

Confounding factors in the detection of species responses to habitat fragmentation

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ABSTRACT

Habitat loss has pervasive and disruptive impacts on biodiversity in habitat remnants. The magnitude of the ecological impacts of habitat loss can be exacerbated by the spatial arrangement – or fragmentation – of remaining habitat. Fragmentation *per se* is a landscape-level phenomenon in which species that survive in habitat remnants are confronted with a modified environment of reduced area, increased isolation and novel ecological boundaries. The implications of this for individual organisms are many and varied, because species with differing life history strategies are differentially affected by habitat fragmentation. Here, we review the extensive literature on species responses to habitat fragmentation, and detail the numerous ways in which confounding factors have either masked the detection, or prevented the manifestation, of predicted fragmentation effects.

Large numbers of empirical studies continue to document changes in species richness with decreasing habitat area, with positive, negative and no relationships regularly reported. The debate surrounding such widely contrasting results is beginning to be resolved by findings that the expected positive species-area relationship can be masked by matrix-derived spatial subsidies of resources to fragment-dwelling species and by the invasion of matrix-dwelling species into habitat edges. Significant advances have been made recently in our understanding of how species interactions are altered at habitat edges as a result of these changes. Interestingly, changes in biotic and abiotic parameters at edges also make ecological processes more variable than in habitat interiors. Individuals are more likely to encounter habitat edges in fragments with convoluted shapes, leading to increased turnover and variability in population size than in fragments that are compact in shape. Habitat isolation in both space and time disrupts species distribution patterns, with consequent effects on metapopulation dynamics and the genetic structure of fragment-dwelling populations. Again, the matrix habitat is a strong determinant of fragmentation effects within remnants because of its role in regulating dispersal and dispersal-related mortality, the provision of spatial subsidies and the potential mediation of edge-related microclimatic gradients.

We show that confounding factors can mask many fragmentation effects. For instance, there are multiple ways in which species traits like trophic level, dispersal ability and degree of habitat specialisation influence species-level responses. The temporal scale of investigation may have a strong influence on the results of a study, with short-term crowding effects eventually giving way to long-term extinction debts. Moreover, many fragmentation effects like changes in genetic, morphological or behavioural traits of species require time to appear. By contrast, synergistic interactions of fragmentation with climate change, human-altered disturbance regimes, species interactions and other drivers of population decline may magnify the impacts of fragmentation. To conclude, we emphasise that anthropogenic fragmentation is a recent phenomenon in evolutionary time and suggest that the final, long-term impacts of habitat fragmentation may not yet have shown themselves.

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I. INTRODUCTION

The magnitude of habitat fragmentation reflects the pervasive influence of humans on the environment at all scales from local (Lord & Norton, 1990) through to regional (Ranta *et al.*, 1998), national (Heilman *et al.*, 2002) and global (Riitters *et al.*, 2000). While the direct effects of habitat loss *per se* are typically considered to pose the greatest current threat to biodiversity (Tilman *et al.*, 1994; Dobson, Bradshaw & Baker, 1997), the size and spatial arrangement of remnant fragments is recognised to have a major effect on population dynamics and species persistence (Barbosa & Marquet, 2002; Hanski & Gaggiotti, 2004), with impacts that are ‘more insidious’ than habitat loss alone (With, 1997). As a consequence, habitat fragmentation has become a central issue in conservation biology (Meffe & Carroll, 1997).

(1) Causes of habitat fragmentation

Fragmentation, as an expression of the size and spatial arrangement of habitat patches, is not a purely anthropogenic process. Naturally fragmented habitats are widely distributed around the world at a range of scales (Watson, 2002). For example, alpine environments that occur as small habitat islands separated by a matrix of sub-alpine and lowland environments (Burkey, 1995), river systems that are isolated from each other by terrestrial and coastal marine habitats (Fagan, 2002), and rock outcrops in alpine grasslands (Leisnham & Jamieson, 2002) are all naturally fragmented systems. However, the most important and largest-scale cause of changes in the degree of fragmentation is anthropogenic habitat modification, with nearly all fragmentation indices being strongly correlated with the proportion of habitat loss in the landscape (Fahrig, 2003).

Fragmentation is the process whereby habitat loss results in the division of large, continuous habitats into smaller, isolated habitat fragments (Ranta *et al.*, 1998; Franklin, Noon & George, 2002). As a landscape becomes progressively fragmented, a greater number of fragments of varying shapes and sizes are created (Baskent & Jordan, 1995) and these are scattered through a matrix of modified habitat (Opdam & Wiens, 2002). The conditions in the matrix surrounding a habitat fragment determine the extent to which exterior environmental conditions penetrate a fragment (Baskent & Jordan, 1995). The portions of a fragment that are altered by external conditions are termed edge habitat, while unaffected portions are called core habitat. The proportion of a fragment that is core habitat is a complex function of fragment size and shape and the nature of the surrounding landscape matrix (Laurance & Yensen, 1991; Baskent & Jordan, 1995).

Fragmentation is not just a patch-level phenomenon, although this is the scale at which many of its biological impacts are observed. In fact, fragmentation only occurs when habitat loss reaches a point at which habitat continuity is broken (Opdam & Wiens, 2002) and this is quite clearly a landscape-level attribute that describes the size and spatial arrangement of remaining habitat (Baskent & Jordan, 1995). The degree of habitat connectivity is partly determined by the physical continuity of habitat, but it is also a function of the degree to which a landscape facilitates or impedes the movement of individuals between fragments (Langlois *et al.*, 2001). As a consequence, connectivity is influenced both by the physical location of habitat fragments as well as by characteristics of the surrounding habitat matrix (Baskent & Jordan, 1995).

(2) Approaches to the study of fragmentation

The study of fragmentation has its roots in classical island biogeography theory (IBT, MacArthur & Wilson, 1967), which emphasised area and isolation effects to the exclusion of landscape structure (Didham, 1997; Laurance & Cochrane, 2001). Theoretical developments in spatial theory (Forman, 1997) and macroecology (Gaston & Blackburn, 2000) saw IBT superseded in the 1980s by landscape ecology, with a new focus on the spatial arrangement of fragments and the structure of the matrix (Laurance & Cochrane, 2001; Haila, 2002). However, the basic tenets of IBT remain relevant to fragmentation, and recent theory has overcome some of the shortcomings of the classical model by incorporating landscape ecological principles (Hanski & Gyllenburg, 1997; Polis, Anderson & Holt, 1997).

In parallel with these changing paradigms underpinning habitat fragmentation studies, the last decade has been witness to an explosion in the amount and types of research being conducted. Complex, community-level studies and cross-species comparisons are now more frequently conducted, reflecting the ease with which multivariate statistics can handle large data sets. Experimental approaches, led by the Biological Dynamics of Forest Fragments Project in the Brazilian Amazon (Bierregaard *et al.*, 1992; Laurance *et al.*, 2002), have become more common (Debinski & Holt, 2000; McGarigal & Cushman, 2002), and the scale of

investigation now ranges from microcosms (Burkey, 1997; Gonzalez & Chaneton, 2002) to the entire globe (Riitters *et al.*, 2000). Advances in associated disciplines such as molecular ecology now allow the investigation of historical (Fisher *et al.*, 2001) and sub-lethal (O'Ryan *et al.*, 1998) genetic impacts, while the application of newly developed 'tools of the trade,' such as stable isotope markers, means that the dispersal of even very small animals can be tracked through time and space (Caudill, 2003).

(3) Structure of this review

Several recent reviews of the fragmentation literature have synthesised the ecological impacts of fragmentation at the landscape scale (Fahrig, 2003; Tschardt & Brandl, 2004), or have focused on a single aspect of habitat fragmentation such as the creation of habitat boundaries (Ries *et al.*, 2004). Nevertheless, fragmentation effects in the empirical literature are still commonly grouped under five categories that together describe the spatial attributes of individual patches in fragmented landscapes: (1) fragment area, (2) edge effects, (3) fragment shape, (4) fragment isolation, and (5) matrix structure. In this review, we examine species and community responses to these five, patch-scale categories. However, one of the most significant advances in the recent fragmentation literature has been the recognition that the effects of processes within these five categories can be either masked or enhanced by confounding factors that operate over large temporal and spatial scales. We discuss how the susceptibility of species to habitat fragmentation varies depending on their particular life history strategies (summarised in Figs 1 & 2). It is also now apparent that the effects of fragmentation can take many decades to be expressed and that synergies between fragmentation and other extrinsic drivers of population decline can magnify the detrimental impacts of fragmentation on species. We stress the importance of taking a mechanistic approach to the study of fragmentation and conclude by highlighting gaps in the current literature and providing some directions for future research.

II. HABITAT AREA

A direct reduction in habitat area is thought to be one of the major causes of species extinctions (Tilman *et al.*, 1994) and typically has a strong, negative effect on biodiversity (Fig. 1A; Fahrig, 2003). Reduced habitat area in a landscape leads to a decrease in the size of fragments and an increase in fragment isolation (Andr n, 1994), with consequent reductions in population size and colonisation rates that directly increase the risk of local extinctions (Bowers & Matter, 1997; Bender, Contreras & Fahrig, 1998; Hanski, 1998; Crooks *et al.*, 2001; Hames *et al.*, 2001; Schoereder *et al.*, 2004). Furthermore, in a recent review, Fahrig (2003) demonstrated the impact of habitat loss on several measures of community structure including species richness, the strength of species interactions and trophic chain length in food webs, as well as on several measures of population

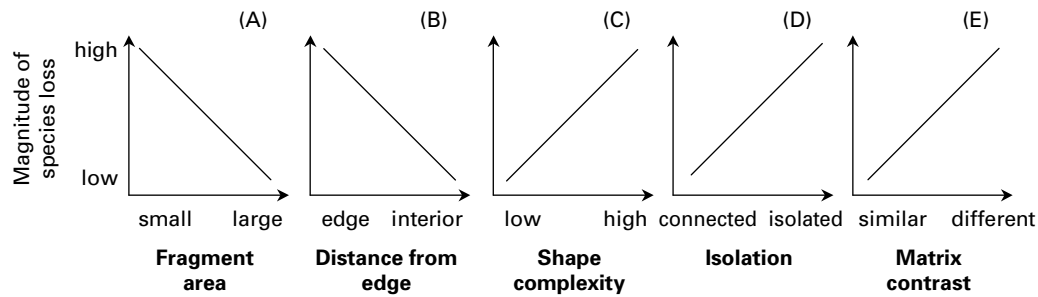


Fig. 1. Widely-held generalisations about community responses to habitat fragmentation. Predictions of how species richness changes as the five main components of the spatial context of habitat fragments are altered. Predictions are derived from current theoretical understanding of fragmentation effects, as discussed in the main text.

structure, including population distribution and abundance, dispersal, reproductive output, foraging success and genetic diversity. However, fragmentation of the remaining habitat has important, additional impacts on biodiversity that are independent of habitat loss (Tscharntke *et al.*, 2002a; Fahrig, 2003). In the context of our review of habitat fragmentation, we explicitly consider habitat loss because habitat area has been consistently used to predict changes in species diversity under the IBT framework. Furthermore, species and population responses are commonly non-linear below threshold values of habitat loss, and these responses are moderated by the size and spatial arrangement of the remaining habitat (With & King, 2001).

(1) Species-area relationships: predicting extinction rates from habitat loss

By explicitly considering habitat fragments as islands, many researchers have followed the IBT approach and constructed species-area (SA) curves to describe rates of species loss with decreasing fragment area (Fig. 1A; Pimm & Askins, 1995; Pimm *et al.*, 1995; Brooks, Pimm & Collar, 1997; Brooks *et al.*, 2002; but see Anderson & Wait, 2001; Cook *et al.*, 2002). The approach itself is relatively straightforward, with the calculation of a simple species loss function $S_{t+1}/S_t = (A_{t+1}/A_t)^z$ (Pimm *et al.*, 1995); where S_t is species richness before habitat loss, S_{t+1} is species richness following habitat loss, A_t is the original amount of habitat area, A_{t+1} is habitat area following habitat loss and z is the slope of the SA curve, which is assumed to average a typical value such as 0.25 for the relationship between habitat area and species richness (Pimm & Askins, 1995; Brooks *et al.*, 1997, 2002). As the species loss function uses the proportion of habitat lost to estimate the proportion of species expected to become extinct, the analysis is assumed to be independent of absolute differences in habitat extent, biogeographic scale, or the size of the total species pool.

Despite the simplicity of the approach, there are a number of important caveats on interpreting observed *versus* predicted extinction rates following habitat loss, most of which stem from the fact that raw SA predictions almost always exceed observed extinction rates (Pimm & Askins, 1995; Pimm *et al.*, 1995; Brooks *et al.*, 1997, 2002;

Cowlishaw, 1999). First and foremost is whether habitat ‘islands’ are analogous to real islands in an IBT context (Anderson & Wait, 2001; Cook *et al.*, 2002; Haila, 2002). For a comparable distance of isolation, populations within fragments are much more likely to be ‘rescued’ by dispersal of individuals between adjacent fragments than are populations within islands (Brown & Kodric-Brown, 1977; Förare & Solbreck, 1997; Menendez & Thomas, 2000). As a result, some species that occur in small fragments may be able to persist by combining resources from a number of fragments (Tscharntke *et al.*, 2002a), so that the area of an individual habitat fragment does not necessarily represent the actual extent of resources available to the species occupying it. The net outcome will be fewer observed extinctions than predicted by the SA model. Of course, fragment isolation is a species-specific variable, so that strong positive slopes for SA curves may be found for some taxa, but not others within the same set of habitat fragments (Fig. 2A–E). For instance, highly dispersive ground beetles have shallower SA curves than do less dispersive groups, because increased dispersal rates can reduce extinction rates in small fragments (Fig. 2B; de Vries, den Boer & van Dijk, 1996).

Second, it is thought that inclusion of both endemic and non-endemic species in SA predictions at a regional scale can cause an overestimate of the number of predicted extinctions, because populations of non-endemic species can be ‘rescued’ by immigration from extra-regional populations in areas not subject to habitat loss (Pimm & Askins, 1995; Pimm *et al.*, 1995; Brooks *et al.*, 1997, 2002). This problem has been countered by taking the more conservative approach of considering only endemic species, globally restricted to the region in which habitat loss rates were estimated, in SA models (Pimm *et al.*, 1995; Brooks *et al.*, 2002).

Third, habitat loss is non-random (Seabloom, Dobson & Stoms, 2002), and in some situations the spatial arrangement of the remaining fragments can have at least as large an impact on total extinction rate as the absolute amount of habitat lost. Moreover, within-fragment extinctions reflect changes in α -diversity (the total number of species at a given site), but ignore the fact that high levels of β -diversity among fragments (a measure of species turnover among sites) may augment total species richness in the landscape

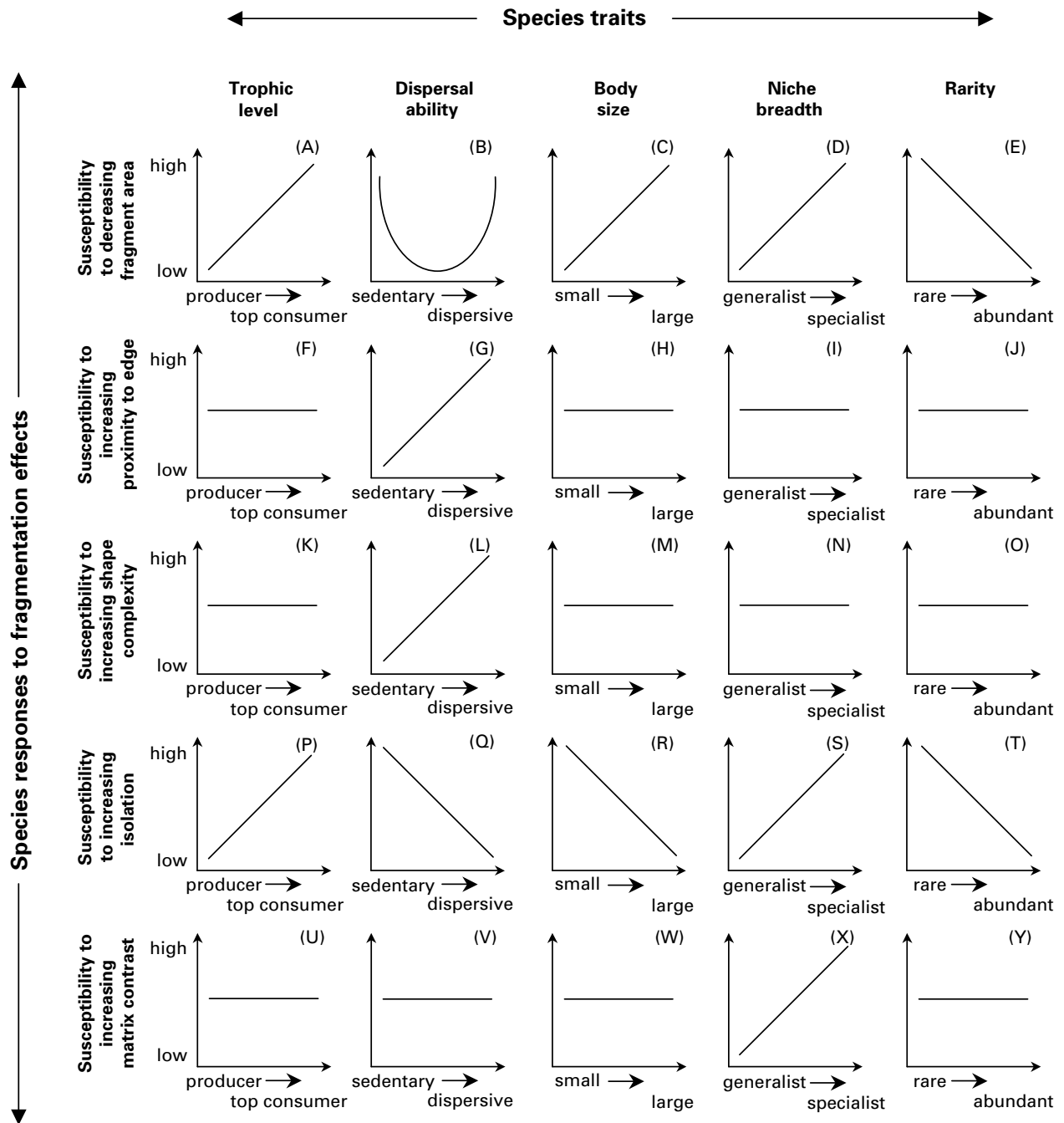


Fig. 2. Trait-mediated differences in species responses to fragmentation. Predictions of how species responses to the five main spatial components of habitat fragmentation vary as a function of species traits. Predictions are derived from current theoretical understanding of fragmentation effects (e.g. Laurance, 1991; Didham *et al.*, 1998*b*; Davies *et al.*, 2000; Tschardtke *et al.*, 2002*a*; Henle *et al.*, 2004), as discussed in the main text.

(Crist *et al.*, 2003). This forms the basis of the ongoing SLOSS (Single Large or Several Small) debate that aims to maximise species diversity within reserve networks (Quinn & Harrison, 1988). For instance, more butterfly species were present in a series of small habitat fragments than in several large fragments of the same total area, in both grasslands in Germany (Tschardtke *et al.*, 2002*b*) and

forests in Spain (Baz & Garcia-Boyer, 1996). Similarly, the β -diversity of aquatic invertebrates was greater in fragmented than continuous floodplain channels (Tockner *et al.*, 1999). These results probably occur because a series of small fragments spread over a wide geographic area encompass a wider range of environmental heterogeneity than does a single large fragment (Tschardtke *et al.*, 2002*b*). However,

large reserves are still considered to be superior to small reserves for the long-term persistence of area-sensitive and extinction-prone species (Burkey, 1995; Ferraz *et al.*, 2003), because they retain larger populations and the habitat is less likely to degrade through time (Connor, Courtney & Yoder, 2000; Tschardt *et al.*, 2002*b*).

Lastly, but often critically, the time-frame across which extinction rates are measured can have a major bearing on the apparent accuracy of SA models, because there can be a long lag-time to extinction for threatened species (Tilman *et al.*, 1994; Brooks, Pimm & Oyugi, 1999; Cowlshaw, 1999) (see Section VII.2). Consequently, some studies (e.g. Brooks *et al.*, 2002) have included threatened species as 'impending extinctions' within extinction rate calculations, providing better fits between observed and predicted extinctions.

(2) Landscape and extinction thresholds

The number, size and spatial arrangement of remaining habitat fragments in the landscape does not change linearly with increasing habitat loss. Instead, there are 'rapid changes in the size and isolation of patches at critical proportions of habitat in the landscape' (Andr n, 1994). These landscape thresholds have important consequences for species persistence in fragmented landscapes. Most of the recent advances in our understanding of landscape thresholds have stemmed from the use of metapopulation models that describe the landscape as a mosaic of patches, and focus on the balance between colonisation and extinction rates (Hill & Caswell, 1999). A simple, but important observation is that populations will not occupy all available sites at any given point in time, and that site occupancy depends greatly on the degree of connectivity in the landscape (Bascompte & Sole, 1996). Consequently, there is a critical amount of habitat cover below which colonisation becomes too infrequent to overcome local extinctions and so metapopulation extinction is inevitable (Kareiva & Wennergren, 1995; Ovaskainen *et al.*, 2002). A large number of theoretical models have been constructed along these lines and they consistently predict the existence of an extinction threshold (Andr n, 1994, 1996, 1999; Bascompte & Sole, 1996; Fahrig, 1997; With, 1997; With, Gardner & Turner, 1997; Boswell, Britton & Franks, 1998). The extinction threshold compounds the risks posed by habitat destruction (Amarasekare, 1998), as even a small loss of habitat near the threshold may result in a precipitous decline in the probability of metapopulation persistence (With & King, 1999). This obviously has serious ramifications for conservation management, but it should not be forgotten that habitat fragmentation effects are only one of many interacting causes of population declines and that many species may well go extinct long before the threshold is reached (Andr n, 1999; M nkk nen & Reunanen, 1999).

Estimates of the level of habitat destruction at which the extinction threshold occurs are varied. Fahrig (1997) suggested that metapopulation survival would be virtually assured if 20% or more of the landscape retained breeding habitat, but the literature belies such a simple rule of thumb, with Bascompte & Sole (1996) and Andr n (1997*a*)

suggesting that the threshold will vary across species and landscapes. For example, experimental estimates of the extinction threshold for rare butterfly species varied from 20 to 60% (Summerville & Crist, 2001). The exact value will likely depend heavily on individual species traits and local landscape structure, as indicated by With & King's (2001) models and small-scale experiments on population persistence for four species 'types' in fractal landscapes. They discovered that the location of the extinction threshold varied from 5 to 90% habitat loss in the landscape, depending on both the species' responses to habitat fragmentation (sensitivity to habitat area and/or edge effects) and the spatial arrangement of the remaining habitat (With & King, 2001). In the null case, where spatial arrangement of fragments is assumed to be random, the extinction threshold is more pronounced and occurs at a lower proportion of habitat loss in the landscape than for fractal landscapes (Hill & Caswell, 1999; With & King, 1999; Fahrig, 2002). Fractal landscapes contain fewer, larger fragments with a more clumped distribution, thus maintaining connectivity across a wider range of habitat loss (With, Caderet & Davis, 1999; With & King, 1999). Such an arrangement serves to enhance dispersal success, allowing populations to occupy nearly all patches at any given time (With & King, 1999) and thereby reducing the likelihood of the extinction threshold occurring. Because the process of habitat loss is patently non-random (Seabloom *et al.*, 2002) and fractal landscapes are probably more representative of natural habitat dispersion (With & King, 1999), the hypothesised effects of spatial arrangement on the extinction threshold are of considerable relevance to conservation management (Ovaskainen *et al.*, 2002).

(3) The population consequences of small habitat area

Near the extinction threshold the majority of fragments are small and almost inevitably contain relatively small populations of most species. For many organisms, this pattern is exacerbated by decreases in population density with decreasing fragment area (Bowers & Matter, 1997; Connor *et al.*, 2000), although for invertebrates such a simple generalisation cannot be made because of inconsistent results in the literature (Didham *et al.*, 1998*a*; Matter, 2000; Steffan-Dewenter & Tschardt, 2000; J. A. Thomas *et al.*, 2001; Krauss *et al.*, 2003*a*). Irrespective of variability in the density-area relationship between species, small fragment area imposes a maximum limit on population size that leaves species vulnerable to local extinction (Lande, 1993; Hanski *et al.*, 1995; Amarasekare, 1998; Burkey, 1999; Brook, Burgman & Frankham, 2000; Brook *et al.*, 2002). The underlying mechanisms driving this relationship can be divided into four categories (Shaffer, 1981): (1) environmental stochasticity, (2) demographic stochasticity, (3) natural catastrophes and (4) reduced genetic diversity (see also review by Gaggiotti & Hanski, 2004). While it is convenient to categorise these processes for discussion, it is important to note that they seldom act independently. Rather, all four have potential to interact with, and magnify the effects of, the other three, creating what have been

described as ‘extinction vortices’ (Leigh, 1981; Gilpin & Soulé, 1986). These processes lie at the heart of population viability analyses (PVA), which comprise a set of analytical and modelling techniques for predicting the probability of species extinction (Soulé, 1987; Beissinger & McCullough, 2002). The wider field of PVA has been extensively and thoroughly reviewed elsewhere (Soulé, 1987; Beissinger & McCullough, 2002), but of particular relevance here is the application of metapopulation concepts and patch occupancy models to PVA for species in highly fragmented landscapes (Hanski, 2002; Holmes & Semmens, 2004). This approach has clearly shown that small populations that are restricted to small habitat remnants (within a patch network) are far more likely to go extinct than populations that remain large (Hanski, 2002). More importantly, though, a species with a small total population size distributed as a metapopulation across a network of habitat patches typically has a greater probability of extinction than a species with the same total population size in which all individuals have a similar chance of encountering each other.

One of the key conclusions from metapopulation modelling is that the probability of population extinction depends not only on habitat area, or quality, but on spatial location within the metapopulation network (Ovaskainen & Hanski, 2004). Furthermore, deterministic drift toward a predicted equilibrium in habitat occupancy and colonisation-extinction dynamics in spatially-explicit models can be strongly influenced by stochastic fluctuations in local conditions. Again, such stochastic extinctions are most important for small populations in situations in which spatially-correlated local dynamics (Gu, Heikkilä & Hanski, 2002), or temporally varying environmental conditions (Ovaskainen & Hanski, 2004), amplify stochastic population fluctuations. The net result is that small populations that might otherwise be predicted to persist, instead have an increased probability of extinction due to spatial correlation in demographic or environmental stochasticity (Casagrandi & Gatto, 1999, 2002).

III. EDGE EFFECTS

(1) Community composition at habitat boundaries

The structure and diversity of invertebrate communities is characteristically altered at habitat edges. Typically, species richness is negatively correlated with distance from the fragment edge into the fragment interior (Ingham & Samways, 1996; Didham *et al.*, 1998*a*; Bolger *et al.*, 2000; Denys & Tschardt, 2002; Magura, 2002; Kitahara & Watanabe, 2003; Klein, Steffan-Dewenter & Tschardt, 2003; Major *et al.*, 2003). The most common explanation for this trend is that there is a mixing of distinct fragment and matrix faunas at habitat edges, giving rise to a zone of overlap with greater overall species richness (Ingham & Samways, 1996; Magura, 2002). While this is the most general species richness pattern, it is by no means universal, as a number of studies have found either no edge effect for species richness (Davies & Margules, 1998; Mönkkönen

& Mutanin, 2003) or a positive correlation (Davies, Melbourne & Margules, 2001*b*; Barbosa & Marquet, 2002; Bieringer & Zulka, 2003). Evidently, in some systems many species avoid edges and the matrix-dwelling fauna is not always speciose enough to compensate for the loss of species at edges (Fig. 1B). Not only is species richness altered at habitat edges, but there can be substantial turnover in species composition, with community similarity decreasing with distance from edge to interior (Didham *et al.*, 1998*a*; Carvalho & Vasconcelos, 1999; Harris & Burns, 2000; Davies *et al.*, 2001*b*; Dangerfield *et al.*, 2003).

Ultimately, changes in both species richness and composition are a composite of individual species responses, which are extremely varied both within and between studies. Studies that have investigated the densities of multiple species at the same sites typically show contrasting edge responses between species with differing life history strategies and habitat requirements, although these contrasts are not necessarily consistent among studies (Fig. 2F–J; Davies & Margules, 1998; Didham *et al.*, 1998*a*; Kotze & Samways, 1999, 2001; Bolger *et al.*, 2000). In a study of spider communities in forest fragments in Finland, it was shown that large hunting spiders were most abundant near forest edges where the environment was warmer, more open, and the leaf litter layer was thick enough to allow stratification of adults and juveniles, which reduced the probability of cannibalism (Pajunen *et al.*, 1995). By contrast, in the same forest fragments, small web-building spiders were more likely to inhabit the forest interior, where the herb and moss cover provided suitable microhabitat structures for web construction (Pajunen *et al.*, 1995). Even different species within a single genus can have completely contrasting responses to edges, as exemplified by the leaf-litter-dwelling beetle genus *Araptus* in Central Amazonia (Didham *et al.*, 1998*a*). Didham *et al.* (1998*a*) showed that some *Araptus* species were apparently insensitive to forest fragmentation, whereas others became locally extinct in small fragments. Furthermore, another *Araptus* species was most abundant in small fragments and at forest edges, while yet another species was most likely to occur deep in undisturbed forest (Didham *et al.*, 1998*a*). Such varied responses to fragmentation within a genus were striking and possibly reflected subtle differences among species life histories and the effects of species-level resource partitioning (Didham *et al.*, 1998*a*).

(2) Edges as ecological traps

Curiously, some animals appear to select or prefer edges as suitable breeding habitat, despite the fact that mortality rates at edges can be much higher than in fragment interiors. This phenomenon has been termed an ‘ecological trap’ and was originally introduced in the avian literature (Gates & Gysel, 1978; Flaspohler, Temple & Rosenfield, 2001; Ries & Fagan, 2003). However, two recent studies of edge effects have expanded the concept to include invertebrates. In a thorough study, McGeoch & Gaston (2000) showed that the abundance of the English holly leaf miner *Phytomyza ilicis* was greatest at woodland edges, indicating that adults prefer to oviposit at edges than in the

woodland interior. Despite this preference, survivorship was lowest at the edge, possibly because of host-plant-induced mortality (McGeoch & Gaston, 2000). Similarly, Ries & Fagan (2003) found the density of mantid egg cases was greatest at the edges of cottonwood and desert shrub riparian zones, where bird predation rates were significantly higher.

(3) Edges alter species interactions

Habitat edges can alter the nature of species interactions and thereby modify ecological processes and dynamics at a wide range of scales (Fagan, Cantrell & Cosner, 1999). Examples of altered herbivory (McKone *et al.*, 2001), seed predation (Burkey, 1993), competition (Remer & Heard, 1998), predation (Ries & Fagan, 2003) and parasitism rates (Tschardt *et al.*, 2002*b*; Cronin, 2003*b*) are relatively common, and explicit recognition of these responses has applied significance in the field of biological control in agroecosystems (Thies & Tschardt, 1999; With *et al.*, 2002). However, habitat edge effects can sometimes be dependent on landscape context, with diverse, structurally complex landscapes negating differences between fragment edges and interiors (Thies & Tschardt, 1999; Tschardt & Brandl, 2004). For instance, Thies & Tschardt (1999) showed that parasitism rates of the rape pollen beetle *Meligethes aeneus* in field interiors were much lower than at field edges when fields were surrounded by homogenous landscapes, but not when the surrounding landscape was heterogeneous.

(4) Variability and hyperdynamism at edges

Perhaps one of the most intriguing aspects of edge effects is that interactions between species may become less stable at edges. This possibility, though not widely tested, is hinted at by the results of several recent studies. In an extensive study of beetle communities in Amazonian forest fragments, Didham *et al.* (1998*a*) showed that the community composition at edges was more variable than in undisturbed forest sites. This result was driven by the fact that most edge species were localised to just one or a few edges, but were seldom located at all edges, indicating that edges support higher β -diversity than fragment interiors (Didham *et al.*, 1998*a*). Similarly, variability in invertebrate predator abundance within an apple orchard decreased with distance from orchard edge to interior (Brown & Lightner, 1997), and the parasitism risk to the planthopper *Prokelisia crocea* was 60% more variable at the edge than in the interior of prairie cordgrass patches (Cronin, 2003*b*). One important outcome of increased variability in trophic interaction strengths may be hyperdynamism in a range of ecosystem process rates, where the frequency and/or amplitude of ecosystem dynamics is increased (Laurance, 2002). Hyperdynamism in fragmented landscapes occurs because habitat fragments are more prone than large areas of continuous habitat to environmental stochasticity and the penetration of external dynamics from the matrix into fragments, and can result in the destabilisation of animal populations (Laurance, 2002). For example, population

outbreaks by the tent caterpillar *Malacosoma disstria* (Roland & Taylor, 1997) and aphids (Kareiva, 1987) were increased in fragmented habitats following reductions in predation and parasitism.

IV. SHAPE COMPLEXITY

Shape complexity is a fragment attribute that has raised surprisingly little interest in fragmentation studies, but may in fact be extremely important. At the most basic level, shape is determined by an interaction between fragment area and perimeter that determines the amount of core habitat remaining in any given habitat fragment (Laurance & Yensen, 1991; Collinge, 1996). It is the relationship between these two variables that forms the basis of most quantitative shape indices (reviewed by Baskett & Jordan, 1995 and Riitters *et al.*, 1995). Unfortunately, the most commonly used shape index is the perimeter to area ratio (Kupfer, 1995), which is not independent of area and can yield large errors when used to estimate the amount of core and edge habitat (Laurance & Yensen, 1991). Furthermore, analyses of large-scale geographic data sets have shown a consistent positive correlation between fragment area and shape complexity (Cochrane & Laurance, 2002). Consequently, many studies that claim to show shape effects may in fact have confounded shape with area effects. For instance, Baz & Garcia-Boyer (1995) found butterfly species richness to be higher in compact shapes, but only if area was not included in the model. The importance of choosing an appropriate shape index was shown clearly by Moser *et al.* (2002), who found that the sign of the relationship between fragment shape and species richness could be either positive or negative for the same data set, depending on how shape complexity was calculated.

Fragments with complex shapes have a much higher proportion of total fragment area that is edge, rather than core habitat (Laurance & Yensen, 1991), accentuating the extent to which edge effects permeate the habitat (Collinge, 1996). Furthermore, the convoluted nature of complex shapes can result in the division of core habitat into multiple, disjunct core areas that are separated by regions of edge-affected habitat (Ewers, 2004). Population estimates based on a literature review of the density-area relationship (Bender *et al.*, 1998; Bowers & Matter, 1997; Connor *et al.*, 2000) showed that disjunct cores in large fragments can reduce invertebrate populations to one-fifth of the population size that could be supported if core habitat were continuous (Ewers, 2004). Moreover, communities in fragments with narrow, elongated shapes may exhibit changes in species richness and abundance that are analogous to area effects (Fig. 1C). Individuals in narrow fragments are likely to have reduced encounter rates relative to individuals in compact fragments, which may lead to shape-induced Allee effects, and reductions in parasitism rates (Thies & Tschardt, 1999).

Perhaps the most consistent pattern that emerges with regard to shape is that complex fragments are colonised more frequently than are compact patches (Game, 1980;

Collinge, 1996; Hamazaki, 1996; Bevers & Flather, 1999; Collinge & Palmer, 2002; Cumming, 2002). This pattern is also found in two-dimensional marine substrates (Minchinton, 1997; Tanner, 2003) and has been applied to three-dimensional patches in marine (Jacobi & Langevin, 1996) and aquatic (Lancaster, 2000) habitats. Increased colonisation of complex fragments occurs because fragments with high shape complexity have a proportionally greater amount of edge, increasing the likelihood that a patch will be encountered by a moving individual (Collinge & Palmer, 2002). However, colonisation probability can be moderated by fragment orientation. When species movements occur in a predictable pattern, such as migration (Gutzwiller & Anderson, 1992) or tidal movements (Tanner, 2003), long thin patches are more likely to be colonised than compact fragments, but only if they are oriented perpendicular to the direction of movement.

The corollary of increased colonisation of complex shapes is that emigration is also likely to be increased (Van Kirk & Lewis, 1999), although this may depend upon boundary permeability (Stamps, Buechner & Krishnan, 1987; Collinge & Palmer, 2002). As a result, the probability of population persistence in fragments with complex shapes is reduced (Fig. 1C; Bevers & Flather, 1999; Van Kirk & Lewis, 1999), leading to higher patch occupancy in compact fragments (Helzer & Jelinski, 1999). Furthermore, the combination of increased emigration and colonisation leads to greater variability in the population size of long, thin patches (Hamazaki, 1996).

Theory suggests that the effects of shape are likely to scale with fragment area. It is likely that small fragments are most heavily impacted by having complex shapes, because any deviation from circularity will greatly reduce the amount of interior habitat (Laurance & Yensen, 1991; Kupfer, 1995). The problem associated with testing for these effects is that shape and area are intimately correlated, as shown by studies including thousands of fragments (Cochrane & Laurance, 2002; Ewers, 2004) or as few as 17 fragments (Watson, 2003). While some experimental studies have varied shape while holding area constant (Hamazaki, 1996), none have independently varied both shape and area.

V. ISOLATION

One of the obvious spatial consequences of habitat fragmentation is that fragments become isolated in space and time from other patches of suitable habitat. Isolation disrupts species distribution patterns (Fig. 1D) and forces dispersing individuals to traverse a matrix habitat that separates suitable habitat fragments from each other. While isolation is most often defined by the Euclidean distance between habitat fragments, it is, in fact, matrix dependent. An extreme example of this was highlighted by Bhattacharya, Primack & Gerwein (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 Section VI.2; Fig. 1E; Ricketts, 2001; Roland, Keyghobadi & Fownes, 2000) and because species differ in their willingness to disperse through matrix environments (Laurance, 1991; Haddad & Baum, 1999; Collinge, 2000), the literature is full of seemingly disparate results regarding the effects of isolation on species and communities. For instance, genetic differentiation between invertebrate populations was clearly related to fragment isolation in some studies (Van Dongen *et al.*, 1998; Schmitt & Seitz, 2002; Krauss *et al.*, 2004), but not in others (Ramirez & Haakonsen, 1999; Wood & Pullin, 2002). Similarly, the relationship between invertebrate species richness and isolation can be positive (Baz & Garcia-Boyer, 1996), negative (Baz & Garcia-Boyer, 1995) or absent (Brose, 2003; Krauss *et al.*, 2003a; Krauss, Steffan-Dewenter & Tschardt, 2003b). One likely reason for these conflicting results is that species with different traits differ in their susceptibility to isolation (see Section VII; Fig. 2P–T).

The intuitive conservation response to isolation is to connect isolated fragments with corridors of suitable habitat (Hill, 1995). Corridors can increase the density and diversity of invertebrate species and communities (Hill, 1995; Gilbert, Gonzalez & Evans-Freke, 1998; Haddad & Baum, 1999; Collinge, 2000), and are most effective for species that never, or rarely, disperse through the matrix surrounding habitat patches (Schultz, 1998). This was convincingly demonstrated in an experimental grassland system by Collinge (2000) and in a natural grassland system by Haddad & Baum (1999). In both studies, species that were restricted to habitat patches benefited from the presence of corridors, whereas no strong benefits were observed for habitat generalists. Corridors have also been shown to have a small positive effect for less vagile species (Collinge, 2000) and strongly increased the survival of predators in an experimentally fragmented moss microecosystem (Gilbert *et al.*, 1998). Interestingly, the current primary role of corridors is to facilitate metapopulation persistence within a landscape (Collinge, 1996; Jordan *et al.*, 2003), but in the future corridors may be required to facilitate species migrations between landscapes in response to climate change (Collingham & Huntley, 2000; Opdam & Wascher, 2004; Stefanescu, Herrando & Paramo, 2004).

VI. MATRIX EFFECTS

A growing body of evidence suggests that matrix quality is crucially important in determining the abundance and composition of species within fragments (Figs 1E, 2U–Y; Laurance, 1991; As, 1999; Gascon *et al.*, 1999; Kotze & Samways, 1999; Cook *et al.*, 2002; Perfecto & Vandermeer, 2002). The traditional IBT approach to the study of habitat fragmentation failed to recognise that the penetration of edge effects from outside a fragment alters habitat characteristics within the fragment (Didham, 1997) and that the matrix may not be completely inhospitable to the fragment-dwelling fauna (Gustafson & Gardner, 1996). In fact, there is often substantial overlap between species that inhabit

fragments and matrix habitat (Cook *et al.*, 2002). This species 'spill-over' is most prevalent in small patches and at the edges of large patches, and may obscure area and isolation effects (Cook *et al.*, 2002; Brotons, Mönkkönen & Martin, 2003). Cook *et al.* (2002) went on to show that IBT predictions had a better fit when species that occurred in the matrix were removed from the analysis. In addition, increasing species' mortality rates in the matrix can have the drastic effect of completely reversing the outcome of competitive interactions within fragments, allowing inferior species to supplant dominant ones within fragments (Cantrell, Cosner & Fagan, 1998).

(1) Can matrix quality mitigate fragmentation effects?

Habitat remnants are not necessarily the only parts of the landscape that provide resources relevant to species persistence, and some fragment-dwelling species are able to compensate for habitat loss by making use of resources available in the matrix (Bierregaard *et al.*, 1992; Davies, Gascon & Margules, 2001*a*; Denys & Tschamtko, 2002; Ries *et al.*, 2004). In these cases, it is not strictly correct to apply the term 'matrix' to the habitat surrounding fragments, as the term carries connotations of inhospitable environments. In fact, for some species the 'matrix' may actually represent a set of resources that are complementary to, and unavailable in, habitat remnants (Ries & Sisk, 2004). Thus, there can be great difficulty involved in arbitrarily splitting components of a landscape into the categories 'patch' and 'matrix.' This is illustrated by the results of Perfecto & Vandermeer (2002), who demonstrated that ants inhabiting forest fragments in Mexican coffee plantations were actively foraging in the surrounding matrix and that some species were even able to survive in matrix habitat in perpetuity. Furthermore, an increase in matrix quality was associated with an increase in the number of species and individuals that occurred in the matrix (Perfecto & Vandermeer, 2002). In other cases, species with complex life histories may require different resources from multiple habitat types during their life cycle (Ries *et al.*, 2004). For instance, Thies & Tschamtko (1999) found that parasitoids required both the availability of hosts within crop fields as well as the availability of perennial hibernation sites within the surrounding landscape matrix.

A species' ability to utilise resources from the matrix can alter the intensity of fragmentation effects (Fig. 2X). In model simulations, Andrén (1997*b*) demonstrated that generalist species maintained higher populations in fragmented landscapes than specialist species that depended on resources available only in fragments. Increasing the degree of habitat specificity further amplified population reductions when habitat was lost and fragmented (Andrén, 1997*b*). In a similar model, Estades (2001) showed that increasing matrix quality (i.e. providing resources in the matrix) increased population density within a fragment. Several empirical studies have now confirmed the importance of matrix quality for population persistence within fragments (Thies & Tschamtko, 1999; Ricketts, 2001; Vandermeer *et al.*, 2001), and that temporal changes in

matrix quality can reverse trends in species abundances. For instance, dramatic declines in the abundances of three *Euglossa* bee species were recorded within months of the creation of experimental forest fragments at the Biological Dynamics of Forest Fragments Project in Brazil (Powell & Powell, 1987; Cane, 2001), yet after several years of matrix regeneration (which provided the bees with a new food source) their numbers had rebounded to become higher in fragments than in continuous forest (Becker, Moure & Peralta, 1991; Cane, 2001). Similarly, variation in the quality of spatial subsidies from matrix habitat can either increase or decrease species richness within fragments by alternately increasing resource availability or competition, respectively (Anderson & Wait, 2001). Studies on oceanic islands have convincingly demonstrated that spatial subsidies from the surrounding environment can increase island productivity, and that subsidies have the greatest relative effect on small islands with greater edge to area ratios (Polis & Hurd, 1995, 1996; Anderson & Wait, 2001). If this concept can reasonably be extrapolated to habitat fragments, it seems likely that spatial subsidies from the surrounding landscape matrix may alter the species richness of small fragments.

(2) Matrix and dispersal

Dispersal between habitat fragments is essential for long-term metapopulation persistence (Gustafson & Gardner, 1996), but is at least partially dependent on matrix properties (Franklin, 1993). Although one of the defining characteristics of a matrix is that movement of individuals is different to that observed in habitat patches (as demonstrated by Schultz, 1998; Kindvall, 1999; Hein *et al.*, 2003), altering the structure of the matrix further influences an animal's movement potential (Szacki, 1999). Differences in matrix quality affect dispersal and movement of individuals in fragmented systems (Gustafson & Gardner, 1996; Bierregaard & Stouffer, 1997; Moilanen & Hanski, 1998; Davies *et al.*, 2001*b*) and may function as a 'qualitative filter' (Szacki, 1999) for individuals at specific life history stages. As a result, matrix structure can alter colonisation-extinction dynamics (Brotons *et al.*, 2003; Cronin & Haynes, 2004), which can lead to changes in population density (Gustafson & Gardner, 1996) and structure (Szacki, 1999). Furthermore, changes to matrix structure can increase variability in species interactions, as demonstrated for host-parasitoid dynamics in cordgrass patches of the North American Great Plains (Cronin & Haynes, 2004).

The degree of contrast between fragment and matrix habitat largely determines the permeability of edges to animal movement across fragment boundaries (Stamps *et al.*, 1987; Holmquist, 1998; Collinge & Palmer, 2002). Typically, low-contrast boundaries are predicted to be more permeable (Collinge & Palmer, 2002), as found in studies on butterflies (Ries & Debinski, 2001), hymenopteran parasitoids (Cronin, 2003*a*) and shrimp (Holmquist, 1998). However, these results are highly species specific and depend entirely on the species' perception of the habitat boundary (Schultz & Crone, 2001). Ries & Debinski (2001) found a link between edge contrast and permeability for

a generalist butterfly, whereas a specialist was unlikely to emigrate from a fragment, regardless of edge structure. Similarly, motile species found edges more permeable than other, more sedentary species (Holmquist, 1998). It should also be noted that edge structure is not the sole determinant of permeability; other factors such as conspecific density, wind direction and time of day or year all significantly influenced edge permeability (Holmquist, 1998; Ries & Debinski, 2001). Changes to edge permeability may be either positive or negative for populations, depending on the particular landscape and species being studied. Long-term persistence of metapopulations requires individuals to cross habitat edges and disperse between habitat remnants (Hanski, 1998), so some degree of permeability is clearly essential. However, edges that are 'too' permeable may act as population sinks. For instance, nocturnal foraging of the carnivorous New Zealand *Paryphanta* spp. landsnails across permeable forest edges leaves them prone to mortality from desiccation in the surrounding pasture matrix during the day, because they are unable to return quickly enough to the shaded safety of the forest (Ogle, 1987).

Once an animal has left a fragment, the structural characteristics of the matrix can resist, hinder or enhance movement behaviour (Gustafson & Gardner, 1996; Roland *et al.*, 2000; Chardon, Adriaensens & Matthysen, 2003). For example, Cronin (2003a) found that hymenopteran parasitoids were most likely to colonise cordgrass fragments that were surrounded by a matrix of native or exotic grass, rather than fragments in a mudflat matrix. Similarly, Ricketts (2001) showed that a meadow-dwelling butterfly species had higher dispersal through willow than conifer matrix, although this result was species specific, with several other species showing no difference. Ricketts (2001) concluded that matrix quality alters 'effective isolation' in ways that vary among even closely-related species. The concept of effective isolation has been applied by other authors under a series of different names including cumulative resistance (Knaapen, Scheffer & Harms, 1992), functional connectivity (Tischendorf & Fahrig, 2000), effective distance (Moilanen & Hanski, 1998; Roland *et al.*, 2000; Ferreras, 2001) and cost-distance (Chardon *et al.*, 2003). Instead of measuring fragment isolation in terms of Euclidean distance, effective isolation weights Euclidean distance according to matrix viscosity (Ferreras, 2001). Ferreras (2001) assigned matrix habitats a 'friction value' based on Jacobs' Selection Index [Jacobs (1974) cited in Ferreras (2001)], which reflects a particular habitat's viscosity to the movement of a particular study animal. Both Ferreras (2001) and Chardon *et al.* (2003) found effective isolation was a more accurate predictor of connectivity than Euclidean distance.

(3) Matrix and edge effects

The strength of an edge effect can be greatly moderated by changes in matrix structure. Edges with a high contrast between the fragment and matrix are more likely to generate stronger edge effects than low-contrast edges (Franklin, 1993; Demaynadier & Hunter, 1998; Zheng & Chen, 2000; Laurance *et al.*, 2002). This has been demonstrated for

edge-related gradients in the density of hymenopteran parasitoids (Cronin, 2003a). Furthermore, Perfecto & Vandermeer (2002) found that ant species richness declined from the fragment edge into the matrix, but the rate of decline was slower when edge contrast was lowest, and Holmquist (1998) showed that edge permeability in the marine environment was a function of edge contrast.

VII. CONFOUNDING FACTORS IN THE DETECTION OF FRAGMENTATION IMPACTS

The literature on habitat fragmentation is replete with examples of apparently contradictory results that cannot be explained solely by reference to differences between the environments or methods used in separate studies. These differences highlight the emerging realisation that a wide range of confounding factors can either obscure or enhance the detection of fragmentation effects.

(1) Trait-mediated differences in species responses to fragmentation

Many seemingly contradictory responses to fragmentation can be adequately explained by investigating the mechanisms driving species-level patterns, and the individual traits that determine species' susceptibilities to those underlying processes. In general, there is a suite of traits that is commonly hypothesised to increase a species' vulnerability to fragmentation, including large body size, low mobility, high trophic level, and matrix tolerance (Fig. 2; Laurance, 1991; Didham *et al.*, 1998b; Davies, Margules & Lawrence, 2000; Tschardtke *et al.*, 2002a; Henle *et al.*, 2004). By explicitly considering the effect of species traits, it becomes possible to explain many of the apparently conflicting results in the fragmentation literature.

For instance, a number of studies have shown that the nature of the SA relationship describing species loss from habitat fragments is confounded by differences in species traits. Species at higher trophic levels, habitat specialists, species with large body size and those with poor dispersal abilities or a reliance on mutualist species are expected to go extinct first when habitat area decreases (Fig. 2A–D; Rathcke & Jules, 1993; Didham *et al.*, 1998a, b; Holt *et al.*, 1999; Davies *et al.*, 2000; Steffan-Dewenter & Tschardtke, 2000; Tschardtke *et al.*, 2002a; Steffan-Dewenter, 2003; Davies, Margules & Lawrence, 2004). Consequently, taxa with these traits frequently exhibit steeper SA curves. For example, Krauss *et al.* (2003a) showed that generalist butterflies had a shallower SA curve than did specialist butterflies. Similarly, Tschardtke and Kruess (1999) found that SA curves for parasitoid species were steeper than for herbivores, although Steffan-Dewenter (2003) failed to find any difference between bees, wasps and their natural predators and parasitoids. Interestingly, recent analyses of nested communities, in which the composition of species-poor communities are hierarchically arranged, non-random subsets of species-rich communities (Patterson, 1987) show that species extinction occurs in a consistent, sequential

pattern as fragment area decreases (Wright *et al.*, 1998; Lövei & Cartellieri, 2000; Loo, Mac Nally & Quinn, 2002), indicating a gradient in extinction vulnerability among species. To date, attempts to integrate the study of nested communities with theoretical predictions of extinction susceptibility for species with particular trait complexes have been largely *ad hoc*, although this emerging field of research promises to shed further light on area-related extinction patterns.

Similarly, many of the contrasting results found in studies of habitat isolation can be explained by more explicit consideration of species traits. Species at higher trophic levels, such as predators and parasitoids, appear to be more heavily affected by isolation than those at lower trophic levels (Fig. 2P; Tschamtko, Gathmann & Steffan-Dewenter, 1998; Zabel & Tschamtko, 1998), and species with high mobility are more likely to survive in fragmented landscapes than species with low mobility (Nieminen, 1996; Thomas, 2000). Interestingly, Thomas (2000) showed that butterfly species with intermediate mobility were more likely to decline in abundance following habitat fragmentation than were butterflies with either high or low mobility (Fig. 3). He explained this unexpected result by reference to the probable underlying mechanism. Highly vagile species were able to disperse freely between fragments and so were relatively unaffected by fragmentation, and at the opposite extreme, species with low vagility tended to stay within a fragment, thereby avoiding dispersal-related mortality. By contrast, intermediate mobility resulted in individuals dispersing away from one fragment but failing to reach the next, leading to an overall increase in the mortality rate for these species. This mechanistic explanation leads directly to the prediction that habitat fragmentation will create local selection pressures to favour simultaneously either of the two extremes of dispersal ability. This prediction is at least partially supported by population-level increases in the dispersal power of butterflies in fragmented landscapes (C. D. Thomas, Hill & Lewis, 1998; Hill, Thomas & Lewis, 1999) and the reduction in mobility of carabid beetles in populations that inhabit fragments for long periods of time (Desender *et al.*, 1998).

Simple tests for the impacts of species traits on species' vulnerability to fragmentation are likely to be confounded by interactions between traits. In a recent review by Henle *et al.* (2004), it was shown that six traits have sufficient empirical support to justify being considered strong predictors of species' sensitivity: population size, population variability, competitive ability and sensitivity to disturbance, degree of habitat specialisation, rarity, and biogeographic location. However, any given species comprises a suite of traits that are strongly intercorrelated (Laurance, 1991; Henle *et al.*, 2004), and can interact with each other to increase susceptibility to fragmentation. For example, Davies *et al.* (2004) showed that a synergistic interaction between the traits of rarity and habitat specialisation made beetle species that were both rare and specialised more vulnerable to fragmentation than predicted by the simple additive effects of the two traits in isolation (Fig. 4). Furthermore, some traits interact with environmental heterogeneity such that the determinants of species vulnerability in one

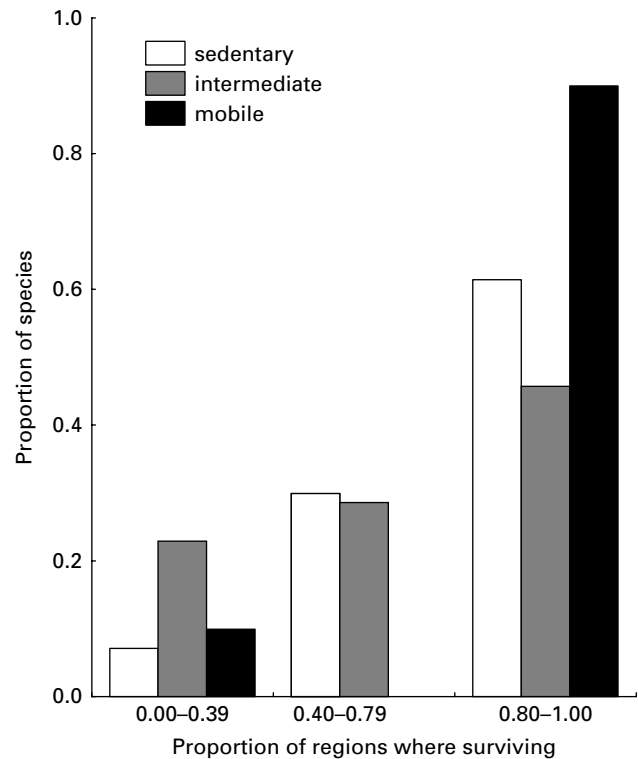


Fig. 3. Some apparently idiosyncratic responses to fragmentation can be explained by reference to the underlying mechanism of species response. On average, UK butterfly species with intermediate mobility (17 species) have smaller geographic ranges and are more likely to go locally extinct than species with either high (10 species) or low (29 species) mobility, which both suffer lower levels of dispersal-related mortality (see text). Proportions of butterfly species surviving in 21 UK regions are plotted for butterflies within each of three classes of differing dispersal ability. A relatively high proportion of species with intermediate mobility survive only in very few (0–39%) of the regions from which they were originally present, implying that many have gone locally extinct from most of their former range. By contrast, species with either high or low mobility are less likely to have suffered local extinctions, and are more likely to have survived in the majority of their original range than species with intermediate mobility. Figure reproduced from Thomas (2000, p. 141).

environment will not necessarily be the same in a different environment (Henle *et al.*, 2004). One potential solution to this problem is to work explicitly in terms of trait complexes, rather than dealing with traits individually. Extinction frequency is seldom randomly distributed across families or genera (Bennett & Owens, 1997; Purvis *et al.*, 2000a), because traits that bias species to extinction are often phylogenetically conservative (McKinney, 1997). By using comparative analyses that control for phylogenetically correlated suites of traits, it should be possible to elucidate more clearly the roles of individual traits (e.g. Owens & Bennett, 2000; Purvis *et al.*, 2000b). This approach has yet to be applied to predictors of species' vulnerability to

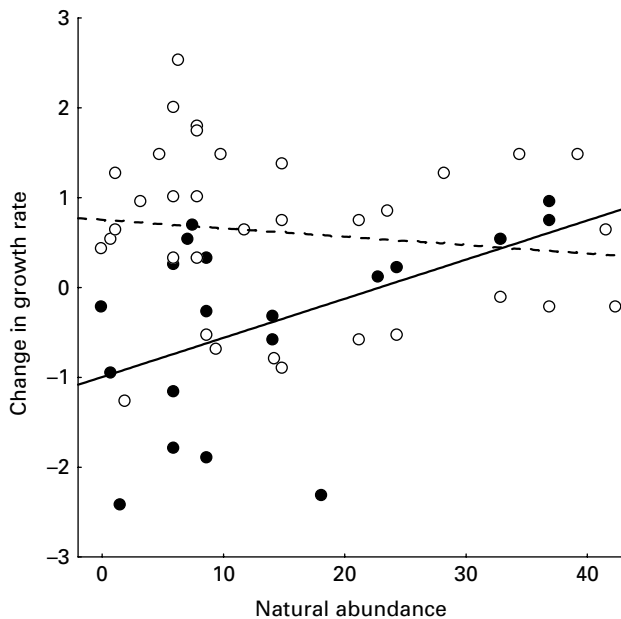


Fig. 4. Single-factor explanations for the influence of individual traits on species responses to fragmentation ignore the fact that synergistic interactions between traits can make some species more susceptible to fragmentation. For 53 beetle species in Australian forest fragments, species that were both rare and specialised were more affected by fragmentation than predicted from either trait operating alone. The y -axis represents the change in the post-fragmentation growth rate of species in fragments compared to continuous forest. Negative values represent reductions in average growth rates. Natural abundance was measured for two years pre-fragmentation. Filled circles (and solid fitted line) are habitat specialists and open circles (and dashed fitted line) are habitat generalists. Figure reproduced from Davies *et al.* (2004, p. 269).

habitat fragmentation, but could be of considerable use in rigorously determining a reliable set of predictor traits.

(2) Time lags in the manifestation of fragmentation effects

The long-term effects of fragmentation are relatively poorly known (McGarigal & Cushman, 2002; Watson, 2003), as most studies of anthropogenically-fragmented landscapes have been conducted less than 100 years after fragmentation (Watson, 2002, 2003). While some authors (e.g. Renjifo, 1999) consider time-scales of 50 to 90 years as 'long-term' and sufficient to ensure that diversity patterns have reached a dynamic equilibrium, this time frame may not be long enough to allow the full spectrum of fragmentation effects to be exhibited (particularly for long-lived organisms). In general, many of the fragmentation effects that are most commonly studied are not exhibited immediately following habitat loss, because not all individuals or species exhibit short-term responses to habitat changes (Wiens, 1994). What we know so far from the spatial and temporal scales applied in the majority of studies, is that short-

medium-term time lags in species responses to fragmentation are almost ubiquitous.

(a) Time lags in population responses to fragmentation

There is a strong temporal component to the manifestation of species responses following fragmentation. In the short term, crowding effects (Bierregaard *et al.*, 1992; Debinski & Holt, 2000) occur when organisms that survive the immediate process of habitat loss are concentrated into the much smaller amount of remaining habitat, thereby increasing population densities and species richness within habitat fragments (Collinge & Forman, 1998). For example, this displacement phenomenon (Hagan, Haegen & McKinley, 1996) occurred almost immediately following habitat loss in Amazonian bird communities (Lovejoy *et al.*, 1986) and in grassland invertebrates of the western USA (Collinge & Forman, 1998), but was not observed at all for Lumholtz's tree kangaroo, *Dendrolagus lumholtzi*, following deforestation in tropical northern Australian (Newell, 1999). In the latter species, individuals exhibited strong site fidelity and chose to remain in the deforested, degraded habitat rather than move to nearby continuous forest (Newell, 1999). While crowding was only discovered by taking an experimental approach to forest fragmentation (Lovejoy *et al.*, 1983; Schmiegelow, Machtans & Hannon, 1997), it paradoxically presents the greatest problem to experimental studies, because many responses to experimental treatments are measured soon after fragmentation.

Typically, fragments are unable to support all surviving individuals and species in the long term, as shown by subsequent reductions in species abundance and richness through time (Debinski & Holt, 2000). For example, the elevated post-fragmentation population densities of species in Amazonian bird communities declined steadily over the following 16 months (Bierregaard *et al.*, 1992, Stouffer & Bierregaard, 1995). A similar pattern was found for birds in the boreal forests of Canada (Schmiegelow *et al.*, 1997). By contrast, reductions in arthropod abundance usually occur over much shorter time frames. For instance, in an experimentally-fragmented moss system in the UK, Gonzalez & Chaneton (2002) found that reductions in microarthropod biomass and abundance occurred over an eight month period. An even shorter time lag was observed in an experimentally-fragmented grassland in Australia, where invertebrate abundance declined over a four month period post-fragmentation (Parker & Mac Nally, 2002). Collinge & Forman (1998) also documented reductions in invertebrate abundance and species richness, and these effects were noticeable after just five weeks.

Reductions in species richness following fragmentation are commonly termed 'extinction debts,' and occur over the medium- to long-term. The term was described by Tilman *et al.* (1994) as a 'time-delayed but deterministic extinction of the dominant competitor in remnant patches,' and describes a time lag between the process of habitat loss and the eventual collapse of populations (Cowlshaw, 1999). The extinction debt is illustrated by negative correlations between species richness and fragment age, measured as time since isolation (Wilcox, 1978; de Vries

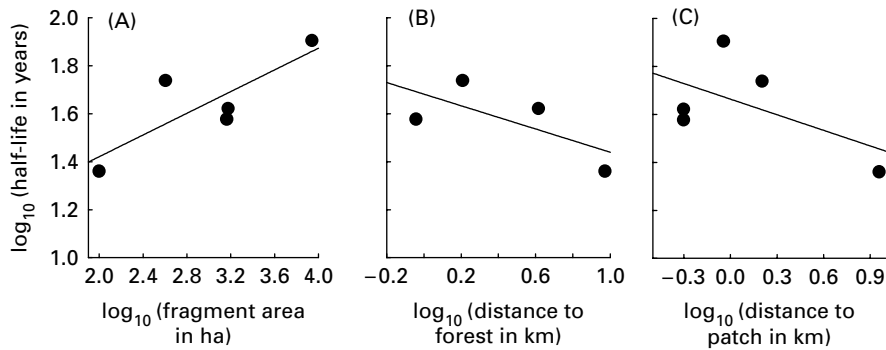


Fig. 5. The spatial attributes of habitat fragments have an important bearing on the time-lag in species loss following habitat loss (the ‘extinction debt’). The y-axis represents the half-life to community relaxation, as the time in years that it took to lose 50% of bird species from forest fragments in Kakamega, Kenya. Figure reproduced from Brooks *et al.* (1999, p. 1146).

et al., 1996; Brooks *et al.*, 1999; Bolger *et al.*, 2000; Parker & Mac Nally, 2002). Furthermore, Komonen *et al.* (2000) showed that the number of insect trophic levels supported by bracket fungus decreased with fragment age, as did the probability of native ants occupying a fragment (Suarez, Bolger & Case, 1998). However, several studies have also found species richness to be greatest in fragments of intermediate (Fahrig & Jonsen, 1998) or old age (Assmann, 1999; Denys & Tschardtke, 2002), because of longer-term temporal changes in habitat diversity that can also result in altered species interactions (Tschardtke & Kruess, 1999; Denys & Tschardtke, 2002).

Extinction debts are paid through time as fragment-inhabiting communities gradually relax to a new equilibrium number of species (Brooks *et al.*, 1999), with the rate of relaxation being a function of fragment area, fragment isolation and generation time of the study organism. Community relaxation approximates an exponential decay with a half-life from 25 to 100 years for birds (Brooks *et al.*, 1999; Ferraz *et al.*, 2003) and 50 to 100 years for prairie-dwelling plants (Leach & Givnish, 1996). Although no direct estimates have yet been made for the half-life of invertebrate extinction debts, Gonzalez (2000) and Gonzalez & Chaneton (2002) found that the extinction debt of microarthropods in an experimentally fragmented moss microsystem was apparently paid in six to twelve months. This probably reflects both the very small size of the fragments in these studies and the rapid generation times of invertebrates relative to vertebrates. The exact value of the half-life may also depend heavily on spatial attributes of the remaining habitat, with small, isolated fragments having much shorter half-lives than large and less-isolated fragments (Fig. 5; Brooks *et al.*, 1999; Ferraz *et al.*, 2003). Similarly, recent modelling studies suggest that the half-life to community relaxation may be a function of the proportion of habitat cover remaining in the landscape, with time lags to extinction being greater at, or below, the extinction threshold (Ovaskainen & Hanski, 2002, 2004). Hanski & Ovaskainen (2002) present an empirical example in which the number of regionally extinct old-growth forest beetles in Finland was proportional to the length of time that forests had been managed for timber production

within different regions, and the amount of available intact habitat. They showed that the extinction debt was especially great for communities in which many species were near the threshold for metapopulation extinction (*i.e.* the ‘capacity’ of the landscape to ensure metapopulation persistence; Hanski & Ovaskainen, 2000), and that some species only survived in the more recently disturbed regions because there had not been enough time for all local populations to become extinct (Hanski & Ovaskainen, 2002). Such transient metapopulation dynamics for individual species has been well described by Ovaskainen & Hanski (2004). They suggest that the length of time taken for a new metapopulation equilibrium to stabilise following habitat loss (whether this is equilibrium persistence or equilibrium extinction) increases with the degree of change in habitat cover, the life span of the organism, the availability of stable large patches within a patch network, and with decreasing habitat cover approaching the extinction threshold. For the well-studied Glanville fritillary butterfly, *Melitaea cinxia*, in Finland, for example, Ovaskainen & Hanski (2004) suggest that the period of transient metapopulation dynamics following habitat loss can be up to 5–10 generations.

(b) Biogeographic factors controlling fragmentation responses

Biogeography and history may offer some clues as to the likely long-term impacts of habitat fragmentation on species and communities. Species’ sensitivity to fragmentation differs between biomes, with particularly low sensitivity recorded in the temperate zones of the Northern Hemisphere (Henle *et al.*, 2004). One likely reason for this is that anthropogenically-driven habitat loss and fragmentation occurred long before scientists recognised it as a problem and began recording species responses (Balmford, 1996). Thus, it is possible that the most sensitive species in this biome have already become extinct, leaving behind just a subset of the original fauna that is resilient to the fragmented landscapes that remain. This process is a type of ‘extinction filter’ (Balmford, 1996), and would explain why species in the more recently degraded habitats of Oceania and many tropical regions appear to be more vulnerable to fragmentation (Henle *et al.*, 2004). It would also suggest that over longer time

scales, human modification of natural habitats will lead to the extinction of many species that are presently considered to be vulnerable to fragmentation. Unfortunately, hypotheses such as this are difficult, if not impossible, to test because we simply do not have the required data on historical extinctions (Balmford, 1996).

(c) *Altered selection pressures and developmental instability*

Morphological changes in individuals in response to fragmentation require time for natural selection to have a noticeable impact. Such phenotypic changes have seldom been investigated, but may hold important clues about species traits that promote population persistence in fragmented landscapes. For example, morphological changes such as increased muscle mass for flight have been observed by comparing butterfly populations in historically fragmented landscapes with those in recently fragmented landscapes (C. D. Thomas *et al.*, 1998; Hill *et al.*, 1999; Norberg & Leimar, 2002). Similar relationships between fragmentation and morphological characters that reflect the dispersal power of individuals have been shown for the damselfly, *Calopteryx maculata* in Canada (Taylor & Merriam, 1995), two species of carabid beetles in western European saltmarshes (Desender *et al.*, 1998), two species of bush cricket in the UK (C. D. Thomas *et al.*, 2001), and the Glanville fritillary butterfly, *Melitaea cinxia*, also in the UK (Norberg & Leimar, 2002). Several species of wing-dimorphic planthoppers also exhibit differences in the relative frequency of wing morphs in relation to fragmentation, with long-winged males more prevalent in fragmented habitats (Denno *et al.*, 2001; Langellotto & Denno, 2001). Long wings confer an advantage over short-winged males when it comes to mate finding (Langellotto & Denno, 2001), but there is also a trade-off between flight capability and reproductive output (Langellotto, Denno & Ott, 2000).

The above examples illustrate the role of habitat fragmentation in altering selection pressures for particular traits of species. Typically, selection occurs on phenotypic variation that occurs naturally within a species, but habitat fragmentation itself may also increase the amount and types of phenotypic variation that are subject to natural selection. For instance, small fragments often contain poor-quality habitats that increase the environmental stresses experienced by individuals and populations (Lens, Van Dongen & Matthysen, 2002). These stresses can result in developmental instability of individuals, which is often shown in the form of fluctuating asymmetry (Weishampel, Shugart & Westman, 1997). Fluctuating asymmetry (FA) was elevated in populations of two gecko species inhabiting fragmented *versus* continuous landscapes in western Australia (Sarre, 1996) and FA rates for seven forest bird species in Kenya were four to seven times greater for birds in the smallest, most degraded fragments sampled by Lens *et al.* (1999). Similarly, the bank vole *Clethrionomys glareolus* had greater rates of FA in fragmented than in continuous landscapes in France (Marchand *et al.*, 2003), as did centipedes in fragmented Amazonian rainforests (Weishampel *et al.*, 1997). Increased levels of FA have been correlated with

reductions in the growth rates and competitive ability of a range of organisms (see reviews by Møller, 1997 and Møller & Thornhill, 1998), as well as reduced survival probabilities for the taita thrush *Turdus helleri* in east Africa (Lens *et al.*, 2002). Furthermore, FA may also leave individuals more susceptible to predation and parasitism (Møller, 1997; F. Thomas, Ward & Poulin, 1998). Interestingly, a meta-analysis by Møller & Thornhill (1998) indicated that FA is a heritable trait, although the exact frequency with which FA is inherited is still being debated (Roff & Réale, 2004). Moreover, it has been demonstrated that phenotypic changes in symmetry can precede genetic changes that may ultimately lead to the fixation of asymmetrical traits in a species (Palmer, 2004). Hence, it now seems evident that environmental stresses, such as those imposed by habitat fragmentation, can result in phenotypic changes that may ultimately lead to morphological divergence between isolated populations (Sarre, 1996).

(3) Synergies magnify the impacts of fragmentation

(a) *Fragmentation and pollination*

There are no data that unequivocally relate habitat fragmentation with long-term pollinator declines (Cane & Tepedino, 2001), perhaps because plant-pollinator systems exhibit wide temporal variation (Roubik, 2001). However, habitat loss and fragmentation can significantly alter the nature of invertebrate pollinator communities and disrupt plant-pollinator interactions (Rathcke & Jules, 1993; Klein *et al.*, 2003). For example, the number of social bee species pollinating coffee crops decreased with isolation from forest edges (Klein *et al.*, 2003), and the taxon richness of native invertebrate pollinators in tropical forest fragments declined with fragment area (Aizen & Feinsinger, 1994). Pollinator communities in small fragments were dominated instead by the exotic honeybee *Apis mellifera* (Aizen & Feinsinger, 1994). Unfortunately, generalist pollinators that replace specialised native species are frequently less effective pollinators, and may result in reduced rates of outcrossing and hence lower genetic variability of fragmented plant populations (Didham *et al.*, 1996; Steffan-Dewenter & Tschamntke, 2002). This point was also demonstrated by Goverde *et al.* (2002), who found that flowers in experimentally fragmented grassland plots were visited less frequently by bumblebee pollinators than were flowers in unfragmented control plots. Moreover, bumblebee foraging behaviour was altered by habitat fragmentation, with lower visiting time per patch and greater flight directionality and distance in fragments (Goverde *et al.*, 2002). However, in other cases introduced pollinators are able to replace sufficiently the loss of natives. For instance, the introduced African honeybee *Apis mellifera scutellata* was a more efficient pollinator of a canopy tree in fragmented Amazonian landscapes than were the native species (Dick, 2001). Furthermore, the introduced honeybee dispersed pollen over greater distances, thereby expanding the area of genetic neighbourhoods and possibly linking fragmented with continuous populations (Dick, 2001; Dick, Etchelecu & Austerlitz, 2003).

Pollinators exhibit species- and scale-specific responses to habitat loss and fragmentation. Steffan-Dewenter *et al.* (2002) showed that the abundance and species richness of solitary bees was positively correlated with the proportion of semi-natural habitat in the landscape at small scales of up to 750 m (circular radius), whereas honeybee density was negatively correlated with semi-natural habitat in the landscape at a much larger scale of 3000 m. These differences occurred because of differences in individual species life histories. Solitary bees have more specific habitat requirements and smaller foraging ranges than do honeybees, leading to contrasting responses to habitat loss. These data clearly support the assertion of Cane (2001) that inter-patch movements and loss of nesting habitat must be considered when investigating pollinator communities, rather than focusing solely on fragments of forage plants.

(b) *Fragmentation and disease*

Deforestation has a significant effect on populations of parasitic disease vectors, with anthropogenic conversion of forest to agricultural land-uses implicated in increased abundances of the insect vectors for malaria, leishmaniasis and trypanosomiasis (Patz *et al.*, 2000). Furthermore, habitat edges can strongly influence species interactions between hosts and pathogens (Fagan *et al.*, 1999; Cantrell, Cosner & Fagan, 2001), but despite this the effect of habitat fragmentation on the dynamics of pathogens has received little attention (McCallum & Dobson, 2002). Nevertheless, it has been convincingly demonstrated that habitat fragmentation can alter the prevalence of disease in a landscape. Langlois *et al.* (2001) found that deer mice *Peromyscus maniculatus* in fragmented Canadian landscapes had a higher hantavirus infection rate than in unfragmented landscapes, probably because habitat fragmentation forces deer mice to disperse over larger areas. In the northeastern U.S.A., Lyme disease also has a dramatically higher prevalence in small forest fragments, because the vector, the blacklegged tick *Ixodes scapularis*, is exponentially more abundant and has higher infection rates in small fragments (Allan, Keesing & Ostfeld, 2003; Fig. 6). In model simulations, Hess (1994) showed that greater fragment isolation typically causes an increased probability of metapopulation extinction, but when host-pathogen interactions are important in host dynamics, then increasing landscape connectivity actually promoted disease transmission, leading to an increased probability of metapopulation extinction. In these circumstances a more fragmented landscape of isolated patches would be preferable for restricting the spread of disease across a landscape (Hess, 1994). A similar conclusion was reached by Perkins & Matlack (2002), who found that increasing the degree of fragmentation in *Pinus* spp. plantations could restrict the spread of fusiform rust *Cronartium quercuum* (Holdenrieder *et al.*, 2004). However, later models by McCallum & Dobson (2002) have indicated that the benefits of corridors that allow species to disperse throughout the landscape (e.g. increased colonisation of empty patches) typically outweigh the risks of increased disease transmission.

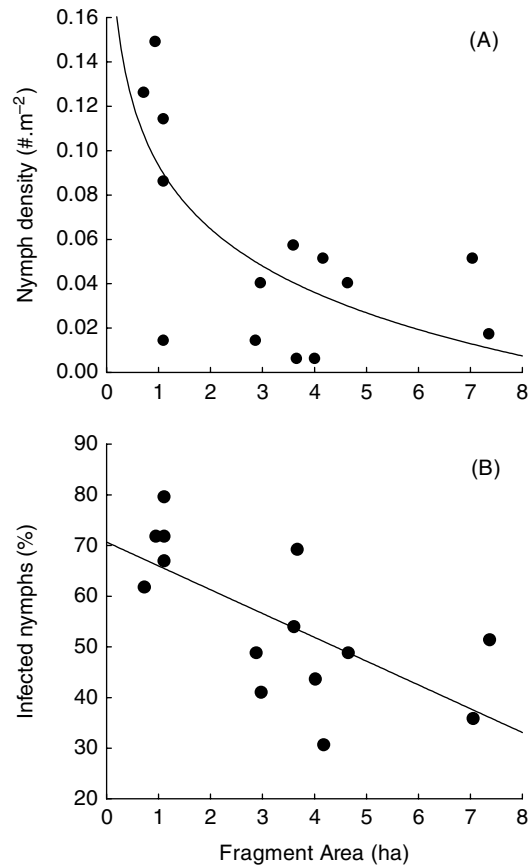


Fig. 6. Synergistic interactions between habitat fragmentation and other drivers of population change, such as disease transmission, can magnify the impacts of fragmentation. Relationship between the prevalence of Lyme disease and forest fragment area in Dutchess County, New York. The density of potential disease vectors, nymphs of the tick *Ixodes scapularis*, is not only exponentially greater in small fragments (A), but there is also a significant density-dependent increase in disease infection rates of ticks in small fragments (B). Figure reproduced from Allan *et al.* (2003, p. 270).

(c) *Fragmentation and climate change*

Worryingly, recent models have indicated that habitat loss and fragmentation may increase a species' susceptibility to climate change, reducing their ability to survive simultaneous changes in both factors (Travis, 2003). During periods of climate change, insects typically shift their distributions rather than adapt *in situ* (Hill *et al.*, 2002). For instance, the northern distributional limits of many European butterflies have recently expanded northward as a result of 20th Century climate warming, and further expansion is considered likely in the future (Hill *et al.*, 2002; Parmesan *et al.*, 1999). However, when populations are isolated by habitat fragmentation, range expansion is restricted and populations may become more vulnerable to the effects of climate change and extreme weather events (Hill *et al.*, 2002; McLaughlin *et al.*, 2002; Opdam &

Wascher, 2004). For example, in the western U.S.A., an increase in yearly variability in precipitation rates amplified population fluctuations in the checkerspot butterfly *Euphydryas editha bayensis* and led to the local extinction of two isolated populations (McLaughlin *et al.*, 2002). Despite the observed climatic changes over recent times, McLaughlin *et al.* (2002) considered that these checkerspot populations must have persisted through much larger historical variations in climate, and have only recently become susceptible to local extinction because of the greatly reduced distribution of suitable habitat. Similarly, metapopulations of the British tiger moth *Arctia caya* increased in variability and populations underwent a dramatic decline in abundance and distribution following a rise in winter temperatures (Conrad, Woiwood & Perry, 2002). In the U.K., the synergistic effects of fragmentation and recent climate change have led to a reduction in the geographic range sizes of 30 out of 35 butterfly species in the last 30 years (Hill *et al.*, 2002), with habitat specialist species exhibiting the largest reductions in distribution and abundance (Warren *et al.*, 2001). Similar effects have also been predicted for butterflies in the Mediterranean (Stefanescu *et al.*, 2004).

(d) *Fragmentation and human-modified disturbance regimes*

The ecology of habitat fragments is often impacted by human-driven external disturbances that amplify the impacts of fragmentation itself. Recent work suggests that focussing on changes in landscape configuration while ignoring these other anthropogenic effects is a dangerously inadequate strategy for conservation (Laurance & Cochrane, 2001). For instance, Amazonian forest remnants are more accessible to hunters than continuous forest, perhaps because of the increased perimeter-area ratio of fragments, but also because fragmentation is accompanied by an influx of human migrants (Peres, 2001). Consequently, many large-bodied birds and mammals are persistently overhunted in small fragments (Peres, 2001), leading directly to their local extinction (Cullen, Bodmer & Valladares Padua, 2000). In this case, the correlative link between fragmentation and species loss was indirect, and the direct cause was over-exploitation due to a synergistic interaction between hunting and habitat fragmentation.

Similarly, fragments of woodland and shrubland in the predominantly agricultural landscapes of southwest Australia are more likely to be grazed and trampled by livestock than continuous forest (Hobbs, 2001). These effects are likely further amplified by the greater ease with which small fragments and fragment edges are invaded by introduced species (Robinson, Quinn & Stanton, 1995; Wiser *et al.*, 1998; Hobbs, 2001; Yates, Levia & Williams, 2004). For instance, trampling by cattle compacts soil structure, reducing the regeneration ability of native tree species that are already struggling with competition from introduced weeds (Hobbs, 2001). Moreover, the presence of introduced animals may be essential for the persistence of many weeds that are unlikely to persist in fragments without the disturbances like external nutrient inputs from cattle and increased soil turnover from rabbits (Hester & Hobbs, 1992; Hobbs, 2001).

Finally, forest fragments in the Brazilian Amazon are highly susceptible to the penetration of fires that originate in the surrounding agricultural matrix (Cochrane & Laurance, 2002). This is because forest edges are associated with elevated rates of leaf litterfall (Sizer, Tanner & Kossmann-Ferraz, 2000) and tree damage and mortality (Laurance *et al.*, 1997, 1998), contributing to an increased standing fuel load (Cochrane & Laurance, 2002). Furthermore, the available fuel in forest fragments likely dries more rapidly at edges than in forest interiors because of selective logging that opens the canopy, causing elevated desiccation rates (Cochrane & Laurance, 2002). Consequently, forest edges are associated with increased fire frequency and intensity (Cochrane, 2001; Cochrane & Laurance, 2002). Unfortunately, the threat to forest remnants from fires in the Brazilian Amazon is amplified greatly by a positive feedback mechanism between habitat loss and disturbance, whereby forest fires increase the susceptibility of fragments to future fires of greater intensity and cause elevated total deforestation rates in the region (Cochrane *et al.*, 1999).

VIII. IMPLICATIONS FOR FRAGMENTATION RESEARCH

The amount of research being conducted on habitat fragmentation is increasing exponentially, as any simple bibliographic search will illustrate. Despite continued debate about the relative importance of habitat fragmentation and habitat loss (Fahrig, 2003; Hanski & Gaggiotti, 2004), it is abundantly clear that the size and spatial distribution of habitat remnants alters the patterns of species distribution and abundance within a landscape. Recent advances in our understanding of habitat fragmentation, the importance of landscape context and complex synergistic interactions with other major drivers of biodiversity loss, have all added considerably to a wider appreciation of the scope and magnitude of the impacts of land use change. However, there are still many facets to the study of habitat fragmentation that remain untested and only vaguely understood. Anthropogenic habitat fragmentation is a relatively recent phenomenon in evolutionary terms, and we still have little real understanding of its long-term implications. Species with certain traits, such as limited mobility or high trophic position, seem disproportionately affected by fragmentation and face the very real possibility of extinction. However, it remains unclear whether the long-term negative effects of fragmentation will be limited to a subset of species with a particular trait complex, or whether these susceptible species are merely the first to respond. Over larger spatial and temporal scales, species with quite different trait complexes may prove to be just as vulnerable to fragmentation.

While field experimental studies are becoming more common, controlled laboratory manipulations of micro-environments to investigate directly the physiological and behavioural mechanisms underlying species responses to fragmentation have still not been widely undertaken. Trials of this nature will be invaluable for determining the exact

process(es) underlying species responses, such as edge avoidance, and will allow the development of specific management actions to remedy, or at least alleviate, the species-level effects of habitat fragmentation in the field. These approaches could also be aided considerably by controlling statistically for the effects of phylogenetically related suites of traits.

Finally, a serious question must be asked about what we are doing with the knowledge we do have. The prevailing attitude toward reserve design is that we do not have a choice and must accept whatever conservation land is available (e.g. Saunders, Hobbs & Magules, 1991). This may be true for most landscapes in temperate nations, but is not a viable argument when applied to many tropical nations where global concern about deforestation is currently focussed (Laurance & Gascon, 1997). In these environments there remains a significant biodiversity resource and the opportunity to plan and implement efficient reserve networks based upon our current understanding of the effects of habitat loss and fragmentation.

IX. CONCLUSIONS

(1) Habitat fragmentation is a pervasive feature of modern landscapes and has contributed to population decline in many species. Fragmentation impacts are effected through changes in habitat area, the creation of habitat boundaries with their associated edge effects, and the isolation of habitat fragments. The relative intensity of each of these factors is mediated by the shape of the remnant habitat areas and the structure of the surrounding matrix habitat.

(2) Species responses to habitat fragmentation are governed by individual species' traits. Species that are highly susceptible to fragmentation are typically characterised by large body size, intermediate mobility, high trophic level, high levels of habitat specialisation, and low pre-fragmentation abundance. Synergies between these traits lead to a greater vulnerability of species with combinations of these traits in severely fragmented landscapes, than might otherwise be predicted from the simple additive effects of multiple traits considered individually.

(3) Habitat fragmentation does not occur in isolation from other threats to biodiversity. Synergistic interactions among multiple drivers of biodiversity loss may magnify the detrimental impacts of fragmentation. For example, fragmentation can disrupt pollination systems, or increase the rate of disease transmission, leaving populations in habitat remnants susceptible to human encroachment, fire and introduced species, and may amplify the vulnerability of species to climate change.

(4) There is a large literature that investigates the effects of habitat fragmentation on species and communities. However, substantial questions remain unanswered. What role does phylogeny play in determining species' susceptibility to fragmentation? What are the physiological and behavioural mechanisms underlying species responses to fragmentation? What are the long term implications of habitat fragmentation? Most importantly, can we predict

and mitigate the effects of habitat fragmentation in the future?

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