

Edge effects in fragmented forests: implications for conservation

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Forest fragmentation is the replacement of large areas of native forest by other ecosystems leaving isolated forest patches, with deleterious consequences for most of the native forest biota. Fragmentation reduces the total area covered by the forest, which may result in the extinction of some species. In addition, forest fragmentation exposes the organisms that remain in the fragment to the conditions of a different surrounding ecosystem and, consequently, to what have been termed 'edge effects'¹. Edge effects are the result of the interaction between two adjacent ecosystems, when the two are separated by an abrupt transition (edge). Although the juxtaposition of two ecosystems can produce effects on both, the concern of conservationists, and of this paper, is the effect of edges on the remnant forest patches.

Edges may affect the organisms in a forest fragment by causing changes in the biotic and abiotic conditions¹⁻³. If exposure to the edge modifies the features of the forest beyond their range of natural intrinsic variation, then the portion of the fragment under the influence of edge effects will be unsuitable for the original ecosystem, and the fragment's area will be effectively reduced for conservation purposes.

Although the general notion that edge effects are deleterious for forest fragments is widely accepted, there is little consensus on what an edge is, how to measure edge effects, or how deleterious they are. Here, I review the concepts of edge and edge effects, the general patterns in the results and weaknesses in current research, and potential future research strategies.

Ecological consequences of edges

Adjacent ecosystems experience flows of energy, nutrients and species across their mutual boundary⁴. As a result, the species composition, structure and ecological processes of an ecosystem near the line of contact with another ecosystem may be changed. The intensity of edge effects has been measured as the distance, d , that these changes penetrate into the habitat.

There are three types of edge effects on the fragments: (1) abiotic effects, involving changes in the environmental conditions that result from proximity to a structurally dissimilar matrix; (2) direct biological effects, which involve changes in the abundance and distribution of species caused directly by the physical conditions near the edge (for example, through desiccation, wind throw and plant growth) and determined by the physiological tolerances of species to the conditions on and near the edge; and (3) indirect biological

Edges are presumed to have deleterious consequences for the organisms that remain in forest fragments. However, there is substantial discrepancy among recent studies about the existence and intensity of edge effects. Most studies have focused on seeking simplistic and static patterns. Very few have tested mechanistic hypotheses or explored the factors that modulate edge effects. Consequently, studies are very site-specific and their results cannot be generalized to produce a universal theory of edges. Although estimates of the intensity and impact of edge effects in fragmented forests are urgently required, little can be done to ameliorate edge effects unless their mechanics are better understood.

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effects, which involve changes in species interactions, such as predation, brood parasitism, competition, herbivory, and biotic pollination and seed dispersal.

Abiotic edge effects

In human-fragmented forests, the fragments are usually surrounded by a matrix of low biomass and structural complexity, such as pastures, croplands or young secondary growth. Differences in structural complexity and biomass result in differences in microclimate. Compared to a forest, crops and pastures allow more solar radiation to reach the ground during the day and higher reradiation to the atmosphere at night⁵. Consequently, diurnal temperatures in pastures and crops tend to be higher near the ground, and

daily temperatures fluctuate more widely⁶. The environment under the forest canopy, in contrast, is cooler, moister and more uniform^{5,6}. The difference in microclimate between the two sides of the edge is likely to create a gradient of temperature and moisture that runs perpendicular to the edge.

Air temperature, air moisture, vapor pressure deficit (VPD), soil moisture and light intensity vary between the edge and the interior in some forest fragments. In those cases, the differences have been estimated to disappear over the first 50 m into the fragment⁷⁻⁹ (Table 1). In other cases, however, there is no change in those variables with distance to the edge^{7,9}.

Two factors seem to modulate the intensity of the physical edge effects: orientation and physiognomy. Compass orientation determines the amount of exposure to solar radiation. The lower the exposure to solar radiation, the weaker are some of the physical edge effects. For example, north-facing edges in southeastern Pennsylvania, USA, exhibit milder edge effects in microclimate than edges facing other directions⁹. One study in the Brazilian Amazon has also reported differences in the penetration of edge effects between northeastern edges and those facing other directions⁷. In the tropics, however, the modulating effect of edge orientation on the light's incidence angle, and the length of daily exposure to the sun is likely to vary through the year. Near the equator, the sun's declination shifts from north to south during the year. Between December and February, when the sun is at its southward declination, north-facing edges should experience milder environmental effects, such as those reported by Kapos⁷; but during May, June and July, when the sun is at its northward declination, the results should be opposite.

Physiognomy also affects the intensity of edge effects by reducing the amount of incident light that reaches the

understorey⁹ (Box 1). In a comparison of three edge types (equivalent to those in Box 1), edges with the least lateral protection exhibited the greatest edge effects in several environmental variables⁹.

Abiotic edge effects can also result from the movement of chemical compounds across the edge that can alter environmental conditions. Chemical fertilizers from adjacent croplands penetrate several meters into the wheat-belt shrubland and the wheat-belt woodland of Australia¹⁰. Also, nitrates, sulfates and herbicides from adjacent croplands are known to penetrate riparian forests in Maryland, USA¹¹. In both cases, values were highest at the edge, and declined with distance into the forest fragment (Table 1).

Direct biological edge effects

Changes in the physical environment caused by edges may directly affect forest structure. The creation of an edge increases the incident light which, in turn, promotes plant growth¹²⁻¹⁴. Thus, even several decades after the creation of the edge, forest structure near the edge remains changed¹⁵. A variety of tropical and temperate-zone forests shows higher stem densities and basal areas within 20 m of the edge¹⁵⁻¹⁸ (but see Ref. 12). The forest stratum that exhibits such plant biomass response, however, differs among forests. In one case, in a sugar maple-beech forest in Michigan, USA, the response was stronger among canopy and subcanopy trees¹⁶, while in a cloud forest fragment in Mexico, the response was stronger among understorey woody plants¹⁹. The physical environment can also affect the forest structure near the edge by causing plant mortality. Near the edge, tree mortality can increase relative to the interior, as a result of wind throw¹², and possibly as a result of fire following the creation of the edge².

Edge effects on the physical and chemical environment can also affect the distribution of species near the edge, because of differences among species in their physiological tolerances. Some forest plants species show lower densities or are absent near the edge^{8,12,13,15,17}, while others show higher densities^{8,12,17}, or no changes at all^{8,17}. The different responses among species to the changes in the physical environment at the edge may result in localized shifts in species composition^{15,16,19}. In other cases, however, differences in species composition do not occur. Studies on tree and seedling species composition have found no differences as a result of proximity to the edge in second growth sugar maple-beech forests in Michigan and in undisturbed lowland rainforests in Panama^{16,18}.

Table 1. Edge effects on a variety of temperate and tropical forests^a

	Higher at edge	No difference	Lower at edge
Abiotic			
Air moisture		9	(50) ^{b)9}
Air Vapor Pressure Deficit	(20) ⁷ (50) ^{b)9}	9	
Air temperature	(20) ⁷ (24) ⁹ (15) ¹⁸	9	
Light (PAR) ^c	(20) ⁷ (44) ⁹	9	
Soil moisture		7	(40) ⁷
Chemical substances	(50) ¹⁰ (?) ¹¹		
Vegetation			
Tree (stem) density	(15) ¹⁶ (30) ¹⁷ (20) ¹⁸ (?) ¹⁹	12,16,19	(56) ¹² (?) ¹⁹
Basal area	(15) ¹⁷	12,19	
Canopy cover			(44) ¹² (150) ²⁷
Subcanopy cover			(?) ²⁷
Understorey cover	(40) ⁹	9,18	
Liana density			(?) ²⁷
Seedling density	(?) ¹²	12,14	(?) ¹²
Plant/seedling growth	(53) ¹² (?) ^{13,14}		
Canopy damage	(150) ²⁷		
Mortality	(56) ¹² (?) ¹⁸	14	
Animals			
Bird density	(60) ²¹	21	(60) ²¹
Processes			
Seed dispersal and/or invasion from matrix	(10) ¹⁰ (80) ²⁶ (500) ²⁷		
Nest predation	(?) ^{25,29} (600) ³⁰ (?) ³⁷	22,25,29,31-33	
Brood parasitism	(?) ³⁴		
Post-dispersal seed predation		13	(?) ¹³
Seed germination			(?) ¹³
Herbivory	(?) ¹³		
Plant species composition and richness			
Species richness	(10) ¹⁵ (15) ¹⁷	15	
Species composition ^d		16,18	(?) ^{15,19} (45) ¹⁶

^aThe numbers in parentheses on each column are the estimated distance (in meters) into the forest that the edge effect penetrated. When more than one replicate (or face) was measured, I used the maximum distance reported. Question marks indicate when the exact distance was not determined. Superscripts are the bibliographic references.

^bMaximum distance measured.

^cPAR: photosynthetically active radiation.

^dNot different from interior, or different from interior.

Forest animal species, also, show diverse responses to the edge. Density and activity of forest animals vary among species from avoidance to preference^{20,21}. Changes in species composition may also result from species from the matrix reacting to the edge as well. A favorable environment that attracts animals²¹⁻²⁵, or facilitates dispersal of plants by abiotic or biotic vectors towards the fragment^{10,26,27}, may cause species from the matrix to converge on the edge, and even penetrate some distance into the fragment.

In contrast to the clear responses exhibited by the forest structure to the abiotic conditions, the response of species compositions is less obvious. Perhaps this variability in responses results from the idiosyncratic responses of different species to the physical conditions (direct biological edge effects), to interactions with other species (indirect biological edge effects), or to both. No study, however, has addressed the relative importance of direct and indirect biological effects on the distribution and abundance of species near the edge.

Indirect biological edge effects

Edge-driven changes in the forest environment and structure may affect the dynamics of species interactions near the edge. For example, a leaf flush that results from increased light incidence at the edge may attract herbivorous insects. These, in turn, may attract nesting birds, which in

Box 1. Cantilevered, canopy dripline and advancing edges¹⁷

Cantilevered edges are those maintained at their point of creation, and are characterized by the overhanging canopy of the branches that grow towards the open space, and a thick understorey among large tree trunks. The overhanging canopy not only offers a more aerodynamic profile that could reduce wind damage, but it could also act as an umbrella that shadows the edge understorey, buffering it from the conditions exerted by the matrix.

Canopy dripline edges are those maintained at the outer tips of the horizontal branches of the canopy trees. These edges have a dense understorey, shaded by the branches of the outermost canopy trees, but have no large tree trunks exposed to the edge. Canopy dripline edges represent an abrupt change in height and plant density between fields and forests, and thus could suffer from higher wind-throw mortality. Also, given the difference in structure associated with the edge, species composition at the edge is likely to differ significantly between the edge and the interior.

Advancing edges are maintained several meters away from their point of creation, or not maintained at all. They are characterized by a dense vegetation that gradually declines in height between the point of edge creation and the point of edge maintenance. Advancing edges are not abrupt as are cantilevered or canopy dripline edges, and consequently I categorize them as ecotones rather than edges. The effects of ecosystems on one another across an ecotone are likely to differ from the effects across an edge because of the long distances separating ecosystems, and, as such, merit their own line of study.

turn could attract nest predators and brood parasites. Thus, the edge effect on light availability, and on the abundance of herbivorous insects, may initiate a series of cascading effects that can spread across the fabric of the ecosystem through species interactions.

The species interactions that have received most attention are nest predation and brood parasitism in birds, but the results have been inconsistent²⁸ (Table 1). Studies have reported higher rates of nest predation on or near the edge in a lowland rainforest in Costa Rica, and in oak forests in Maryland and Tennessee, USA^{29,30}. Other studies have reported inconsistent or no significant edge effects on bird nest predation in a variety of temperate zone forests in North America, Europe and Costa Rica^{20,25,29,31–33} (see Ref. 28 for a reanalysis of some data sets). Studies carried out in the USA on the relationship between avian brood parasitism and exposure to the edge also show inconsistent results. In a Wisconsin (USA) deciduous forest³⁴, and an oak–hickory forest in Michigan²³, cowbirds (*Molothrus ater*) parasitized nests more frequently near the edge than far from it. Another study in an oak–hickory forest in Maryland, however, found no relationship between nest parasitism by cowbirds and proximity to the edge²⁰.

Studies on other species interactions are scarce. These studies have found that at the edge there is lower post-dispersal seed predation¹³ and higher herbivory than in the forest interior of an oak–hickory forest in Michigan¹³. In a tropical rainforest in Queensland, Australia, animal-dispersed seeds from the matrix moved a distance of up to 80 m into the forest²⁶.

Why is there little consensus in the results?

Edge effects have been measured in a large variety of forest types with different edge characteristics, and surrounded by a variety of matrices. Yet we are still unable to draw clear-cut general patterns (Table 1). Possible generalizations have been obscured by at least three factors that may act simultaneously: poor design, lack of consistency in methodology, and oversimplification of the perception of edge and edge effects.

Some of the lack of consistency in the results on edge effects may be attributed to improper design. Table 1 lists the results as they were reported by the authors, without

interpretation or re-analysis on my part. Eleven of the 24 studies listed failed to select appropriate replicates, or did not replicate at all. Lack of replication limits the generality of the conclusions, if not their validity. Inadequate replication usually involved confounding of effects. In two cases, penetration of edge effects was estimated by measuring a variable at the core of a series of fragments that ranged greatly in size^{27,35}. This design confounds fragment size with exposure to the edge, and therefore the conclusions drawn are inappropriate. Additionally, several studies confounded treatments with replicates. Two studies, for example, confounded two levels of nest density with two different edge types^{29,31}. Lack of replication was common, involving pseudo-replication – that is, several transects were surveyed, but all were located in one forest-clearing edge.

Many factors are potential modulators of the intensity of edge effects, and must be taken into account when selecting appropriate replicates. Some of these factors are: age^{9,15,18}, physiognomy^{9,15,17}, orientation^{7,9,15,17}, matrix type^{10,20,22,29,31} and management history of forest and matrix^{2,9,16,17,19–21}. One could argue that finding adequate replicates for landscape-level studies is very difficult when so many variables must be considered. If proper replication is not possible, then such limitations in the design must be taken into account when formulating hypotheses and interpreting results.

Most studies also fail to provide a proper description of the edge and where it lies, which makes the interpretation of results difficult. The description of the study area is important in assessing whether the purported edge effects are independent from landscape elements different from the edge. If the edges fall along, or parallel to, topographic accidents (e.g. streams, terrain depressions or elevations) or soil discontinuities, edge effects may be confounded and impossible to separate from such incidental factors.

Most studies measure edge effects relative to a point indicated by a zero meter mark, yet only a few specify the precise placement of this zero meter mark with respect to tree trunks and understorey growth^{15,16,19,20,23}. Ranney *et al.*¹⁷ identified two important factors with respect to the position of the edge: the point of edge creation (canopy tree trunks of the original forest will reach to this point) and the point of edge maintenance (limit of undergrowth). These two factors determine the physiognomy of the edge, which can act as a modulator of edge effects⁹ (Box 1) and therefore become an important issue when designing studies and reporting results.

It is likely that edge effects interact with each other. Therefore, it may be unrealistic to expect all edge effects to vary monotonically with distance from the edge. So far, studies have been designed to test for significant differences between samples on or near the edge and samples at some distance into the forest; or else, for the intercept between two monotonic linear functions (Fig. 1a). Yet, several studies have found peaks and depressions in edge effects at intermediate distances from the edge (usually around 20–30 m), but have not attributed any importance to them^{7,10,16,19,21}. It is possible that those peaks are part of the inherent variation of the measured variable, but it is also conceivable that they are the result of an interaction among two or more variables. For example, light, a limited resource to the forest plants, increases at the edge creating a concentration of leaf biomass at the edge that, in turn, casts a shadow behind it limiting plant growth beyond natural levels. The result is a peak of leaf density at the edge, followed by a trough at some distance from the edge, and intermediate values further behind. This phenomenon has been termed a competition-induced wave of biomass, and seems to occur whenever

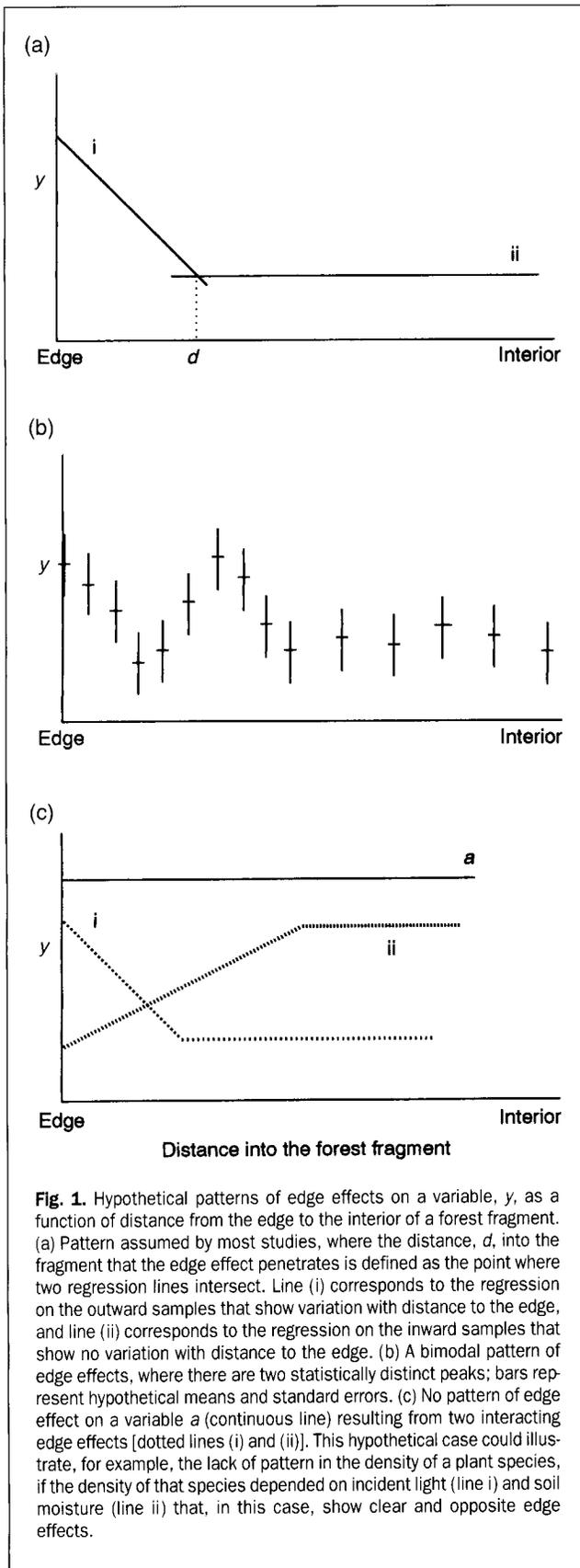


Fig. 1. Hypothetical patterns of edge effects on a variable, y , as a function of distance from the edge to the interior of a forest fragment. (a) Pattern assumed by most studies, where the distance, d , into the fragment that the edge effect penetrates is defined as the point where two regression lines intersect. Line (i) corresponds to the regression on the outward samples that show variation with distance to the edge, and line (ii) corresponds to the regression on the inward samples that show no variation with distance to the edge. (b) A bimodal pattern of edge effects, where there are two statistically distinct peaks; bars represent hypothetical means and standard errors. (c) No pattern of edge effect on a variable a (continuous line) resulting from two interacting edge effects [dotted lines (i) and (ii)]. This hypothetical case could illustrate, for example, the lack of pattern in the density of a plant species, if the density of that species depended on incident light (line i) and soil moisture (line ii) that, in this case, show clear and opposite edge effects.

there is a release of an otherwise limited resource³⁶. Therefore future studies should be designed bearing in mind that edge effects need not be monotonic (Fig. 1b).

Species respond in different ways to the edge^{8,15,16,21,36}. Thus, measurement of edge effects should consider which spatial and temporal scales are most relevant for each species. For example, the scale used for measuring edge effects in

one species may be unrealistic for another species with a home range, or a life span, an order of magnitude different. Studies should not only take into account the scale but also the grain size of the measurements. Most studies have found edge effects to disappear within the first 50 m into the forest. Yet, few have used a fine enough scale to give precise estimates or detect significant fluctuations. On the other hand, studies such as those on nest predation of territorial birds may have to incorporate edge effect measurements over hundreds of meters, in order to encompass several territories between the edge and the interior.

To summarize, most deficiencies pointed out here are simply the reflection of our simplistic view of edges. The scant descriptions of study sites, edges and criteria used for determining the location of the edge, and for selecting replicates, indicate how unaware researchers have been of the importance of such factors on determining edge effects. Also, given the complexity of biological interactions, it is perhaps naive to expect finding simple (unimodal) patterns of edge effects at all ecological levels. Processes at one level could obscure or neutralize edge effects at the same or different levels (Fig. 1c).

Future directions

The study of edges and their effects on forest fragments has been, for several decades, descriptive and uninquisitive of the mechanisms that cause edge-related modifications in the forest. The research accumulated in the past five years, while valuable for guiding site-specific management plans, has not sought the underlying principles that will allow us to make realistic generalizations and projections. At this stage, in spite of the number of studies on edge effects, we have no idea whether there are any 'edge principles', or if we must describe every situation as a unique case study. While some of our confusion resides in the methodological inconsistencies cited above, it is the general aim of the studies that presents the biggest conceptual constraint. For example, a recent review on the evidence available for edge effects on bird nesting success permitted some generalizations of patterns²⁸. Yet, neither the review itself, nor the bulk of reanalyzed data sets, shed much light on whether edge effects are omnipresent, or if inconsistencies among studies are because of failure in finding edge effects or if edge effects occur only under particular circumstances.

I propose a two-pronged approach to studying edge effects on forest fragments. First, because abiotic edge effects have given the clearest (and perhaps the simplest) responses to edges, focusing on abiotic edge effects may allow us to assess the modulating potential of factors such as age, physiognomy, orientation, geometry of the edge and matrix type on edge effects. The current perception of edges is that they are either static, or bound to experience a series of effects that 'eat away' the fragment from the outside. Yet, some studies indicate that it is not necessarily so, and that edges are dynamic. The short- and long-term persistence of edge effects, however, have rarely been addressed. Most studies are short, and few have explored the effect of time on edge dynamics. Edge effects need not be permanent year-round, or year after year. Indeed, the few studies that have considered time as a modulating factor suggest that older edges experience milder abiotic edge effects than younger ones^{9,18}. Once the vegetation at the edge 'seals' a few years after edge creation, the impact of the matrix on the fragment is likely to decline^{8,9,18}. Likewise, the possibility that other factors, such as those mentioned above, could modulate edge effects has been suggested by circumstantial evidence, but remains largely untested.

The second approach is to formulate and test mechanistic hypotheses. Most studies have used a correlative approach, inferring the sensitivity of a process to the edge by looking for patterns. Because of the complexity of most ecological processes, however, it is likely that looking for patterns at this level becomes a sterile and frustrating endeavor. The high inconsistency among results shown here proves the point. Rather, future research based on the causal mechanisms behind edge effects may be more rewarding. Many studies have proposed mechanistic explanations to the patterns found. For example, an increase in nest density near the edge caused by an increased cover or insect availability at the edge; or an increased stem density near the edge that results from higher light availability, or changes in density of one or several plant species caused by changes in soil moisture. No study so far has independently tested any mechanistic hypothesis concerning edge effects. Perhaps it is time that the field moved from pattern-seeking to a search for causal relationships between edge-associated patterns and mechanisms, well supported by rigorous design and testing.

The failure of studies carried out so far to find repeatable patterns may lead us to underestimate the potential deleterious effect that edges may have on the species diversity, structure and function of the forest fragments. Given the rate at which forest is disappearing, and the stakes for conserving what little is left, it is imperative to consolidate as fast as possible a sound conceptual background. Only well-designed, preferably long-term, studies will be able to determine which patterns are universal to edges in general, and the factors that potentially modulate edge effects in each particular case. To the extent that we are able to predict when and how strongly an edge effect will occur, we will be able to design management plans that attenuate the detrimental effects of forest fragmentation and exposure to the edge.

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