Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects

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ABSTRACT

The pervasive influence of island biogeography theory on forest fragmentation research has often led to a misleading conceptualization of landscapes as areas of forest/habitat and ‘non-forest/non-habitat’ and an overriding focus on processes within forest remnants at the expense of research in the human-modified matrix. The matrix, however, may be neither uniformly unsuitable as habitat nor serve as a fully–absorbing barrier to the dispersal of forest taxa. In this paper, we present a conceptual model that addresses how forest habitat loss and fragmentation affect biodiversity through reduction of the resource base, subdivision of populations, alterations of species interactions and disturbance regimes, modifications of microclimate and increases in the presence of invasive species and human pressures on remnants. While we acknowledge the importance of changes associated with the forest remnants themselves (e.g. decreased forest area and increased isolation of forest patches), we stress that the extent, intensity and permanence of alterations to the matrix will have an overriding influence on area and isolation effects and emphasize the potential roles of the matrix as not only a barrier but also as habitat, source and conduit. Our intention is to argue for shifting the examination of forest fragmentation effects away from a patch-based perspective focused on factors such as patch area and distance metrics to a landscape mosaic perspective that recognizes the importance of gradients in habitat conditions.

Keywords

Dispersal, forest fragmentation, habitat quality, heterogeneity, island biogeography, matrix, spatial landscape ecology.

INTRODUCTION

Many long-standing theories concerning the ecological effects of forest fragmentation stem from conceptualizations of landscapes in which forested ecosystems are viewed as islands of habitat embedded in an uninhabitable matrix of non-forested uses (Haila, 2002). While intuitively appealing, such a depiction has severe limitations for a range of reasons (Margules et al., 1982; Kupfer, 1995), including its inability to account for variability in habitat quality in both the forested and non-forested habitats (Lindenmayer & Franklin, 2002). The ‘remnants as islands’ analogue is also conceptually flawed, in that it focuses attention almost solely on population (or metapopulation) dynamics within forested habitats while ignoring dynamic linkages and feedbacks with the non-forested habitat (e.g. Koelle & Vandermeer, 2005). Often, the most important aspects of non-forested habitats, from the viewpoint of ecologists concerned with biodiversity in forest remnants, are whether they provide adequate habitat for forest species and whether species can disperse through the nonforested habitats to other forest habitats.

The purpose of this paper is to present a conceptual model of forest fragmentation effects that addresses not only aspects of the forest remnants themselves (recently reviewed and criticized by Fahrig, 2003), but how the effects of changing forest area and isolation are mediated by a range of matrix effects identified by recent studies. Throughout this paper, we use the terms ‘remnants’ for forest areas not affected by specific human-caused disturbances and ‘matrix’ for the disturbed areas, which may include recently logged areas, agricultural fields, pastures and other areas of human disturbance (Fig. 1). Although this usage of matrix does not necessarily agree with other formal definitions of this term (e.g. the matrix defined as the most extensive or dominant area; Forman, 1995), it is intuitive and matches the usage of Lindenmayer & Franklin (2002), who have theorized it most effectively. This definition also recognizes that the matrix can take on a variety of forms in a given landscape and can contain a range of varying habitat quality.
It is also important to clarify that forest fragmentation can refer to either the broad process of forest loss and isolation or more specifically to changes in the spatial configuration of forest remnants that are a result of deforestation. Bunnell (1999), Fahrig (1997, 1999, 2003) and Haila (1999), among others, argue that the ecological consequences of habitat loss (deforestation) and isolation (fragmentation, in a narrow sense) need to be distinguished. While we agree that this distinction is important from a scientific standpoint and believe that it may be possible to separate such effects in simulations and some controlled experiments (Caley et al., 2001; Davies et al., 2001), it is difficult or impossible to do so in studies of natural ecosystems. Further, we contend that all effects should be considered collectively in an attempt to understand forest fragmentation in the broader,

Figure 1 Examples of modified matrixes. Top left: row cropping of *Phaseolus* near Hill Bank, Belize (photograph by John Kupfer); top right: active slash and burn *milpa* (field) near Indian Church, Belize (photograph by John Kupfer); middle left: recent selection cut of floodplain forest along the White River, Arkansas, USA (photograph by John Kupfer); middle right: aspen (*Populus tremuloides*) regrowth on a former clear cut in *Pseudotsuga menziesii* forest in Valles Caldera National Preserve, New Mexico, USA (photograph by Jeff Balmat); bottom left: urbanized area in Tela, Honduras (photograph by John Kupfer); bottom right: fern regeneration on a boreal forest clearcut and subsequent burn, southwestern Newfoundland, Canada (photograph by Scott Franklin).
process-based sense of the term, and rather than trying to isolate each, we include their interaction across a range of effects. Finally, although the term ‘biodiversity’ has many meanings, we focus primarily on aspects at the population and community levels (e.g. issues of species persistence and extinction, changes in species richness) because these are the levels at which most land stewards make their decisions.

A CONCEPTUAL MODEL OF FRAGMENTATION EFFECTS

Based in part on principles from island biogeography theory, metapopulation models and source–sink dynamics, Zuidema et al. (1996) developed a conceptual model that identified four effects of forest fragmentation leading to the loss of biodiversity. These effects focused primarily on the effects of pattern on processes in the remnants. Here, we build on their scheme by rethinking the effects of fragmentation and incorporating additional matrix heterogeneity concepts (Fig. 2). We chose this starting point because it includes an explicit pattern-process connection and because it is at a landscape scale appropriate for management decisions.

Forest fragmentation: effects of forest remnant area, isolation and edge

The process of forest fragmentation results in three distinct changes in forest ecosystem pattern: reduced forest area, increased isolation of resulting remnants, and the creation of edges where remnant forest abuts modified ecosystems. Each of these influences a range of population, community and ecosystem processes that may affect biodiversity. In this section, we assume an inhospitable matrix, focusing attention solely on characteristics of the forest remnants.

Reductions in forest area

Island biogeography (MacArthur & Wilson, 1967) provides a starting point in evaluating the effects of forest loss associated with deforestation. Habitat loss has two consequences: (1) a reduction in the range of habitat types results in fewer species; and (2) a reduction in resources for species leads to smaller populations that are more vulnerable to extinction. The latter is related to niche packing and the inability of species to subdivide a habitat into extremely narrow niches if the total resources are limited. We represent these effects as changes in the resource base in Fig. 2.

Changes in the resource base are linked inextricably to the subdivision of populations. Smaller populations lead to higher extinction rates (although such effects may not be immediately manifested; Tilman et al., 1994) and changes in population genetics (e.g. Templeton et al., 1990; Ricklefs & Miller, 2000). Changes in trophic relations (Zanette et al., 2000), competition (Huxel & Hastings, 1998), dispersal vectors (Cordeiro & Howe, 2001) and other species interactions can also lead to population declines. Abundances of many species have thus been linked to forest habitat loss, although local extinction following fragmentation is species-specific as some taxa are more vulnerable than others (e.g. Newmark, 1991; Kattan et al., 1994; Marsden, 1998; Henle et al., 2004).
The amount of forest removed and the resulting patch sizes may constrain the types, extents, frequencies and even intensities of disturbances. Some types of disturbances may depend directly on area; for example, small forest remnants in non-forested landscapes may be more subject to wind destruction than comparably sized areas in continuous forest (Esseen, 1994). Specific disturbance characteristics such as fireline intensity may be influenced by the amount of area over which the disturbance develops, and the area of a disturbance per se can be part of a disturbance regime. The combination of these aspects of disturbance regime will affect the dynamics of species and the resulting biodiversity (e.g. Malanson, 1984).

The degree to which area-related changes occur is a function of not only the total amount of forest loss, but also (1) the size of remaining forest remnants, and (2) where in a landscape the destruction occurs. These latter two effects are correlated with, but not typically the same as, the total area of habitat destruction, although all are components of reduced forest area. Even in a continuously forested landscape, spatial structure (e.g. pattern of heterogeneity or interspersion of forest types) is present. Rarely are patterns of deforestation across a landscape random (Thiollay & Meyburg, 1988; Kupfer & Franklin, 2000), so the spatial selectivity of forest clearing affects the degree to which forest fragments represent the original forest. Further, populations in the remnants are merely a sample of the original population and may not be representative of the precut populations, not only in terms of numbers but also in terms of a range of other characteristics (e.g. genetic diversity and demographic structure) (Terborgh et al., 1997).

**Increased isolation of forest remnants**

Landscape structure has been shown to affect plant and animal dispersal for colonization, movement patterns and gene flow. Changes in population dispersal and dynamics ultimately affect community assembly and interactions. Processes occurring at the population and community level drive landscape-level processes (e.g. metapopulation dynamics) while landscape pattern (e.g. distance to seed pool) constrains population (e.g. extinction) and community (e.g. succession) processes. The spatial adjacency of existing patches, especially source patches, is an important factor affecting animal movement so if landscape fragmentation is severe, the adjacency of existing habitat patches is crucial for maintaining populations. Isolation through fragmentation is also important because it forces more cross-landscape movement (Forman, 1995), which may be energetically costly or increase risks of predation (one factor that makes matrix habitat a barrier to dispersal).

Given an uninhabitable matrix, the immigration rate to an isolated forest remnant will generally be lower than an equal area surrounded by contiguous forest habitat. Fragmentation can thus lead to the subdivision of a single population into multiple disjunct but interacting subpopulations (e.g. a metapopulation) or, if isolation is extreme enough, individual non-interacting populations, which has attendant ramifications associated with small population sizes. Further, because many disturbances are spatially contagious processes, isolation and the resulting subdivision of populations may alter disturbance frequency and thus threats from environmental fluctuations and catastrophes (Akcakaya & Baur, 1996; Perkins & Matlack, 2002).

Isolation effects may feedback to affect species interactions. Species that could interact because they were in a contiguous area may no longer be able to do so because of isolation, and species interactions can be altered to the extent that local extinctions may occur if some species are missing and cannot be rescued by immigration. Among a group of interacting species, a particular spatial configuration will mean different degrees of isolation depending on the mobility of the species, and individuals may be in a remnant without a primary predator or competitor. Such effects may be interrelated to changes in area. For example, if top carnivores are left on small remnants they are likely to become locally extinct should the remnants be too isolated for interpatch movement. Competition may also be affected if species are released from competitors by local extinctions (Hanson et al., 1990; Huxel & Hastings, 1998), and mutualisms or commensalisms can be lost if one interacting species becomes locally extinct and cannot be rescued (e.g. Anstett et al., 1997).

**Edge effects**

Forest fragmentation results in the increased susceptibility of forest remnants to edge effects: changes in microclimate, forest structure, biotic composition and ecological function that occur along forest edges exposed to non-forested habitats. Edges are distinguished primarily by changes in microclimate, including incoming solar radiation, temperature, wind speed and evapotranspiration (Ranney et al., 1981). A wide range of studies have documented the depth to which various microclimatic edge effects may be observed (e.g. Baker & Dillon, 2000), but it is important to recognize that edges represent gradients of multiple physical factors (e.g. Cadenasso et al., 1997) rather than discrete forest communities. It is also important to note that edge effects, while related to the effects of reduced forest area through the ratio of edginterior habitat, are a function of spatial configuration independent of habitat amount.

Changes in abiotic conditions along edges lead typically to biotic responses. Edge species are those adapted to edge microclimates and are often species found in the early stages of forest succession in a given region (cf. Kupfer & Malanson, 1993). The responses of forest interior species to conditions that develop along the new edge vary, but some species are unable to survive in the newly created conditions. For these species, the amount of habitat lost to fragmentation is greater than that simply converted.

Invasions by exotic species may also be enhanced by habitat destruction (Medley, 1997), as many invasive plant species are prolific seed producers that thrive in higher light conditions and have widely dispersed seeds. These traits make them more likely to establish and thrive along edges, after which they may be able to play an increasing role in vegetation dynamics within remnant interiors (Burke & Nol, 1998).

Finally, edge effects alter species interactions by increasing the degree of interaction among edge and interior species (e.g. brood...
parasitism and nest predation of bird populations; Gustafson et al., 2002). Fagan et al. (1999) synthesized recent empirical results concerning the effects of habitat edges on population dynamics with contemporary theoretical developments to outline the ways in which species interactions, and the dynamics of the communities in which they are embedded, can be changed.

Interactions among area, isolation and edge

The effects of changes in forest extent and spatial configuration are not independent. Isolation, for example, tends to be a function of area in that the two change simultaneously (albeit non-linearly) for a given landscape (i.e. there is no isolation in real landscapes without a simultaneous loss of area; Andrén, 1999; Fahrig, 2003). When isolation is low, the remnants function as a larger whole. Further, tests of island biogeography theory and metapopulation models have demonstrated that patch area affects their role as target and thus the rate of immigration because larger patches are easier to locate (e.g. Lomolino, 1990). Finally, there is arithmetic and geometric dependence between the proportionate importance of edge effects in a patch and its area and shape. Managers are often interested in maintaining the species that existed in an area prior to its becoming a remnant; because of edge effects, these species and their functions may be confined to a core. Edge–interior relationships for a forest fragment are thus often quantified using metrics such as core-area models, which provide an approximation of total edge and core habitat based on a measure of edge penetration depths and forest geometry (e.g. Laurance, 1991).

Forest fragmentation: the role of the matrix

The consequences of altering forest area, isolation and edge have generally been conceptualized using a binary division of the landscape into forested vs. non-forested habitats. Fragmentation effects have thus often been interpreted with an explicit focus on changing forest patterns, as we have discussed in the previous section. In this section, we consider how the effect of pattern on process is moderated by matrix characteristics. Specifically, as we discuss the effects of a diminished resource base, population subdivision, altered disturbance regimes, modified microclimate, and increased presence of invasive species and human pressures on remnants, we do so with the understanding that the extent to which each of these affects diversity in forest remnants is dependent on processes in the matrix.

Effects of the matrix on population subdivision

Population subdivision is typically associated with increased isolation of forest remnants during the process of forest fragmentation; therefore, fragmentation effects should be affected by the characteristics of the adjacent habitat as it influences inter-remnant movement (Lord & Norton, 1990; Wiens, 1994). Plant and animal movement across fragmented landscapes depends not only on the species’ dispersal ability and the isolation and characteristics of suitable patches but also on species’ responses to potential movement barriers. Specifically, the isolation of forest habitat is based not only on a species’ means of dispersal but also its tolerance to matrix habitat and edges, which can vary in their effectiveness as landscape barriers. When species are readily able to cross the matrix, the amount of available habitat decreases largely as a function of total remaining forest, whereas available habitat within a matrix more restrictive to movement decreases at a disproportionately greater rate than the rate of forest clearing (Dale et al., 1994). These results match other modelled expectations based on life-history trade-offs between competitive ability and dispersal ability (Tilman et al., 1997; Malanson, 2002). The matrix can thus reduce the effect of isolation on population degree to which they are habitat specialists or generalists, and some may experience little difference between a remnant and the matrix even if the matrix differs substantially in structure, while others respond to even minor differences (Krauss et al., 2003; Wethered & Lawes, 2003). Thus the functional notion of remnant and matrix is dependent on the scale of operation for specific species and may not always be clear.

Several studies have found that populations in forest remnants are influenced strongly by the surrounding habitat (e.g. Hinsley et al., 1995; Stouffer & Bierregaard, 1995; Metzger, 2000; Lindenmayer et al., 2001), although the effects have sometimes been attributed to an increased resource base in terms of additional foraging or breeding area (discussed here), increased immigration through the matrix (discussed in the next section) or some combination of the two. Studies of avian populations, in particular, have cited the importance of an expanded resource base in the matrix as a factor determining the presence of specific species in remnants (e.g. Jokimaki & Huhta, 1996; Sisk et al., 1997), and some species may even be able to compensate for a loss of their natural forest habitat by moving into other habitat types (e.g. plantations or other modified habitats) (Norton et al., 2000; Cook et al., 2002).

Gascon et al. (1999) provided one of the most comprehensive assessments of matrix effects on the resource base in their study of birds, frogs, small mammals and ants in fragmented central Amazonian landscapes. Their results showed that for all four groups, a high proportion of nominally primary-forest species were detected in matrix habitats, with 8–25% of species in each group found exclusively in the matrix. The three vertebrate groups (birds, small mammals, frogs) exhibited positive and significant correlations between matrix abundance and vulnerability to fragmentation, suggesting that species that avoid the matrix tend to decline or disappear in fragments, while those that tolerate or exploit the matrix often remain stable or increase.

Effects of the matrix on the resource base

When the matrix is uninhabitable, changes in the resource base associated with forest loss and fragmentation are most closely tied to reductions in forest area. However, the degree to which the matrix differs from the remnants alters the resource base differently for different species (Brotos et al., 2003), and the definition of patch size (equated typically with forest patch size) becomes less obvious if species are able to use the matrix as feeding or nesting habitat (Sisk et al., 1997). Species differ in the extent to which they tolerate or exploit the matrix as a complement to forest remnants. Thus, matrix effects can be considered as a function of area in that the two change simultaneously (albeit non-linearly) for a given landscape (i.e. there is no isolation in real landscapes without a simultaneous loss of area; Andrén, 1999; Fahrig, 2003).
subdivision if it is not impassible, as often seems to be the case in terrestrial landscapes.

As with the effects of the matrix on the resource base, a number of studies have focused on the influence of matrix quality on interpatch isolation. Renjifo (2001), for example, found an increased connectivity among forest remnants surrounded by exotic-tree plantations compared to pastures and observed that structurally complex anthropogenic matrices have potential as management tools for bird conservation by complementing habitat protection and restoration. Although the distinct contribution of matrix permeability to reducing isolation (as opposed to increasing resource base) cannot always be demonstrated clearly (Cooper et al., 2002), the well-documented existence of species-specific responses to changes in habitat quality and arrangement necessitates recognition of the varying resistance of the matrix to species’ movements rather than a simple measure of isolation such as interpatch distance (Tischendorf et al., 2003; Verbeylen et al., 2003). Metrics based on life history strategies (r-selected, K-selected species), behaviour (social vs. solitary) and ecological tolerance (generalist vs. specialist) may help predict the effects of fragmentation on communities (e.g. Wolff, 1999).

The extent to which fragmentation results in the subdivision of populations revolves around the level of isolation actually caused by changes in the matrix from the pre-disturbance conditions, which raises an important distinction between structural and functional connectivity. The former refers to the degree of habitat connectedness and so is clearly altered by fragmentation. Functional connectivity, while related to structural connectivity, refers to the ease with which organisms move across a landscape and also includes the effects of matrix quality, stepping stones, width and quality of corridors, gap-crossing willingness of the species and the ways in which species move along or across edges (Tischendorf & Wissel, 1997; Malanson & Cramer, 1999; Haddad, 2000; Sondgerath & Schroder, 2001; Belisle & Desrochers, 2002; Bowman & Fahrig, 2002; Bakker & Van Vuren, 2004). At low levels of forest loss, structural and functional connectivity both remain high. Structural connectivity changes most rapidly around some threshold value (e.g. 60% forest cover in random landscapes; lower values in real landscapes; Andrén, 1994), but functional connectivity may remain higher until much lower levels of remaining habitat (e.g. Andrén, 1999). Measures of structural connectivity are thus important only to the extent that they capture the underlying functional connectivity, unless they can somehow account for the heterogeneity of the matrix as well.

**Effects of the matrix on disturbance regimes**

While patch area and isolation affect the size, frequency and intensity of disturbances in forest remnants (Baker, 1989), alterations of a remnant’s disturbance regime may be determined to a similar or even greater degree by the nature of the matrix, which may serve as a source of disturbance or modify the degree of isolation. The probability of both fire ignition and rate of fire spread, for example, have been shown to differ across different types of human-modified habitat (Cochrane et al., 1999; Román-Cuesta et al., 2003). As with population subdivision, the degree to which a matrix operates as a barrier, filter or conduit will vary with the type of disturbance. It is even possible that the matrix can act as a super-conduit for disturbance, increasing the rates of disturbance transmission over what would have occurred in a contiguous forest, as was probably true for the extensive fires in Wisconsin in 1871, following logging that left a matrix of fine dead wood. Research in western and northern forests has similarly linked the amount of cutover area and forest susceptibility to bark beetle and fungal attacks (Franklin & Forman, 1987).

**Effects of the matrix on microclimate**

Forest fragmentation significantly alters microclimate across the landscape (e.g. Olejnik et al., 2002; Laurance, 2004), which in turn can feed back to influence disturbance regime (Holdsworth & Uhl, 1997). The degree to which the matrix contrasts with the remnant in structure, roughness, albedo and evapotranspiration will modify microclimatic (and thus biotic) edge effects (e.g. Matlack, 1994; Cadenasso et al., 2003). Didham & Lawton (1999), for example, found that edge penetration distances for most microclimate and vegetation structure variables were as much as two to five times greater at open, fire-encroached forest edges than at closed, non-fire-encroached edges in central Amazonian forest remnants. The matrix can thus reduce the effect of small size and edge on microclimate, if the matrix’s structure, albedo and roughness are similar to that of the remnant forest.

**Effects of the matrix on invasive species**

With (2002) noted that landscape structure (and by association, fragmentation) may affect the spread of invasive species and the invisibility of communities by enhancing spread above some threshold level of landscape disturbance directly or indirectly (e.g. through landscape effects on dispersal vectors), interacting with the distribution of invasive species to facilitate spread, promoting or altering species, interactions in ways that enhance the invisibility of communities, compromising the adaptive potential of native species to resist invasion or enhancing the adaptive response of invasive species and interacting with the dynamics of the disturbance architecture to create spatiotemporal fluctuations in resource availability, which enhance system invasibility. Many of these processes are directly affected by the nature of the intervening matrix, and as with native species the matrix can serve as a habitat, conduit, barrier or filter for invasive species. In fact, as a habitat or conduit the matrix may function better, from the perspective of the invasive species, than would a contiguous forest.

Previous studies have proposed that forest fragments, often disturbed by winds and other factors from the surrounding matrix, may be prone to invasions of species adapted to recurring disturbance (Janzen, 1983; Laurance, 1997). Indeed, studies of exotic species mobility in the landscape corroborate this relationship (National Research Council, 2002). Many highly invasive exotics have similar life histories to 'fragmentation-positive' taxa, including generalist habitat preferences and adaptations for...
disturbances, such as high dispersal ability (Bazzaz, 1986; Usher, 1988; Rejmánek & Richardson, 1996). The invasion of exotic species whose primary use is aesthetic may be ignited by their intensive use in urban centres (e.g. privet, Ligustrum sinense and L. vulgare, Rudis and Jacobs, in review). The matrix may also serve as habitat for generalist predator species that cause mortality in patch-resident prey species (Cantrell et al., 2001). Thus disturbance, in general, tends to result in increased numbers of exotics (Pyle, 1995).

Effects of the matrix on human pressure

The matrix is fundamentally associated with human pressure, but the nature of human land use in the matrix will affect fragmentation impacts. Where forest clearing is for forestry or agriculture, increased human pressures on remnants may come from hunting or fuelwood gathering (An et al., 2001; Bousquet et al., 2001). Unless the remnants are small, edges will generally have more activity than the interior. Cochrane (2001), for example, demonstrated that fire occurrence in two areas in the eastern Brazilian Amazon was concentrated disproportionately near forest edges, suggesting a synergism between forest fragmentation and fire that has been seen elsewhere. Where cutting is due to land use such as housing, human pressures in terms of light, noise, pets and local recreation will also have a strong distance decay (Theobald et al., 1997).

The role of matrix extent, contrast and recovery

The importance of matrix-based processes in different landscapes will vary, but we believe that it is possible to generalize their importance by coupling three key features: the extent and pattern of modification in a given landscape, the contrast of the matrix and remnant habitats, and the permanence of the matrix disturbance.

Matrix extent, pattern and quality

The extent and pattern of human-caused changes in a forested landscape (and thus the extent and pattern of the matrix) can be defined by comparing pre- and post-disturbance landscapes (e.g. the amount of canopy area affected by selective logging of canopy trees; Anderson et al., 2000). Forman (1995) described a loosely ordered set of stages in the modification of landscapes, ranging from perforation and dissection (the initial creation of openings in a forested landscape by patches or linear features, respectively) through fragmentation (in which pieces of forest become isolated from one another) to shrinkage and attrition (where remnants decrease in size and are eventually lost). These stages correspond to a gradient of potential importance in matrix processes. That is, processes in the matrix are likely to be less important when disturbed areas represent a small percentage of the landscape and remnant forests are widespread and well connected (e.g. a forested landscape with a few small patch cuts vs. a formerly forested landscape dominated by agriculture). As the matrix becomes more extensive in a landscape its potential importance as habitat grows, and the importance of matrix permeability (e.g. as it affects interpatch movements) increases. Thus, the value of agricultural fields as habitat or dispersal avenues may be of less concern in cultivated areas where clearings represent a small percentage of the landscape than in areas where agricultural extensification leaves only scattered forest remnants in a primarily agricultural landscape.

Forman’s stages relate to changes in the spatial structure of the landscape associated with fragmentation but not necessarily to changes in habitat quality in either the matrix (i.e. the clearing may not reduce habitat quality to zero) or the remnants (e.g. increased susceptibility to invasion). McIntyre & Hobbs (1999) provide an alternative approach in which landscapes are represented as intact, variegated, fragmented or relictual as the amount of cutting increases; each portion could also be unmodified, modified, highly modified and destroyed. Although they show modification only on edges, one can consider impacts across both the remnants as well as variability in the matrix. The effects of the matrix on the remnants and thus landscape dynamics as a whole depend particularly on how similar it is to the remnant and how well it supports fluxes among remnants (e.g. Ricketts, 2001), which are not necessarily directly related.

Matrix contrast

A number of studies have shown the importance of contrast (often structural contrast of the plant community) between the remnants and the matrix (e.g. Åberg et al., 1995; Marzluff & Ewing, 2001), including contrast of the boundary between the two (Collinge & Palmer, 2002). We can consider the varied roles of matrix functions with a modified version of Forman’s (1995) typology for edge-related processes. One function of the matrix is habitat; the degree to which some forest species can live in or utilize the matrix as alternative habitat will affect landscape functioning. In terms of flux, we can think of the matrix as a conduit (allowing or facilitating the movement of individuals), a source (serving as an origin of individuals that move into the remnants), a sink (accepting individuals from the remnants but not allowing them to leave) or a non-permeable barrier, blocking all movement. Many of these functions are determined by structural contrast between the matrix and remnant areas, and previous research has even shown that the type(s) of disturbance within a landscape may influence community composition more than disturbance extent through its effect on habitat contrast (Rodewald & Yahner, 2001). In cases with an extensive matrix that offers little for forest species, the forest remnants do essentially become habitat islands (Driscoll, 2004), but in many or most cases the matrix will serve as a filter, allowing selective passage of certain species while restricting others.

Matrix recovery

In most studies of fragmentation, the matrix has been treated not only as uninhabitable but also static. This may effectively be true in some cases (e.g. a densely urbanized matrix) but not in others (e.g. selectively logged or cultivated areas). In the first situation,
the modified habitat may be affected indefinitely and have little or no habitat value for forest species, whereas the latter situation may involve only a temporary reduction in habitat for species that rely on mature forests. In general, changes in forest structure and composition are relatively rapid following disturbances that impact primarily forest canopies but considerably slower following disturbances that heavily impact all aboveground vegetation or, even more so, soils, such as bulldozing, heavy or long-term grazing and severe fires (Chazdon, 2003).

Recovery of the matrix will be through the process of plant succession, which is driven by processes of mortality, colonization and the abiotic characteristics of the area, all of which may be altered significantly by forest fragmentation. Much has been written about mechanisms of plant succession (e.g. Glenn-Lewin et al., 1992), and we have no intention of summarizing this literature. Instead, we want to emphasize that the role of the matrix in shaping fragmentation effects will change through time so that, for example, the effects of changes in spatial pattern on the resource base or the subdivision of populations vary with the recovery of the matrix.

The state of the matrix following disturbance as well as its subsequent recovery are a function of the amount of vegetation removed, the presence of regenerating roots, stems and seeds (e.g. advanced regeneration), and the availability of propagules from offsite sources. The first two factors are largely a function of the severity of the disturbance, while the latter factor, which is a key determinant of colonization (Hewitt & Kellman, 2002), is influenced by the spatial arrangement of seed sources in the mosaic of remnant and disturbed areas and the response of dispersal agents to landscape structure (e.g. Darley-Hill & Johnson, 1981; McClanahan & Wolfe, 1987; Hughes & Fahey, 1988). Seed density generally decreases with distance from a seed source, and patterns of arrival will vary by species because of differences in seed morphometry. Patterns of seedling establishment and, as a result, plant recruitment and colonization, during recovery will vary spatially because seeds will not be dispersed uniformly into the adjacent matrix from the remnants (McClanahan, 1986; Silva et al., 1996; Kupfer et al., 2004). In addition, predation of seeds and seedlings will vary spatially (Ostfeld et al., 1999).

There are a number of direct feedbacks between recovery processes in the matrix and population processes in the remnants. Dispersal of seeds from the matrix may subsequently affect recruitment in remnant forests (e.g. Cadenasso & Pickett, 2000), and edges may influence seed banks, recruitment and population dynamics within forest interiors, at least temporarily, by acting as seed sources for shade-intolerant plant species in forest remnants (Ranney et al., 1981; Matlack, 1993; Kupfer & Runkle, 1996, 2003; Kupfer et al., 1997; Laurance, 1997; Goldblum & Beatty, 1999; Landenberger & McGraw, 2004).

Overall, the dynamics of the matrix affect remnants by increasing the area of remnants as matrix adjacent to remnant edge approaches full recovery, by reducing isolation as forest recovery increases the permeability of the intervening matrix, and by changing the edge effect as edge becomes interior. These effects are interactive and non-trivial; for example, the contrast between the matrix and remnants and how quickly the matrix recovers following habitat destruction may govern the extinction debt (sensu Tilman et al., 1994), because extinctions can potentially be prevented if recovery occurs quickly enough.

A MATRIX-INCLUSIVE APPROACH TO FRAGMENTATION

Despite the widespread recognition that forest fragmentation is a pressing environmental issue, there continues to be an active debate concerning the most appropriate areas for future study of fragmentation effects and the manners by which theory can be applied to real-world situations (Villard, 2002). Whether the explicit focus has been on specific species or more generally on biodiversity, research on the effects of deforestation and forest fragmentation has concentrated typically on pattern and process within habitat remnants. Understanding the effects of forest loss on biota in the remnants is critical to assessing impacts on the diversity of species and community composition, and a considerable amount of work on forest fragmentation has stressed how declining forest area and/or increasing isolation of forest remnants influences both richness and species survival. The underlying theory (stemming from applications of island biogeography and metapopulation theory) is that as forests are fragmented, populations decline in size and become increasingly isolated from one another, leading to higher extinction rates, lower immigration rates and lower species richness in remaining forests.

The application of island biogeography theory to forest fragmentation rests on the definition of forest remnant area and the distance from other patches irrespective of how the matrix affects habitat area and patch isolation, and even few applications of metapopulation theory, island biogeography’s more recent conceptual cousin, have addressed the importance of matrix effects (e.g. Vandermeer & Carvajal, 2001). The matrix may be neither uniformly unsuitable nor serve as a fully absorbing barrier to the dispersal of forest taxa, while remaining forest areas represent typically a gradient of conditions and habitat quality. Studies of mosaic landscapes containing old-growth forest, successional habitats and agriculture (e.g. Fox et al., 2000; Perfecto & Vandermeer, 2002) exemplify how landscapes can represent a range of conditions from deforestation to varying degrees of forest degradation in otherwise ‘intact’ forest. After a long period in which comparatively little attention had been paid to how processes in the matrix affect longer-term responses of forest remnants to fragmentation, a number of papers have: (1) addressed the effects of spatial variation on the propagation of ecological entities (e.g. individuals, disturbances) across heterogeneous landscapes (Reiners & Driese, 2001), (2) highlighted the diverse roles of the matrix in fragmented landscapes (e.g. Cantrell et al., 1998; Lomolino & Perault, 2001; Rodewald, 2003), and (3) argued that management in fragmented landscapes needs to focus as much or more on processes in the intervening matrix (Crome, 1997; Franklin et al., 1997; Hobbs, 2001; Lindenmayer & Franklin, 2002; Lomolino & Smith, 2003).

Patch-orientated measures of fragmentation such as patch area or interpatch distance have become popular because they...
are perceived to capture the effects of a diminished resource base or population subdivision and because they are easy to implement with modern geospatial tools (e.g. geographical information systems). However, we argue in this paper that ecologists need to move beyond solely documenting fragmentation effects from a remnant-based perspective (e.g. determining whether patch area or isolation have unique effects) to focus on how processes in the matrix contribute to patterns of species persistence across modified landscapes as a whole. In fact, we posit that the degree to which ‘typical’ fragmentation effects (i.e. those attributed to area and isolation) are exhibited in any given case is as much a function of characteristics in the matrix as those in the remnants. In particular the extent, degree and permanence of alterations to the matrix have a tremendous and under-appreciated potential to mediate the negative effects of changes in forest area, isolation and edge. Such a view argues for greater emphasis on the spatial and temporal dynamics of deforestation, including not only patterns of forest loss and fragmentation, but also spatial heterogeneity of recovery (e.g. Messina & Walsh, 2001). Recognizing the variability of conditions in the matrix and its potential role as habitat, source, conduit and filter (rather than as a simple barrier) also helps to shift the examination of forest fragmentation effects away from a patch-based perspective (focused on factors such as patch area and distance metrics) to a landscape mosaic perspective that recognizes the importance of gradients in habitat conditions (e.g. Murphy & Lovett-Doust, 2004).

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REFERENCES


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