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RESEARCH REVIEW

Landscape modification and habitat fragmentation: a synthesis

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ABSTRACT

Landscape modification and habitat fragmentation are key drivers of global species loss. Their effects may be understood by focusing on: (1) individual species and the processes threatening them, and (2) human-perceived landscape patterns and their correlation with species and assemblages. Individual species may decline as a result of interacting exogenous and endogenous threats, including habitat loss, habitat degradation, habitat isolation, changes in the biology, behaviour, and interactions of species, as well as additional, stochastic threats. Human-perceived landscape patterns that are frequently correlated with species assemblages include the amount and structure of native vegetation, the prevalence of anthropogenic edges, the degree of landscape connectivity, and the structure and heterogeneity of modified areas. Extinction cascades are particularly likely to occur in landscapes with low native vegetation cover, low landscape connectivity, degraded native vegetation and intensive land use in modified areas, especially if keystone species or entire functional groups of species are lost. This review (1) demonstrates that species-oriented and pattern-oriented approaches to understanding the ecology of modified landscapes are highly complementary, (2) clarifies the links between a wide range of interconnected themes, and (3) provides clear and consistent terminology. Tangible research and management priorities are outlined that are likely to benefit the conservation of native species in modified landscapes around the world.

Keywords

Connectivity, countryside biogeography, edge effects, extinction proneness, habitat loss, habitat fragmentation, keystone species, landscape heterogeneity, matrix, threatening processes.

INTRODUCTION

Landscape modification and habitat fragmentation have become major research themes in conservation biology (Haila, 2002; Fazey *et al.*, 2005). They are considered severe threats to global biodiversity (Sala *et al.*, 2000; Foley *et al.*, 2005), and are believed to negatively affect virtually all taxonomic groups including birds and mammals (Andrén, 1994; Recher, 1999), reptiles (Gibbons *et al.*, 2000), amphibians (Stuart *et al.*, 2004), invertebrates (Didham *et al.*, 1996) and plants (Hobbs & Yates, 2003). Although 'fragmentation' has become a major research theme, progress in the field has been hampered by overly restrictive conceptual paradigms (Haila, 2002) and the imprecise or inconsistent use of important terminology (Bunnell, 1999; Fahrig, 2003).

A range of reviews have investigated fragmentation-related topics to date. Most of these have dealt with specific sub-components of the enormous body of literature on landscape modification and habitat fragmentation, such as the amount of native vegetation cover in relation to birds and mammals (Andrén, 1994), the relative effects of habitat loss and habitat sub-division (Fahrig, 2003), experimental approaches to studying 'fragmentation' (Debinski & Holt, 2000; McGarigal & Cushman, 2002), the history of fragmentation research (Haila, 2002), metapopulation dynamics (Hanski 1998), or edge effects (Ries *et al.*, 2004; Harper *et al.*, 2005). To date, only the review by Saunders *et al.* (1991) — which is now 15 years old — has covered a breadth of inter-related topics that are relevant to conservation biologists working in modified landscapes. The separate treatment of different sub-components of landscape change has led to a range of parallel research paradigms. Much research currently approaches modified landscapes from one particular perspective, such as metapopulation dynamics or vegetation thresholds. Such highly

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focused research has produced useful insights, but arguably, it can also be problematic because it can lead to the oversight of valuable insights from other perspectives (e.g. Moilanen & Hanski, 2001).

The aim of this paper is to provide a holistic view of the ecology of modified landscapes by synthesising recent developments across a range of different research themes. By necessity, this breadth means that any given sub-component of landscape change is covered only in a cursory manner, emphasizing recent key insights over areas of internal disagreement. We believe that this conscious focus on breadth is needed to help researchers from a range of backgrounds to appreciate work from different backgrounds that is equally relevant to understanding the ecology of modified landscapes. We acknowledge that our choice of material included in this review may be contentious. Most importantly, we hope this review will stimulate more holistic thinking about the ecology and management of modified landscapes.

First, we introduce a conceptual framework for understanding the effects of landscape modification on species and assemblages. Second, threatening processes associated with landscape modification, and how they affect individual species and immediate species interactions, are discussed. Third, the relationships between human-perceived patterns in modified landscapes and assemblages of species are investigated, and cascading effects arising from landscape modification are considered. Finally, key knowledge gaps are identified, and a short list of tangible management recommendations for conservation management in modified landscapes is provided.

The main emphasis of this review is on animals, with plants largely referred to in the context of their interactions with animals. Despite this bias, we acknowledge that landscape modification also may change plant assemblages (Hobbs & Yates, 2003; Mayfield & Daily, 2005). The themes covered in this paper are outlined in Fig. 1. Frequently used terms that have contributed to confusion in past work are defined explicitly in Table 1.

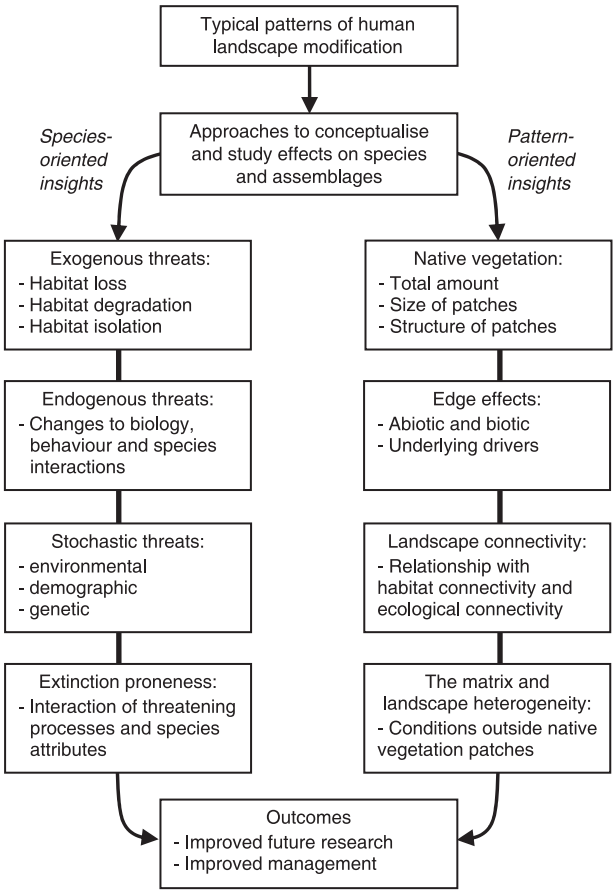

Figure 1 Conceptual framework and structure of this review showing a range of connected themes associated with landscape modification and habitat fragmentation.

A CONCEPTUAL FRAMEWORK OF LANDSCAPE MODIFICATION

Typical patterns of landscape modification

In this paper, we are concerned with landscape modification that has occurred within the last few centuries and that has negatively affected native species diversity. Broadly similar patterns of this type of landscape modification have been documented around the world (e.g. Sharpe *et al.*, 1987; Bennett, 1990; Saunders *et al.*, 1993; Webb, 1997). Typically, as landscape modification increases, more native vegetation is lost, land-use intensity in modified areas increases, and remnants of native vegetation are increasingly influenced by processes originating in modified areas (McIntyre & Hobbs, 1999; Fig. 2). Common spatial patterns in human-modified landscapes include the perforation, dissection, sub-division, shrinkage, and attrition of native vegetation (Forman, 1995; Fahrig, 2003). Generally, native vegetation is cleared first in areas with high primary productivity (e.g. Norton *et al.*, 1995; Landsberg, 1999), although this trend is somewhat modified by jurisdictional and cultural aspects of land-use history (Lunt & Spooner, 2005).

A continuum of research approaches

Fragmentation-related research has suffered from a lack of a clear conceptual basis and reliance on overly restrictive conceptual models of modified landscapes (reviewed by Bunnell, 1999; Haila, 2002). In addition, many themes are widely agreed to be important, but have usually been treated separately in existing reviews. To overcome these problems, an integrated rather than a divisive conceptual framework is briefly introduced here, which recognises the complementary contributions of many different types of research.

Two extremes can be identified along a continuum of approaches to understanding the effects of landscape modification on species and assemblages. The first extreme is 'species-oriented'. Species-oriented approaches are often centred around individual species, which are believed to respond individualistically to their environment (Gleason, 1939; Austin & Smith, 1989; Manning *et al.*, 2004). Species-oriented approaches recognise that each species responds individualistically to a range of processes

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Table 1 Selected key terms to conceptualise the ecology of modified landscapes

Term	Definition
Ecological connectivity	Connectedness of ecological processes at multiple spatial scales (see Soulé *et al.*, 2004, for details)
Fragmented landscape	Following McIntyre & Hobbs (1999), a landscape characterised by a strong contrast between vegetation patches and their surrounding matrix (native vegetation cover typically *c.* 10–60%); often seen in formerly forested areas
Habitat	The range of environments suitable for a particular species
Habitat connectivity	Connectedness of habitat for a particular species; the opposite of habitat isolation
Habitat isolation	Degree of isolation between habitat patches used by a particular species; opposite of habitat connectivity
Habitat loss	Loss of habitat for a particular species
Habitat sub-division	Sub-division of habitat for a particular species
Landscape	A human-defined area ranging in size from *c.* 3 km^2 to *c.* 300 km^2
Landscape connectivity	A human perception of the connectedness of native vegetation cover in a landscape
Landscape heterogeneity	A human perspective of environmental gradients and land-cover types in a landscape
Matrix	The dominant background patch type in a landscape; in modified landscapes usually not native vegetation
Relictual landscape	Following McIntyre & Hobbs (1999), a landscape characterised by sharp boundaries between a minimal amount of remnant native vegetation (< 10%) and surrounding modified land; often seen in areas with intensive agriculture
Variegated landscape	Following McIntyre & Hobbs (1999), a landscape characterised by gradual boundaries between native vegetation and surrounding modified land (native vegetation cover typically *c.* 60–90%); often seen in areas with extensive livestock grazing

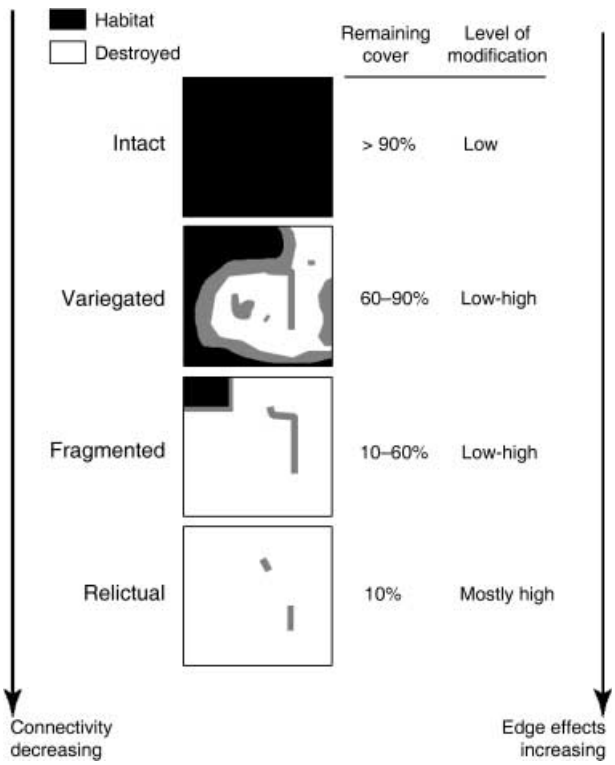

Figure 2 Conceptual model of landscape modification states (modified from McIntyre & Hobbs, 1999).

related to its requirements for food, shelter, space and suitable climatic conditions, as well as interspecific processes like competition, predation and mutualisms (Fischer & Lindenmayer, 2006; Fig. 3). A key limitation of species-oriented approaches is that it is impossible to study every single species in any given landscape.

At the other end of the continuum are 'pattern-oriented' approaches. Here, the focus is typically on human-perceived landscape patterns and their correlation with measures of species occurrence, including aggregate measures such as species richness. Pattern-oriented approaches originate from island biogeography (MacArthur & Wilson, 1967) and are the traditional stronghold of 'fragmentation-related' research (Haila, 2002). Two widely used pattern-oriented conceptual landscape models are the patch–matrix–corridor model (Forman, 1995) and to a lesser extent the variegation model (McIntyre & Barrett, 1992; Ingham & Samways, 1996). Although various pattern-oriented approaches differ in their assumptions, all are based on human-defined land cover (often native vegetation), and seek to establish correlations with species or groups of species to infer potential ecological causalities (Fig. 3). The main limitation of pattern-oriented approaches is that they frequently aggregate across individual species and ecological processes. In some cases, this aggregation may lead to an under-appreciation of the complexity of ecological processes and differences between individual species.

Given the unique practical and theoretical strengths and weaknesses of species-oriented and pattern-oriented approaches, the two approaches are highly complementary for understanding and managing modified ecosystems. The two approaches are considered separately below, and research priorities and management recommendations are derived that recognise the value of both approaches.

SPECIES-ORIENTED APPROACHES

A useful way to understand potentially negative effects of landscape modification on native taxa is to consider the range of processes that may threaten a given individual species. Threatening processes associated with landscape modification may be broadly classified as exogenous (originating independently of the

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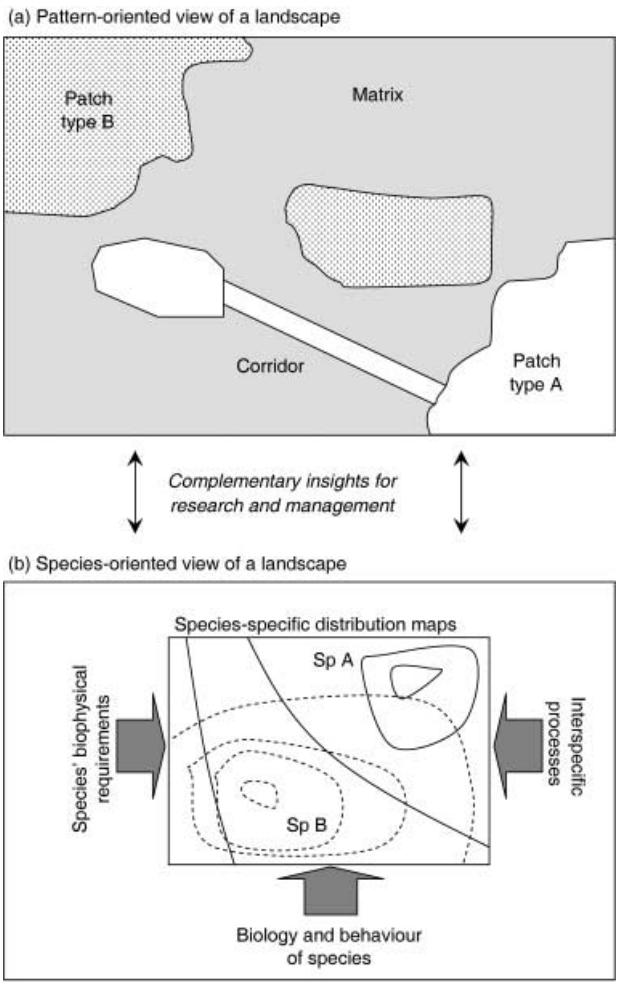

Figure 3 Graphical summary of (a) a pattern-oriented view of a modified landscape, and (b) a species-oriented view of a modified landscape. Pattern-oriented approaches and species-oriented approaches can lead to complementary insights into the ecology of modified landscapes (see Fischer *et al.*, 2004; Fischer & Lindenmayer, 2006).

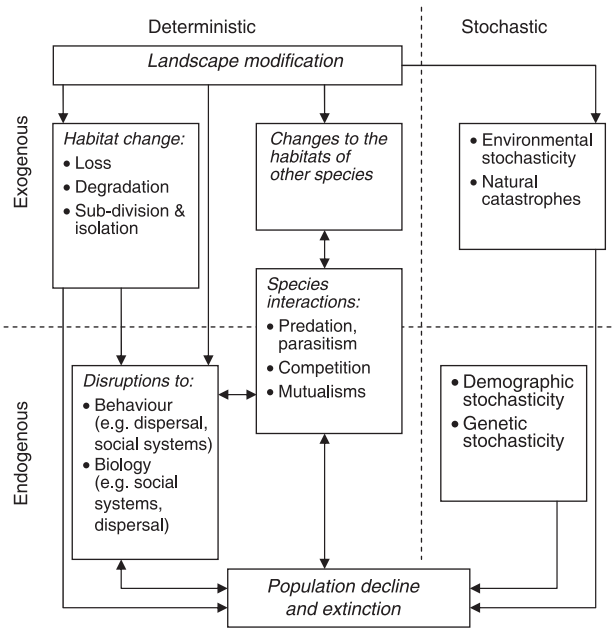

Figure 4 Threatening processes arising from landscape modification as experienced by a declining species. Threatening processes are broadly classified as deterministic versus stochastic, and exogenous versus endogenous. Deterministic threats predictably lead to declines, whereas stochastic threats are driven by chance events. Exogenous threatening processes are external to a species' biology, whereas endogenous threats arise as part of a species' biology (see text for details).

species' biology) or endogenous (originating as part of the species' biology), although this distinction may be blurred in some instances.

Exogenous threatening processes

Habitat may be broadly defined as the range of environments suitable for a given species. That is, it is a species-specific concept. Habitat loss is the dominant threat to species around the world (Sala *et al.*, 2000). Landscape modification for agriculture and urbanisation typically causes habitat loss for many species (Kerr & Deguise, 2004; Luck *et al.*, 2004). Because native vegetation is important for many species, numerous authors have equated 'habitat' with 'native vegetation' (e.g. Andrén, 1994). Although this classification may be appropriate in some situations (Terborgh *et al.*, 2001), in many situations it can be misleading. This is because a binary classification of land into habitat (native vegetation) and non-habitat (other land cover) ignores habitat suitability gradients and differences between species with respect to what constitutes suitable habitat for them (Fig. 3; Andrén *et al.*, 1997); importantly, many native species can be conserved in well-managed production landscapes (Daily, 2001; Lindenmayer & Franklin, 2002). On this basis, we suggest that the term 'habitat' and associated terms like 'habitat fragmentation' be used only in a single-species context (Table 1). The broader use of the term habitat (i.e. equating it with native vegetation) can result in the under-appreciation of differences between the unique habitat requirements of different species, and the under-appreciation of the potential habitat value of modified environments for some species. For a given species, habitat loss rarely occurs in isolation from other threats, but tends to coincide with habitat degradation, habitat sub-division and a range of additional threatening processes (Liu *et al.*, 2001; Fig. 4).

Habitat degradation is the gradual deterioration of habitat quality. In degraded habitat, a species may decline, occur at a lower density, or may be unable to breed (Temple & Cary, 1988; Felton *et al.*, 2003; Hazell *et al.*, 2004). Degraded habitat may constitute an 'ecological trap' to which individuals of a species are attracted but in which they cannot reproduce (Battin, 2004). Habitat degradation can be difficult to detect because: (1) some types of degradation take a long time to manifest (e.g. recruitment failure of cavity trees; Saunders *et al.*, 2003), and (2) some species with slow life cycles may continue to be present in an area

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even if they are unable to breed (e.g. cockatoos reliant on nesting hollows; Saunders, 1979). Factors related to habitat degradation vary widely between species, and may include pressure from grazing (Spooner *et al.*, 2002), logging (Recher & Serventy, 1991), or changed thermal regimes (Jäggi & Baur, 1999). Detailed autoecological studies and monitoring are often required to detect and counteract habitat degradation (Borghesio & Giannetti, 2005).

Habitat sub-division is the breaking apart of continuous habitat into multiple patches; it is synonymous with what some authors have termed 'fragmentation' (Fahrig, 2003). Smaller habitat patches can lead to population declines (Bender *et al.*, 1998), for example because resources in smaller patches may be more limited (Zanette *et al.*, 2000). In addition, habitat sub-division increases the isolation of remaining habitat areas. Habitat isolation can negatively affect day-to-day movements of a given species (e.g. between nesting and foraging resources; Saunders, 1980; Luck & Daily, 2003). Habitat isolation also may negatively affect the dispersal of juveniles (Cooper & Walters, 2002). Metapopulations, i.e. 'set[s] of local populations which interact via individuals moving between local populations' sometimes develop as a result of habitat isolation (Hanski & Gilpin, 1991). Notably, patchy populations are true metapopulations only if movement between sub-populations is neither very uncommon nor very common (Hanski & Simberloff, 1997). Finally, habitat isolation may negatively affect large-scale movements of species such as seasonal migration or range shifts in response to climate change (Soulé *et al.*, 2004). The extent to which landscape modification results in habitat isolation depends on the interaction between a given species' dispersal behaviour, mode and scale of movement, what constitutes suitable habitat for it, and how a given landscape has been modified. Habitat connectivity is the opposite of habitat isolation, and is contrasted against other connectivity concepts in the section entitled *Connectivity* below.

Endogenous threatening processes

In addition to direct negative impacts on a species' habitat, declining species in modified landscapes often experience disruptions or changes to their biology, behaviour and interactions with other species. These changes are often triggered by exogenous threats, but may constitute threatening processes in their own right. Landscape modification can lead to altered breeding patterns and social systems. For example, birds may have shorter breeding seasons, lay fewer eggs, and rear fewer nestlings (Hinsley *et al.*, 1999; Zanette *et al.*, 2000), or their mating systems may change (Ims *et al.*, 1993). Many other types of behavioural and biological changes have been observed for animals in modified landscapes, including disruptions to dispersal (Brooker & Brooker, 2002), changed movement patterns over greater distances (Recher *et al.*, 1987; Norris & Stutchbury, 2001), altered home ranges (Pope *et al.*, 2004), higher incidences of fluctuating body asymmetry (Sarre, 1996), changed vocalisation patterns (Slabbekoorn & Peet, 2003; Lindenmayer *et al.*, 2004), and disrupted group behaviours (Gardner, 2004).

Changes to species interactions may affect competition, predation, parasitism and mutualisms. Increased competition can occur, for example, for insectivorous woodland birds in many Australian farming landscapes where the aggressive noisy miner (*Manorina melanocephala*) has increased in abundance (Grey *et al.*, 1997). Increased predation and parasitism have both been frequently reported in modified landscapes, especially for birds (Robinson *et al.*, 1995; Lahti, 2001; Zanette *et al.*, 2005), but more recently also for complex insect–plant food webs (Valladares *et al.*, 2006). Increased pressure from competition and predation can be particularly severe when introduced species are involved. For example, competition by exotic snails has severely decimated Hawaii's native snail fauna (Hadfield *et al.*, 1980).

Landscape modification also may disrupt mutualisms. For example, Cordeiro & Howe (2003) demonstrated the disruption of the mutualism between the endemic tree *Leptonychia usambarensis* and fruit-dispersing birds in a modified landscape in Tanzania. Similarly, Kearns *et al.* (1998) argued that landscape modification may disrupt pollination throughout the world, as recently emphasized by Ricketts *et al.* (2004) for Costa Rican coffee farms.

Disruptions to species interactions have particularly severe effects when strongly interacting species are involved, which play a disproportionate role in maintaining ecosystem function (Terborgh *et al.*, 2001; Soulé *et al.*, 2005). Such species are sometimes also termed keystone species (Paine, 1969; Power *et al.*, 1996), and their importance is discussed in more detail below in the section entitled *Extinction cascades*.

Stochastic threatening processes

The exogenous and endogenous threatening processes discussed above are deterministic. Deterministic threatening processes are those which predictably lead to declines (Gilpin & Soulé, 1986; Fig. 4). In addition to deterministic processes, stochastic processes may threaten species in modified landscapes. Exogenous stochastic threats are related to environmental variability, such as fluctuations in climate or natural catastrophes like hurricanes or wildfires (Simberloff, 1988). Endogenous stochastic threats occur as part of a species' life cycle, and include demographic stochasticity (e.g. year-to-year variability in reproductive success) and genetic stochasticity (e.g. genetic drift). Endogenous stochastic threats are more pronounced in small populations (Roughgarden, 1975; Keller & Waller, 2002).

Interactions among threatening processes and extinction proneness

Species declining as a result of landscape modification are typically affected by both deterministic and stochastic threats. Exogenous threats often lead to the initial decline of a species. The resulting smaller populations, in turn, are more susceptible to endogenous threats that reinforce the decline of the species (Clark *et al.*, 1990; Fig. 4).

Many factors have been suggested to be related to the extinction proneness of species in modified landscapes,

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Table 2 Proposed relationship between key threatening processes associated with landscape modification and biological attributes of species which ameliorate extinction proneness

Threatening process	Ameliorating biological attribute	Explanation
Habitat loss and habitat degradation	Low habitat specialisation	Specialised species are more likely to lose their habitats as a result of landscape change
	Disturbance tolerance	Disturbance-tolerant species are more likely to find suitable habitat in modified landscapes
	Ability to live in the matrix	Species that can live in the matrix experience no habitat loss as a result of landscape modification
Habitat isolation and sub-division	Ability to move through the matrix	Species that can move through the matrix are less likely to suffer the negative consequences of habitat isolation
	Dispersal ability	Strong dispersers may be more likely to maintain viable metapopulations (but note this is contentious — see text)
Disrupted species interactions	Limited dependence on particular prey or mutualist species	Species that can switch prey or mutualists are more likely to withstand landscape change
	Competitive ability	Species that are strong competitors are less likely to be outcompeted by species whose habitat expands as a result of landscape change
Disrupted biology	Low biological and behavioural complexity	Species with a complex biology (e.g. social or breeding systems) are more likely to have their biological processes disrupted as a result of landscape change than species with simpler biological systems
Stochastic events	Population density	High density populations contain many individuals even in a small area, and hence are more resilient to stochastic threats

including habitat or niche specialisation, home range size, mobility, extent of geographic distribution, population density or rarity, edge sensitivity, body size and dietary specialisation (Johns & Skorupa, 1987; Brashares, 2003; Koh *et al.*, 2004; Cardillo *et al.*, 2005; Kotiaho *et al.*, 2005). Although these factors are often considered as equally plausible in studies on extinction proneness, it is important to note that some of them are more directly related to extinction proneness in a causal sense than others. For example, body size is a proxy for a range of other ecological attributes, including area requirements, mobility and dietary specialisation (Laurance, 1991), whereas habitat specialisation is directly linked to the threatening process of habitat loss. Table 2 outlines some of the most direct links between known threatening processes and likely factors contributing to (or ameliorating) extinction proneness. Notably, some of these links are complex, and potentially contentious. For example, although high mobility can help species to move between habitat patches (Table 2), it may also lead to an increased number of individuals dispersing into unsuitable habitat, thereby threatening population persistence (Gibbs 1998; Casagrandi & Gatto 1999). Further investigation of the links between threatening processes and extinction proneness in the future may lead to an increasingly robust, process-based understanding of species extinctions. A likely emergent pattern is that a given species' ability to withstand human landscape modification is related to the extent to which landscape modification causes habitat loss and isolation, and the disruption of biological and interspecific processes for that individual species. Small population size (natural or human-induced) will further exacerbate a species' risk of extinction due to stochastic events (Fig. 4; Table 2).

PATTERN-ORIENTED APPROACHES

Assessing the relationship between human-perceived landscape patterns and individual species or species assemblages has been a popular, albeit controversial, research area in ecology and conservation biology (Haila, 2002). Some key attributes of landscape pattern are discussed below.

Amount and condition of native vegetation

For many species of plants and animals, habitat conditions are ideal in large areas of unmodified native vegetation. Hence, the loss of native vegetation at landscape and regional scales has been linked to the loss of native species around the world (e.g. Andrén, 1994; Kerr & Deguise, 2004). Similarly, the loss of native vegetation at the local scale tends to reduce native species richness. Other things being equal, small patches of native vegetation support fewer native species than large patches (e.g. Bellamy *et al.*, 1996; Rosenblatt *et al.*, 1999). Such species–area relationships have long been known (Arrhenius, 1921). Several mechanisms are likely to underlie species–area relationships (McGuinness, 1984). Larger patches may have a higher ratio of colonisations to extinctions (MacArthur & Wilson, 1967), are more likely to contain undisturbed areas which are required by some species (Harris, 1984), are more likely to capture a range of environmental conditions which constitute habitat for different sets of species (Harner & Harper, 1976; Fox, 1983), and are more likely to capture patchily distributed species by chance (Connor & McCoy, 1979).

Despite strong evidence of the importance of large areas of native vegetation, it is important to recognise that: (1) small areas

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of native vegetation can be important complements to large areas (Fischer & Lindenmayer, 2002; Tscharntke *et al.*, 2002); (2) land management outside patches of native vegetation can have both positive and negative context effects on patches (Wethered & Lawes, 2005); and (3) different types of native vegetation will support different sets of species (Austin & Smith, 1989; Sabo *et al.*, 2005). For these reasons, the exclusive focus on large patches of native vegetation is often overly restrictive and represents an outdated conceptual model of landscape modification (Haila, 2002; Manning *et al.*, 2004).

Even where extensive areas of native vegetation remain, deterioration of vegetation structure and deterioration of the physical environment can negatively affect many native species. For example, domestic livestock grazing can simplify vegetation structure and exacerbate the replacement of native species by introduced species (Hobbs, 2001), as well as reduce regeneration rates of native woody vegetation (Spooner *et al.*, 2002). In dry environments, these processes may eventually result in desertification (Milton *et al.*, 1994). Many other land management practices such as logging or firewood collection can be linked to the deterioration of vegetation structure and the physical environment (Driscoll *et al.*, 2000; Chettri *et al.*, 2002; Lindenmayer & Franklin, 2002). Typically, the loss and degradation of native vegetation co-occur in modified landscapes (Liu *et al.*, 2001; Klink & Machado, 2005).

Edge effects

Edge effects are changes in physical and biological conditions at an ecosystem boundary or within adjacent ecosystems. Abiotic edge effects refer to changes in physical variables such as radiation, moisture, temperature, humidity, wind speed and soil nutrients (Chen *et al.*, 1990; Matlack, 1993; Weathers *et al.*, 2001). Biotic edge effects are changes in biological variables such as species composition of plants and animals, or patterns of competition, predation and parasitism (Malcolm, 1994; Robinson *et al.*, 1995; Lahti, 2001; Valladares *et al.*, 2006). The penetration depth of edge effects can vary widely from tens of metres for variables like soil moisture (Laurance *et al.*, 1997) to several kilometres in the case of recruitment failure of Dipterocarpaceae in Gunung Palung National Park in western Borneo (Curran *et al.*, 1999).

Despite substantial regional variation in edge effects (e.g. for nest predation; Batary & Baldi, 2004), several factors are likely to enhance the presence and magnitude of edge effects. These include high structural contrast at the edge, high wind speeds and temperatures, and the presence of pioneer, exotic and invasive taxa that may benefit from edge environments (Harper *et al.*, 2005). In addition, a large amount of variability in ecological patterns around edges may be effectively explained by distinguishing between four fundamental underlying mechanisms: ecological flows, access to spatially separated resources, resource mapping and species interactions (Ries *et al.*, 2004). Although edge effects are considered to have negative effects on native ecosystems, not all edges are necessarily detrimental for all native species (Yahner, 1988), especially where edges are gradual or of low structural contrast (Tubelis *et al.*, 2004).

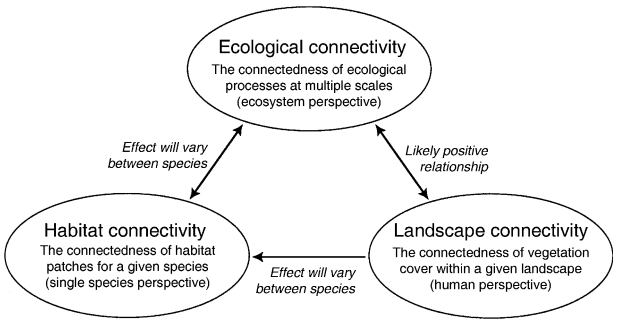

Figure 5 Relationship between the three connectivity concepts defined in this paper.

Connectivity

It is widely agreed that connectivity is important for biological conservation (Taylor *et al.*, 1993). However, the term 'connectivity' is often used loosely, and different authors use the term in different ways. For example, Tischendorf & Fahrig (2000) considered landscape connectivity to be an attribute of landscapes that resulted from the interaction of land cover with individual species' movement rates. In contrast, Moilanen & Hanski (2001) took a metapopulation perspective and suggested that connectivity was better understood as an attribute of individual patches. Other authors have distinguished between structural connectivity and functional connectivity. Using this distinction, structural connectivity is related to landscape pattern and results from the density and complexity of corridors, the distance between patches, and the structure of the matrix (Uezu *et al.*, 2005). In contrast, functional connectivity is often defined by the extent to which an individual species of interest can move through a landscape (Uezu *et al.*, 2005). The many different, and often implicit, definitions of connectivity have contributed to considerable confusion and debate; for example, regarding the question if corridors provide connectivity (Simberloff *et al.*, 1992; Beier & Noss, 1998; Procheş *et al.*, 2005).

To overcome existing confusion, we differentiate between three types of connectivity (Fig. 5).

1 *Habitat connectivity* is the connectedness between patches of suitable habitat for a given individual species. It may be defined at the patch scale (e.g. Moilanen & Hanski 2001) or at the landscape scale (e.g. Hanski & Ovaskainen 2000; Tischendorf & Fahrig 2000). The term is chosen to include the word 'habitat' to emphasize its species-specific nature.

2 *Landscape connectivity* is a human perspective of the connectedness of native vegetation cover in a given landscape. It may be expressed using various buffer- or distance-based metrics that can be calculated from maps of human-defined land cover (e.g. Gustafson 1998; Moilanen & Nieminen 2002). The term is chosen to include the word 'landscape' to emphasize its anthropocentric nature — the concept of a landscape is a human construct (Table 1).

3 *Ecological connectivity* is the connectedness of ecological processes across multiple scales, including trophic relationships, disturbance processes and hydroecological flows. The measurement

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of ecological connectivity is not straightforward and depends on which aspect of ecological connectivity is to be estimated. Despite this difficulty, ecological connectivity is an important concept that is not adequately captured by existing definitions of connectivity. The term is based on a discussion by Soulé *et al.* (2004).

The three connectivity concepts are related but not synonymous (Fig. 5). Landscape connectivity may translate into habitat connectivity for some but not all species. For example, corridors and stepping stones (i.e. small vegetation patches scattered through a landscape) always contribute to landscape connectivity, but may not be used by all native species – that is, they do not contribute to habitat connectivity for those species (Forman, 1995; Beier & Noss, 1998). Similarly, the relationship between landscape connectivity and ecological connectivity tends to be positive, but not all ecological processes are effectively facilitated through all types of landscape connectivity. For example, seed-dispersing birds used corridors in a study in South Carolina (USA). Here, enhanced landscape connectivity increased one aspect of ecological connectivity, that is, the process of seed dispersal (Levey *et al.*, 2005a). However, neither corridors nor stepping stones may effectively maintain some aspects of ecological connectivity such as natural hydrological flows or the natural spread of fire throughout a landscape (Soulé *et al.*, 2004).

In practice, landscape connectivity is the most easily manageable aspect of connectivity because it requires no detailed understanding of individual species' habitat requirements or ecological processes. Landscape connectivity may be enhanced through corridors, stepping stones, and the maintenance of a 'soft' matrix which is structurally similar to native vegetation (*sensu* Franklin, 1993). Despite some ecological risks such as potentially facilitating the spread of introduced species (Simberloff *et al.*, 1992; Procheş *et al.*, 2005), increased landscape connectivity is usually more likely to have desirable effects on native species and ecological processes than undesirable effects (Noss & Beier, 2000; Haila, 2002; Levey *et al.*, 2005b).

The matrix and landscape heterogeneity

The analysis of modified landscapes as 'island-like' systems represents the traditional stronghold of the fragmentation literature (Fig. 3a; Haila, 2002). However, in many situations, thinking about modified landscapes as mosaics of patches and corridors within a hostile or uniform matrix is not appropriate (Wiens, 1994; Gascon *et al.*, 1999; Kupfer *et al.*, 2006). First, the matrix may provide habitat for some native species, especially if it is structurally similar to remaining native vegetation (Barrett *et al.*, 1994; Pardini, 2004). Second, by enhancing landscape connectivity, a structurally similar matrix may enhance habitat connectivity for some species reliant on native vegetation (Ricketts, 2001; Bender & Fahrig, 2005). Third, the matrix provides an important ecological context for patches of native vegetation, which may positively or negatively affect species in the patches (Ås, 1999; Ries *et al.*, 2004; Tubelis *et al.*, 2004; Harper *et al.*, 2005).

Some landscapes are so heterogeneous that it becomes difficult to delineate patches and a matrix in a meaningful way. Heterogeneous landscapes are characterised by a diversity of environmental gradients and land-cover types (August, 1983). Although situations where heterogeneity reduces species richness may exist, generally, heterogeneous modified landscapes support more species than otherwise similar but less heterogeneous modified landscapes (Tscharntke *et al.*, 2005). For example, landscape heterogeneity is recognised as beneficial for native species in European farming landscapes (Benton *et al.*, 2003; Hole *et al.*, 2005), Central American farming landscapes (Luck & Daily, 2003; Mayfield & Daily, 2005), and forestry landscapes around the world (Lindenmayer & Franklin, 2002). Heterogeneity arising from natural disturbance processes often provides a useful indication of the landscape or vegetation patterns most likely to benefit native species (Lindenmayer & Franklin, 2002).

Extinction cascades

Landscape modification typically results in the loss of native vegetation and changes to its spatial distribution, altered disturbance regimes and deterioration of vegetation structure (see above). These processes can interact and cause cascading ecosystem changes and regime shifts in ecosystem functioning. Regime shifts occur when inter-relationships between key variables in an ecosystem change fundamentally — they can be thought of as transitions where an ecosystem 'flips' from one state to another (Scheffer *et al.*, 2001; Folke *et al.*, 2004; Groffman *et al.*, 2006). Extinction cascades occur where the extinction of one species triggers the loss of one or more other species, which in turn leads to further species extinctions (e.g. Terborgh *et al.*, 2001).

Amount and configuration of native vegetation cover

Cascading effects on native species can result from the simultaneous reduction of the total amount of native vegetation and landscape connectivity. Several studies have suggested that connectivity loss is particularly severe below a 30% threshold of native vegetation cover, leading to increased losses of species reliant on native vegetation (Andrén, 1994; Fahrig, 2003; Radford *et al.*, 2005). Notably, not all species depend on native vegetation, and many other aspects of landscape modification also affect the distribution of species. Hence, the '30% rule' does not apply for all species or all ecosystems (Parker & Mac Nally, 2002; Lindenmayer *et al.*, 2005). Perhaps the most useful, albeit general, conclusion from the literature on vegetation thresholds is that extinction cascades are particularly likely to occur at low levels of native vegetation cover.

Disturbance regimes and structural complexity

Both natural and human disturbances can alter the vegetation structure in modified landscapes. For example, fire is a major disturbance agent that has been significantly altered in modified landscapes around the world (Agee, 1993; Turner *et al.*, 2003). Anthropogenic disturbances, like livestock grazing or logging, also can significantly alter vegetation structure (see above).

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The loss of some structural elements can have particularly severe negative effects on native species, and is especially likely to trigger extinction cascades. Tews *et al.* (2004) defined elements of structural complexity that are particularly important to many species as 'keystone structures'. Examples of keystone structures include scattered trees in dry savannas, which alter the abiotic environment and provide habitat for a large number of plants and animals (Vetaas, 1992; Dean *et al.*, 1999; Manning *et al.*, 2006).

Species composition

A change in species composition *per se* can trigger extinction cascades. The loss of individual species is particularly likely to trigger extinction cascades when 'keystone' or 'strongly interacting' species are involved because they exert a disproportionate effect on ecosystem function relative to their abundance (Paine, 1969; Power *et al.*, 1996; Soulé *et al.*, 2005). Strong ecological interactions may be apparent via habitat enrichment, predation, competition or mutualisms (Soulé *et al.*, 2005). For example, Terborgh *et al.* (2001) showed that the absence of predators from forest fragments in Venezuela had led to dramatic increases in herbivores. This, in turn, had a range of cascading effects throughout the food chain, including reduced levels of tree recruitment.

Ecosystems are more likely to absorb external shocks and maintain their function if multiple species fulfil similar ecological roles (Elmqvist *et al.*, 2003; Tscharntke *et al.*, 2005). Such 'functional redundancy' among species increases the chances of some species being able to compensate for a given species' ecological role if it becomes rare or goes extinct (Walker, 1992, 1995). Functional redundancy across multiple scales is considered an important aspect of ecosystem resilience (Elmqvist *et al.*, 2003; Folke *et al.*, 2004).

SUMMARY: KEY INSIGHTS FROM EXISTING WORK

Complementary insights on the ecology of modified landscapes have been gained from species-oriented and pattern-oriented work. Species-oriented work has the advantage of being based on well-established ecological causalities, but its main limitation is that it is impossible to study every individual species in any given landscape. In contrast, pattern-oriented work provides broadly applicable general insights, but may oversimplify complex causal relationships and subtle differences between individual species. Key insights from existing work are listed below.

- Habitat is a species-specific concept, and should not be equated with native vegetation.
- Threats for a given species arise from negative changes to its specific habitat, and disruptions to its biology, behaviour and interactions with other species.
- Extinction proneness can be studied in direct causal relation to the above threats.
- A large amount of unmodified native vegetation tends to benefit native species, but there appears to be no universally applicable minimum 'threshold' amount of native vegetation.
- Edge effects are diverse in their consequences and penetration depth, but recent reviews suggest they may be less idiosyncratic than previously thought.
- Existing debates on connectivity may be partly solved by distinguishing between landscape connectivity, habitat connectivity and ecological connectivity.
- Conditions in the matrix and landscape heterogeneity are fundamentally important in modified landscapes, and deserve equal attention in research and management as patches of native vegetation.
- Regime shifts and extinction cascades are particularly likely to arise when native vegetation cover is severely reduced, when vegetation structure throughout the landscape is greatly simplified, and when entire functional groups or keystone species are lost.

Management recommendations derived from these insights are discussed in detail by Fischer *et al.* (2006) and are summarised in Table 3.

FUTURE RESEARCH PRIORITIES

The conceptual framework outlined above recognises the complementary contributions of pattern-oriented and species-oriented research approaches in work on landscape modification and habitat fragmentation (Figs 1 & 3). Already, a combination of work on patterns and individual species has led to particularly useful insights on ecosystem functioning, as demonstrated by examples on metapopulation dynamics (Hanski 1994; Wiegand *et al.*, 2003), species distribution patterns (Bennett 1987) and amphibian declines (Pounds *et al.*, 2006). The explicit recognition of complementarity between species-oriented and pattern-oriented work may contribute to a further closing of the perceived gap between pattern and process in the ecological sciences (Hoekstra *et al.*, 1991; Hobbs, 1997; Fischer *et al.*, 2004). The proposed framework (Figs 1 & 3) may improve future work for several reasons. First, it overcomes vagueness in terminology, especially the confusion of species-specific concepts like habitat loss or habitat connectivity with pattern-based concepts like vegetation clearing or landscape connectivity (Table 1). Second, it provides a conceptual basis to simultaneously appreciate subtle species-specific differences while maintaining the search for general patterns (Fig. 3). Third, it provides greater conceptual clarity, thereby facilitating improved synthesis of past work and improved hypothesis generation for future work (e.g. Table 2). Fourth, it covers a wide breadth of inter-related issues, thereby encouraging holistic thinking about the ecology of modified landscapes.

Particularly interesting research opportunities exist in the following areas.

1 At the species level, the process of dispersal warrants further research. It may be best studied using a combination of field, modelling and genetic techniques (Peakall *et al.*, 2003; Bender & Fahrig, 2005; Levey *et al.*, 2005a).

2 At the ecosystem level, biases towards birds and mammals need to be overcome, and more work is required on plants and invertebrates (Didham *et al.*, 1996; Hobbs & Yates, 2003; Tscharntke *et al.*, 2005).

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Table 3 List of pattern-oriented and species-oriented management strategies to mitigate potential negative effects of landscape modification on native species (summarised from Fischer *et al.*, 2006)

Management strategy	Main purposes
Pattern-oriented strategies	
1. Maintain and/or restore large and structurally complex patches of native vegetation	Provide core habitat for species which depend on native vegetation
2. Maintain and/or restore a matrix that is structurally similar to native vegetation	Provide habitat for many species throughout the landscape Provide habitat connectivity for many species throughout the entire landscape Reduce structural contrast between modified and unmodified areas, thereby reducing edge effects throughout the landscape
3. Maintain and/or restore buffers around sensitive areas	Protect sensitive areas like aquatic systems Reduce edge effects at specific locations
4. Maintain and/or restore corridors and stepping stones	Provide habitat connectivity for species that cannot move through the matrix Provide additional habitat for species that use native vegetation but are not area-sensitive
5. Maintain and/or restore landscape heterogeneity and capture environmental gradients	Provide a diversity of habitats that are useful to a range of different species Distribute different land-use intensities across natural gradients in climate, topography, and primary productivity
Species-oriented strategies	
1. Maintain key species interactions and functional diversity	Protect important ecosystem processes Protect characteristic ecosystem structure and feedbacks
2. Maintain or apply appropriate disturbance regimes	Encourage characteristic vegetation structure Create characteristic spatial and temporal variability in vegetation patterns
3. Maintain species of particular concern	Ensure the continued survival of rare or threatened species
4. Control aggressive, over-abundant and invasive species	Reduce competition and predation by undesirable species which could negatively affect desirable species Maintain characteristic species composition
5. Minimise ecosystem-specific threatening processes	Identify problems that may affect biodiversity but are not directly related to landscape modification Establish protocols to eliminate these problems

3 More studies need to investigate biodiversity throughout entire modified landscapes, including outside patches of native vegetation (Daily, 2001).
4 Increased efforts are needed to identify cascading effects of landscape modification before they occur, for example through scenario planning (Peterson *et al.*, 2003; Scholes & Biggs, 2004).
5 Future research could be strengthened by investigating larger spatial and temporal scales than have been typical in the past (Fazey *et al.*, 2005), for example through the use of well-designed natural experiments (*sensu* Diamond, 1986).
6 Given potential trade-offs and synergies between biodiversity conservation and other objectives of human land use, ecologists should further strengthen links with other academic disciplines such as economics, agriculture and ethics (Daily & Ehrlich, 1999) as well as conservation policy and management (Mattison & Norris, 2005; Soulé *et al.*, 2005).

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REFERENCES

Agee, J.K. (1993) *Fire ecology of the Pacific Northwest forests*. Island Press, Washington, D.C.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat — a review. *Oikos*, **71**, 355–366.

Andrén, H., Delin, A. & Seiler, A. (1997) Population response to landscape changes depends on specialization to different landscape elements. *Oikos*, **80**, 193–196.

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Ås, S. (1999) Invasion of matrix species in small habitat patches. *Conservation Ecology*, **3**, 1 (online). http://www.consecol.org/vol3/iss1/art1.

August, P.V. (1983) The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology*, **64**, 1495–1507.

Austin, M.P. & Smith, T.M. (1989) A new model for the continuum concept. *Vegetatio*, **83**, 35–47.

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Barrett, G.W., Ford, H.A. & Recher, H.F. (1994) Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology*, **1**, 245–256.

Batary, P. & Baldi, A. (2004) Evidence of an edge effect on avian nest success. *Conservation Biology*, **18**, 389–400.

Battin, J. (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, **18**, 1482–1491.

Beier, P. & Noss, R.F. (1998) Do habitat corridors provide connectivity? *Conservation Biology*, **12**, 1241–1252.

Bellamy, P.E., Hinsley, S.A. & Newton, I. (1996) Factors influencing bird species numbers in small woods in south-eastern England. *Journal of Applied Ecology*, **33**, 249–262.

Bender, D.J., Contreras, T.A. & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, **79**, 517–529.

Bender, D.J. & Fahrig, L. (2005) Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology*, **86**, 1023–1033.

Bennett, A.F. (1987) Conservation of mammals within a fragmented forest environment: the contribution of insular biogeography and autecology. *Nature conservation: the role of remnants of native vegetation* (ed. by D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J. Hopkins), pp. 41–52. Surrey Beatty & Sons, Chipping Norton, NSW.

Bennett, A.F. (1990) Land use, forest fragmentation and the mammalian fauna at Naringal, south-western Victoria. *Australian Wildlife Research*, **17**, 325–347.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.

Borghesio, L. & Giannetti, F. (2005) Habitat degradation threatens the survival of the Ethiopian bush crow *Zavattariornis stresemanni. Oryx*, **39**, 44–49.

Brashares, J.S. (2003) Ecological, behavioural, and life-history correlates of mammal extinctions in West Africa. *Conservation Biology*, **17**, 733–743.

Brooker, L. & Brooker, M. (2002) Dispersal and population dynamics of the Blue-breasted Fairy-wren, *Malurus pulcherrimus*, in fragmented habitat in the Western Australian wheatbelt. *Wildlife Research*, **29**, 225–233.

Bunnell, F.L. (1999) Let's kill a panchreston: giving fragmentation meaning. *Forest fragmentation — wildlife and management implications* (ed. by J.A. Rochelle, L.A. Lehman and J. Wisnewski), pp. vii–xiii. Brill, Leiden.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple causes of high extinction risk in large mammal species. *Science*, **309**, 1239–1241.

Casagrandi, R. & Gatto, M. (1999) A mesoscale approach to extinction risk in fragmented habitats. *Nature*, **400**, 560–562.

Chen, J., Franklin, J.F. & Spies, T.A. (1990) Microclimatic pattern and basic biological responses at the clearcut edges of old-growth Douglas fir stands. *Northwest Environmental Journal*, **6**, 424–425.

Chettri, N., Sharma, E., Deb, D.C. & Sundriyal, R.C. (2002) Impact of firewood extraction on tree structure, regeneration and woody biomass productivity in a trekking corridor of the Sikkim Himalaya. *Mountain Research and Development*, **22**, 150–158.

Clark, T.W., Warneke, R.M. & George, G.G. (1990) Management and conservation of small populations. *The management and conservation of small populations* (ed. by T.W. Clark and J.H. Seebeck), pp. 1–18. Chicago Zoological Society, Brookfield, Illinois.

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. *The American Naturalist*, **113**, 791–833.

Cooper, C.B. & Walters, J.R. (2002) Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*, **16**, 471–478.

Cordeiro, N.J. & Howe, H.F. (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 14052–14056.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E. & Haeruman, H. (1999) Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science*, **286**, 2184–2188.

Daily, G.C. (2001) Ecological forecasts. *Nature*, **411**, 245.

Daily, G.C. & Ehrlich, P.R. (1999) Managing Earth's ecosystems: an interdisciplinary challenge. *Ecosystems*, **2**, 277–280.

Dean, W.R.J., Milton, S.J. & Jeltsch, F. (1999) Large trees, fertile islands, and birds in arid savanna. *Journal of Arid Environments*, **41**, 61–78.

Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.

Diamond, J. (1986) Overview: laboratory experiments, field experiments, and natural experiments. *Community ecology* (ed. by J. Diamond and T.J. Case), pp. 3–23. Harper & Row Publishers, New York.

Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A.J. (1996) Insects in fragmented forests: a functional approach. *Trends in Ecology & Evolution*, **11**, 255–260.

Driscoll, D., Milkovits, G. & Freudenberger, D. (2000) *Impact and use of firewood in Australia*. CSIRO Sustainable Ecosystems, Canberra.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.

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

Fazey, I., Fischer, J. & Lindenmayer, D.B. (2005) What do conservation biologists publish? *Biological Conservation*, **124**, 63–73.

Felton, A.M., Engstrom, L.M., Felton, A. & Knott, C.D. (2003) Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests

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in West Kalimantan, Indonesia. *Biological Conservation*, **114**, 91–101.

Fischer, J. & Lindenmayer, D.B. (2002) Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. *Biological Conservation*, **106**, 129–136.

Fischer, J. & Lindenmayer, D.B. (2006) Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos*, **112**, 473–480.

Fischer, J., Lindenmayer, D.B. & Fazey, I. (2004) Appreciating ecological complexity: habitat contours as a conceptual landscape model. *Conservation Biology*, **18**, 1245–1253.

Fischer, J., Lindenmayer, D.B. & Manning, A.D. (2006) Biodiversity, ecosystem function and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment*, **4**, 80–86.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, **35**, 557–581.

Forman, R.T.T. (1995) *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, New York.

Fox, B.J. (1983) Mammal species diversity in Australian heathlands: the importance of pyric succession and habitat diversity. *Mediterranean-type ecosystems: the role of nutrients* (ed. by F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis), pp. 473–489. Springer-Verlag, Berlin.

Franklin, J.F. (1993) Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications*, **3**, 202–205.

Gardner, J.L. (2004) Winter flocking behaviour of speckled warblers and the Allee effect. *Biological Conservation*, **118**, 195–204.

Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Jr, Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M. & Borges, S. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation*, **91**, 223–229.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S. & Winne, C.T. (2000) The global decline of reptiles, déjà vu amphibians. *Bioscience*, **50**, 653–666.

Gibbs, J.P. (1998) Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology*, **13**, 263–268.

Gilpin, M.E. & Soulé, M.E. (1986) Minimum viable populations: processes of species extinctions. *Conservation biology: the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 19–34. Sinauer Associates, Sunderland, Massachusetts.

Gleason, H.A. (1939) The individualistic concept of plant association. *American Midland Naturalist*, **21**, 92–110.

Grey, M.J., Clarke, M.F. & Loyn, R.H. (1997) Initial changes in the avian communities of remnant eucalypt woodlands following a reduction the abundance of Noisy Miners, *Manorina melanocephala*. *Wildlife Research*, **24**, 631–648.

Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., LeRoy Poff, N., Rejeski, D.W., Reynolds, J.F., Turner, M.G., Weathers, K.C. & Wiens, J. (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*, **9**, 1–13.

Gustafson, E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems*, **1**, 143–156.

Hadfield, M.G., Miller, S.E. & Carwile, A.H. (1980) The decimation of endemic Hawaiian tree snails by alien predators. *American Zoologist*, **33**, 610–622.

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

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

Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151–162.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, **42**, 3–16.

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

Hanski, I. & Simberloff, D. (1997) The metapopulation approach, its history, conceptual domain and application to conservation. *Metapopulation biology* (ed. by I. Hanski and M.E. Gilpin), pp. 5–26. Academic Press, San Diego.

Harner, R.F. & Harper, K.T. (1976) The role of area, heterogeneity, and favorability in plant species diversity of Pinyon–Juniper ecosystems. *Ecology*, **57**, 1254–1263.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Essen, P.-E. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, **19**, 768–782.

Harris, L.D. (1984) *The fragmented forest: island biogeography theory and the preservation of biotic diversity*. University of Chicago Press, Chicago.

Hazell, D., Hero, J.M., Lindenmayer, D. & Cunningham, R. (2004) A comparison of constructed and natural habitat for frog conservation in an Australian agricultural landscape. *Biological Conservation*, **119**, 61–71.

Hinsley, S.A., Rothery, P. & Bellamy, P.E. (1999) Influence of woodland area on breeding success in Great Tits *Parus major and* Blue Tits *Parus caeruleus*. *Journal of Avian Biology*, **30**, 271–281.

Hobbs, R. (1997) Future landscapes and the future of landscape ecology. *Landscape and Urban Planning*, **37**, 1–9.

Hobbs, R.J. (2001) Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conservation Biology*, **15**, 1522–1528.

Hobbs, R.J. & Yates, C.J. (2003) Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. *Australian Journal of Botany*, **51**, 471–488.

© 2007 The Authors

Hobbs, R.J. & Yates, C.J. (2003) Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. *Australian Journal of Botany*, **51**, 471–488.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.

Hoekstra, T.W., Allen, T.F.H. & Flather, C.H. (1991) Implicit scaling in ecological research. *Bioscience*, **41**, 148–154.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, F. & Evans, A.D. (2005) Does organic farming benefit biodiversity? *Biological Conservation*, **122**, 113–130.

Ims, R.A., Rolstad, J. & Wegge, P. (1993) Predicting space use responses to habitat fragmentation: can voles *Microtus oeconomus* serve as an experimental model system (EMS) for Capercaillie Grouse *Tetrao urogallus* in boreal forest? *Biological Conservation*, **63**, 261–268.

Ingham, D.S. & Samways, M.J. (1996) Application of fragmentation and variegation models to epigaeic invertebrates in South Africa. *Conservation Biology*, **10**, 1353–1358.

Jäggi, C. & Baur, B. (1999) Overgrowing forest as a possible cause for the local extinction of *Vipera aspis* in the northern Swiss Jura mountains. *Amphibia-Reptilia*, **20**, 25–34.

Johns, A.D. & Skorupa, J.P. (1987) Responses of rain-forest primates to habitat disturbance — a review. *International Journal of Primatology*, **8**, 157–191.

Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998) Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics*, **29**, 83–112.

Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, **17**, 230–241.

Kerr, J.T. & Deguise, I. (2004) Habitat loss and the limits to endangered species recovery. *Ecology Letters*, **7**, 1163–1169.

Klink, C.A. & Machado, R.B. (2005) Conservation of the Brazilian Cerrado. *Conservation Biology*, **19**, 707–713.

Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology*, **18**, 1571–1578.

Kotiaho, J.S., Kaitala, V., Kolmonen, A. & Paivinen, J. (2005) Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 1963–1967.

Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography*, **15**, 8–20.

Lahti, D.C. (2001) The 'edge effect on nest predation' hypothesis after twenty years. *Biological Conservation*, **99**, 365–374.

Landsberg, J. (1999) Status of temperate woodlands in the Australian Capital Territory region. *Temperate eucalypt woodlands in Australia: biology, conservation, management and restoration* (ed. by R.J. Hobbs and C.J. Yates), pp. 32–44. Surrey Beatty & Sons, Chipping Norton, NSW.

Laurance, W.F. (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology*, **5**, 79–89.

Laurance, W.F., Bierregaard, R.O., Gascon, C., Didham, R.K., Smith, A.P., Lynam, A.J., Viana, V.M., Lovejoy, T.E., Sieving, K.E., Sites, J.W., Andersen, M., Tocher, M.D., Kramer, E.A., Restrepo, C. & Moritz, C. (1997) Tropical forest fragmentation: synthesis of a diverse and dynamic discipline. *Tropical forest remnants. Ecology, management and conservation of fragmented communities* (ed. by W.F. Laurance and R.O. Bierregaard), pp. 502–525. University of Chicago Press, Chicago.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005a) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146–148.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. (2005b) Landscape corridors: Possible dangers? Response. *Science*, **310**, 782–783.

Lindenmayer, D.B., Cunningham, R.B. & Fischer, J. (2005) Vegetation cover thresholds and species responses. *Biological Conservation*, **124**, 311–316.

Lindenmayer, D.B., Cunningham, R.B. & Lindenmayer, B.D. (2004) Sound recording of bird vocalisations in forests. II. Longitudinal profiles in vocal activity. *Wildlife Research*, **31**, 209–217.

Lindenmayer, D.B. & Franklin, J. (2002) *Conserving forest biodiversity*. Island Press, Covelo, California.

Liu, J.G., Linderman, M., Ouyang, Z.Y., An, L., Yang, J. & Zhang, H.M. (2001) Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science*, **292**, 98–101.

Luck, G.W. & Daily, G.C. (2003) Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. *Ecological Applications*, **13**, 235–247.

Luck, G.W., Ricketts, T.H., Daily, G.C. & Imhoff, M. (2004) Alleviating spatial conflict between people and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 182–186.

Lunt, I.D. & Spooner, P.G. (2005) Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. *Journal of Biogeography*, **32**, 1859–1873.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.

Malcolm, J.R. (1994) Edge effects in central Amazonian forest fragments. *Ecology*, **75**, 2438–2445.

Manning, A.D., Fischer, J. & Lindenmayer, D.B. (2006) Scattered trees are keystone structures — implications for conservation. *Biological Conservation*, **132**, 311–321.

Manning, A.D., Lindenmayer, D.B. & Nix, H.A. (2004) Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos*, **104**, 621–628.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Matlack, G.R. (1993) Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation*, **66**, 185–194.

Mattison, E.H.A. & Norris, K. (2005) Bridging the gaps between agricultural policy, land-use and biodiversity. *Trends in Ecology & Evolution*, **20**, 610–616.

Mayfield, M.M. & Daily, G.C. (2005) Countryside biogeography

© 2007 The Authors

of neotropical herbaceous and shrubby plants. *Ecological Applications*, **15**, 423–439.

McGarigal, K. & Cushman, S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, **12**, 335–345.

McGuinness, K.A. (1984) Equations and explanations in the study of species–area curves. *Biological Reviews*, **59**, 423–440.

McIntyre, S. & Barrett, G.W. (1992) Habitat variegation, an alternative to fragmentation. *Conservation Biology*, **6**, 146–147.

McIntyre, S. & Hobbs, R. (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology*, **13**, 1282–1292.

Milton, S.J., Dean, W.R.J., du Plessis, M.A. & Siegfried, W.R. (1994) A conceptual model of arid rangeland degradation — the escalating cost of declining productivity. *Bioscience*, **44**, 70–76.

Moilanen, A. & Hanski, I. (2001) On the use of connectivity measures in spatial ecology. *Oikos*, **95**, 147–151.

Moilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131–1145.

Norris, D.R. & Stutchbury, B.J.M. (2001) Extraterritorial movements of a forest songbird in a fragmented landscape. *Conservation Biology*, **15**, 729–736.

Norton, D.A., Hobbs, R.J. & Atkins, L. (1995) Fragmentation, disturbance, and plant distribution — mistletoes in woodland remnants in the Western Australian wheatbelt. *Conservation Biology*, **9**, 426–438.

Noss, R.F. & Beier, P. (2000) Arguing over little things: response to Haddad *et al. Conservation Biology*, **14**, 1546–1548.

Paine, R.T. (1969) A note on trophic complexity and community stability. *The American Naturalist*, **103**, 91–93.

Pardini, R. (2004) Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodiversity and Conservation*, **13**, 2567–2586.

Parker, M. & Mac Nally, R. (2002) Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation*, **105**, 217–229.

Peakall, R., Ruibal, M. & Lindenmayer, D.B. (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes. Evolution*, **57**, 1182–1195.

Peterson, G.D., Cumming, G.S. & Carpenter, S.R. (2003) Scenario planning: a tool for conservation in an uncertain world. *Conservation Biology*, **17**, 358–366.

Pope, M.L., Lindenmayer, D.B. & Cunningham, R.B. (2004) Patch use by the Greater Glider in a fragmented forest ecosystem. I. Home range size and movements. *Wildlife Research*, **31**, 559–568.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature*, **439**, 161–167.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. (1996) Challenges in the quest for keystones. *Bioscience*, **46**, 609–620.

Procheş, Ş., Wilson, J.R.U., Veldtman, R., Kalwij, J.M., Richardson, D.M. & Chown, S.L. (2005) Landscape corridors: possible dangers? *Science*, **310**, 779–783.

Radford, J.Q., Bennett, A.F. & Cheers, G.J. (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, **124**, 317–337.

Recher, H.F. (1999) The state of Australia's avifauna: a personal opinion and prediction for the new millennium. *Australian Zoologist*, **31**, 11–29.

Recher, H.F. & Serventy, D.L. (1991) Long term changes in the relative abundance of birds in Kings Park, Perth, Western Australia. *Conservation Biology*, **5**, 90–102.

Recher, H.F., Shields, J., Kavanagh, R.P. & Webb, G. (1987) Retaining remnant mature forest for nature conservation at Eden, New South Wales: a review of theory and practice. *Nature conservation: the role of remnants of vegetation* (ed. by D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J. Hopkins), pp. 177–194. Surrey Beatty & Sons, Chipping Norton, NSW.

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

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Michener, C.D. (2004) Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 12579–12582.

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

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.

Rosenblatt, D.L., Heske, E.J., Nelson, S.L., Barber, D.H., Miller, M.A. & MacAllister, B. (1999) Forest fragments in east-central Illinois: islands or habitat patches for mammals? *American Midland Naturalist*, **141**, 115–123.

Roughgarden, J. (1975) A simple model for population dynamics in stochastic environments. *The American Naturalist*, **109**, 713–736.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., Soykan, C., Watts, J. & Welter, A. (2005) Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, **86**, 56–62.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Sarre, S. (1996) Habitat fragmentation promotes fluctuating asymmetry but not morphological divergence in two geckos. *Researches on Population Ecology*, **38**, 57–64.

Saunders, D.A. (1979) The availability of tree hollows for use as

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nest sites by White-tailed Black Cockatoos. *Australian Wildlife Research*, **6**, 205–216.

Saunders, D.A. (1980) Food and movements of the short-billed form of the White-tailed Black Cockatoo. *Australian Wildlife Research*, **7**, 257–269.

Saunders, D.A., Hobbs, R.J. & Arnold, G.W. (1993) The Kellerberrin project on fragmented landscapes: a review of current information. *Biological Conservation*, **64**, 185–192.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Saunders, D.A., Smith, G.T., Ingram, J.A. & Forrester, R.I. (2003) Changes in a remnant of salmon gum *Eucalyptus salmonophloia* and York gum *E. loxophleba* woodland, 1978 to 1997. Implications for woodland conservation in the wheat-sheep regions of Australia. *Biological Conservation*, **110**, 245–256.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Scholes, R.J. & Biggs, R. (2004) *Ecosystem services in southern Africa: a regional assessment*. Council for Scientific and Industrial Research, Pretoria, South Africa.

Sharpe, D.M., Gunterspergen, G.R., Dunn, C.P., Leitner, L.A. & Stearns, F. (1987) Vegetation dynamics in a southern Wisconsin agricultural landscape. *Landscape heterogeneity and disturbance* (ed. by M.T. Turner), pp. 137–155. Springer-Verlag, New York.

Simberloff, D.A. (1988) The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, **19**, 473–511.

Simberloff, D.A., Farr, J.A., Cox, J. & Mehlman, D.W. (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology*, **6**, 493–504.

Slabbekoorn, H. & Peet, M. (2003) Birds sing at a higher pitch in urban noise — Great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature*, **424**, 267–267.

Soulé, M.E., Estes, J.A., Miller, B. & Honnold, D.L. (2005) Strongly interacting species. conservation policy, management, and ethics. *Bioscience*, **55**, 168–176.

Soulé, M.E., Mackey, B.G., Recher, H.F., Williams, J.E., Woinarski, J.C.Z., Driscoll, D., Dennison, W.C. & Jones, M.E. (2004) The role of connectivity in Australian conservation. *Pacific Conservation Biology*, **10**, 266–279.

Spooner, P., Lunt, I. & Robinson, W. (2002) Is fencing enough? The short-term effects of stock exclusion in remnant grassy woodlands in southern NSW. *Ecological Management and Restoration*, **3**, 117–126.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571–573.

Temple, S.A. & Cary, J.R. (1988) Modelling dynamics of habitat interior bird populations in fragmented landscapes. *Conservation Biology*, **2**, 340–347.

Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. & Balbas, L. (2001) Ecological meltdown in predator-free forest fragments. *Science*, **294**, 1923–1926.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.

Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7–19.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, **12**, 354–363.

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

Tubelis, D.P., Lindenmayer, D.B., Saunders, D.A., Cowling, A. & Nix, H.A. (2004) Landscape supplementation provided by an exotic matrix: implications for bird conservation and forest management in a softwood plantation system in south-eastern Australia. *Oikos*, **107**, 634–644.

Turner, M.G., Romme, W.H. & Tinker, D.B. (2003) Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, **1**, 351–358.

Uezu, A., Metzger, J.P. & Vielliard, J.M.E. (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological Conservation*, **123**, 507–519.

Valladares, G., Salvo, A. & Cagnolo, L. (2006) Habitat fragmentation effects on trophic processes of insect–plant food webs. *Conservation Biology*, **20**, 212–217.

Vetaas, O.R. (1992) Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science*, **3**, 337–344.

Walker, B. (1995) Conserving biological diversity through ecosystem resilience. *Conservation Biology*, **9**, 747–752.

Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.

Weathers, K.C., Cadenasso, M.L. & Pickett, S.T. (2001) Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies and the atmosphere. *Conservation Biology*, **15**, 1506–1514.

Webb, N.R. (1997) The development of criteria for ecological restoration. *Restoration ecology and sustainable development* (ed. by K.M. Urbanska, N.R. Webb and P.J. Edwards), pp. 133–158. Cambridge University Press, Cambridge.

Wethered, R. & Lawes, M.J. (2005) Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. *Biological Conservation*, **123**, 125–137.

Wiegand, T., Jeltsch, F., Hanski, I. & Grimm, V. (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. *Oikos*, **100**, 209–222.

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Wiens, J. (1994) Habitat fragmentation: island vs landscape perspectives on bird conservation. *Ibis*, **137**, S97–S104.

Yahner, R.H. (1988) Changes in wildlife communities near edges. *Conservation Biology*, **2**, 333–339.

Zanette, L., Doyle, P. & Tremont, S.M. (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology*, **81**, 1654–1666.

Zanette, L., MacDougall-Shakleton, E., Clinchy, M. & Smith, J.N. (2005) Brown-headed Cowbirds skew host offspring sex ratios. *Ecology*, **86**, 815–820.

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