitat patches immediately following disturbance of the surrounding landscape, with the most common of these being a short-term increase in population densities of mobile taxa that 'crowd' into the remaining intact patches (Bierregaard *et al.*, 1992; Collinge & Forman, 1998). Ecological observations made during this time-frame can give a highly biased impression of the ecological condition of the patch and the ecological impact of fragmentation (Ewers & Didham, 2006a). Transient crowding effects may also impose a strong destabilising effect on species interactions and community structure for resident organisms within habitat patches, and might even be one of the factors that exacerbates the rate or magnitude of community change in the long term.

Over the succeeding trajectory of species relaxation, populations decline and are lost at varying rates depending on the spatial attributes of the remaining habitat and the traits of the remaining species (Brooks *et al.*, 1999; Ferraz *et al.*, 2003), with rates being very rapid (on the order of months to a few years) for short-lived invertebrate species in small habitat patches (Collinge & Forman, 1998; Gonzalez, 2000). In some regions where habitat loss has been exceptionally rapid and severe (such as the Atlantic Forest of Brazil, and many regions of tropical South East Asia), there is considerable concern that long time-lags to extinction for many taxa could mean that we are facing a very large ‘extinction debt’ (Tilman *et al.*, 1994; Brooks *et al.*, 1999), that will inevitably lead to many hundreds, if not thousands, of rare and endangered species disappearing over the coming century. Although at one time the concept of extinction debts was largely theoretical (Tilman *et al.*, 1994), there is a now a growing body of empirical evidence supporting the strong temporal dependence of community change following fragmentation (Ewers & Didham, 2006a; Kuussaari *et al.*, 2009). The same concept has also been extended to temporal dependence in a range of other processes occurring concurrently in modified landscapes, including the concept of an ‘invasion debt’ (reflecting the number of species yet to invade a patch from incipient populations in the landscape; Seabloom *et al.*, 2006), and a ‘colonisation credit’ (reflecting the number of species yet to colonize a patch during community re-assembly following habitat restoration; Cristofoli *et al.*, 2010), although these may eventually be seen as one in the same concept (Jackson & Sax, 2010).

Synergistic interactions between fragmentation and other threatening processes

Finally, habitat fragmentation is not the only anthropogenically-driven process threatening species in habitat patches, and in many cases it may not even be the most important factor. Other components of land-use change, such as land-use intensification in the matrix for example, can be the key determinant of patch processes (Tscharntke *et al.*, 2005), and there can be strong historical or environmental context dependence in the effects of other components of global environmental change which blurs or confounds determination of species responses to fragmentation (Didham *et al.*, 2005; Didham *et al.*, 2007). For instance, in most, if not all, modified landscapes there is strong intercorrelation between loss of habitat, invasion of non-native species and decline of native species, making it difficult to separate whether it really is habitat loss or invasion that is the cause of decline (Didham *et al.*, 2005).

Of even greater concern is the weight of emerging evidence showing that multiple drivers of global change interact synergistically, rather than independently, such that the effects of one driver exacerbate the effects of other drivers (Didham *et al.*, 2007; Brook *et al.*, 2008; Tylianakis *et al.*, 2008). Such synergies operate frequently, if not ubiquitously, between habitat fragmentation and species invasion (Didham *et al.*, 2007). For example, invasion of the predatory beetle *Coccinella septempunctata* into cropland in the USA led to a three-fold increase in predation pressure on a native aphid *Bipersona* sp. in natural grassland patches within a crop matrix, compared to control sites in a more pristine grassland-dominated landscape (Rand & Louda, 2006). Habitat fragmentation may also exacerbate future impacts of climate change. For example, the geographical distribution of butterflies tracks climate warming (Thomas *et al.*, 2006) but in fragmented landscapes the movement of habitat specialists is restricted by adverse conditions in the matrix, such that climate change impacts are likely to be much more severe in heavily fragmented landscapes than in less modified landscapes (Thomas *et al.*, 2006). Numerous other examples of synergistic and antagonistic interactions have also been recorded among all components of land-use change, atmospheric CO_2 increase, climate change, anthropogenic nitrogen deposition and species invasion processes (Didham *et al.*, 2007; Brook *et al.*, 2008; Darling & Côté, 2008; Tylianakis *et al.*, 2008). Ecological understanding of the interactions among multiple drivers of global change is still in its infancy and presents an important future challenge for conservation management in fragmented landscapes (Didham *et al.*, 2007; Tylianakis *et al.*, 2008).

Conclusions

When considered in the broadest sense as an on-going process of human modification of the amount, spatial arrangement and quality of semi-natural habitats remaining in the landscape, ‘habitat fragmentation’ continues to be the most widely-accepted and useful umbrella concept for ecology, conservation and management in modified landscapes. The discipline of habitat fragmentation is constantly developing, so that today most studies are either implicitly or explicitly linking both patch and landscape perspectives on the ecological consequences of land-use change for organisms living in networks of remnant patches surrounded by a mosaic of modified or novel land use types. The most important recent advances in our understanding of the ecological effects of habitat fragmentation all stem from recognition of the strong context dependence of ecosystem responses, and the synergistic interactions between habitat fragmentation and other components of global environmental change.

References

Andrén H (1997) Habitat fragmentation and changes in biodiversity. *Ecological Bulletins* **46**, 171-181.

Banks-Leite C & Ewers RM (2009) Ecosystem Boundaries. In *Encyclopedia of Life Sciences*. Chichester: John Wiley & Sons, Ltd.

Beissinger SR & McCullough DR (2002) *Population Viability Analysis*. Chicago, IL, USA: University of Chicago Press.

Bhattacharya M, Primack RB & Gerwein J (2003) Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation* **109**, 37-45.

Bierregaard RO, Lovejoy TE, Kapos V, Santos AA & Hutchings RW (1992) The biological dynamics of tropical forest fragments. A prospective comparison of fragments and continuous forest. *BioScience* **42**, 859-866.

Brook BW, Sodhi NS & Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* **23**, 453-460.

Brooks TM, Pimm SL & Oyugi JO (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* **13**, 1140-1150.

Brotons L, Mönkkönen M & Martin J-L (2003) Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *American Naturalist* **162**, 343-357.

Cadenasso ML, Pickett STA, Weathers KC & Jones CG (2003) A framework for a theory of ecological boundaries. *BioScience* **53**, 750-758.

Cadenasso ML, Traynor MM & Pickett STA (1997) Functional location of forest edges: gradients of multiple physical factors. *Canadian Journal of Forest Research* **27**, 774-782.

Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, Mroz GD, Brookshire BL & Franklin JF (1999) Microclimate in forest ecosystem and landscape ecology. *BioScience* **49**, 288-297.

Collinge SK (1996) Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landscape and Urban Planning* **36**, 59-77.

Collinge SK (2000) Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. *Ecology* **81**, 2211-2226.

Collinge SK (2009) *Ecology of Fragmented Landscapes*. Baltimore, MD, USA: The Johns Hopkins University Press.

Collinge SK & Forman RTT (1998) A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos* **82**, 66-84.

Collinge SK & Palmer TM (2002) The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecology* **17**, 647-656.

Connor EF, Courtney AC & Yoder JM (2000) Individuals-area relationships: the relationship between animal population density and area. *Ecology* **81**, 734-748.

Cook WM, Lane KT, Foster BL & Holt RD (2002) Island theory, matrix effects and species richness in habitat fragments. *Ecology Letters* **5**, 619-623.

Cristofoli S, Piqueray J, Dufrêne M, Bizoux JP & Mahy G (2010) Colonization credit in restored wet heathlands. *Restoration Ecology* **in press**.

Cumming GS (2002) Habitat shape, species invasions, and reserve design: insights from simple models. *Conservation Ecology* **6**, 3.

Damschen EI, Haddad NM, Orrock JL, Tewksbury JJ & Levey DJ (2006) Corridors increase plant species richness at large scales. *Science* **313**, 1284-1286.

Darling ES & Côté IM (2008) Quantifying the evidence for ecological synergies. *Ecology Letters* **11**, 1278-1286.

Davies KF, Margules CR & Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**, 1450-1461.

Davies KF, Melbourne BA & Margules CR (2001) Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. *Ecology* **82**, 1830-1846.

Didham RK (1997) An overview of invertebrate responses to forest fragmentation. In *Forests and Insects*, pp. 303-320 [A Watt, NE Stork and M Hunter, editors]. London: Chapman and Hall.

Didham RK, Hammond PM, Lawton JH, Eggleton P & Stork NE (1998) Beetle species responses to tropical forest fragmentation. *Ecological Monographs* **68**, 295-323.

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA & Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution* **22**, 489-496.

Didham RK, Tylianakis JM, Hutchison MA, Ewers RM & Gemmell NJ (2005) Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* **20**, 470-474.

Donald PF & Evans AD (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology* **43**, 209-218.

Ewers RM & Didham RK (2006a) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* **81**, 117-142.

Ewers RM & Didham RK (2006b) Continuous response functions for quantifying the strength of edge effects. *Journal of Applied Ecology* **43**, 527-536.

Ewers RM & Didham RK (2007a) The effect of fragment shape and species' sensitivity to habitat edges on animal population size. *Conservation Biology* **21**, 926-936.

Ewers RM & Didham RK (2007b) Habitat fragmentation: panchreston or paradigm? *Trends in Ecology and Evolution* **22**, 511.

Ewers RM & Didham RK (2008) Pervasive impact of large-scale edge effects on a beetle community. *Proceedings of the National Academy of Sciences U.S.A.* **105**, 5426-5429.

Ewers RM, Thorpe S & Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* **88**, 96-106.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* **34**, 487-515.

Ferraz G, Russell GJ, Stouffer PC, Bierregaard RO, Pimm SL & Lovejoy TE (2003) Rates of species loss from Amazonian forest fragments. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 14069-14073.

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**, 570-574.

Fonseca CR & Joner F (2007) Two-sided edge effect studies and the restoration of endangered ecosystems. *Restoration Ecology* **15**, 613-619.

Forman RTT (1995) *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge, UK: Cambridge University Press.

Franklin AB, Noon BR & George TL (2002) What is habitat fragmentation? In *Effects of Habitat Fragmentation on Birds in Western Landscapes: Contrasts with Paradigms from the Eastern United States*, pp. 20-29 [TL George and DS Dobkin, editors]: Cooper Ornithological Society.

Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman BL, Tocher M & Borges S (1999) Matrix effects and species richness in tropical forest remnants. *Biological Conservation* **91**, 223-229.

Gilbert F, Gonzalez A & Evans-Freke I (1998) Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 577-582.

Gilpin ME & Soulé ME (1986) Minimum viable populations: processes of species extinction. In *Conservation Biology. The Science of Scarcity and Diversity*, pp. 19-34 [ME Soulé, editor]. Massachusetts, USA: Sinauer associates, Inc.

Gonzalez A (2000) Community relaxation in fragmented landscapes: the relation between species richness, area and age. *Ecology Letters* **3**, 441-448.

Gonzalez A (2009) Metacommunities: spatial community ecology. In *Encyclopedia of Life Sciences*. Chichester: John Wiley & Sons, Ltd.

Haddad NM & Baum KA (1999) An experimental test of corridor effects on butterfly densities. *Ecological Applications* **9**, 623-633.

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* **12**, 321-334.

Hamazaki T (1996) Effects of patch shape on the number of organisms. *Landscape Ecology* **11**, 299-306.

Hanski I (1998) Metapopulation dynamics. *Nature* **396**, 41-49.

Hanski I & Gaggiotti OE (2004) *Ecology, Genetics, and Evolution of Metapopulations*. San Diego, CA, USA: Elsevier.

Hanski I & Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755-758.

Harper KA, MacDonald SE, Burton PJ, Chen J, Brosofske KD, Saunders SC, Euskirchen ES, Roberts D, Jaiteh MS & Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* **19**, 768-782.

Henle K, Davies KF, Kleyer M, Margules C & Settele J (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* **13**, 207-251.

Hilty JA, Lidicker WZ & Merenlender AM (2006) *Corridor Ecology: the Science and Practice of Linking Landscapes for Biodiversity Conservation*. Washington, DC, USA: Island Press.

Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* **124**, 377-406.

Jackson ST & Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution* **25**, 153-160.

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. *Global Ecology and Biogeography* **15**, 8-20.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Ockinger E, Partel M, Pino J, Roda F, Stefanescu C, Teder T, Zobel M & Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology & Evolution* **24**, 564-571.

Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation* **141**, 1731-1744.

Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG & Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* **16**, 605-618.

Laurance WF & Yensen E (1991) Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* **55**, 77-92.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M & Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601-613.

Levey DJ, Bolker BM, Tewksbury JJ, Sargent S & Haddad NM (2005) Effects of landscape corridors on seed dispersal by birds. *Science* **309**, 146-148.

Lindenmayer DB & Fischer J (2007) Tackling the habitat fragmentation panchreston. *Trends in Ecology and Evolution* **22**, 127-132.

Lomolino MV (2000) Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* **27**, 17-26.

MacArthur RH & Wilson EO (1967) *The theory of island biogeography*. Princeton, N.J.: Princeton University Press.

Matlack GR (1994) Vegetation dynamics of the forest edge - trends in space and successional time. *Journal of Ecology* **82**, 113-123.

Myers N & Knoll AH (2001) The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences U.S.A.* **98**, 5389-5392.

Perfecto I & Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* **16**, 174-182.

Pickett STA & Cadenasso ML (1995) Landscape ecology: spatial heterogeneity in ecological systems. *Science* **269**, 331-334.

Pimm SL, Russell GJ, Gittleman JL & Brooks TM (1995) The future of biodiversity. *Science* **269**, 347-350.

Rand TA & Louda SA (2006) Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conservation Biology* **20**, 1720-1729.

Ranta P, Blom T, Niemelä J, Joensuu E & Siitonen M (1998) The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiversity and Conservation* **7**, 385-403.

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* **158**, 87-99.

Ries L, Fletcher RJJ, Battin J & Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models and variability explained. *Annual Review of Ecology, Evolution and Systematics* **35**, 491-522.

Roland J, Keyghobadi N & Fownes S (2000) Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* **81**, 1642-1653.

Saunders DA & Hobbs RJ (1991) The role of corridors in conservation: what do we know and where do we go? In *Nature Conservation 2: The Role of Corridors*, pp. 421-427 [DA Saunders and RJ Hobbs, editors]. Australia: Surrey Beatty & Sons.

Saunders DA, Hobbs RJ & Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**, 18-32.

Seabloom EW, Dobson AP & Stoms DM (2002) Extinction rates under nonrandom patterns of habitat loss. *Proceedings of the National Academy of Sciences U.S.A.* **99**, 11229-11234.

Seabloom EW, Williams JW, Slayback D, Stoms DM, Viers JH & Dobson AP (2006) Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications* **16**, 1338-1350.

Simberloff DS (1992) Do species-area curves predict extinction in fragmented forest? In *Tropical Deforestation and Species Extinction*, pp. 75-89 [TC Whitmore and JA Sayer, editors]. London: Chapman and Hall.

Skole D & Tucker CJ (1993) Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. *Science* **260**, 1904-1910.

Tewksbury J, Levey D, Haddad N, Sargent S, Orrock J, Weldon A, Danielson B, Brinkerhoff J, Damschen E & Townsend P (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences U.S.A.* **99**, 12923-12926.

Tewksbury JJ, Garner L, Garner S, Lloyd JD, Saab V & Martin TE (2006) Tests of landscape influence: Nest predation and brood parasitism in fragmented ecosystems. *Ecology* **87**, 759-768.

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London Series B Biological Sciences* **267**, 139-145.

Thomas CD, Franco AMA & Hill JK (2006) Range contractions and extinction in the face of climate change. *Trends in Ecology and Evolution* **21**, 415-416.

Tilman D, May RM, Lehman CL & Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* **371**, 65-66.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I & Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters* **8**, 857-874.

Tscharntke T, Steffan-Dewenter I, Kruess A & Thies C (2002) Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* **17**, 229-239.

Tylianakis JM, Didham RK, Bascompte J & Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters* **11**, 1351-1363.

Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G & Hermy M (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* **87**, 542-548.

Wilcove DS, McLellan CH & Dobson AP (1986) Habitat fragmentation in the temperate zone. In *Conservation Biology. The Science of Scarcity and Diversity,* pp. 237-256 [ME Soulé, editor]. Massachusetts,USA: Sinauer associates, Inc.

Williams-Linera G, Domínguez-Gastelú V & García-Zurita ME (1998) Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology* **12**, 1091-1102.

Young A & Mitchell N (1994) Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* **67**, 63-72.

Zabel J & Tscharntke T (1998) Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* **116**, 419-425.

Further reading

Bierregaard RO Jr, Gascon C, Lovejoy TE and Mesquita R (2001) *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest.* Yale, CT, USA: Yale University Press.

Gutzwiller KJ (2002) *Applying Landscape Ecology in Biological Conservation*. New York: Springer.

Harris LD (1984) *The Fragmented Forest*. Chicago, IL, USA: University of Chicago Press.

Laurance WF and Bierregaard RO Jr (1997) *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities.* Chicago, IL, USA: University of Chicago Press.

Lindenmayer D and Fischer J (2006) *Habitat Fragmentation and Landscape Change: an Ecological and Conservation Synthesis.* Collingwood, Vic., Australia: CSIRO.

Rochelle JA, Lehmann LA and Wisniewski J (1999) *Forest Fragmentation: Wildlife and Management Implications.* Boston, MA: Brill.

Schelhas J and Greenberg R (1996) *Forest Patches in Tropical Landscapes*. Washington, DC, USA: Island Press.

Wiens JA and Moss MR (2005) *Issues and Perspectives in Landscape Ecology*. Cambridge, UK: Cambridge University Press.

Figure captions

Figure 1. Land-use change in a fragmented tropical forest landscape in the highlands near Sapa, Vietnam, showing the scale of habitat loss, the altered spatial arrangement of remaining rainforest habitats, and the mosaic of human land-use intensification in the surrounding landscape matrix. Photo reproduced with permission from iStock Photo (http://www.istockphoto.com).

Figure 2. Defining habitat fragmentation. There is strong debate about whether the term 'habitat fragmentation' should be used to describe: (A) the entire spatio-temporal *process* by which habitat loss leads to the subdivision of large, continuous habitats into a greater number of smaller patches of lower total area, isolated from each other by a matrix of dissimilar habitats; or (B) solely the differences that occur due to the differing *pattern* of spatial arrangement of remaining habitat after the amount of habitat remaining in the landscape has been taken into account. The satellite images in (A) show typical correlated changes in habitat loss and habitat fragmentation in the same landscape east of Santa Cruz, Bolivia, over three time intervals (images courtesy of NASA/Goddard Space Flight Center Scientific Visualization Studio; http://visibleearth.nasa.gov). The satellite images in (B) show three different landscapes in southern Mato Grosso, Brazil, with approximately the same amount of habitat loss, but very differing spatial arrangement (images courtesy of Jacques Descloitres, MODIS Land Rapid Response Team, NASA/GSFC, 29 May 2001; http://visibleearth.nasa.gov).

Figure 3. A schematic representation of the problem of attributing causality to 'habitat loss' versus 'habitat fragmentation per se'. (A) In modified landscapes, all measures of spatial habitat configuration are strongly intercorrelated with the amount of remaining habitat,

making separation of ‘independent’ effects impossible. (B) The reason for the strong intercorrelation is that the effects of habitat amount do not only operate directly and separately from the effects of habitat fragmentation, they predominantly operate through indirect pathways mediated by altered spatial configuration. For clarity, not all possible indirect pathways are shown in (B).

Figure 4. Widely-held generalisations about community responses to habitat fragmentation. Predictions of how species richness typically changes as the five main components of the spatial context of habitat fragments are altered. Redrawn from Ewers & Didham (2006a).

Figure 1

Figure 2

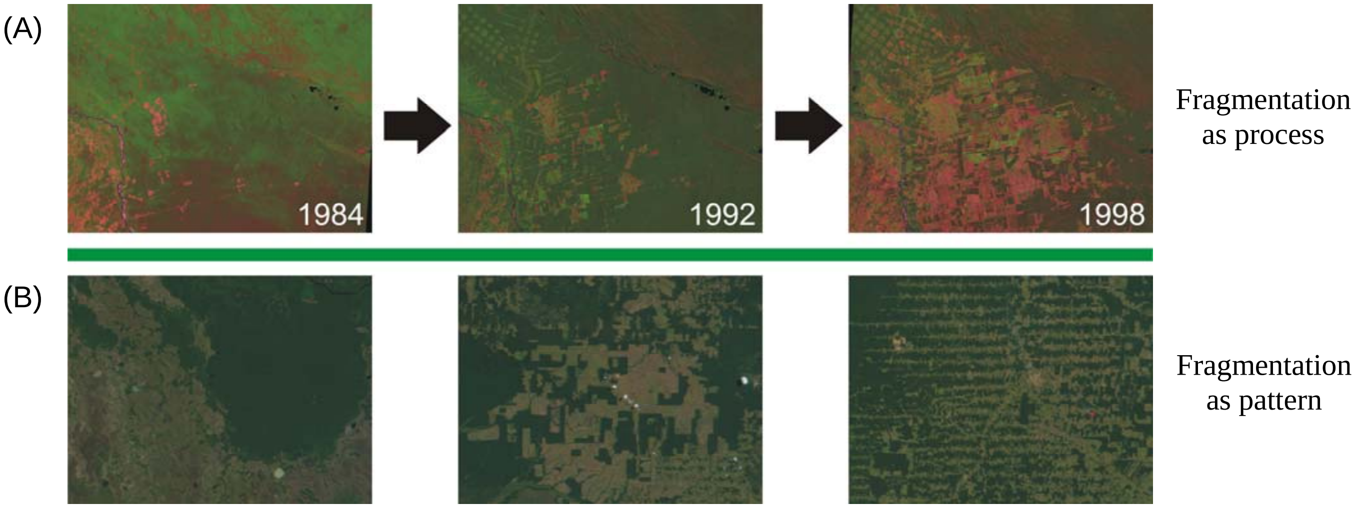

(A)
1984
1992
1998
Fragmentation
as process
(B)
Fragmentation
as pattern

Figure 3

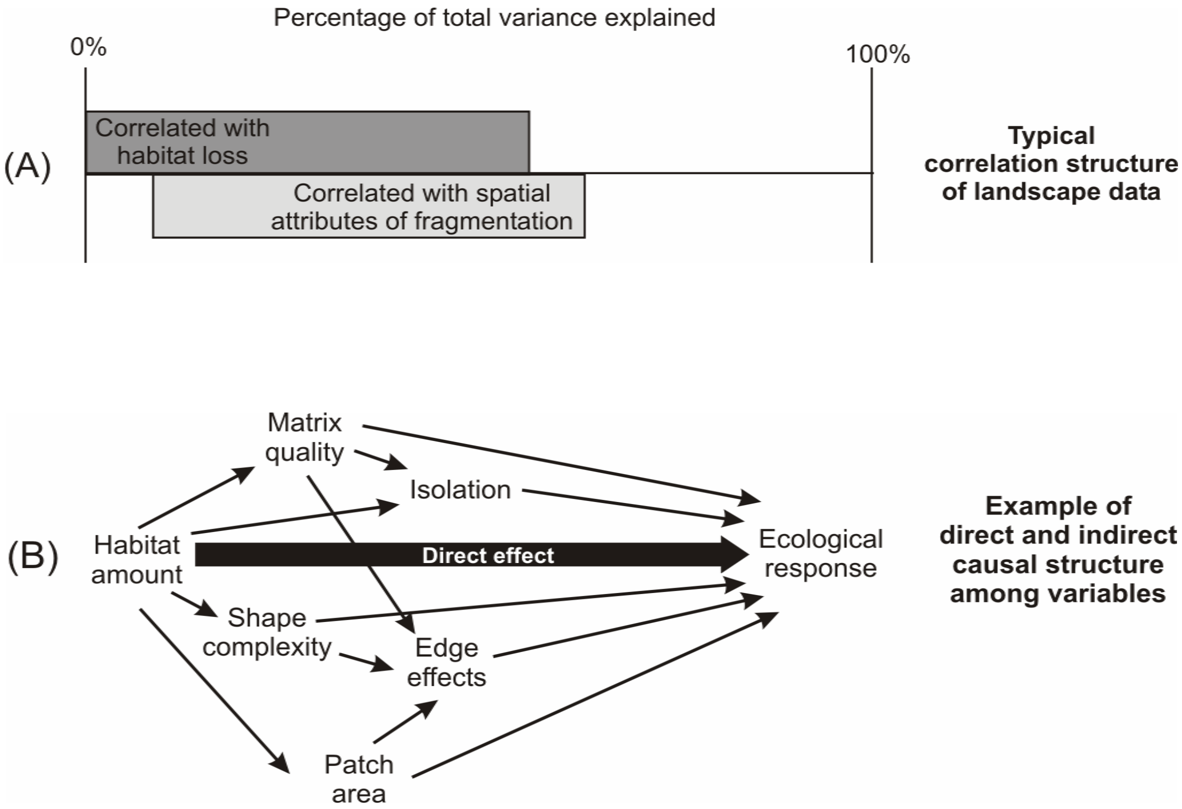
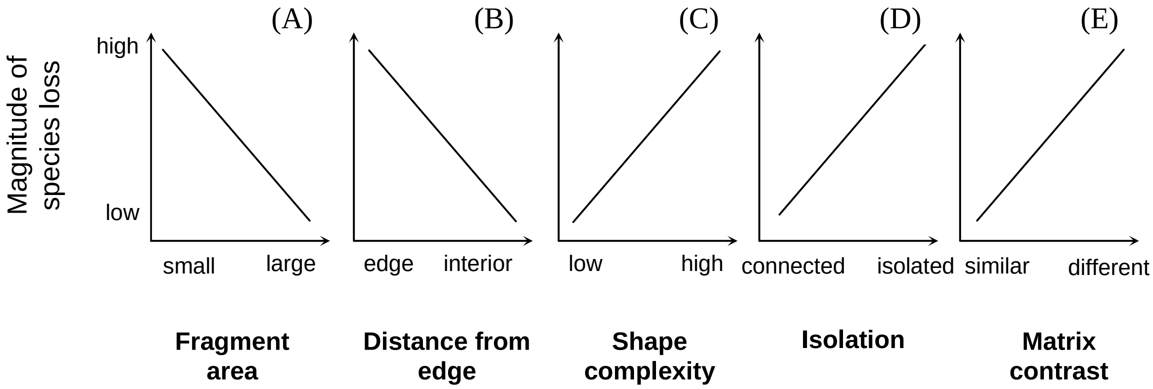

Percentage of total variance explained
0%
100%
(A)
Correlated with habitat loss
Correlated with spatial attributes of fragmentation
Typical correlation structure of landscape data
(B)
Matrix quality
Isolation
Habitat amount
Direct effect
Ecological response
Shape complexity
Edge effects
Patch area
Example of direct and indirect causal structure among variables

Figure 4


(A)
(B)
(C)
(D)
(E)
Magnitude of species loss
high
low
small
large
edge
interior
low
high
connected
isolated
similar
different
Fragment area
Distance from edge
Shape complexity
Isolation
Matrix contrast