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Fragmentation and Edge Effects on Plant–Animal Interactions, Ecological Processes and Biodiversity

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A fragment of tropical montane forest in central Veracruz, Mexico. Note the high contrast ('hard edge') with the surrounding pasture land. Photo: Adrian Newton

We summarize studies of forest fragmentation and edge effects on a diverse range of ecological processes and abiotic variables in neotropical montane and south temperate rainforests. The main findings from these studies are that: (i) anthropogenic edge effects significantly altered forest regeneration processes occurring over small spatial and temporal scales; (ii) adjacent vegetation type not only affected the probabilities of tree invasion and regeneration, but also the extent of microclimatic edge effects within the forest interior; and (iii) edge structure and function are linked as a habitat for plants and animals and as a front for forest expansion. We found that the main modulators of edge effects were: (i) forest edge to non-forest matrix contrast (hard and soft edges); (ii) edge orientation with respect to biotic or abiotic fluxes; (iii) season (dry or wet) or year of study (temporal variance); and (iv) species-specific responses. Future edge studies should consider the modulators of edge effects for the particular response variable being studied. The consequences of edge effects for the conservation of regional biodiversity and changes in forest structure in fragmented forest landscapes are discussed.

Introduction

Forest fragmentation and its effects

Global forest fragmentation has been documented extensively, with an emphasis on the substantial loss of tropical rainforests in Central Africa and Amazonia (Fearnside, 1996; Justice *et al.*, 2001; Semazzi and Yi, 2001; Zhang *et al.*, 2001). The tropical montane forests of Mexico and Central America and the temperate rainforests of southern South America have been less studied, but are also suffering rapid changes in land use leading to increased forest fragmentation and larger perimeter/forest patch area ratios (see Chapter 2). Such patterns are threatening the conservation of regional biodiversity, especially narrow endemics and forest specialists in each forest type (Chapter 3), as well as the dynamics of biotic interactions in rural landscapes. In general, the main trends associated with anthropogenic forest fragmentation are: (i) increasing habitat loss; (ii) increasing number of forest fragments; (iii) decreasing size of forest fragments; and (iv) increasing isolation of remnant forest habitats (Fahrig, 2003). A higher number of isolated forest patches leads to the creation of more edge habitat or forest-matrix transitions. Loss of forest cover, therefore, changes the habitat mosaic not only by creating new edges, but also by changing the edge contrast, from low to high contrast between the forest and the adjacent degraded or human-used habitat (Wiens *et al.*, 1985). These changes are likely to affect wildlife habitat quality, ecological processes and ultimately regional and local biodiversity.

Edges are a transition zone separating two contiguous habitat types that are perceived by some focal organism as being of significantly different quality (Lidicker, 1999). Hence, edge definition and measurement depend upon habitat use by focal species and the spatial scale of the study (Murcia, 1995; Sarlov-Herlin, 2001). Accordingly, the study of habitat edges is subjected to several restrictions (Lidicker, 1999): (i) recognition of habitat edges depends on the human observer; (ii) responses to habitat edges will be species-specific and possibly sex- and age-specific as well; and (iii) assessing the width and length of habitat edges is difficult, as various abiotic and biotic factors, which

may influence the focal organism, penetrate to different distances across an edge. Considering these restrictions, it is not surprising that it has been difficult to generate a unifying theory of habitat edges (see reviews by Ries *et al.*, 2004; Harper *et al.*, 2005). However, extensive reviews suggest that the magnitude and distance of edge influences are a direct function of the contrast in structure and composition between adjacent habitats, resulting in different edge types. Therefore edge responses are more predictable where specific focal species, distributed along specific edge types, are defined a priori (Ries *et al.*, 2004).

Different functional edge types have been compared in a small number of experimental studies, the results of which have suggested the following a priori edge type classifications: (i) thinned versus intact (Cadenasso and Pickett, 2000, 2001; Kollmann and Buschor, 2002); (ii) natural versus anthropogenic (Song and Hannon, 1999); (iii) hard versus soft (Fenske-Crawford and Niemi, 1997; López-Barrera and Newton, 2004; López-Barrera *et al.*, 2005); and (iv) border-edge cuts versus uncut edges (Fleming and Giuliano, 1998). The characteristics of the edge itself (thickness, sharpness, etc.) influence not only the movement within or across edges, but also the movement to and from adjacent patches in the landscape (Sarlov-Herlin, 2001). Duelli *et al.* (1990) suggested that permeability to the movement of organisms is an important edge feature and proposed six edge types based on the 'hardness' for the focal organism. However, permeability can also refer to physical influences across edges, such as the effects of atmospheric chemistry and fertilizers derived from activities in the surrounding matrix.

Edge effects and ecological processes

The term 'edge effect' was first used in 1933 by Leopold, a wildlife ecologist, to explain the increased richness of generalist game species at edges between two habitats or 'ecotones' (Sarlov-Herlin, 2001). Later the concept was broadened to include the negative impacts of edges within large and well-preserved forest fragments (Fox *et al.*, 1997; Benitez-Malvido, 1998; Gascon *et al.*, 2000). As applied to tropical countries, studies of reserve design first addressed the issue of edges in planning protected areas (Laurance, 1991). Today the concept comprises a wide range of ecological processes occurring at edges (Murcia, 1995), as mutual influences on physical and biological flows result in changes of species composition and structure (Fagan *et al.*, 1999; Lidicker, 1999; Cadenasso and Pickett, 2000, 2001; Laurance *et al.*, 2001).

Edge effects may be defined by changes in physical or biotic response variables, which occur at the transition between adjoining habitats (Lidicker, 1999). The current use of the edge-effect concept in the literature summarizes a diversity of responses. Edges may have both positive and negative consequences for focal organisms and may produce emergent response properties (Fig. 4.1). Lidicker (1999) differentiated two general edge effects depending on emergent properties: the *matrix* effect and the *ecotone* effect. The matrix effect is an abrupt change in some response variable as the edge is crossed,

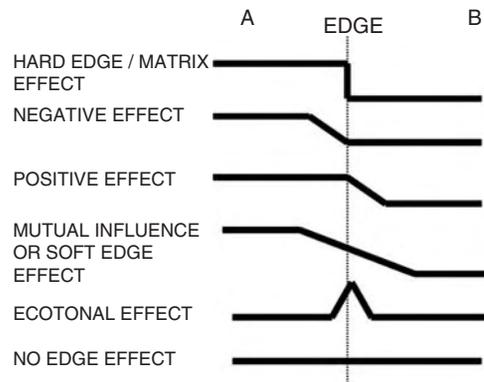


Fig. 4.1. Simple representation of potential edge effects for physical or biotic response variables (thick line). A and B are two juxtaposed habitat types. Modified from Duelli *et al.* (1990).

where the response of organisms at an edge can be explained strictly by the organism's behaviour in the two habitat types (away from the edge). This type of boundary is defined as a 'hard edge' by Duelli *et al.* (1990; Fig. 4.1). The ecotonal effect is characterized by the presence of emergent properties (negative, positive or mutual influences), therefore the response of the organism at the edge cannot be explained solely by its contrasting behaviour in each habitat type (Lidicker and Peterson, 1999). Emergent properties could produce either increasing or decreasing responses near the edge (Fig. 4.1).

Studies of habitat fragmentation have often examined the effects of edges on bird nest predation by mammals and other birds (see review by McCollin, 1998). Edges are believed to be detrimental to some bird species because of reduced reproductive success and increased rates of nest parasitism and predation. However, studies of the effects of distance from edge on the nesting success of birds have produced mixed results. Not all studies have documented edge effects and the general pattern seems to vary according to region, ecosystem, predator assemblage, forest size and type of adjoining habitat (Andren, 1994; Murcia, 1995; Hinsley *et al.*, 1998; Bergin *et al.*, 2000; Brand and George, 2000; Hansson, 2000). It seems that an edge-related increase in nest predation is most common inside small forest patches surrounded by farmland or highly fragmented anthropogenic landscapes, and is rarely present or undetectable in forest mosaics or continuous landscapes (Donovan *et al.*, 1997; McCollin, 1998).

Edge effects on seed and seedling herbivory have been less studied than bird nest predation. There are no comparisons of these effects in forests mosaics or forests surrounded by rural or urban habitats. Small mammals are important seed predators and/or dispersers in many forest landscapes. Habitat use (specialist or generalist) by small mammals will have a great influence on seed-predator interactions in edges (Lidicker, 1999; Manson *et al.*, 1999) by determining the ability of the seed predators and/or dispersers to move between adjacent habitat patches of different quality (Rodriguez

et al., 2001). Increased herbivory in edges may also be associated with greater insect activity, as insects may be attracted to greater productivity in open canopy habitats (Chacón and Armesto, 2006).

Edge effects on seed dispersal are associated with changes in vegetation structure (Kollmann and Buschor, 2002), however most studies of edge effects on tree regeneration do not provide a precise description of edge structure. There is substantial discrepancy among recent studies regarding the existence and intensity of edge effects on seed predation (Kollmann and Buschor, 2002). Some lack of consistency in the results may be attributed to improper design (lack of true replication), differences in edge definition, lack of temporal replication and oversimplification of the perception of edge dynamics (Murcia, 1995) and also to temporal and spatial variability in the occurrence of different seed predators.

Although negative consequences of fragmentation and resulting edge effects have been documented in a large number of studies performed mainly in lowland tropical rainforest (Williams-Linera, 1990a,b; Malcolm, 1994; Fox *et al.*, 1997; Kapos *et al.*, 1997; Laurance, 1997; Turton and Freiburger, 1997; Benitez-Malvido, 1998; Laurance *et al.*, 1998; Didham and Lawton, 1999; Sizer and Tanner, 1999; Gascon *et al.*, 2000; Laurance and Williamson, 2001), research has been sparse in tropical montane and high-latitude temperate rainforests, such as those in Mexico and Chile. Despite their globally recognized conservation importance (Myers *et al.*, 2000), we know little about the impact of fragmentation in these ecosystems that results from the increased land use change and logging in recent decades (Chapter 2). In this chapter, we present a synthesis of ongoing research to assess the effects of such fragmentation on a variety of ecological processes in these two study regions. Although the studies were not designed to be directly comparable, we consider it important to examine the generality of these findings and their value to forest managers in efforts to conserve regional biodiversity. Finally, we propose several directions for future research in these regions based on the results presented.

General predictions and aims

The following general predictions were tested as part of the research summarized here:

1. Forest edges are habitats with emergent properties different to forest interior and tree-fall gaps.
2. Edge-related changes in abiotic conditions (light, soil moisture, etc.) relative to the forest interior or tree-fall gaps may result in measurable differences in forest structure, species composition and ecological interactions along edges.
3. Edges may induce changes in the abundance and distribution of species, which will in turn produce changes in species interactions, such as predation, herbivory, pollination and seed dispersal.

4. Edge orientation modulates the intensity of abiotic effects (such as fog penetration in cloud-dependent forests), thereby affecting resource distribution and consequently forest structure and dynamics.
5. According to landscape ecology theory, as structural similarity between two adjacent habitats increases, the edge created becomes less abrupt and the edge effect less evident. Hence, ecological flows (such as animal movements) across edges may be enhanced by uniformity and reduced by sharpness or abruptness of edges.

Research Approaches

Edges, forests and canopy gaps

Because of the considerable heterogeneity among study systems and research foci, several different experimental and descriptive approaches were employed (Table 4.1). Most of the studies defined a priori the habitat contrasts compared, for instance forest edges versus canopy gaps, edges versus forest interior, trees in forest patches versus isolated trees in pastures, forests versus shrublands, etc. Six of the studies ('experimental-habitat') introduced artificial avian nests, seeds or seedlings to evaluate the effect of the habitat on ecological process, and eight studies ('descriptive-habitat') estimated attributes of plants and animals (species richness, abundance, etc.) living in contrasting adjacent habitats. Two studies estimated forest structure and composition along forest-edge–exterior gradients and six studies ('experimental-gradient') tested different ecological processes along forest-edge–exterior gradients (using distance from the edge as a factor); most of these studies also tested the effects of edge type.

Varying sized forest patches, isolated trees and riparian corridors

Other studies within this project compared ecological processes such as pollination and seed dispersal, focusing on landscape elements including isolated trees in pastures, remnant forest patches in rural areas (1 ha, small; 8–23 ha medium; > 150 ha large patches; Smith-Ramírez and Armesto, 2003), and the function of riparian vegetation strips in rural landscapes (Box 4.10).

Main Research Findings

Edge effects

Owing to the broad range of methodological approaches, differences among the study regions, and variation in the response variables measured, we summarize the main results in Table 4.2 comparing edge versus interior habitat in forest patches. To integrate the extensive range of response variables we developed a conceptual framework to compare the patterns

Table 4.1. Different descriptive and experimental approaches used in the studies of forest edges summarized in this review.

Approach	Response variables or ecological processes measured	Spatial scale (m)	Reference
Experimental Habitat contrasts: Forest edges were defined as habitats and were compared with other habitats such as forest interior, canopy gaps, isolated trees in pastures, shrublands, old-fields	Nest predation risk	5-50	Willson <i>et al.</i> (2001)
	Seed and seedling survival	1-50	Guzmán-Guzmán and Williams-Linera (2006)
	Seed predation	1-100	Diaz <i>et al.</i> (1999)
	Seedling growth, survival, specific leaf area and foliar damage	<100	Chacón and Armeστο (2005, 2006)
	Foliar damage	1-30	Reynoso-Moran and Williams-Linera (Box 4.2)
	Seed rain density and composition	20-100	Armeστο <i>et al.</i> (2001)
	Epiphyte cover and diversity	1-100	Salinas and Armeστο (Box 4.5)
	Bryophyte diversity	1-300	Larriain and Armeστο (Box 4.6)
	Seedling and sapling density	10-50	Gutiérrez <i>et al.</i> (Box 4.8)
	Tree composition		
Descriptive Habitat contrasts: Forest edges were defined as habitats and were compared with other habitats such as forest interior, forest exterior, gaps or riparian corridors	Tree growth rate	10-50	Gutiérrez <i>et al.</i> (Box 4.9)
	Plant species richness and diversity	1-50	Muñiz-Castro <i>et al.</i> (2006)
	Avian species richness	1-500	Jaña <i>et al.</i> (Box 4.1)
	Seed rain		
	Small mammals; abundance and composition	8-80	Ruán-Tejeda and Manson (Box 4.7)
	Plant species richness and forest structure		Guzmán-Guzmán and Williams-Linera (Box 4.4)
	Germination success	1-60	López-Barrera (Box 4.3)
	Rate of acorn removal	1-50	López-Barrera and Newton (2005)
	Acorn removal and movement	1-60	López-Barrera <i>et al.</i> (2005)
	Distribution of small mammals	1-60	López-Barrera <i>et al.</i> (2007)
Descriptive Gradient: Different distances from the edge into the interior	Seedling establishment	1-60	López-Barrera <i>et al.</i> (2006)
	Nesting success	1-50	De Santo <i>et al.</i> (2002)
	Fog capture	10-200	del Val <i>et al.</i> (2006)
	Seedling and sapling densities		
Experimental Gradient: Different distances from the edge into the interior and into the matrix were compared; edge type distinction made			

Table 4.2. Summary of studies measuring ecological processes, patterns and microclimate at the forest edge (zero metres) compared to forests interior (except in the case of ecological flows), showing higher or lower values of the response variable at the edge, or no difference. Modulators are factors that conditioned the observed response.

Response variable	Region	Modulators	Higher	Lower	No difference	Potential effects		Reference
						on species richness	on species richness	
<i>Dynamic processes</i>								
Seed rain	Chiloé	Only fleshy-fruited species Landscape	X			Positive		Armeño <i>et al.</i> (2001)
	Chiloé	type Landscape		X		Neutral		Jaña <i>et al.</i> (Box 4.1)
Avian nest predation	Chiloé		X			Negative		Willson <i>et al.</i> (2001)
	Chiloé			X		Positive		De Santo <i>et al.</i> (2002)
Seed germination	Chiapas	Species identity	X			Positive		López-Barrera and Newton (2005)
Seed removal and/or predation	Chiapas	Only non-masting years	X			Uncertain		López-Barrera <i>et al.</i> (2005)
	Veracruz			X				Guzmán-Guzmán and Williams-Linera (2006)
	Chiloé	Species identity, season and canopy opening		X		Neutral		Díaz <i>et al.</i> (1999)
Seedling herbivory	Chiloé			X		Positive		Chacón and Armeño (2005)
	Chiapas	Edge specific: only in hard edges	X			Negative in hard edges		López-Barrera <i>et al.</i> (2006)

	Veracruz	Season specific: only in the soft edge during the dry season	X	Reynoso-Moran and Williams-Linera (Box 4.2)
Seedling performance (survival and growth)	Chiapas		X	López-Barrera <i>et al.</i> (2006)
	Chiloé		X	Chacón and Armesto (2006)
	Veracruz		X	Guzmán-Guzmán and Williams-Linera (2006)
			X	Reynoso-Moran and Williams-Linera (Box 4.2)
			X	Gutiérrez <i>et al.</i> (Box 4.9)
Tree growth rate		Species- dependent		Positive
Ecological flows				
Fog interception and tree regeneration	Fray Jorge	Fog influx direction	X	del Val <i>et al.</i> (2006)
Seed movement from edge into the exterior	Chiapas	Edge specific: only in soft edges	X	López-Barrera <i>et al.</i> (2007)
<i>Patterns</i>				
Woody species richness/ diversity	Chiapas		X	López-Barrera (Box 4.3)
	Veracruz		X	Guzmán-Guzmán, and Williams-Linera (Box 4.4)
			X	Muñiz-Castro <i>et al.</i> (2006)
Epiphyte cover and species richness	Chiloé		X	Salinas and Armesto (Box 4.5)
Bryophyte species richness	Chiloé		X	Larráin and Armesto (Box 4.6)
Avian species richness	Chiloé		X	Jaña <i>et al.</i> (Box 4.1)

Continued

Table 4.2. Continued

Response variable	Region	Modulators	Higher	Lower	No difference	Potential effects on species richness	Reference
Diversity and abundance of native small mammals	Chiapas	Edge specific: only in soft edges	X			Positive in soft edges	López-Barrera <i>et al.</i> 2007
	Veracruz	Only in fragments with soft edges	X			Positive in soft edges	Ruán-Tejeda and Manson (Box 4.7)
	Chiloé	Species identity and shade tolerance	X			Positive	Gutiérrez <i>et al.</i> (Box 4.8)
Overall tree seedling and sapling density	Chiapas				X	Uncertain	López-Barrera (Box 4.3)
	Veracruz				X	Uncertain	Guzmán-Guzmán and Williams-Linera (Box 4.4)
Microclimate Soil moisture	Semi-arid Chile	Fog influx direction	X				del Val <i>et al.</i> (2006)
	Veracruz			X			Reynoso-Moran and Williams-Linera (Box 4.2)
Light	Chiapas				X	Uncertain	López-Barrera (Box 4.3)
	Chiapas	Edge specific: only in hard edges	X			Uncertain	López-Barrera (Box 4.3)
Air temperature	Veracruz		X				Reynoso-Moran and Williams-Linera (Box 4.2)

recorded along habitat edges. This framework is based on the description of modulators of edge effects, i.e. the factors that determine the recorded change of the response variable along the edge habitat versus the forest interior. Published work is cited in Table 4.2 and briefly discussed in the text, while an abstract of unpublished (or submitted) work is presented as case studies (included in individual Boxes) appended at the end of this chapter.

We reviewed 22 studies that recorded 34 response variables that compared forest edge and forest interior habitats in tropical montane and south temperate rainforests. From these 34 response variables, 19 resulted in positive edge effect (higher values of the response variable in the edge versus forest), 9 in a negative edge effect (lower values of the response variable in the edge versus forest) and six recorded no edge effect. Considering all positive and negative edge effects documented, 40% recorded an additional factor (modulator) that determined the occurrence of the edge effect. It is interesting to note that for the 18 response variables that characterized ecological processes (seed rain, seedling herbivory, seed movements across borders, etc.), all recorded higher or lower values of the response variable comparing edges versus forest interior habitats (Fig. 4.2). However, from the 16 studies that characterized ecological patterns (plant and animal species richness, seedling and sapling densities, etc.) in edges and forest interior habitats, six did not detect significant differences between these two habitats (Fig. 4.2). As patterns arise from processes, this difference is difficult to understand, but may reflect the loss of a detectable signal as one moves from one level of an ecological hierarchy to another, much as the pattern observed in trophic cascades (Finke and Denno, 2004). Another possible explanation is that some of the species studied are habitat generalists and have sufficient phenotypic plasticity to use interior and edge habitats, as is the case for most avian species in Chilean forests (Rozzi *et al.*, 1996) and for several tree species that are

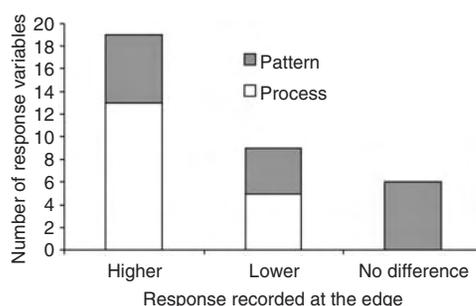


Fig. 4.2. Number of response variables that showed higher, lower or no difference (no edge effect) in the values of a response variable that was compared at the edge versus forest interior. The response variables were divided according their type; pattern refers to forest attributes such as plant species richness, tree seedling abundance, etc. Process refers to ecological attributes and interactions, such as seed removal by animals, seed dispersal, seedling herbivory, fog capture, etc.

intermediate in light requirements (Figueroa and Lusk, 2001; Aravena *et al.*, 2002).

In terms of edge theory, it has been argued that edge versus matrix contrasts may influence edge effects and therefore edge-related changes in the response variable will be weaker near soft edges (low contrast) than hard edges (high contrast edges; Ries *et al.*, 2004). Differences in edge responses, in the cases reported here, were mainly attributable to different mean vegetation heights and density between adjacent habitats. Studies in México considered this modulator of edge effects in two study areas where hard and soft edges were compared (Table 4.3). In both study areas, studies in both hard and soft edges recorded different emergent properties, but only when ecological processes were studied as a response variable. When static patterns such as forest plant species and tree seedling abundance were studied, no significant differences were recorded in either study region.

The studies that compared ecological processes among forest edges versus forests interior and versus canopy gaps generally found that canopy gaps represented a qualitatively different habitat for variables relevant to forest dynamics compared to the forest interior. Forest edges represented intermediate conditions between these two contrasting environments, but differed from canopy gaps. Changes in vegetation structure generally associated with edge creation increased incident light availability, which in turn promoted plant growth, often to a greater extent than occurs within forest canopy gaps. From all the response variables tested in the different study regions, only tree seedling growth and survival exhibited consistent responses in the three regions, showing enhanced response in edges compared to the forest interior. In all of these experimental studies, nursery-grown tree seedlings were established, to control for age and initial seedling status.

Ecological flows across edges, such as seed movement via biotic vectors and fog penetration, were dependent on edge type. Soft edges were more permeable to the movement of seeds by small mammals compared to hard edges, and windward edges (owing to their orientation) were more important for fog capture by trees, and as a consequence presented higher soil moisture and enhanced tree regeneration.

Discussion

Species-modulated responses

As species differ in their physiological requirements, edge responses may differ between species with respect to processes such as seed germination (López-Barrera and Newton, 2005), seed removal and/or predation by birds and rodents (Díaz *et al.*, 1999), and patterns such as tree seedling and sapling densities relative to the forest interior (Box 4.8). Although the different responses of species may result in changes in tree species composition between edges and the forest interior, these contrasts are not always associated with overall differences in tree species richness or floristic diversity

Table 4.3. Comparisons between study areas in Mexico, in sites with hard (open) and soft edges in each habitat (forest, edge and open) for each of the (*Quercus* spp.) tree regeneration processes and patterns.

	Forest						Edge						Open					
	Hard		Soft		Hard		Soft		Hard		Soft		Hard		Soft			
	Chiapas	Veracruz																
<i>Processes</i>																		
Acorn removal	High	High	High	Med	Low	High	High	High	High	Low	Low	Med	Med	High	High	High	High	
Seedling performance	Low	Low	Low	Med	Low	Low	Low	Low	Low	Low	Low	Med	Med	Low	Low	High	Med	
<i>Patterns</i>																		
Forest species richness	High	High	High	Low	Low	Low	High											
Tree seedling abundance	High	High	High	Low	Low	Low	Med											

(Boxes 4.3 and 4.4). However, it is interesting to note that in both temperate and tropical forest types, when seedlings were established experimentally there was an overall positive edge effect on seedling survival and growth. This suggests that the edges should generally exhibit higher densities of tree seedlings and saplings than the forest interior. However, in field studies where local seedling densities were sampled along gradients from edges to forest interior, responses were mixed, and for some species seedling densities were lower in edges than in the forest interior habitat. These findings suggest that while edges may generally favour seedling growth in controlled experiments, the resulting pattern at the community level is not predictable due to other factors operating at temporal and spatial scales (e.g. disturbance events and herbivory pulses) beyond the period of this study. These factors should be considered in future studies.

Animal species also showed different responses in their habitat preferences, which in turn affected ecological processes such as seed dispersal. Some species preferred edge habitat, while others avoided edges owing to increased predation risks. Consequently the observed species-specific response, such as seed predation rate, was not only attributable to differences in seed mass and chemical quality among plant species, but also to changes in the specific plant–animal interactions along edges. This supports the idea that changes in plant or animal species distribution and abundance along edges may have cascading effects on local assemblage structure (Ries *et al.*, 2004).

Temporal variability

Studies of edge effects should span a range of different timescales (Ries *et al.*, 2004). In this research, intra-annual variability produced different responses in variables relevant to forest dynamics, such as tree seed predation (Díaz *et al.*, 1999) and seedling herbivory (Box 4.2). Inter-annual variability owing to the occurrence of seed masting was also recorded in a study of acorn removal by small mammals (López-Barrera *et al.*, 2005) and in a study of seed rain in Chiloé forests (Armesto *et al.*, 2001). Some temporal changes in response variables along the edges are attributable to temporal differences in resource use and distribution, life cycles, stochastic events, lags in species responses or to relatively gradual changes in the quality of the edges compared to adjacent habitats (Ries *et al.*, 2004). Such differences must be documented by performing studies with longer time frames. Long-term studies of edge effects are an important gap in our current knowledge of this ecological feature in human-modified landscapes, especially considering that edges may change rapidly in structure and composition after creation.

Edge type effects

Differences in edge location and structural differences between edges and adjacent habitat are critical as they influence the strength and quality of edge

responses (Ries *et al.*, 2004). Habitat use by different organisms is related to edge-adjacent habitat contrasts and therefore to the edge types, generally characterized as hard (high contrast) and soft (low contrast) edges. In this research we found that hard and soft edges produce different responses in seed removal and seed dispersal across edges (López-Barrera, 2003; López-Barrera *et al.*, 2007; Guzman-Guzman and Williams-Linera, 2006), seedling herbivory (López-Barrera *et al.*, 2006 and Box 4.2), diversity and abundance of small mammals (López-Barrera, 2003), and edge microclimate (López-Barrera, 2003). A recent review of the edge literature concluded that the magnitude and distance of penetration of edge influences are a direct function of the contrast in structure and composition between adjacent habitats on either side of the edge (Harper *et al.*, 2005). In this review we provide experimental data supporting the idea that edge structure contrast is a strong modulator of the magnitude of edge effects. For example, we found that edge type affected the permeability of edges to animal movement with soft or regenerating (expanding) edges enhancing small mammal dispersal of seeds from the forest edge into adjacent old-fields, whereas hard or more stable edges tended to concentrate seed dispersal along edges (López-Barrera *et al.*, 2007).

Geographical position and edge orientation can also affect the degree of habitat contrast with respect to the matrix, as orientation relative to prevailing winds can affect the magnitude and distance of physical influences across edges (Harper *et al.*, 2005). This effect was documented by del Val *et al.* (2006), as reflected in greater fog capture by vegetation at the edge facing the incoming wind, in contrast to leeward edges. The difference in fog interception between opposite edges was so great that it affected patterns of tree regeneration and mortality in forest patches located on fog-influenced coastal mountaintops. The presence of fog can also diminish abiotic differences in light, temperature and humidity gradients, and as a consequence biotic responses to such vegetation gradients. This seems to be the case in Veracruz and Chiapas, for example, where soil moisture was similar along the edges compared to forest interiors (Boxes 4.2 and 4.3).

Spatial and temporal scales and region-specific fragmentation effects

To understand the effects of habitat fragmentation it is essential to specify the spatial scale of habitat fragmentation and connectivity, which is related to the habitat area requirements of organisms, home range boundaries and movement patterns of individuals (Andren, 1994). Most of the studies summarized in this chapter were conducted in small areas within forest patches in agricultural or rural mosaics. This may constrain the scaling up of edge effects recorded in these field studies (Manson, 2000). For instance, in many cases only one edge type was represented at an individual study site and different matrix characteristics were not evaluated, making it difficult to test the site or landscape effect. For future experimental designs we recommend that different edge types are examined in the same fragmented landscape. For instance, it may be possible to use large, abandoned clearings within the

forest and manipulate part of the vegetation in order to see how vegetation structure at different spatial scales affects response variables at the edge. On the other hand, the effects documented in small forests patches are likely to prevail over entire regions that are being rapidly transformed by increasing deforestation. Effects on regional biodiversity predicted from present and other studies are expected to be large.

Research summarized here suggests that the documentation of simple, descriptive patterns associated with edge creation in fragmented forests should be complemented by testing of mechanistic hypotheses in order to relate vegetation structure to function and understanding interactions between adjacent habitats. This review suggested that edge effects (emergent properties at the edge habitat) were always detected when ecological processes were recorded; however, some studies detected no effect of edges on plant species richness or other descriptive forest attributes. By long-term monitoring of spatial patterns of tree regeneration in edges, we should advance our understanding of the feedbacks from edge dynamics on tree regeneration (Conner and Perkins, 2003).

Another important observation regarding our findings is that their applicability to lowland tropical rainforests, particularly in Amazonia (Laurance and Bierregaard, 1997; Laurance *et al.*, 1998, 2001), may be limited as these landscapes may differ considerably in the degree to which they are subjected to intensive human disturbance (road density, higher population size, etc.). For example, research in Chiapas and Veracruz documented widespread, frequent human disturbance occurring within forest fragments (Ramírez-Marcial *et al.*, 2001; Chapters 3 and 10); precisely the same result was obtained in Region X of Chile (Chapter 3). Such disturbance, including harvesting of timber or firewood and browsing by livestock, makes it more difficult to measure and detect edge effects. Increased disturbance near an edge may increase the edge width and result in edge effects becoming more diffuse. For example, Fox *et al.* (1997) found that Australian rainforest fragments with minor disturbance had an abrupt increase in the abundance of forest interior species with increasing distance from the edge. However, in sites with major disturbance (mainly by cattle) the increase in abundance of core rainforest species was more gradual and the density of pioneer species remained high within the forest as well as at the edge. In effect, the contrast between edge and forest interior is not as pronounced as in areas such as lowland Amazonia, where research has focused on fragmentation of pristine rainforest (Laurance and Bierregaard, 1997).

Fragmentation effects on biodiversity

It has been stated that edges may have negative consequences for biodiversity of forest communities as edges modify forest structure, tree regeneration and mortality, enhancing the loss of forest fragment areas for conservation purposes (Murcia, 1995; Laurance *et al.*, 1998). Nevertheless, the variety of results found in recent years and evidence from the studies summarized in Table 4.2 indicate that edge effects on biodiversity are not straightforward

and need to be assessed at a landscape scale. The timing of the study is also important in comparing such effects in old versus new fragments and considering extinction debts and thresholds (Fahrig 2002; Schrott *et al.*, 2005; Helm *et al.*, 2006).

Edges habitats may generate positive or negative conditions for forest biodiversity, and in some ecosystems, such as fog-dependent rainforest fragments on coastal mountaintops of semi-arid Chile or the cloud forests of central Veracruz, edge habitats may represent opportunities for forest regeneration and forest fragment expansion. Fog-capture in these patches greatly influences biological diversity, as many species (e.g. ferns, bryophytes) depend on the water dripping from trees. For some tree species in forest edges we have also documented species-rich insect pollinator assemblages, as their flower displays become more attractive than in the forest interior. A similar effect was recorded in edges of riparian vegetation strips (Box 4.1), where frugivorous birds deposit a greater number and diversity of seeds than in the forest interior. In general, in landscapes that may be subjected to frequent large-scale disturbance (such as multiple tree falls, fire or landslides), as may be the case of montane tropical forests and south temperate rainforests, a relatively high proportion of species may be habitat generalists able to exploit the new opportunities. Such species may be able to take advantage of the increasing amount of edge habitats resulting from forest fragmentation.

Future studies of edge effects should examine the changes in ecological processes and structure over long time frames, as edges change because of decline in the size of fragments or successional expansion. Edge effects should be combined with information about landscape variables (fragment size, shape, isolation and habitat contrasts). Attention should be given to the factors that modulate edge effects, in order to conduct a comprehensive analysis of the consequences of fragmentation on forest biodiversity. By comparing different landscapes such as forest mosaics versus intensively managed areas, and by performing cross-scale edge studies, it may be possible to assess the scale-dependency of edge effects (Donovan *et al.*, 1997). Quality of edges, and not just quantity (e.g. width and length), should be considered as variables when fragmentation patterns are examined. For instance, edge effects may be more severe in forest-prairie mosaics than in relatively homogeneous forests because the edge effect at any point is a function of the nearest edge (Malcolm, 1994). However, if there is longer edge length with lower contrast or abruptness, this may have less negative effects on the forest patches than lower edge length with high contrast or hard edges in a relatively continuous forest. This may also be related to the ability of seeds of forest tree species to reach edges (Armesto *et al.*, 2001) and the ability of seedlings to survive in the new habitats, therefore reducing the contrast between edge and adjacent matrix habitat.

Conclusions

The particular hypotheses addressed in this review and a summary of the main related findings are detailed below.

Forest edges are habitats with emergent properties different to forest interior and tree-fall gaps

Significant differences in response variables occurred between the forest edge and the forest interior or tree-fall gaps, indicating that forest edges are indeed habitats with emergent properties. However, these differences were recorded more frequently when response variables were ecological processes (predation, dispersal, seedling growth, etc.) rather than patterns (seedling abundance, plant diversity, etc.).

Edge-related changes in abiotic conditions (light, soil moisture, etc.) relative to the forest interior or tree-fall gaps may result in measurable differences in forest structure, species composition and ecological interactions along edges

In this review, the abiotic conditions of edges in the two study regions had an effect in the following patterns and processes: seed rain, avian nest predation, seed germination, seed removal and/or predation, seedling herbivory, seedling performance (survival and growth), tree growth rate, fog interception and tree regeneration, seed movement from edge into the exterior, epiphyte and bryophyte cover and species richness, diversity and abundance of native small mammals and overall tree seedling and sapling density.

In the two study regions, tree seedling survival and growth were higher along the edge than in the forest interior (Chacón and Armesto, 2006; López-Barrera *et al.*, 2006; Guzmán-Guzmán and Williams-Linera, 2006; and Box 4.2). However, such experimental differences were not always reflected in higher density and diversity of naturally established tree seedlings along the same edges (Boxes 4.3 and 4.4), highlighting the need for long-term studies that consider all factors that might affect population- and community-level dynamics along such borders.

Edges may induce changes in the abundance and distribution of species, which will in turn produce changes in species interactions, such as predation, herbivory, pollination and seed dispersal

In all the studies where a response variable related to species interactions was compared, an edge effect was recorded (i.e. significant differences were recorded in the response variable between the edge and the forest interior). We need to assess whether these changes are transient or persistent and their overall net impact on ecosystem structure and function along this gradient. Changes in distribution and/or abundance of seed predators and/or dispersers along the forest-edge gradient affected seed predation and dispersal (Díaz *et al.* 1999; López-Barrera *et al.* 2005, 2007; Guzmán-Guzmán and Williams-Linera, 2006). However, these edge effects were determined by factors such as species, canopy opening and the occurrence of mast-seeding years. Changes in distribution and/or abundance of insects along the forest-edge gradient affected seedling herbivory (Chacón and Armesto, 2005;

López-Barrera *et al.*, 2006; and Box 4.2), but these differences were determined by factors such as species, edge type and season. Edge effects on patterns of nest predation reflected the different distribution and/or abundance of nest predators (Willson *et al.*, 2001; De Santo *et al.*, 2002). While pollination was not studied along forest edges–interior gradients, results comparing isolated trees in pastures, remnant forest patches in rural areas and riparian vegetation strips in rural landscapes suggest that this ecological interaction is strongly affected by forest fragmentation (Smith-Ramírez and Armesto, 2003; and Box 4.10).

Edge orientation modulates the intensity of abiotic effects (such as fog penetration in cloud-dependent forests), thereby affecting abiotic factors (light, humidity, wind, temperature, etc.), resource distribution and consequently forest structure and dynamics

All forest patches studied in the rainforest patches in the Chilean semiarid region displayed new tree establishment concentrated in the windward (or fog receiving) edge, where oceanic fog inputs are three-times higher than in the opposite edges, providing a suitable microhabitat for seedling and sapling growth. In contrast, tree mortality was largely concentrated in the patch centre and particularly in the edges opposite to the direction of fog input (LE), where the oldest trees in the patch are found (del Val *et al.*, 2006). This underlines how edge orientation modulates fog penetration in cloud-dependent forests, thereby affecting resource distribution and consequently forest structure and dynamics.

According to landscape ecology theory, as structural similarity between two adjacent habitats increases, the edge created becomes less abrupt and the edge effect less evident; hence, ecological flows (such as animal movements and seed dispersal) across edges may be enhanced by uniformity and reduced by sharpness or abruptness of edges

This prediction was tested comparing the differences between hard and soft edges. Hard edges presented an abrupt change in micro-environmental conditions at the soil, herbs and shrub level, whereas changes along soft edges were more gradual. These differences, mostly due to changes in microenvironment at the soil level, affected oak regeneration processes (López-Barrera and Newton, 2005; López-Barrera *et al.*, 2005, 2006). Along hard edges the response variables change abruptly and we recorded a diversity of edge effects (negative or matrix effects). In contrast, along soft edges effects were more gradual or not observed at all. A positive relationship was observed between the structural similarity of the matrix and forest vegetation and the permeability of edges to small mammal acorn consumers (López Barrera *et al.*, 2007).

Forest fragmentation and associated edge effects are widespread in forested landscapes in tropical and temperate South America. The ecological studies presented here were performed at relatively small spatial scales

owing to the particular pattern of forest fragmentation in the regions studied (Chapter 3). Remnant forest patches often represent important resources for human populations that have been using these ecosystems for centuries. The loss of forest habitat and biological diversity resulting from land conversion and deforestation threatens the sustainability of productivity and ecosystem services (e.g. water and resource availability and erosion control) provided to local people. However, a general theory about the net consequences of forest fragmentation (including edge creation) on forest biodiversity and ecosystem services remains elusive, as species-specific and site-specific responses are common. Inferred or observed effects of edges on biodiversity in the tropical montane and south temperate areas compared in this study were not always negative. Edge theory is largely derived from data collected in tropical rainforests of South America at larger spatial scales and comparing well-preserved forest fragments with a highly disturbed surrounding matrix. This research highlights the fact that edge effects depend on the specific patterns of forest fragmentation, the spatial scale of the clearings (edges versus canopy gaps), current land-use practices and the relative abundance of regenerating (soft) and static (hard) edges (not always related to the edge age), the additive effects of superimposed edges, the importance of small but frequent canopy gaps occurring along the edges, and the continuous impact of human-related activities within forest fragments, such as collection of firewood and livestock use of edges.

Our review provides evidence supporting the conclusions of Ries *et al.* (2004) and Harper *et al.* (2005) that future edge studies should consider landscape complexity in developing a theoretical, predictive framework for multiple regions. The research summarized here shows that a number of factors modulate the intensity, direction and type of edge effect. These modulators must be taken into account in studies of edge effects on ecological interactions or patterns of diversity. Studies documenting the edge effects of vegetation structure and composition in the same study sites indicate that the responses are modulated by the unique responses of particular species and landscape contexts. This makes it necessary to explicitly incorporate a landscape approach in the study of edges in order to integrate matrix composition and structure and measurable attributes of edges, length, width and connectivity into model building exercises. Particularly important in future studies is to assess the additive effects of humans on edges through the collection of timber and firewood, livestock trampling and grazing, and direct interference with the biotic interactions through hunting and increased predation by domestic animals.

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Case Studies

Box 4.1. Seed dispersal and avian species richness in riparian vegetation edges (R. Jaña, S. Reid, J. Cuevas and J.J. Armesto)

This study compared avian species diversity and seed rain of fleshy-fruited tree species in riparian and upland forests in a rural landscape of northern Chiloé Island (42° S), southern Chile. Riparian vegetation strips are relevant for the conservation of biodiversity in this and other rural landscapes, as forests are converted to pastures or crops, or become highly degraded by logging and fire. We expected riparian forest habitats to function in a similar way as forest edges, supporting a higher diversity of bird and plant species owing to a more heterogeneous seed rain and colonization from the surrounding matrix. Our study was conducted in two sites (landscape units, LU) in a rural mosaic of pastures and forest patches in northern Chiloé Island. In each LU (c.50 ha) we distinguished three habitats: riparian forest strips, edges of upland forest fragments and interior of upland forest fragments. In each habitat and LU we measured: (i) seed rain of fleshy fruits falling in 21 seed traps (30 cm diameter, 1 m above ground) evenly distributed along 500 m transects; (ii) bird species richness and abundance through monthly point censuses along the same transects; and (iii) tree species richness in a 2-m radius circle around each seed trap. Seeds (> 3 mm) retrieved bi-weekly from seed traps were counted and identified to species during the entire fruiting period (December–April). All statistical comparisons among habitats were made using two-sample permutation tests based on 10,000 iterations. The two LUs were not exact replicates and differed in some attributes. In one landscape (LU1), seed rain of bird-dispersed propagules was significantly higher by two orders of magnitude in the riparian forest strip than in the edge or interior of upland forests (Fig. 4.1). In the second landscape, however, there was only a marginally significant difference in total seed rain between habitats, and the tendency was the same as in LU1. The deposition of entire fruits (fallen by gravity) did not differ between forest edges and interior, but it was again significantly higher in riparian forests for LU1. Bird-dispersed seed rain was significantly higher than gravity seed rain in the three habitats. No significant differences were detected in avian species richness or abundance (frugivorous species only) among habitats. Consequently differences in seed deposition patterns can be attributed primarily to differences in tree species composition, fruit productivity and forest structure among habitats within landscapes.

Box 4.2. Edge effect and insect folivory on *Quercus xalapensis* seedlings in two cloud forest fragments in central Veracruz, Mexico (J.A. Reynoso-Moran and G. Williams-Linera)

Two tropical cloud forest fragments in Veracruz, Mexico were selected to experimentally contrast insect herbivory on *Quercus xalapensis* seedlings. In each forest edge, four sets of five seedlings were planted along four parallel bands located at the forest interior, forest and field edges, and old-field. The

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Box 4.2. *Continued*

experiments were conducted in the warm-dry (April–May) and warm-wet seasons (July–August). Herbivore damage was measured at the beginning and end of each season. Weekly environmental variables were measured in the same positions at which seedlings were planted. During the wet season, herbivory was similar on seedlings planted at different distances (c.2%), whereas during the dry season, herbivory was higher for seedlings planted at the forest border (3–12%) than for those planted at the old-field border (0.50–0.75%). Herbivory and air temperature were higher, and air relative humidity and soil water content were lower in the abrupt than in the soft forest edge. Herbivory damage was negatively correlated with air and soil humidity. Our results suggest that herbivory level on oak seedlings depends on modulator factors such as edge type and season of the year.

Box 4.3. Edge effects on plant diversity and vegetation structure in a forest mosaic in the Highlands of Chiapas, Mexico (F. López-Barrera)

Forest edges created by scattered-patch clear-cutting have become a common landscape feature in neotropical montane forest. A study was carried in the Highlands of Chiapas, Mexico in order to assess changes in vegetation structure and floristic composition along a gradient from the interior of the forest into adjacent clearings. At six sites an 80 × 10 m belt transect was established perpendicular to the forest/pasture edge. Plant species presence was recorded and seedling, sapling and tree stem diameter and height were assessed. A single-factor (distance) analysis of variance showed no significant effect of distance from the forest interior towards the edge in plant density and basal area ($P > 0.05$). Richness and floristic composition did not vary with the depth-of-edge influence (Chi-square tests, $P > 0.05$). The level of recurrent disturbance may be influencing the response of the vegetation to the edge to interior gradient, and hence the observed results can be explained by the interaction of low but frequent human disturbance and fragmentation. Abandoned grasslands showed the presence of patches of secondary vegetation and recovering forests up to 20 m into the grassland. Expected spatio-temporal changes include the evenness of the forest/grassland edge as time advances. Results suggest that edge effects on vegetation are not measurable with conventional methods in sites where forests are mosaics with small clearings (0.5–2 ha) and widespread, low and frequent human disturbance is occurring.

Box 4.4. Vegetation structure and floristic composition at forest edges in central Veracruz, Mexico (J. Guzmán-Guzmán and G. Williams-Linera)

The fragmentation of tropical montane cloud forest has resulted in patches of forest vegetation connected (or separated) by different land uses. One of the consequences of fragmentation is the increment in forest edges. The objective of this study was to estimate changes in vegetation structure (basal area, density and height) and woody species composition in the forest interior, edge and old-field. In

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Box 4.4. *Continued*

central Veracruz, Mexico, four forest fragments adjacent to old and young abandoned pastures were selected. Basal area, density and height of woody plants ≥ 5 cm dbh, < 5 cm dbh but > 2 m height, and < 2 m height were determined in plots located in six bands parallel to the border, two in the old-fields and four in the forest edge. Recorded woody species were classified as primary or secondary. Vegetation structure data were analysed using ANOVA and principal component analyses. A total of 158 woody plant species was recorded, and the number of species was similar in the four sites (60–67). Most secondary species were found in edges, 69 species were trees > 5 cm dbh, 127 were understorey species ≤ 5 cm dbh and > 2 m height, and 85 were advanced regeneration ≤ 2 m height. The most abundant tree species were *Carpinus caroliniana*, *Quercus xalapensis*, *Q. germana*, *Q. leiophylla*, *Q. salicifolia*, *Turpinia insignis*, *Liquidambar styraciflua* and *Clethra mexicana*. In addition, *Rapanea myricoides*, *Lippia myriocephala* and *Palicourea padifolia* were recorded in the understorey. Advanced regeneration included *Q. xalapensis*, *Q. leiophylla*, *Hoffmannia excelsa*, *Urera caracasana*, *Ardisia* sp. and *Hampea* sp. Few species were recorded in all study sites and 28 were found both in abandoned pasture and edges such as *Lippia myriocephala*, *Acacia pennatula*, *Cestrum* sp., *Citharexylum* sp., *Leucaena leucocephala*, *Myrica cerifera* and *Cnidocolus multilobus*. The edge effect was different in each site, but in general, it was more similar in the sites located at the boundary of forest–older abandoned pasture. The age of the adjacent old-field may be an important factor modulating the depth of edge effects.

Box 4.5. Vascular epiphyte diversity associated with *Nothofagus nitida* (Phil.) Krasser (Nothofagaceae) trees in a Chilean temperate rainforest: effects of edges and successional habitat (F. Salinas and J.J. Armesto)

Vascular epiphytes constitute an important functional element of temperate rainforests of southern South America because of their large species richness, high biomass and relevance to ecosystem processes, such as nutrient capture. We assessed vascular epiphyte communities associated with old growth and mid-successional forests and edges of forest fragments adjacent to pastures in a rural landscape in northern Chiloé Island. To control for differences in host-tree composition and age among habitats, we compared epiphyte assemblages only on adult trees of *Nothofagus nitida* (Phil.) Krasser (Nothofagaceae). Sampling considered only vascular epiphytes (angiosperms and ferns) growing on tree trunks up to 2 m height, because of accessibility limitations. Total epiphyte cover on tree trunks, composed mainly of ferns and vines, was higher in old-growth forest habitat than in mid-successional forest and in edge habitats. However, species richness of epiphytes did not differ among successional forests (old-growth versus mid-successional) or forest edges. Average vascular epiphyte species richness per sample unit was 17, 15 and 12 species for old-growth, mid-successional and forest edge habitats respectively. A dendrogram of taxonomic affinity of epiphytic floras among trees in the three

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Box 4.5. *Continued*

habitats revealed two statistically different epiphyte assemblages; one formed by old-growth forest species and a second one grouping mid-successional and edge species. Using a discriminant function analysis to determine whether forest habitats differed in their species composition and total epiphyte cover produced two functions. The first canonical function separated forest edge from old-growth forest samples, and the second canonical function separated mid-successional samples from the other two habitats. Most important distinctive taxa were Hymenophyllaceae ferns as different species characterized each habitat type. *Hymenophyllum plicatum*, *Serpilopsis caespitosa* and *H. dentatum* were most important on *Nothofagus* trees located at forest edges, while *H. plicatum* occurred mainly on trees in mid-successional forest. *H. dicranotrichum* and *Hymenoglossum cruentum* were largely restricted to trees in old-growth forests. Accordingly, the composition of vascular epiphyte communities was strongly affected by forest structure, through microhabitat conditions independent of the host tree species, and these effects should be considered when managing forests to protect biodiversity.

Box 4.6. The diversity of bryophyte species associated with rural landscapes in northern Chiloé Island (J. Larraín and J.J. Armesto)

We characterized the patterns of species richness of mosses in the rural landscape of northern Chiloé Island (42° 30' S). We compared moss species assemblages among four common habitats in this human-dominated environment: an abandoned anthropogenic prairie (previously grazed), a secondary shrubland (originated after slash-and-burn), a secondary forest edge (a roughly even age structure, 30–50 years old trees) and an old-growth forest patch (with uneven age structure and complex vertical layering). The secondary forest habitat occurred along the edge of the old-growth forest and for comparison purposes is considered the forest edge adjacent to an open pasture. In artificial prairies, shrublands and forests, we recorded all the mosses present in the soil within 20 sampling quadrats of 50 × 50 cm, located at random distances along a linear transect crossing the habitat patch along its longest axis. In addition, to characterize epiphytic species in shrublands, we randomly selected 20 shrubs (< 1.5 m tall), recording all mosses present in stems and branches of each sample shrub. In second-growth forest edges and in old-growth forests, we sampled the moss species occurring on the bark of the trunks of 20 randomly selected trees (> 10 cm diameter at breast height, dbh), from the base of the main trunk up to a height of 2 m. We were unable to record canopy mosses in either second-growth or old-growth forests because of the height of tree crowns (> 15–20 m) and as a consequence forest epiphyte diversity is underestimated. Old-growth forest habitats accumulated 59% of the total number of species of mosses recorded in all habitats in the study area. From the old-growth moss species, 30.4% were restricted to the old-growth habitat and therefore absent from forest edges and shrublands. The most common and habitat-restricted moss species found in old-growth forests were endemic to South American temperate rainforests. Although some moss taxa are yet to be identified to species, these patterns are unlikely to change significantly. Secondary forest edge species contained a subset of those species found in old-growth habitats.

Box 4.7. Fragmentation effects on small mammal communities in remnants of cloud forest in central Veracruz, Mexico (I. Ruán-Tejeda and R.H. Manson)

Habitat fragmentation is an increasingly prevalent problem affecting both tropical and subtropical forests. Habitat loss, isolation, smaller sized remnants and increased edge often combine to affect microclimate and ecological processes, through which wildlife is also affected. In central Veracruz, tropical montane cloud forests are rapidly being replaced and fragmented by urban expansion and land conversion for economic gain via coffee, cattle ranching, or sugar cane and other crops.

Using a well-known indicator group, this research sought to evaluate the effects of fragmentation on the distribution, abundance and richness of small mammals inhabiting cloud forest remnants in central Veracruz. Three main objectives of this research included: (i) determining the degree to which the species of small mammals in cloud forest fragments are interior forest specialists, generalists or prefer edge habitat; (ii) comparing the richness and diversity of small mammal communities inhabiting cloud forest fragments of different sizes; and (c) estimating how edge effects for small mammals change as a function of cloud forest fragment shape, disturbance and isolation.

Eight cloud forest remnants in the centre of Veracruz were selected for sampling of small mammals, including four with hard edges delineated by cattle pastures and four with soft edges characterized by old-fields with secondary vegetation at least 1 m high. Two 3-day trapping sessions were conducted at each site using an array of 80 Sherman live-traps distributed in a rectangular 8 × 10 grid with 8 m between traps. The long axis of this grid extended towards the forest interior from each edge under study and was oriented perpendicular to the forest edge in areas where the last trap row did not reach the centre of the fragment. All small mammals captured were identified to species, measured, weighed, sexed and then marked with a small numbered eartag prior to release at the point of capture. In addition, the size, form and degree of isolation of each fragment were calculated using a combination of field measurements and the program ARCVIEW 3.2. A disturbance index was also calculated for all fragments using information about the presence of hunters, trails, trash, cattle, wood extraction and active stewardship of owners.

A total of 694 captures of 325 individuals from nine species (31% of the 29 species registered historically in the region) were registered with a capture success of 18%. These species include *Oryzomys alfaroi*, *Oligoryzomys fulvescens*, *Peromyscus furvus*, *P. aztecus*, *P. leucopus*, *Reithrodontomys fulvescens*, *R. mexicanus*, *Microtus quasiater* and *Cryptotis mexicana*. *O. alfaroi*, *O. fulvescens* and *P. furvus* were captured more frequently in trap-rows farther from the forest edge, suggesting a preference for forest interior habitat. In contrast, *P. leucopus* and *R. fulvescens* were captured most frequently in traps located near the forest border, suggesting a preference for edge or open habitats. *M. quasiater* and *C. mexicana* were also captured in traps adjacent to the forest edge, although the small number of individuals captured precluded a statistical test of this pattern. *P. aztecus* and *R. mexicanus* showed no significant changes in abundance or activity with distance from the forest edge and therefore may be habitat generalists. These patterns were consistent irrespective of edge type

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Box 4.7. Continued

except for *P. aztecas*, which was captured more frequently in the forest interior and forest edge at sites with soft and hard edges, respectively.

Contrary to expectations, there was an inverse relationship between small mammal species richness and the size of forest fragments in this study. The smallest site (1.9 ha) recorded the highest number of species (7), whereas only three species were captured in the largest forest fragment (18.6 ha). The smallest forest fragment was also the site with the highest diversity of small mammals. Despite a trend of more individuals in smaller fragments, there were no significant differences in the abundance of forest interior species, nor those favouring forest edges, across the range of forest fragment sizes included in this study, therefore highlighting the importance of the focal species chosen for study.

Similarly, there was a non-significant trend of increased abundance of both forest interior and edge species in sites with a more circular shape. In contrast, the degree of perturbation appears to be an important explanatory variable, especially for forest interior species. We found a decrease in the abundance of interior species in sites with greater disturbance, while there was no such relationship for forest edge specialists. The degree of forest fragment isolation was not found to be significantly correlated with the abundance or diversity of small mammals in this study.

Our results contrast somewhat with previous studies suggesting that smaller forest fragments have relatively low wildlife conservation value, and highlight the need to consider other factors such as the shape and disturbance of forest fragments simultaneously with measures of forest patch size in predicting the effects of fragmentation on small mammal communities.

Box 4.8. Edge effects on tree recruitment processes in Valdivian and North Patagonian rainforests: anthropogenic edges versus canopy gaps
(A.G. Gutiérrez, N.V. Carrasco, D.A. Christie, J.C. Aravena, M. Fuentes and J.J. Armesto)

Regeneration responses of tree species to natural disturbance (canopy openings created by tree falls) and anthropogenic edges of remnant forest fragments in agricultural landscapes were compared in two lowland forests in northern Chiloé Island (42° 30' S). We sampled the two main types of evergreen rainforest present in southern Chile and hence maximized the regional representation of tree species: North Patagonian, sampled in Senda Darwin Biological Station, and a Valdivian rainforest, sampled in the Guabún Peninsula. The Valdivian rainforest was more diverse than the North Patagonian forest, containing a greater number of epiphytes and vines, as well as canopy trees (Aravena *et al.*, 2002). Owing to differences in habitat conditions between anthropogenic forest edges and canopy gaps (i.e. greater exposure to the matrix along edges), we proposed that the density and composition of tree regeneration should differ between them, presumably leading to changes in forest composition in fragmented forests compared to continuous protected forest.

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Box 4.8. *Continued*

We found interspecific differences in tree regeneration density among tree-fall gaps, forest interior and edge habitats in Valdivian and North Patagonian forests. Canopy gaps concentrated a greater heterogeneity and quantity of microsites suitable for tree regeneration, because of the greater presence of logs and stumps, which are favourable substrates for tree recruitment. The environment under canopy gaps (pooling data from both gap centre and edge) presented higher tree seedling densities and species richness compared to forest interior and anthropogenic edge habitats. We conclude that natural disturbance regimes associated with tree-fall gaps affect tree regeneration differently than anthropogenic forest-prairie edges, primarily because of differences in microsite availability and light environment. Dense stands of juvenile trees along forest edges tend to reduce tree recruitment for many years.

Box 4.9. Growth responses of eight canopy tree species to natural disturbance and anthropogenic edges (A.G. Gutiérrez, M.P. Peña, D.A. Christie and J.J. Armesto)

The effect of anthropogenic forest edges on tree growth responses is important for understanding the impact of habitat fragmentation on forest dynamics. In two old-growth forest patches located in a rural landscape of northern Chiloé Island, Chile, we conducted a comparative analysis of growth responses, measured by tree-ring width increments, of eight canopy tree species to natural (tree-fall gaps) and anthropogenic (edge adjacent to pasture) disturbances. The objective was to determinate the magnitude and duration of changes in tree-ring width following disturbance. The study sites were two large remnant forest fragments in northern Chiloé Island, representing the species composition of Valdivian and North Patagonian rainforests respectively. Five habitats were analysed for comparing tree responses: forest interior under closed canopy, open pastures outside forests, canopy openings within forest patches (tree-fall gaps), forest edges adjacent to open pastures and tree-fall gap edges within forest patches. Light availability was measured in each habitat using a PAR radiation sensor. We quantified the patterns of tree regeneration from the matrix (open pasture) outside the forest match, to the interior of the forests and tree-fall gaps. Regeneration (tree seeds and seedlings) was sampled using 20 1-m² plots along 50m transects. We also collected sections taken at the base or 1.3m above ground level (dbh), for all those trees <5cm diameter at breast height (1.3m). Using standard dendrochronological techniques, we assessed the year of occurrence of disturbance events (tree-fall gaps and edge creation), and the tree-ring growth responses.

The diversity of regenerating trees varied among habitats, with a higher number of recruits and greater species richness in tree-fall gaps (pooling gaps centres and edges). These differences were strongly correlated with differential PAR values recorded in each habitat. Shade-tolerant trees regenerated more abundantly in the forest interior, whereas shade-intolerant and early successional

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Box 4.9. Continued

trees recruited in edges and open areas. In contrast, tree-fall gaps have greater light heterogeneity, and hence both types of species recruited in these habitats. Time required to reach 1.3 m height differed among species and habitats. For the shade-tolerant conifer *Podocarpus nubigena* (mañío), growth was lower in edges and open habitats than inside forests (under the canopy and tree-fall gaps). However, one of the main pioneer species, *Drimys winteri* (canelo), did not show differences among habitats in the time required to reach 1.3 m height. These represent two contrasting strategies between late and early successional tree species. Radial increments did not show clear patterns across species. Few species showed marked responses: *Nothofagus nitida* showed notable growth responses to edge creation and *Aextoxicon punctatum* to tree-fall gaps.



Fig. 4.3. Forest edge in Guabun peninsula in Chiloé island, Chile (Gutierrez *et al.*, Box 4.9). The forest edge is dominated by *Drimys winteri* and the forest interior by *Eucryphia cordifolia* and *Aextoxicon punctatum* (photo by J.J. Armesto).

We suggest that persistence of each tree species in forest patches may be determined mainly by its ability to survive the seedling stage rather by differences in radial growth among later stages of development.

Box 4.10. Abundance of the rare arboreal marsupial *Dromiciops gliroides* in riparian forest remnants in southern Chile (C. Smith-Ramírez, J.L. Celis-Diez, J. Jiménez and J.J. Armesto)

Riparian vegetation strips found along rivers crossing the predominantly farmed Chilean central valley, separating the relatively more forested coastal and Andean mountains, are important remnants from extensive forest cover that covered the area two centuries ago. We estimated the abundance of the rare arboreal marsupial *Dromiciops gliroides* (only living member of the order Microbiotheridae) along riparian vegetation strips in an intensely managed agricultural landscape of the Chilean Lake District (UTM: 707.175/5.526.969). Riparian vegetation occurred along a major tributary of the large River Bueno, crossing about 49 km through the central valley. We correlated the abundance of this small marsupial, estimated by live trapping over three nights at each site, with the distance from each sampling point to the nearest large tract of continuous forest, found in the foothills of the Andes. In addition, we correlated *Dromiciops* abundance with the width of the riparian vegetation strip as well as with the presence and number of the hemiparasite *Tristerix corymbosus* in the riparian habitat. The fruits of this plant are an important food resource for this arboreal marsupial. Furthermore, we compared the abundance of *Dromiciops gliroides* in the riparian vegetation strip with its abundance in the nearest continuous forest in the Andean foothills and with its abundance in remnant forest fragments in the rural landscape < 1 km away from the riparian vegetation strip.

During the 2 years of the study, we captured a total of 32 individuals of the rare *Dromiciops gliroides*. Of these, 22 (70%) were found in the riparian vegetation strip. We found a statistically significant correlation between the width of the riparian vegetation strip and the abundance of *Dromiciops* ($R=0.749$, $P=0.033$). No correlation was found between the local abundance of the hemiparasite *Tristerix corymbosus* (Loranthaceae) in riparian or forest patch habitats and the local abundance of *Dromiciops*. The number of individuals trapped in remnant forest fragments of the central valley and in the continuous Andean forest was similar to the number of individuals trapped in the narrow (around 30 m wide on average) riparian forest strip. We suggest that narrow vegetation strips (minimum width 30 m) along rivers in the intensely farmed and deforested central depression of the Chilean Lake District may be key habitats for the survival of species restricted to forest habitats, such as this endangered arboreal marsupial.

References

- Aizen, M.A. (2003) Influences of animal pollination and seed dispersal on winter flowering in temperate mistletoe. *Ecology* 84, 2613–2627.
- Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Aravena, J.C., Carmona, M.R., Pérez, C.A. and Armesto, J.J. (2002) Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Revista Chilena de Historia Natural* 75, 339–360.

- Armesto, J.J., Díaz, I., Papic, C. and Willson, M.F. (2001) Seed rain of fleshy and dry propagules in different habitats in the temperate rainforests of Chiloé Island, Chile. *Austral Ecology* 26, 311–320.
- Benitez-Malvido, J. (1998) Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology* 12, 380–389.
- Bergin, T.M., Best, L.B., Freemark, K.E. and Koehler, K.J. (2000) Effects of landscape structure on nest predation in roadsides of a midwestern agroecosystem: a multiscale analysis. *Landscape Ecology* 15, 131–143.
- Brand, L.A. and George, T.L. (2000) Predation risks for nesting birds in fragmented coast redwood forest. *Journal of Wildlife Management* 64, 42–51.
- Cadenasso, M.L. and Pickett, S.T.A. (2000) Linking forest edge structure to edge function: mediation of herbivore damage. *Journal of Ecology* 88, 31–44.
- Cadenasso, M.L. and Pickett, S.T.A. (2001) Effect of edge structure on the flux of species into forest interiors. *Conservation Biology* 15, 91–97.
- Chacón, P. and Armesto, J.J. (2005) Effect of canopy openness on growth, specific leaf area, and survival of tree seedlings in a temperate rainforest of Chiloé Island, Chile. *New Zealand Journal of Botany* 43, 71–81.
- Chacón, P. and Armesto, J.J. (2006) Do carbon-based defences reduce foliar damage? Habitat-related effects on tree seedling performance in a temperate rainforest of Chiloé Island, Chile. *Oecologia* 146, 555–565.
- Conner, L.M. and Perkins, M.W. (2003) Nest predator use of food plots within a forest matrix: an experiment using artificial nests. *Forest Ecology and Management* 182, 371–380.
- De Santo, T.L., Willson, M.F., Sieving, K.E. and Armesto, J.J. (2002) Nesting biology of tapaculos (family Rhinocryptidae) in fragmented south-temperate rainforests of Chile. *Condor* 104, 482–495.
- del Val, E., Barbosa, O., Armesto, J.J., Christie, D., Gutiérrez, A.G., Jones, C.G., Marquet, P. and Weathers, K.C. (2006) Rain forest islands in the Chilean semiarid region: fog-dependency, ecosystem persistence and tree regeneration. *Ecosystems* 9, 598–608.
- Díaz, I., Papic, C. and Armesto, J.J. (1999) An assessment of postdispersal seed predation in temperate rain forest fragments in Chiloé Island, Chile. *Oikos* 87, 228–238.
- Didham, R.K. and Lawton, J.H. (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31, 17–30.
- Donovan, T.M., Jones, P.W., Annand, E.M. and Thompson, F.R. (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78, 2064–2075.
- Duelli, P., Studer, M., Marchand, I. and Jakob, S. (1990) Population movements of arthropods between natural and cultivated areas. *Biological Conservation* 54, 193–207.
- Fagan, W.F., Cantrell, R.S. and Cosner, C. (1999) How habitat edges change species interactions. *American Naturalist* 153, 165–182.
- Fahrig, L. (2002) Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* 12, 346–353.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34, 487–515.
- Fearnside, P.M. (1996) Amazonian deforestation and global warming: carbon stocks in vegetation replacing Brazil's Amazon forest. *Forest Ecology and Management* 80, 21–34.
- Fenske-Crawford, T.J. and Niemi, G.J. (1997) Predation of artificial ground nests at two types of edges in a forest-dominated landscape. *Condor* 99, 14–24.
- Figueroa, J.A. and Lusk, C.H. (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytologist* 152, 483–489.
- Finke, D.L. and Denno, R.F. (2004) Predator diversity dampens trophic cascades. *Nature* 429, 407–410.

- Fleming, K.K. and Giuliano, W.M. (1998) Effect of border-edge cuts on birds at woodlot edges in southwestern Pennsylvania. *Journal of Wildlife Management* 62, 1430–1437.
- Fox, B.J., Taylor, J.E., Fox, M.D. and Williams, C. (1997) Vegetation changes across edges of rainforest remnants. *Biological Conservation* 82, 1–13.
- Gascon, C., Williamson, G.B. and da Fonseca, G.A.B. (2000) Receding forest edges and vanishing reserves. *Science* 288, 1356–1358.
- Guzmán-Guzmán, J. and Williams-Linera, G. (2006) Edge effect on acorn removal and oak seedling survival in Mexican lower montane forest fragments. *New Forests* 31, 487–495.
- Hansson, L. (2000) Edge structures and edge effects on plants and birds in ancient oak–hazel woodlands. *Landscape and Urban Planning* 46, 203–207.
- Harper, K.A., MacDonald, E., Burton, P.J., Chen, J., Brososke, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. and Esseen, P. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19, 768–782.
- Helm, A., Hanski, L. and Patel, M. (2006) Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters* 9, 72–77.
- Hinsley, S.A., Bellamy, P.E., Enoksson, B., Fry, G., Gabrielsen, L., McCollin, D. and Schotman, A. (1998) Geographical and land-use influences on bird species richness in small woods in agricultural landscapes. *Global Ecology and Biogeography Letters* 7, 125–135.
- Justice, C., Wilkie, D., Zhang, Q., Brunner, J. and Donoghue, C. (2001) Central African forests, carbon and climate change. *Climate Research* 17, 229–246.
- Kapos, V., Wandelli, E., Camargo, J.L. and Ganade, G. (1997) Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In: Laurence, W.F. and Bierregaard, R.O.J. (eds) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, Illinois, pp. 33–43.
- Kollmann, J. and Buschor, M. (2002) Edge effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology* 164, 249–261.
- Laurance, W.F. (1991) Edge effects in tropical forest fragments: applications of a model for the design of nature-reserves. *Biological Conservation* 57, 205–219.
- Laurance, W.F. (1997) Hyper-disturbed parks: edge effects and the ecology of isolated rainforest reserves in tropical Australia. In: Laurence, W.F. and Bierregaard, R.O.J. (eds) *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, Illinois, pp. 71–83.
- Laurance, W.L. and Bierregaard, R.O. (1997) *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, Illinois.
- Laurance, W.F. and Williamson, G.B. (2001) Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology* 15, 1529–1535.
- Laurance, W.F., Ferreira, L.V., Rankin-De Merona, J.M., Laurance, S.G., Hutchings, R.W. and Lovejoy, T.E. (1998) Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12, 460–464.
- Laurance, W.F., Didham, R.K. and Power, M.E. (2001) Ecological boundaries: a search for synthesis. *Trends in Ecology and Evolution* 16, 70–71.
- Lidicker, W.Z.J. (1999) Responses of mammals to habitat edges: an overview. *Landscape Ecology* 14, 333–343.
- Lidicker, W.Z.J. and Peterson, J.A. (1999) Responses of small mammals to habitat edges. In: Barrett, G.W. and Peles, J.D. (eds) *Landscape Ecology of Small Mammals*. Springer, Berlin, Germany, pp. 211–227.
- López-Barrera, F. (2003) Edge effects in a forest mosaic: implications for the oak regeneration in the Highlands of Chiapas, Mexico. PhD thesis. Institute of Atmospheric and Environmental Science, University of Edinburgh, Edinburgh, UK.

- López-Barrera, F. and Newton, A.C. (2005) Edge type effect on acorn germination of oak species in the Highlands of Chiapas, Mexico. *Forest Ecology and Management* 217, 67–79.
- López-Barrera, F., Newton, A.C. and Manson, R. (2005) Edge effects in a tropical montane forest mosaic: experimental tests of post-dispersal acorn removal. *Ecological Research* 20, 31–40.
- López-Barrera, F., Manson, R., González-Espinosa, M. and Newton, A.C. (2006) Effects of the type of montane forest edge on oak seedling establishment along forest-edge-exterior gradients. *Forest Ecology and Management* 225, 234–244.
- López-Barrera, F., Manson, R., Newton, A.C. and González-Espinosa, M. (2007) Effects of varying forest edge permeability on seed dispersal in a neotropical montane forest. *Landscape Ecology* 22, 189–203.
- Malcolm, J.R. (1994) Edge effects in central Amazonian forest fragments. *Ecology* 75, 2438–2445.
- Manson, R.H. (2000) Spatial autocorrelation and the interpretation of patterns of tree seed and seedling predation by rodents in old-fields. *Oikos* 91, 162–174.
- Manson, R.H., Ostfeld, R.S. and Canham, C.D. (1999) Responses of a small mammal community to heterogeneity along forest–old-field edges. *Landscape Ecology* 14, 335–367.
- McCollin, D. (1998) Forest edges and habitat selection in birds: a functional approach. *Ecography* 21, 247–260.
- Muñiz-Castro, M.A., Williams-Linera, G. and Rey-Benayas, J.M. (2006) Distance effect from cloud forest fragments on plant community structure in abandoned pastures in Veracruz, Mexico. *Journal of Tropical Ecology* 22, 431–440.
- Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10, 58–62.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Ramírez-Marcial, N., González-Espinosa, M. and Williams-Linera, G. (2001) Anthropogenic disturbance and tree diversity in montane rain forest in Chiapas, Mexico. *Forest Ecology and Management* 154, 311–326.
- Ries, L., Fletcher, R.J., Batin, J. and Sisk, T.D. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution and Systematics* 35, 491–522.
- Rodriguez, A., Andren, H. and Jansson, G. (2001) Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* 95, 383–396.
- Rozzi, R., Martínez, D.R., Willson, M.F. and Sabag, C. (1996) Avifauna de los bosques templados de Sudamérica. In: Armesto, J.J., Villagrán, C. and Arroyo, M.T.K. (eds) *Ecología de los Bosques Nativos de Chile*. Editorial Universitaria, Santiago, Chile, pp. 135–152.
- Sarlov-Herlin, I. (2001) Approaches to forest edges as dynamics structures and functional concepts. *Landscape Research* 26, 27–43.
- Schrott, G.R., With, K.A. and King, A.T.W. (2005) On the importance of landscape history for assessing extinction risk. *Ecological Applications* 15, 493–506.
- Semazzi, F.H.M. and Yi, S. (2001) A GCM study of climate change induced by deforestation in Africa. *Climate Research* 17, 169–182.
- Sizer, N. and Tanner, E.V.J. (1999) Responses of woody plant seedlings to edge formation in a lowland tropical rainforest, Amazonia. *Biological Conservation* 91, 135–142.
- Smith-Ramírez, C. and Armesto, J.J. (2003) Behaviour of nectar-feeding birds visiting *Embothrium coccineum* (Proteaceae) trees on edges of forest fragments in Chiloé Island, Chile. *Austral Ecology* 28, 53–60.
- Song, S.J. and Hannon, S.J. (1999) Predation in heterogeneous forests: a comparison at natural and anthropogenic edges. *Ecoscience* 6, 521–530.

- Turton, S.M. and Freiburger, H.J. (1997) Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, Northeastern Australia. In: Laurence, W.F. and Bierregaard, R.O.J. (eds) *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities*. University of Chicago Press, Chicago, Illinois, pp. 45–54.
- Wiens, J.A., Crawford, C.S. and Gosz, J.R. (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45, 421–427.
- Williams-Linera, G. (1990a) Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78, 356–373.
- Williams-Linera, G. (1990b) Origin and early development of forest edge vegetation in Panama. *Biotropica* 22, 235–241.
- Willson, M.F., Morrison, J.L., Sieving, K.E., De Santo, T.L., Santisteban, L. and Díaz, I. (2001) Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conservation Biology* 15, 447–456.
- Zhang, H., Henderson-Sellers, A. and McGuffie, K. (2001) The compounding effects of tropical deforestation and greenhouse warming on climate. *Climatic Change* 49, 309–338.