Edge Influence on Forest Structure and Composition in Fragmented Landscapes

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Abstract: *Although forest edges have been studied extensively as an important consequence of fragmentation, a unifying theory of edge influence has yet to be developed. Our objective was to take steps toward the development of such a theory by (1) synthesizing the current knowledge of patterns of forest structure and composition at anthropogenically created forest edges, (2) developing hypotheses about the magnitude and distance of edge influence that consider the ecological processes influencing these patterns, and (3) identifying needs for future research. We compiled data from 44 published studies on edge influence on forest structure and composition in boreal, temperate, and tropical forests. Abiotic and biotic gradients near created forest edges generate a set of primary responses to edge creation. Indirect effects from these primary responses and the original edge gradient perpetuate edge influence, leading to secondary responses. Further changes in vegetation affect the edge environment, resulting in ongoing edge dynamics. We suggest that the magnitude and distance of edge influence are a direct function of the contrast in structure and composition between adjacent communities on either side of the edge. Local factors such as climate, edge characteristics, stand attributes, and biotic factors affect patch contrast. Regional factors define the context within which to assess the ecological significance of edge influence (the degree to which the edge habitat differs from interior forest habitat). Our hypotheses will help predict edge influence on structure and composition in forested ecosystems, an important consideration for conservation. For future research on forest edges in fragmented landscapes, we encourage the testing of our hypotheses, the use of standardized methodology, complete descriptions of study sites, studies on other types of edges, synthesis of edge influence on different components of the ecosystem, and investigations of edges in a landscape context.*

Key Words: created edges, edge effects, forest edge, fragmentation, landscape processes, plant communities, vegetation structure

Influencia del Borde sobre la Composición y Estructura de Bosques en Paisajes Fragmentados

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Resumen: *Aunque los bordes de bosque han sido extensivamente estudiados como una importante consecuencia de la fragmentación, aún no se ha desarrollado una teoría unificadora de la influencia del borde. Nuestros objetivos fueron acercarnos al desarrollo de tal teoría mediante (1) la síntesis del conocimiento actual de los patrones de estructura y composición del bosque en bordes de bosque creados antropogénicamente; (2) el desarrollo de hipótesis relacionadas con la magnitud y distancia de la influencia del borde considerando procesos ecológicos que influyen sobre esos patrones; y (3) la identificación de futuras necesidades de investigación. Recopilamos datos de 44 estudios publicados sobre la influencia del borde sobre la estructura y composición de bosques boreales, templados y tropicales. Los gradientes bióticos y abióticos creados cerca de los bordes de bosque generan una serie de respuestas primarias a la creación del borde. Los efectos indirectos de estas respuestas primarias y el borde original perpetúan la influencia del borde, conduciendo a respuestas secundarias. Los cambios posteriores en la vegetación afectan al ambiente del borde, lo que resulta en una dinámica continua del borde. Sugerimos que la magnitud y la distancia de la influencia del borde son una función directa del contraste en la estructura y composición entre comunidades adyacentes en cualquier lado del borde. Los factores locales, como el clima, las características del borde, los atributos del bosque y los factores bióticos, afectan al contraste de parches. Los factores regionales definen el contexto en el cual evaluar la importancia ecológica de la influencia del borde (el grado en que el hábitat del borde difiere del hábitat del interior del bosque). Nuestras hipótesis ayudarán a predecir la influencia del borde sobre la estructura y composición de ecosistemas boscosos, una consideración de importancia para la conservación. Para futuras investigaciones sobre bordes de bosque en paisajes fragmentados recomendamos: que nuestras hipótesis sean probadas, metodologías estandarizadas, descripciones completas de los sitios de estudio, estudios sobre otros tipos de borde, síntesis de la influencia del borde sobre diferentes componentes del ecosistema e investigaciones sobre bordes en un contexto paisajístico.*

Palabras Clave: borde de bosque, bordes artificiales, comunidades de plantas, efectos de borde, estructura de la vegetación, fragmentación, procesos paisajísticos

Introduction

The influence of the adjacent nonforest environment on forest structure and species composition at created edges is now widely recognized. The altered habitat may be contributing to forest degradation and the loss of biodiversity in fragmented landscapes (Saunders et al. 1991; Gascon et al. 2000; Laurance et al. 2002). Forest edges are becoming more abundant in many regions around the globe because of the loss of forest arising from human activity, including settlement, agriculture, resource extraction, and timber harvesting (Fig. 1). Consequently, a large portion of the landscape may be experiencing edge influence (EI). Depending on the spatial configuration of fragmentation, the area of edge influence might be the dominant component of the landscape matrix (Fig. 1; see Table 1 for terminology).

Edge influence has been a major topic of interest in studies of the landscape patterns and processes associated with edge creation and fragmentation during the last few decades. Research on forest edges began with Leopold's (1933) recognition that edge habitat supported a high abundance and diversity of game species ("edge effect"). This realization fostered management practices aimed at increasing the amount of edge created by logging (Thomas et al. 1979). Negative effects of edge creation have since become apparent, including structural damage (Lovejoy et al. 1986; Laurance et al. 1998*a*) and depressed breeding success of songbirds (Gates & Gysel 1978) at forest edges. More recently, research on changes at forest edges has revealed that EI can lead to the degradation of forest fragments (Gascon et al. 2000; Laurance et al. 2002). These negative consequences have fostered much interest in edges and fragmentation in conservation biology.

Edge influence on forest structure and composition at created edges has been studied in tropical, temperate, and boreal ecosystems (Table 2). Although these studies have provided empirical evidence for understanding patterns of response in the focal ecosystem, a unifying theoretical framework relating to the mechanisms of EI has yet to arise (Murcia 1995). A theory on created forest edges would contribute to our understanding of forest ecosystem function by addressing commonalities of forest response to edge creation and would be more detailed and scale- and system-specific than the framework provided by Cadenasso et al. (2003) on boundaries. A useful step toward such a theory is to synthesize the available literature on empirical studies of EI on plant communities. A synthesis could provide testable hypotheses that, once validated or refuted, may allow for predictions of EI in forest types for which there are no empirical data. The ability to predict the extent and strength of EI is a prerequisite to developing conservation strategies aimed at reducing the negative effects of forest fragmentation (Murcia 1995).

We synthesized the available knowledge on responses of plant communities at created forest edges. We focused on vegetation structure and composition because these

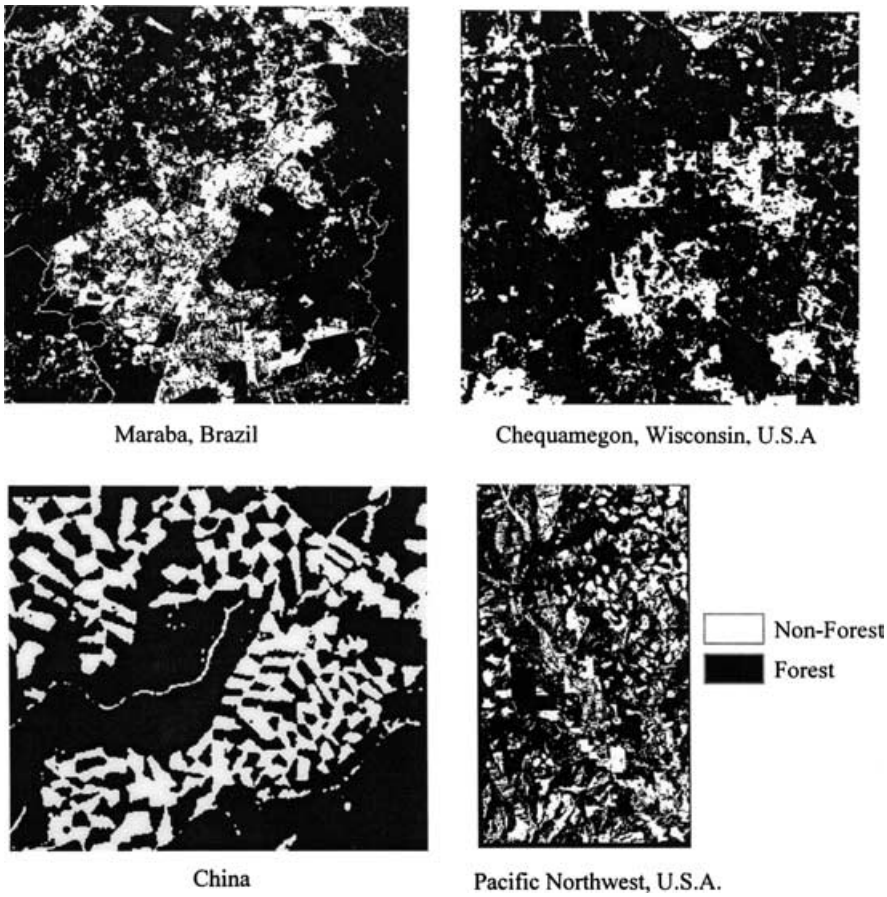

Figure 1. Fragmentation patterns within 20 × 20 km landscapes (11.7 × 34 km for Pacific Northwest). The configuration of edges is largely determined by human-induced disturbances including timber harvesting, agricultural expansion, and urbanization. Different fragmentation patterns can result in varying amounts of edge in the landscape. About 70–81% of these landscapes are still described as forest, but the amount of forested area falling within 60 m of edges is 34, 24, 33, and 56%, respectively. In all these landscapes, the area of edge influence has the potential to be a dominant component of the landscape.

constitute some of the most dominant components of the ecosystem, provide habitat for fauna, and physically manifest the effects of many ecological processes. We concentrated on impacts of the nonforest community on the adjacent forest (and not the converse) because this type of EI is of primary importance for conservation. Likewise, we considered only anthropogenically created edges because these are the most commonly studied type of edge in fragmented landscapes worldwide. We take into account created edges at all stages of development, however. Our specific objectives were (1) to synthesize the current understanding of ecological patterns and processes as reflected in forest structure and composition at anthropogenically created edges between forested and nonforested ecosystems, (2) to develop hypotheses, based on evidence from the literature, that predict the nature and extent of EI on plant communities at created edges in forested ecosystems, and (3) to identify research needs and scientific challenges for future research.

Connecting Pattern to Process

Many factors control the magnitude and distance of EI (Table 1) in a particular ecosystem; thus, vegetation responses to edge creation are necessarily site specific. Although it is difficult to find generalities among studies with different methodologies (Murcia 1995), a synthesis of the literature on the magnitude and distance of EI reveals some general trends in forest structure and composition at created edges. We compiled data from 44 published studies on edge influence on forest structure and composition in boreal, temperate, and tropical forests (Appendix 1). Studies were found in previous data compilations (Baker & Dillon 2000) and from a literature review of ecology journals. We developed hypotheses from our literature synthesis based on the assumption that responses to EI are monotonic and linear. Although more complex responses have been found (e.g., Murcia 1995; Euskirchen et al. 2001; Harper & Macdonald 2002), we use this simplistic approach as a starting point to provide generalizations about edges. Under this assumption, the magnitude and distance of EI can be envisioned as quantifying a gradient that could range from steep and short (large magnitude, small distance) to shallow and long (small magnitude, large distance; Fig. 2). Magnitude and distance of EI are, therefore, functionally independent and do not necessarily respond to edge creation and subsequent dynamics in a similar manner. We sought to connect these general patterns of EI to the underlying mechanisms by examining the processes driving EI at the stand level and the importance of local and regional context.

Table 1. Proposed standard terms and definitions for common concepts used in research on forest edges, following consideration of past definitions and common usage in the literature, ecological relevance, and usefulness of terms.

Term	*Definition*	*Comments*
Edge	interface between different ecosystem types	
Created edge	an edge formed as a result of a natural or anthropogenic disturbance, also called an induced edge	Steep gradients in topography, soil type, microclimate and/or geomorphology can result in inherent edges (Thomas et al. 1979). We considered only anthropogenically created edges, whether maintained artificially or left to regenerate. Edges can also be created, however, by fire, wind, insect outbreaks, or other natural phenomena.
Forest edge	interface between forested and nonforested ecosystems or between two forests of contrasting composition or structure	In practice, a forest edge can be defined as the limit of the continuous canopy or the boundary in canopy composition.
Forest interior	forest that shows no detectable edge influence	Interior conditions are typically characterized using samples located in large blocks of unfragmented forest or in the center of the largest patches available for study.
Edge influence (EI)	the effect of processes (both abiotic and biotic) at the edge that result in a detectable difference in composition, structure, or function near the edge, as compared with the ecosystem on either side of the edge	Both edge influence (Chen et al. 1992; Harper & Macdonald 2002) and edge effects (Harris 1984; Murcia 1995) have been used extensively and interchangeably in the literature. We use the term *edge influence* because *edge effect* is sometimes used to refer specifically to the phenomenon of increased diversity at edges (e.g., Leopold 1933).
Magnitude of edge influence	a measure of the extent to which a given parameter differs at the edge, as compared with the reference "nonedge" ecosystem	Both significance of EI (Chen et al. 1995) and magnitude of EI (Burton 2002) have been defined this way. To avoid confusion, we propose using the magnitude and significance of EI to distinguish between the magnitude of an ecological effect and its statistical significance, respectively. We recommend calculating the magnitude of EI as $(e-i)/(e+i)$, where e = value of the parameter at the edge, i = value of the parameter in the interior (nonedge) forest; the magnitude of EI thus varies between -1 and $+1$ and is equal to 0 when there is no EI. If $e+i = 0$, a transformation of the data should be used so that the magnitude of EI would not be undefined. The magnitude of EI has also been computed as the ratio between the edge and interior values (e.g., Burton 2002).
Distance of edge influence	the set of distances from the edge into the adjacent community over which there is a statistically significant EI; also known as depth of EI (Chen et al. 1992; Euskirchen et al. 2001)	The distance of EI may be considered to represent a zone of EI that extends to both sides of the edge, in which structure or composition is different from either of the adjacent communities. This zone may actually begin some distance into the forest or in the adjacent nonforested area (e.g., Harper & Macdonald 2002).
Area of edge influence	the total area of a given patch or landscape subject to significant EI; an extension of the distance of EI in two dimensions	Because the distance of EI varies with edge orientation, edge contrast, surrounding topography, and other factors, the area of EI typically appears as a belt of variable width surrounding all edges in the landscape.
Core area	the total patch or landscape area that consists of interior forest outside the zone of significant EI (i.e., total forested area – edge area)	
Patch contrast	the difference in composition, structure, function, or microclimate between adjoining ecosystems on both sides of the edge	

Table 2. Number of studies reporting edge influence in which the response variable is higher (H) or lower (L) at the edge compared with the interior forest (each study reported only once per category of response variable and per edge type).

	Young tropical[a]		*Maintained tropical*[b]		*Maintained Australian*[c]		*Regen. east N. Amer.*[d]		*Maintained east N. Amer.*[e]		*Regen. west N. Amer.*[f]		*Regen. boreal*[g]		*Maintained European*[h]		*All studies*	
Response	*H*	*L*	*H*	*L*	*H*	*L*	*H*	*L*	*H*	*L*	*H*	*L*	*H*	*L*	*H*	*L*	*H*	*L*
Primary																		
Processes																		
Tree mortality or damage	2										1		3	1			6	1
Forest structure																		
Canopy tree abundance	1	1		3	1				5	1		1		3			7	9
Canopy cover	1	4		1	1	2				2	1	3		2			3	14
Snags and logs	1		2		1	1					3			2			7	3
Secondary																		
Processes																		
Recruitment	3		1	2		1			1				2	1			7	4
Growth rate	2										1		2	1			5	1
Canopy foliage (growth)		1	1														1	1
Understory foliage (growth)	1								1								2	
Seedling mortality	2												1				3	
Changes in understory structure																		
Understory (or total) tree density	2		2	1		1			6	1			1				11	3
Herb cover									1				1	1			2	1
Shrub abundance							1	1	1				1	1	1		4	2
Changes in species composition																		
Species composition[i]							1		4		1					6		
Exotic species abundance									5								5	
Individual species abundance	2				2		1	1	3	3	1	2	1	2	1	1	11	9
Species richness or diversity					1		1		4				1	1			7	1

[a] *South and Central American tropical edges generally <7 years old (Williams-Linera 1990a, 1990b; Kapos et al. 1993; Malcolm 1994; Kapos et al. 1997; Laurance et al. 1998a, 1998b; Williams-Linera et al. 1998; Mesquita et al. 1999; Sizer & Tanner 1999).*

[b] *South and Central American tropical edges generally 7–12 years (but up to 25 years) at which the disturbed forest was maintained in a nonforested state (Williams-Linera 1990b; Viana et al. 1997; Benitez-Malvido 1998; Williams-Linera et al. 1998; Didham & Lawton 1999; Oosterhoorn & Kappelle 2000).*

[c] *Edges of tropical forests in Australia and temperate forests in New Zealand at which the disturbed forest was maintained in a nonforested state. Ages were not always reported but were often around 100 years (Laurance 1991, 1997; Young & Mitchell 1994; Turton & Freiburger 1997; Lloyd et al. 2000).*

[d] *Regenerating (regen.) eastern North America: young (1–5 years) and regenerating (<115 years) edges in temperate forests in northeastern United States (Matlack 1993; Euskirchen et al. 2001).*

[e] *North America: edges in temperate forests in northeastern United States at which the disturbed forest was maintained in a nonforested state. Ages were not always reported but were often >40 years (Ranney et al. 1981; Whitney & Runkle 1981; Miller & Lin 1985; Palik & Murphy 1990; Brothers & Springarn 1992; Brothers 1993; Matlack 1993; Fraver 1994; Luken & Goessling 1995; Burke & Nol 1998; Gelhausen et al. 2000; Cadenasso & Pickett 2001; MacQuarrie & Lacroix 2003).*

[f] *Regenerating (regen.) western North America: regenerating edges <27 years in old-growth Douglas-fir forests in northwestern United States (Gratowski 1956; Chen et al. 1992; Jules et al. 1999; Toms & Lesperance 2003).*

[g] *Regenerating (regen.) boreal: regenerating edges <25 years in boreal and sub-boreal forests in Canada and Sweden (Esseen & Renhorn 1998; Burton 2002; Cienciala et al. 2002; Harper & Macdonald 2002; Rheault et al. 2003).*

[h] *Edges in forests in continental Europe at which the disturbed forest was maintained in a nonforested state. Ages >200 years (Honnay et al. 2002; Kollman & Buschor 2002).*

[i] *Edge influence means species composition is different than in the interior.*

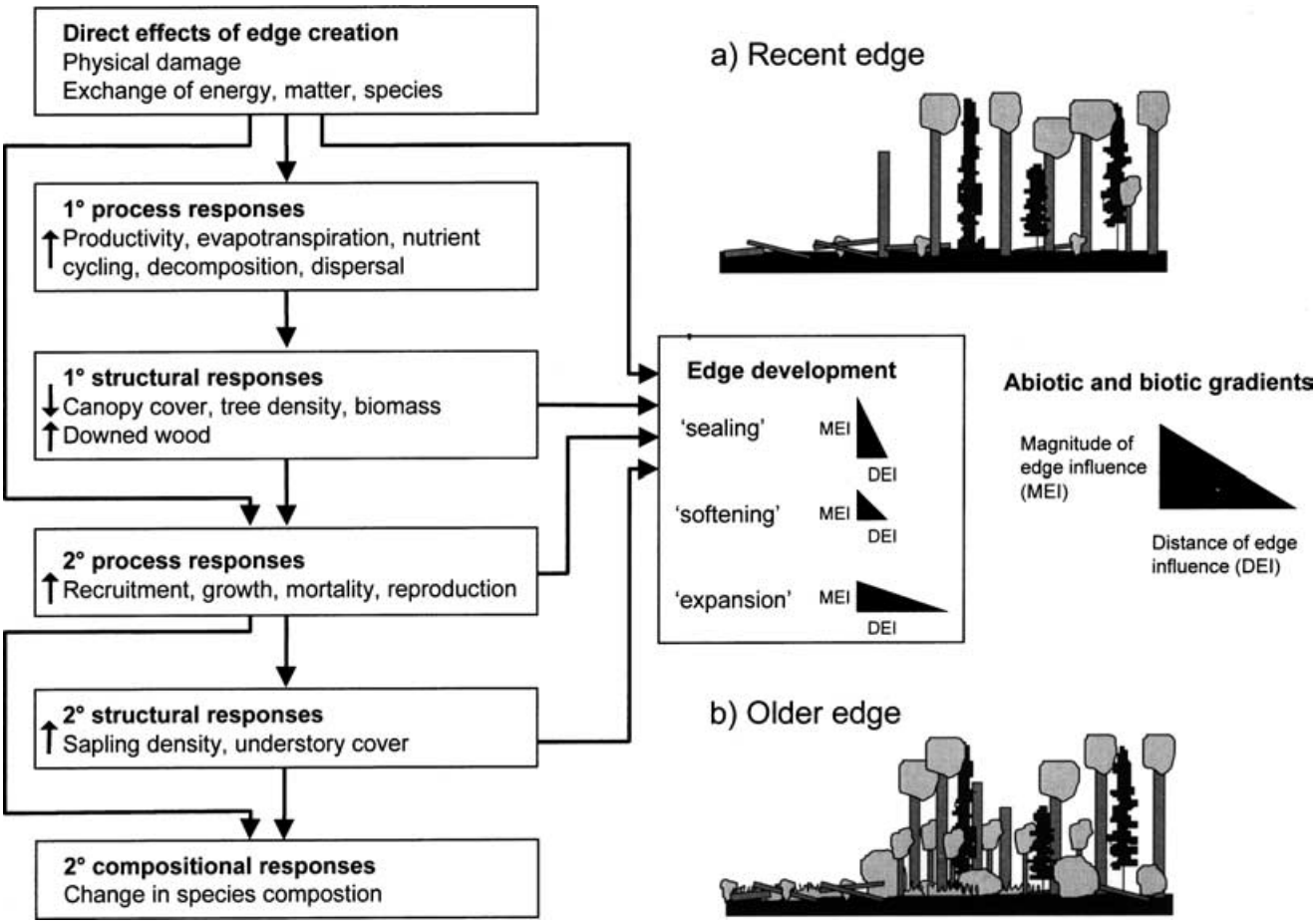

Figure 2. Conceptualized diagram of processes and responses following edge creation including (a) a recently created edge and (b) an older edge. Upward and downward arrows within the boxes denote increases and decreases, respectively. Abiotic and biotic gradients (triangles with the height representing the magnitude of edge influence [MEI] and length representing the distance of edge influence [DEI]) are strong at the newly created edge (a) and become steeper, weaker, or longer at older edges with edge sealing, softening, or expansion (b). Edge sealing is the development of dense vegetation at maintained edges, edge softening is the reduction of edge influence at regenerating edges, and edge expansion is the increase in the extent of edge influence over time.

Ecological Processes near Edges

All edges share at least two commonalities: exchange or flow of energy, material, and/or organisms across the boundary (Cadenasso et al. 2003), and alterations in biophysical processes and ecosystem composition and structure. Direct effects of edge creation include (1) physical disturbance of vegetation and soil, (2) abiotic environmental gradient changes in attributes such as light, wind, and moisture, and (3) increased access for organisms, material (pollen, seeds, pollutants) and energy (Fig. 2). All edges are characterized by distinct abiotic and biotic gradients associated with these direct effects (Fig. 2). Flows across edges driven by these gradients have been likened to movement across a semipermeable membrane (Wiens 1992).

Responses to edge creation can be termed primary or secondary (Fig. 2). Primary responses are those resulting immediately and directly from the effects of edge creation. In forests, primary process responses include damage to trees and other vegetation; disruption of the forest floor and soil; increased dispersal of pollen and seeds; and changes in evapotranspiration, nutrient cycling, and decomposition. These ecological processes are the mechanisms responsible for primary structural responses such as changes in forest structure (including canopy cover, tree density, downed wood, leaf area, and vegetative biomass).

Subsequently, secondary responses (or indirect effects of edge creation) arise because these primary responses confound the original abiotic and biotic gradients. Secondary process responses to edge creation (e.g.,

regeneration, growth, reproduction, mortality) reflect both the edge-related gradients and primary responses to it. These changes lead to secondary responses in forest structure (e.g., sapling density, understory cover, shrub height) and species composition (as species differences in responses are manifest). Over time, secondary responses to edge creation will further influence the forest environment and associated ecological processes, feeding back into ongoing processes of edge development (cf "higher order effects," Baker & Dillon 2000).

It is evident from the literature that tree damage—a common response to edge creation—leads to reduced canopy cover and greater abundance of snags and logs at edges (Table 2). We found that the primary process response of tree mortality has greater magnitude and distance of EI than primary structure responses (Fig. 3). The apparent disconnect between EI for these process and structure responses may result from compensatory increases in leaf area of individual trees or increased turnover of downed wood near edges. Edge influence on the abundance of downed wood extends farther into the interior forest than EI on canopy cover, likely because the former is related to the physical footprint of fallen trees (Fig. 3).

Following primary edge responses, the accentuation of abiotic gradients near edges is the probable mechanism for secondary process responses of regeneration, growth, and mortality (Table 2). These secondary process responses tend to have distance and magnitude of EI similar to, or greater than, primary responses (Fig. 3). The greater distance of EI for secondary (versus primary) responses likely occurs because primary structural responses initiate secondary responses that occur farther from the edge. Because secondary responses arise as a result of primary responses, they may start later and last longer. Recruitment, a secondary process influenced by increased light following canopy opening at the edge, has been measured as seedling abundance or a change in tree abundance (Table 2). The primary process response of seed dispersal, however, has not been extensively studied along the edge-to-interior gradient (but see Cadenasso & Pickett 2001).

Secondary process responses, in turn, result in EI on understory structure and species composition, including increased diversity and abundance of saplings, herbs, and shrubs, and changes in species composition at the edge (versus interior forest; Table 2). The magnitude and distance of EI are relatively low for secondary responses in understory structure (Fig. 3), reflecting the combined

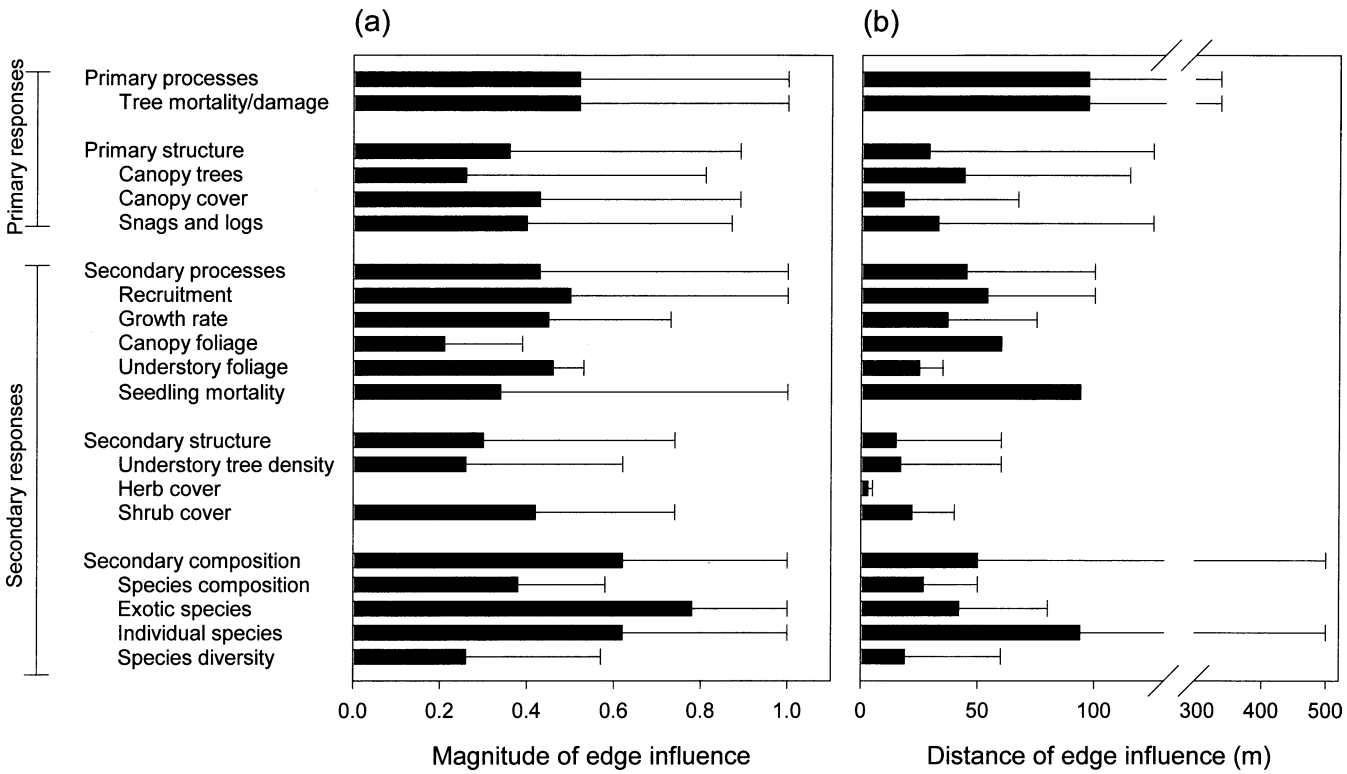

Figure 3. (a) Magnitude and (b) distance of edge influence (EI) for different categories of response variables. Means (bars) of the mean absolute value per study were calculated for each category of response variables. Maximum absolute values (lines) are for individual values (i.e., not averaged by study). The magnitude of EI was calculated from mean values at the edge and interior reported in the articles (see Table 1 for equation).

effect of greater growth and recruitment of some species but reduced growth or increased mortality of others. In contrast, subtle species differences in EI on recruitment, growth, and mortality likely underlie the greater distance of EI observed for species composition than for structure (Fig. 3). Further, the magnitude of EI is substantially higher for secondary responses in species composition than for any other edge responses (Fig. 3). These compositional changes typically involve increased abundance of exotics and shade-intolerant species and lower abundance of shade-tolerant species.

Although abiotic and biotic gradients change over time and process responses may diminish, we expect that the arising structure and composition responses will persist. Edge influence caused by microclimate can decline over time because of changes in species composition or acclimation (Laurance et al. 2002). At some edges, the distance of EI may increase over time even as the magnitude of EI declines ("edge expansion," Fig. 2; Ranney et al. 1981; Gascon et al. 2000; Harper & Macdonald 2002), as a result of factors such as exogenous disturbance (e.g., fire, Cochrane & Laurance 2002) or persistent wind effects (Laurance et al. 2002).

At "maintained" edges, where the nonforested community is maintained as such, secondary responses often result in the development of a "sidewall" of dense vegetation or side canopy as canopy trees, regenerating trees, and shrubs grow to fill in open spaces at the edge (Didham & Lawton 1999; Laurance et al. 2002). This may reduce the depth of penetration of energy and matter into the forest, shortening the length of the gradient (distance) while the magnitude of edge influence remains strong ("edge sealing," Strayer et al. 2003; Fig. 2). Maintained tropical edges had lower average distance of EI than young tropical edges (Fig. 4), but also lower magnitude of EI, possibly reflecting the high patch contrast (Table 1) of newly created edges in this forest type. The edge zone at maintained edges may become a highly competitive, deeply shaded habitat with increased abundance of canopy trees and reduced recruitment and growth of the understory (Table 2).

Patch contrast is reduced over time at "regenerating" edges when the adjacent community redevelops to forest. If regeneration is rapid, both the distance and magnitude of EI may be reduced ("edge softening," Fig. 2) and would be lower than at maintained edges. The magnitude of EI is slightly higher for maintained (versus regenerating) edges in eastern North America (Fig. 4). In summary, older, maintained edges could be sharp and narrow (large magnitude, small distance), whereas older, regenerating edges could be soft and narrow (small magnitude, small distance), and either could also be soft and wide (small magnitude, large distance).

The Context of Edge Influence

Energy exchange between two adjacent ecosystems is a major driver of EI. Direct effects of edge creation are a reflection of the steepness of the resulting gradients, which is in turn a function of patch contrast. Flows of energy across an edge increase with greater patch contrast (Laurance et al. 2001) and regulate magnitude and distance of EI. This premise is inherent in the proposal by Harris (1984) that EI can be minimized by reducing the contrast in age or structure of adjacent forest stands. The ecological importance of responses to edge creation is mediated by the nature of the ecosystem. In particular, inherent heterogeneity of the interior forest affects the ecological importance and distance of EI (Harper & Macdonald 2002). The context of EI thus includes patch-level factors close to the edge that affect both the magnitude and distance of EI, and regional-level factors that affect the ecological importance and distance of EI.

With information from our literature search (Table 2, Fig. 4, Appendix 1), we were able to compare EI on plant

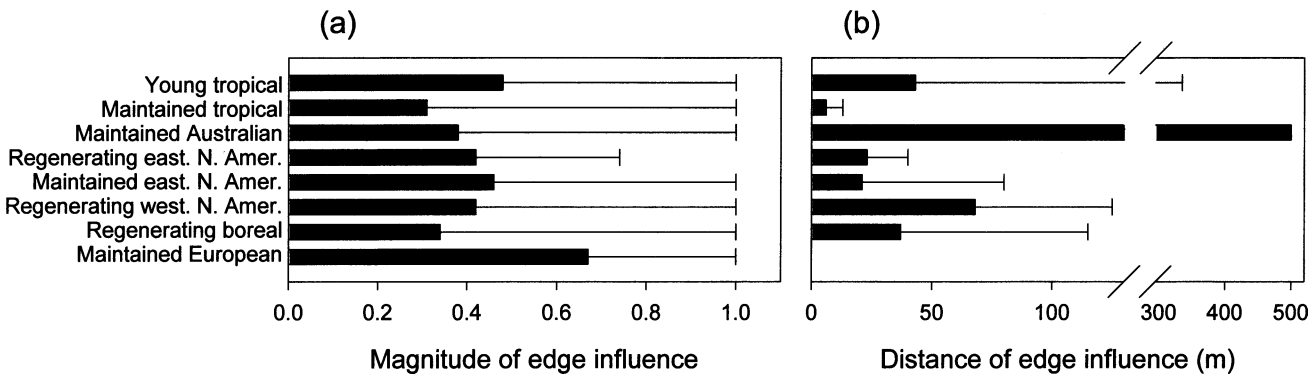

Figure 4. (a) Magnitude and (b) distance of edge influence (EI) for different categories of region and edge type (Table 2). Means (bars) of the mean absolute value per study were calculated for each category. Maximum absolute values (lines) are for individual values (i.e., not averaged by study). The magnitude of EI was calculated from mean values at the edge and interior reported in the articles (see Table 1 for equation).

communities in different forested biomes to develop hypotheses about the context of EI. Unfortunately we were somewhat limited by a paucity of data for some regions (e.g., Asia, Africa) and edge types (fewer studies on regenerating edges) and by variability in measured response variables and methodologies. For example, at regenerating and maintained edges in eastern North America, most research has focused on understory responses, whereas investigations at young tropical edges have emphasized processes and primary responses.

Factors Affecting Patch Contrast

Climatic factors, location, edge characteristics, stand attributes, and biotic factors can determine the contrast between forested and nonforested areas and thus affect EI for vegetation. Compared with colder boreal and subboreal regions, young and regenerating edges in tropical regions and in western North America had greater magnitude (Fig. 4a) and distance (Baker & Dillon 2000) of EI. Conditions in open areas are more "severe" (i.e., more different than interior forest understory conditions) where solar energy is higher and air temperatures are more extreme. The unexpectedly high magnitude of EI at maintained edges in continental Europe, which has a temperate climate (Fig. 4a), may result from the long time period since edge creation (>200 years) for the available studies.

A cloudy and/or rainy climate has the potential to reduce the contrast in ground-level energy balance between open and forest interior understory environments. Regenerating forest edges in western temperate North America, which is well known for high precipitation and cloud cover, have much greater magnitude and distance of EI than similar edges in eastern North America (Fig. 4). We expected, however, to see the opposite trend of lower magnitude and distance of EI in regions with high cloud cover than in regions at similar latitudes with less cloud cover. Although cloud cover may affect EI on some response variables, there appears to be greater impact from increased precipitation, productivity, and canopy height, such that patch contrast may be greater in western North America.

We expect that higher average wind speed, more frequent extreme winds, and shallow soils will be associated with more tree damage and blowdown near edges and farther into the forest, resulting in greater magnitude and distance of EI. Unfortunately, because of the lack of published information on wind speed and soil depth in studies, we were unable to make comparisons from the literature.

Geographical location and aspect of edges can also affect the degree of patch contrast. Edge orientation relative to prevailing winds will affect the magnitude and distance of EI for tree damage and windthrow (Burton 2002). Greater distance and magnitude of EI for microclimate and vegetation occur at south- or southwest-facing edges (versus north) in the northern hemisphere (Palik & Murphy 1990; Chen et al. 1995; Burton 2002). In terms of geographic location, we found lower magnitude of EI at regenerating boreal and sub-boreal edges compared with young and regenerating temperate and tropical edges. But the trend for distance of EI was not as clear (Fig. 4). For edges facing the equator, distance of EI might be expected to increase toward the poles, where a greater solar angle results in deeper penetration of solar radiation into the forest. Alternatively, a longer optical path and greater solar attenuation in the atmosphere may reduce contrast with interior forest conditions, resulting in reduced magnitude and distance of EI at high-latitude edges.

Edge structure is a crucial factor that determines EI. It is affected by time since edge creation and by whether the edge is maintained or regenerating. Forests with open edges often have greater distance of EI than forests with closed or sealed edges (Didham & Lawton 1999). We hypothesize that both the magnitude and distance of EI will persist longer when high patch contrast is maintained over time. Edge influence is expected to be relatively short lived at regenerating edges because patch contrast declines with forest redevelopment. The type and speed of canopy closure at regenerating edges, or the sealing process at maintained edges, is context specific and depends on climate and vegetation.

Patch contrast is also affected by the structural features of the forest stand, notably canopy height, canopy cover, and susceptibility to windthrow. In the absence of quantitative data, the distance of EI has often been estimated as two to three canopy heights into the forest (Harris 1984). Unfortunately, few published studies report both canopy height and the distance of EI. Canopy structure affects patch contrast by controlling gradients of wind and light into the forest. Greater canopy cover and height increase patch contrast and therefore the magnitude and distance of EI. Forest structure will determine tree susceptibility to wind damage and blowdown once neighboring trees are removed. In tropical rainforests, where lianas often interconnect adjacent trees, tree damage extends much farther from the edge (Laurance et al. 1998*a*) than in mixed-wood boreal forests (Harper & Macdonald 2002), even after accounting for differences in canopy height.

There is also a biotic component to the context of EI. Forests hosting many pioneer species, which are already adapted to the range of microclimatic conditions found at newly created edges, may exhibit lower magnitude or distance of EI than forests dominated by late-successional species. This is particularly evident in ecosystems that are subject to frequent natural disturbance, where component species may exhibit strong persistence, and in broad niches (such as in the boreal forest with frequent wildfires [Johnson 1992]), where the magnitude of EI is lower compared to that of other forests (Fig. 4). As such, edge creation may have relatively little impact on the

composition of the forest community (Harper & Macdonald 2002). Thus there would be greater magnitude and distance of EI on species composition (i.e., a more distinctive edge vegetation) at edges in forest landscapes characterized by infrequent stand-replacing disturbances.

Factors Affecting the Regional Importance of Edge Influence

Regional factors can affect the ecological importance of EI by defining the ecological context within which to assess the significance of EI. If edge habitat is not significantly different from what may be encountered within the regional landscape, the ecological importance of EI may be minimal, even though there may still be a high magnitude of EI. Because the relationship between the distance of EI and regional factors depends on the method of calculation, we assume that the distance of EI is quantified as the set of distances from the edge that are significantly different from the range of variation within interior forest (e.g., Laurance et al. 1998*a*; Harper & Macdonald 2002). Thus, in landscapes with a high degree of inherent heterogeneity, the distance of EI is low and EI may also be less ecologically important.

Heterogeneity in topography, soils, or parent materials and the presence of many bodies of water or pronounced cliffs or ridges all promote the development of internal plant community boundaries or inherent gaps within forest stands (Lertzman et al. 1996). We hypothesize that this internal variability will result in a smaller distance of EI such that the influence of imposed edges may be more difficult to detect in heterogeneous landscapes.

Edge influence will also be less pronounced in forests with a more open and diverse canopy; thus, EI is difficult to detect (statistically) and probably less important ecologically. We further hypothesize that EI changes with stand age. Edge influence for structural responses is likely to increase as the stand matures and trees become larger, and are weakened by rot and therefore more susceptible to wind damage. But because forests experience canopy breakup and develop horizontal and vertical patchiness as they age (Spies & Franklin 1988), older forests that have progressed through a canopy breakup phase may show lower EI than younger forests. Nevertheless, some secondary responses, particularly by species adapted to old-growth conditions, may have greater distance of EI in older forests.

We suggest that landscapes naturally characterized by a patchy composition (e.g., of coniferous and deciduous species or of tree-, shrub- and grass-dominated cover) may also have more edge-adapted species, making significant EI on composition less likely. Compared with forested landscapes with no invasive species, however, landscapes with many exotics in the regional species pool (e.g., landscapes fragmented by human activity) will likely have greater EI on species composition because of the presence of exotic species at edges. Many invasive species are adapted to disturbed soils and/or high light and hence can be effectively excluded from forest interiors while proliferating in adjacent open areas and at edges.

Conclusions

The direct effects of edge creation and the resulting abiotic and biotic gradients lead to primary responses of biophysical processes, which in turn lead to primary structural responses. The indirect effects of edge creation result from the confounding effect of primary responses on the original edge gradient, leading to a perpetuation of EI in terms of both distance and magnitude. Subsequent secondary responses in plant population dynamics and ecosystem processes arise from these indirect effects and then lead to secondary structural and compositional responses. Ultimately, changes in understory structure and species composition will influence the edge environment and combine with the influence of the original edge gradient and primary responses to it, feeding back into an ongoing process of edge development that could include edge sealing, softening, or expansion.

Because patch contrast determines energy exchanges across an edge, it has a prevailing influence on the strength of the direct effects of edge creation. Factors such as climate, edge characteristics, stand attributes, and biotic factors affect patch contrast and therefore largely determine the magnitude of EI. Regional factors affect the ecological importance of EI by defining the context within which the distance of EI can be measured. The distance of EI is expected to be a function of the magnitude of EI, solar angle, and inherent heterogeneity of the forest community. Ecologically, edge influence should be less important in forests that are more structurally heterogeneous. The statistical significance of EI on forest structure and composition depends on the degree to which the edge habitat or edge community can be distinguished from interior forest habitat in a given landscape. To summarize the factors that affect patch contrast or the regional importance of edge influence, the following are the situations in which edge influence is hypothesized to be relatively more pronounced and more ecologically important, all other conditions being equal: (1) high mean annual (or growing season) air temperature, (2) low latitudes with high solar radiation, (3) low mean annual (or growing season) cloud cover, (4) frequent, extreme windy conditions, (5) edges facing the equator or into prevailing winds, (6) shallow soil depth, (7) abrupt, open edges, (8) edges where patch contrast is maintained over time, (9) forests with tall, dense canopies, (10) closed-canopy (generally mid-successional or mature) stands, (11) regional flora or fauna with many pioneer species, (12) regional flora or fauna with many exotic and invasive

species, (13) biomes or forest types subject to infrequent stand-replacing disturbances, or (14) forest communities or landscapes with low inherent heterogeneity in vegetation, topography, or soils.

We have synthesized the current understanding of ecological patterns of and processes influencing forest structure and composition at created edges between forested and nonforested ecosystems. We developed the following testable hypotheses that apply to forest structure and composition at created edges at the time of edge creation, unless otherwise stated: (1) the distance of EI will be greater for secondary responses than for primary responses, (2) secondary responses will start later and last longer than primary responses, (3) for both primary and secondary responses, those involving structure and composition will last longer than process responses, (4) the magnitude and distance of EI will persist longer at edges that are maintained compared with edges that are regenerating, (5) the magnitude and/or distance of EI will be greater at edges with greater patch contrast, (6) the magnitude of EI will be a function of local context, whereas the distance of EI will reflect both local and regional factors, and (7) the distance of EI will be greater, and EI will be more ecologically important, in more homogeneous forests and landscapes.

Future Directions and Challenges

Our hypotheses reflect the state of knowledge and the current paradigm regarding EI. We presented the results of our synthesis in hypothesis form to encourage independent testing of the hypotheses in a scientifically rigorous way across different geographic locations. There are major obstacles to overcome, however, before any meta-analyses of edge research can be conducted, including inconsistent methodology (Murcia 1995) and incomplete descriptions of study sites. To ensure generalizations among future studies, we strongly recommend using a standardized methodology that assesses the significance of EI against background heterogeneity in interior forest, and reporting both the magnitude and distance of EI. Standardized methods are also needed to define and report patch contrast. At a minimum, studies should include a complete study site description with information on location (latitude, longitude, elevation, aspect), regional climate (temperature, precipitation, cloudiness, wind), forest stand characteristics (canopy height, canopy cover, tree species composition), and attributes of the disturbed area next to created edges (size and shape, time since disturbance, regeneration height). Future research could consider developing an index of patch contrast based on differences in species composition, life form, age, height, and density.

Scientific experimentation, particularly involving creation of forest edges with different contrasts and/or long-term permanent plot sampling, would be particularly useful (Laurance et al. 2001). Although most researchers have attempted to control for contrast (e.g., by performing studies across similar edge sites), important insights could be obtained by varying patch contrast in edge investigations and by defining specific factors that contribute to contrast. Researchers could also experimentally test hypotheses that differentiate mechanisms for EI. Long-term examination of edges might also offer insight into the development of nonmonotonic responses.

Our synthesis of forest structure and composition at created edges is intended as a focal point for the development of a comprehensive theory of EI that relates to all components of the ecosystem at all types of terrestrial edges. To achieve this broader goal, however, additional research is needed on EI at natural or inherent edges and at types of created edges that have not been as well studied. Investigations of different edge types have already begun, and the number of studies has increased in recent years. Our hypotheses can be tested for plant responses in a diversity of ecosystems and edge types. Additional data need to be collected for belowground processes and communities. Vegetation structure and composition can also be affected by EI on plant and animal interactions. Edge effects resulting from these secondary influences, which include herbivory of seedlings, insect outbreaks, browsing, and seed predation, might be considered tertiary effects. Wildlife biologists could explore these relationships and develop additional hypotheses for ecological processes pertaining to mobile organisms, such as behavioral responses including predation and parasitism (Fagan et al. 1999).

As forest fragmentation becomes increasingly prevalent, an understanding of landscape-scale processes will be essential for modeling efforts that attempt to characterize ecological properties across the landscape. The structure of many landscapes is complex, and a majority of land area may be influenced by two or more edges, each with a different age, history, and adjacent land cover. Only a few studies, however, have focused on the interaction of EIs within fragmented areas (e.g., Malcolm 1994). Additive effects from two or more edges may influence the core area (Table 1) in fragmented landscapes and therefore be particularly important for conservation.

Our hypotheses are intended as a first step toward constructing a theory of edge influence. The usefulness of any theory depends on how well its related hypotheses can withstand rigorous scientific testing. We encourage such efforts in the hope that this body of knowledge will advance quickly and contribute to our broader understanding of ecological pattern and process relationships. Our hypotheses should help predict and guide experimental design for examining EI on forest structure and composition in forested ecosystems, an important consideration in the effort toward efficient conservation strategies in fragmented landscapes.

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Appendix 1. To synthesize the literature on edge influence (EI) on forest structure and composition at anthropogenically created edges, we compiled the following database from published refereed studies.[a]

Edge category[b]	*Response*[c]	*Mean MEI*[d]	*Mean absolute MEI*[e]	*MEI range*[f]	*Mean DEI*[g] *(m)*	*DEI range*[h] *(m)*	*Study*
Tree mortality or damage							
1	H	0.51	0.51	0.49 to 0.52	210	85 to 335	Laurance et al. 1998*a*
1	H	0.47	0.47	0.31 to 0.60	NA		Mesquita et al. 1999
6	H	0.32	0.32		NA		Gratowski 1956
7	H	0.36	0.36	0.12 to 0.56	58	54 to 62	Burton 2002
7	H	0.85	0.85		NA		Esseen & Renhorn 1998
7	H & L	0.11	0.61	−1.00 to 0.74	22	0 to 60	Harper & Macdonald 2002
Canopy tree abundance							
1	H & L	0.06	0.06	−0.01 to 0.12	NA		Williams-Linera 1990*b*
2	H & L	−0.16	0.56	−0.79 to 0.81	NA		Oosterhoorn & Kappelle 2000
2	L	−0.39	0.39	−0.60 to −0.27	NA		Viana et al. 1997
2	H & L	0	0.09	−0.23 to 0.08	NA		Williams-Linera 1990*b*
3	H	0.1	0.1		NA		Young & Mitchell 1994
5	H	0.42	0.42	0.37 to 0.47	NA		Brothers 1993
5	H	0.6	0.6	0.47 to 0.68	9	5 to 15	Palik & Murphy 1990
5	H	0.17	0.17		NA		Ranney et al. 1981
5	L	−0.2	0.2		10		Burke & Nol 1998
6	L	−0.09	0.09	−0.12 to −0.06	85		Chen et al. 1992
7	L	−0.2	0.2	−0.33 to −0.11	113	111 to 115	Burton 2002
7	L	−0.42	0.42	−0.55 to −0.30	2.5	0 to 5	Harper & Macdonald 2002
7	L	−0.06	0.06	−0.08 to −0.05	NA		Rheault et al. 2003
Canopy cover[i]							
1	L	−0.79	0.79		NA		Kapos et al. 1993
1	L	−0.76	0.76		NA		Kapos et al. 1997
1	L	−0.89	0.89		NA		Williams-Linera 1990*a*
1	L	0.83	0.83	0.80 to 0.86	7.5	5 to 10	Williams-Linera 1990*b*
1	H	0.14	0.14		NA		Williams-Linera et al. 1998
2	L	−0.7	0.7	−0.60 to −0.78	5.4	5 to 6	Williams-Linera 1990*b*
2	L	0.25	0.25		0		Williams-Linera et al. 1998
3	L	−0.52	0.52		NA		Laurance 1991
3	L	−0.13	0.13		NA		Laurance 1997
3	H	0.4	0.4		NA		Turton & Freiberger 1997
5	L	NA	NA		5		Burke & Nol 1998
5	L	−0.44	0.44	−0.20 to −0.64	16	5 to 40	Gehlhausen et al. 2000
6	L	−0.37	0.37		44		Chen et al. 1992
7	L	−0.11	0.11	−0.07 to −0.15	67		Burton 2002
7	H & L	0	0.02	−0.02 to 0.01	10		Harper & Macdonald 2002
7	L	−0.14	0.14		5		Rheault et al. 2003
Snag or log abundance							
1	H	0.66	0.66	0.45 to 0.87	10.3	8 to 13	Williams-Linera 1990*b*
2	H	0.52	0.52	0.33 to 0.78	7.6	7 to 9	Williams-Linera 1990*b*
3	H & L	0.41	0.45	−0.17 to 1.00	NA		Young & Mitchell 1994
6	H	0.51	0.51		125		Chen et al. 1992
7	H	0.25	0.25	0.23 to 0.27	NA		Burton 2002
7	L	−0.2	0.2		NA		Esseen & Renhorn 1998
7	H & L	0.02	0.2	−0.21 to 0.27	17	10 to 20	Harper & Macdonald 2002
7	H	0.37	0.37	0.34 to 0.41	5		Rheault et al. 2003
Recruitment[j]							
1	H	0.3	0.3		100		Laurance et al. 1998*b*
1	H	0.53	0.53	0.33 to 0.69	10		Sizer & Tanner 1999
1	H	0.33	0.33	0.00 to 0.78	NA		Williams-Linera 1990*a*
2	H & L	0	0.67	−1.00 to 1.00	NA		Oosterhoorn & Kappelle 2000
2	L	−0.2	0.2	−0.6 to 0.00	NA		Viana et al. 1997
3	L	−0.67	0.67		NA		Turton & Freiberger 1997
5	H	0.65	0.65	0.89 to 1.00	NA		Cadenasso & Pickett 2001
7	H & L	−0.11	0.26	−0.37 to 0.15	70		Burton 2002
7	H	0.89	0.89	0.88 to 0.91	35	10 to 60	Harper & Macdonald 2002
Growth rate							
1	H	0.73	0.73	0.57 to 1.00	10		Sizer & Tanner 1999
1	H	0.33	0.33		NA		Williams-Linera 1990*a*
6	H	0.53	0.53	0.31 to 0.76	40	26 to 53	Chen et al. 1992
7	H & L	0.12	0.28	−0.38 to 0.69	61	45 to 75	Burton 2002
7	H	0.38	0.38		NA		Cienciala et al. 2002
Canopy foliage							
1	L	−0.39	0.39		60		Malcolm 1994
2	H	0.03	0.03		NA		Didham & Lawton 1999
Understory foliage							
1	H	0.53	0.53		35		Malcolm 1994
5	H	0.39	0.39		15		Miller & Lin 1985
Seedling mortality							
1	H	0.05	0.05	0.00 to 0.17	NA		Sizer & Tanner 1999
1	H	0.38	0.38	0.00 to 1.00	NA		Williams-Linera 1990*a*
7	H	0.59	0.59	0.44 to 0.74	94		Burton 2002
Understory tree density[k]							
1	H	0.16	0.16	0.04 to 0.27	3.8	1 to 6	Williams-Linera 1990*b*
1	H	0.28	0.28		5		Williams-Linera et al. 1998

(continued)

Appendix 1. continued

Edge category[b]	*Response*[c]	*Mean MEI*[d]	*Mean absolute MEI*[e]	*MEI range*[f]	*Mean DEI*[g] *(m)*	*DEI range*[h] *(m)*	*Study*
2	L	−0.19	0.19	−0.34 to −0.01	NA		Benitez-Malvido 1998
2	H	0.26	0.26	0.11 to 0.34	10.8	7 to 13	Williams-Linera 1990*b*
2	H	0.05	0.05		NA		Williams-Linera et al. 1998
3	L	−0.28	0.28		NA		Young & Mitchell 1994
5	H	0.11	0.11	0.03 to 0.18	NA		Brothers 1993
5	H	0.33	0.33		20		Burke & Nol 1998
5	H	0.38	0.38	0.25 to 0.50	5	0 to 10	Fraver 1994
5	H	0.35	0.35	0.00 to 0.62	NA		Gehlhausen et al. 2000
5	H & L	−0.17	0.29	−0.60 to 0.22	NA		Palik & Murphy 1990
5	H	0.5	0.5		NA		Ranney et al. 1981
7	H	NA	NA		60		Harper & Macdonald 2002
Herb cover							
5	H	NA	NA		5		Burke & Nol 1998
7	H & L	NA	NA		1.25	0 to 5	Harper & Macdonald 2002
Shrub abundance							
4	H & L	0.37	0.42	−0.08 to 0.74	40		Matlack 1993
5	L	−0.48	0.48		NA		Matlack 1993
7	L	NA	NA		3.75	0 to 5	Harper & Macdonald 2002
8	H	0.35	0.35		NA		Kollman & Buschor 2002
Species composition[l]							
4	H	NA	NA		20		Euskirchen et al. 2001
5	H	NA	NA		35	20 to 50	Fraver 1994
5	H	0.45	0.45	0.35 to 0.58	20	10 to 40	Gehlhausen et al. 2000
5	H	NA	NA		19	5 to 45	Palik & Murphy 1990
5	H	0.31	0.31		NA		Whitney & Runkle 1981
6	H	NA	NA		40	35 to 42	Toms & Lesperance 2003
Exotic species abundance							
5	H	0.69	0.69	0.68 to 0.69	NA		Brothers & Spingarn 1992
5	H	NA	NA		10		Burke & Nol 1998
5	H	1	1		35	10 to 60	Fraver 1994
5	H	1	1		NA		Gehlhausen et al. 2000
5	H	0.97	0.97		NA		Luken & Goessling 1995
5	H	0.23	0.23		80		MacQuarrie & Lacroix 2003
Individual species abundance							
1	H	NA	NA		60		Laurance et al. 1998*b*
1	H	1	1		10		Sizer & Tanner 1999
3	H	NA	NA		500		Laurance 1991
3	H	0.27	0.27	0.20 to 0.33	NA		Laurance 1997
4	H & L	NA	NA		9	0 to 30	Euskirchen et al. 2001
5	H & L	NA	NA		27	20 to 35	Palik & Murphy 1990
5	H & L	0.46	0.70	−1.00 to 1.00	NA		Ranney et al. 1981
5	H & L	0.31	0.74	−1.00 to 1.00	NA		Whitney & Runkle 1981
6	H & L	0.10	0.47	0.66 to 0.91	71	41 to 92	Chen et al. 1992
6	L	−0.63	0.63	−1.00 to −0.02	NA	0 to 60	Jules et al. 1999
7	L	−0.18	0.18		50		Esseen & Renhorn 1998
7	H & L	NA	NA		25	0 to 60	Harper & Macdonald 2002
8	H & L	0.59	0.98	−1.00 to 1.00	NA		Honnay et al. 2002
Species diversity							
2	H	0.08	0.08	0.04 to 0.13	NA		Oosterhoorn & Kappelle 2000
3	H	0.57	0.57		NA		Lloyd et al. 2000
5	H	0.13	0.13	0.08 to 0.19	NA		Brothers 1993
5	H	NA	NA		7.5	5 to 10	Burke & Nol 1998
5	H	0.21	0.21	0.19 to 0.23	30	20 to 40	Fraver 1994
5	H	0.33	0.33	0.17 to 0.54	37	15 to 60	Gehlhausen et al. 2000
7	H & L	NA	NA		1.25	0 to 5	Harper & Macdonald 2002

[a] *Studies were found in previous data compilations (Baker & Dillon 2000) and from a literature review of common ecology journals. We included only studies that report the magnitude or distance of EI or with values for both edge and interior sites in either tables or figures. We used these latter values to calculate the magnitude of EI (see Table 1 for equation). We considered interior sites as the sampled sites that were farthest from the forest edge.*

[b] *Results subdivided into seven categories of edge type and region: 1, young tropical; 2, maintained tropical; 3, maintained Australian; 4, regenerating eastern North American; 5, maintained eastern North American; 6, regenerating western North American; 7, regenerating boreal; and 8, maintained European (more complete descriptions of categories provided in Table 2 footnotes). Each study is reported only once per category of response variable and per edge type; multiple results within each category and study were averaged, and the range of results is noted (see below).*

[c] *High (H) or low (L) in edges relative to interior.*

[d] *Results of the magnitude of EI (MEI) (see Table 1 for equation) were averaged within each study and category of response variable; positive and negative values represent positive and negative edge influence, respectively.*

[e] *Absolute values of the magnitude of EI (MEI) were averaged within each study and category of response variable to measure the strength of edge influence.*

[f] *Range of values of the magnitude of EI within each study and category of response variable.*

[g] *Distance of EI (DEI) averaged within each study and category of response variable based on results reported in the studies.*

[h] *Range of values of the distance of EI (DEI) within each study and category of response variable.*

[i] *Canopy tree density or tree basal area.*

[j] *Seedling abundance or a change in tree abundance.*

[k] *Understory tree density or total tree density.*

[l] *High means species composition is different than in the interior.*