An Amazonian forest and its fragments as a laboratory of global change

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Abstract

We synthesize findings from the world's largest and longest-running experimental study of habitat fragmentation, in central Amazonia. Over the past 35 years, Amazonian forest fragments (1 to 100 ha in size) and intact forests have experienced a wide array of ecological changes. Edge effects have been a dominant driver of fragment dynamics, strongly affecting forest microclimate, tree mortality, carbon storage, fauna, and other aspects of fragment ecology. The matrix of vegetation surrounding fragments has changed markedly over time (evolving from large cattle pastures to mosaics of abandoned pasture and regrowth forest), and this in turn has strongly influenced fragment dynamics and faunal persistence. Both rare weather events and apparent global-change drivers have significantly influenced forest structure and dynamics across the study area. Such drivers are likely to interact synergistically with habitat fragmentation and other disturbances such as logging, hunting, and fire, creating an even greater peril for the Amazonian biota.

Keywords: Amazonia, Biodiversity, Climate change, Edge effects, Ecosystem services, Environmental synergisms, Global change, Habitat fragmentation, Rainforest

1. Introduction

1.1 Amazonia and global change

Amazonia stands at the intersection of several key questions for global change, both for study and for action. The Amazon is believed to be one of the regions that will be most impacted by projected climate changes (Dai 2012; IPCC 2013). It has the potential to contribute significantly to efforts to mitigate climate change during the narrow window of time that we have to avert "dangerous" warming. It is also one of the places where avoiding greenhouse-gas emissions (by avoiding forest destruction) brings with it the greatest social and environmental co-benefits (Stickler et al. 2009).

The Biological Dynamics of Forest Fragments Project (BDFFP), with 35 years of research in fragmented and continuous forest in Central Amazonia (Fig. 1), contributes to quantifying all of these roles in global change. BDFFP studies assess the vulnerability of the forest to changes in meteorological parameters (Laurance et al. 2009a), including those that are aggravated by fragmentation (Laurance 2004). The long-term monitoring of thousands of individual forest trees, and of populations of various other species in the same locations, means that changes are likely to be first detected and understood here.

The BDFFP is a source of invaluable long-term datasets. These include high-quality estimates of Amazon forest biomass and carbon stocks (Phillips et al. 1998, Baker et al. 2004)—needed to reduce uncertainties in estimating the climatic impact of destroying the forest and the consequent benefit of avoiding this destruction. The project also contributes greatly to knowledge of the diversity of species and their relationships in an Amazon forest ecosystem (Laurance et al. 2010a, ter Steege et al. 2013). Biodiversity and ecosystem processes represent part of what is lost when the forest is destroyed or degraded, whether by direct human action, by climate change, or by the interaction of both together. Understanding these processes is also essential for assessing not only the vulnerability of forests, but also their potential resilience in the face of global change.

The rapid loss and fragmentation of old-growth forests are among the greatest threats to tropical biodiversity (Lovejoy et al. 1986, Sodhi et al. 2004, Laurance and Peres 2006). More than half of all surviving tropical forest occurs in the Amazon Basin, which is being seriously altered by large-scale agriculture (Fearnside, 2001a, Gibbs et al. 2010), industrial logging (Asner et al. 2005), proliferating roads (Laurance et al. 2001a, Fearnside 2002, 2007, Killeen 2007), and oil and gas developments (Finer et al. 2008).

The exploitation of Amazonia is driving forest fragmentation on a vast spatial scale. By the early 1990s, the area of Amazonian forest that was fragmented (<100 km^2) or vulnerable to edge effects (<1 km from edge) was over 150% greater than the area that had been deforested (Skole and Tucker 1993). From 1999 to 2002, deforestation and logging in Brazilian Amazonia respectively created ~32,000 and ~38,000 km of new forest edge annually (Broadbent et al. 2008). Prevailing land uses in Amazonia, such as cattle ranching and small-scale farming, produce landscapes dominated by small (<400 ha) and irregularly shaped forest fragments (Cochrane and Laurance 2002, Broadbent et al. 2008). Such fragments are highly vulnerable to edge effects, fires, and other deleterious consequences of forest fragmentation (Laurance et al. 2002, Barlow et al. 2006, Cochrane and Laurance 2008).

While model predictions for future climate in Amazonia vary considerably, there is broad agreement that the region will be hotter and drier under expected global warming (Dai 2012, IPCC 2013). What this portends for Amazonian forest is a matter of some controversy. Disastrous die-off projected by the UK Meteorological Office Hadley Centre at atmospheric CO_2 concentrations approximately two times those in the pre-industrial atmosphere (Cox et al. 2000, 2004) have now been countered by a new model version from the same group indicating the Amazon forest almost entirely intact, even with up to four times the pre-industrial CO_2 concentration (Cox et al. 2013, Good et al. 2013, Huntingford et al. 2013). The main difference is inclusion of CO_2-fertilization effects, making the trees grow faster, resist stress better, and close their stomata more frequently such that they use and need less water.

The BDFFP has made a significant contribution to debate over climatic influences on the Amazon via its monitoring of lianas (Laurance et al. 2014). Lianas evidently make better use of rising CO_2 than do trees (e.g., Condon et al. 1992), and contribute significantly to tree damage and mortality (Ingwell et al. 2010). They also are most prone to form heavily vine-dominated “liana forests” in drier parts of Amazonia, where climate is similar to that expected over much wider areas of the region in the future (Fearnside 2013). BDFFP plots show a marked increase in liana abundance and biomass between censuses in 1997-99 and 2012. Since liana increases have also been found in tropical forests in Western Amazonia, Central America, the Guianas, and elsewhere, with rising CO_2 levels being one of the more likely explanations. This negative effect of CO_2 enrichment is not included in the Hadley Centre models, and would likely cancel out some of the benefits indicated in a high-CO_2 future.

BDFFP data also help reveal the direct effects of a warmer, drier climate on the forest. The microclimate on forest edges is significantly hotter and drier than that in the continuous forest (Kapos 1989, Kapos et al. 1993, Camargo and Kapos 1995). Canopy trees are vulnerable to changing microclimates on forest edges during the dry season, with desiccation detected up to 2 km from clearings (Briant et al. 2010). At the BDFFP, edge-associated tree mortality and “biomass collapse” have been extensively documented (Laurance et al. 1997, 1998, 2000, Nascimento and Laurance 2004). Because the entire forest can be expected to face comparable conditions under projected climate change, the dead trees in the BDFFP fragment edges stand as a clear warning of the power of these changes.

Better estimates of how the forest will fare under changed climate are essential for many reasons, including providing the scientific basis needed to convince both world leaders and the general public that containing climate change is worth the cost. But just as basic is the question of what to do about climate change once the world finally decides that it is time to act. The role of tropical forests is critical to this debate, as they contain a large stock of carbon that could either be released by deforestation, logging, and fire, or conserved for their crucial environmental values. The ways that avoiding these emissions could be incorporated into global mitigation efforts, how carbon benefits would be rewarded, and how they should be calculated have been the subject of longstanding controversy dividing environmental groups, national governments, and scientists (see Fearnside 2001b, 2012a,b).

One aspect of this discussion to which the BDFFP makes an important contribution is in reducing the uncertainty surrounding biomass and carbon-stock estimates for Amazon forest. The BDFFP tree survey is much more complete and carefully done than, for example, the data from about 3000 ha of 1-ha plots surveyed by the RADAMBRASIL Project (Nogueira et al. 2008). RADAMBRASIL only considers trees ≥ 31.8 cm diameter-at-breast height (DBH), whereas the BDFFP measures trees ≥ 10 cm DBH, and down to 1 cm diameter within a subsample of sites. The BDFFP also has data on other forest components not included in the RADAMBRASIL surveys, such as palms, lianas, strangler figs, understory vegetation and dead vegetation (necromass). In addition, the tree-species identifications are much better, with about 98% of the trees ≥ 10 cm DBH identified to species or morphospecies. This allows better matching with wood-density data (e.g., Fearnside 1997, Nogueira et al. 2005, 2007, Chave et al. 2006).

Crucially, the BDFFP forest data allow one to see the variability in biomass from one hectare to another. The mean aboveground biomass of live trees across 69 1-ha plots was 355.8 ± 47 tons per ha (Mg ha^{-1}), ranging from 230.7 to 491.6 Mg ha^{-1} for individual plots (Laurance et al. 1999). This great variability indicates the need for many plots, rather than relying on only a few plots of 1 ha or less scattered around the region as the basis for calibrating satellite imagery for biomass mapping and for estimating greenhouse-gas emissions from deforestation (see Fearnside 2014). The relationships of biomass with soil characters in the BDFFP (Laurance et al. 1999), and the corresponding relationships with topography and distance above the water table found in other studies in the state of Amazonas (de Castilho et al. 2006, Schietti et al. 2013), are essential to future improvement in biomass estimates across the region. These estimates form the basis of any form of reward for maintaining Amazonian forest as a global-warming mitigation measure.

1.2. The Biological Dynamics of Forest Fragments Project

Starting in 1979, the Biological Dynamics of Forest Fragments Project (BDFFP) has been assessing the impacts of fragmentation on the Amazon rainforest and biota (Lovejoy et al. 1986, Bierregaard et al. 1992, Pimm 1998, Laurance et al. 2002, 2011). Today, 35 years later, it is the world's largest and longest-running experimental study of habitat fragmentation, as well as one of the most highly cited ecological investigations ever conducted (Gardner et al. 2009, Peres et al. 2010, Pitman et al. 2011). The BDFFP has also been a global leader in research, training, and capacity development, with over 640 publications (http://pdbff.inpa.gov.br), more than 180 student theses, over 700 graduate students and conservation professionals participating in sponsored courses, and over 1000 student interns to date.

The BDFFP is located 80 km north of Manaus, Brazil and spans ~1000 km^2 . The topography is relatively flat (80–160 m elevation) but dissected by numerous stream gullies. The heavily weathered, nutrient-poor soils of the study area are typical of large expanses of the Amazon Basin. Rainfall ranges from 1900 to 3500 mm annually with a moderately strong dry season from June to October. The forest canopy is 30–37 m tall, with emergent trees to 55 m. Species richness of trees (≥ 10 cm DBH) often exceeds 280 species ha^{-1} (Oliveira and

Mori 1999, Laurance et al. 2010b) with a comparably high level of diversity also evident in many other plant and animal taxa.

The study area includes three large cattle ranges (~5000 ha each) containing 11 forest fragments (five of 1 ha, four of 10 ha, and two of 100 ha), and expanses of nearby continuous forest that serve as experimental controls. In the early 1980s, the fragments were isolated from nearby intact forest by distances of 80–650 m by clearing and burning the surrounding forest. A key feature was that pre-fragmentation censuses were conducted for many animal and plant groups (e.g. trees, understory birds, small mammals, primates, frogs, many invertebrate taxa), thereby allowing long-term changes in these groups to be assessed far more confidently than in most other fragmentation studies.

Because of poor soils and low productivity, the ranches surrounding the BDFFP fragments were largely abandoned after government fiscal incentives dried up from 1984 onwards. Secondary forests (initially dominated by *Vismia* spp. in areas that were cleared and burned, or by *Cecropia* spp. in areas that were cleared without fire) proliferated in many formerly cleared areas (Mesquita et al. 2001). Some of the regenerating areas initially dominated by *Cecropia* spp. later developed into quite mature (>20 m tall), species-rich secondary forests. *Vismia*-dominated regrowth, which is relatively species poor, is changing far more slowly (Norden et al. 2010). To help maintain isolation of the experimental fragments, 100 m-wide strips of regrowth were cleared and burned around each fragment on 4–5 occasions, most recently in 2013-2014. Additional human disturbances that harm many fragmented landscapes in the Amazon, such as major fires and logging, are largely prevented at the BDFFP. Hunting pressure has been very limited until recently. Laurance and Bierregaard (1997) and Bierregaard et al. (2001) provide detailed descriptions of the study area and design.

3. Sample and area effects

3.1. Sample effects are important in Amazonia

Many species in Amazonian forests are rare or patchily distributed. This phenomenon is especially pronounced in the large expanses of the basin that overlay heavily weathered, nutrient-poor soils (e.g. Radtke et al. 2008), where resources such as fruits, flowers, and nectar are scarce and plants are heavily defended against herbivore attack (Laurance 2001). This has a key implication for understanding forest fragmentation: given their rarity, many species may be absent from fragments not because their populations have vanished, but because they were simply not present at the time of fragment creation—a phenomenon termed the ‘sample effect’ (Wilcox and Murphy 1985). Such sample effects are the hypothesized explanation for the absence of many rare understory bird species from fragments (Ferraz et al. 2007). In addition, many beetles (Didham et al. 1998a), bats (Sampaio et al. 2003), ant-defended plants (Bruna et al. 2005), and trees (Bohlman et al. 2008, Laurance et al. 2010b) at the BDFFP exhibit high levels of habitat specialization or patchiness. In a region where rarity and patchy distributions of species are the norm, sample effects appear to play a major role in structuring fragmented communities. Given these sample effects, nature reserves will have to be especially large to sustain viable populations of rare species (Lovejoy and Oren 1981, Laurance 2005, Peres 2005, Radtke et al. 2008).

3.2. Fragment size is vital

Although fragments range from just 1–100 ha in the BDFFP study area, understanding fragment-area effects has long been a central goal of the project (Lovejoy and Oren 1981, Lovejoy et al. 1984, 1986). The species richness of many organisms declines with fragment area, even with constant sampling effort across all fragments. Such declines are evident in leaf bryophytes (Zartman 2003), tree seedlings (Benítez-Malvido and Martinez-Ramos 2003a), palms (Scariot 1999), understory insectivorous birds (Stratford and Stouffer 1999; Ferraz et al. 2007), gleaning animal-eating bats (Sampaio 2000, Rocha et al., 2013), primates (Gilbert and Setz 2001, Boyle and Smith 2010a), and larger herbivorous mammals (Timo 2003), among others. For these groups, smaller fragments are often unable to support viable populations and deleterious edge effects—ecological changes associated with the abrupt, artificial edges of forest fragments— can also rise sharply in intensity (Didham et al. 1998a). A few groups, such as ant-defended plants and their ant mutualists, show no significant decline in diversity with fragment area (Bruna et al. 2005).

Fragment size also influences the rate of species losses, with smaller fragments losing species more quickly (Lovejoy et al. 1986, Stouffer et al. 2008). Assuming the surrounding matrix is hostile to bird movements and precludes colonization, Ferraz et al. (2003) estimated that a 1000-fold increase in fragment area would be needed to slow the rate of local species extinctions by 10-fold. Even a fragment of 10,000 ha in area would be expected to lose a substantial part of its bird fauna within one century (Ferraz et al. 2003). Similarly, mark-recapture data suggest that very large fragments will be needed to maintain fully intact assemblages of some faunal groups, such as ant-following birds, which forage over large areas of forest (Van Houtan et al. 2007).

4. Edge effects

4.1. Forest hydrology is disrupted

The hydrological regimes of fragmented landscapes differ markedly from those of intact forest (Kapos 1989). Pastures or crops surrounding fragments have much lower rates of evapotranspiration than do forests because they have far lower leaf area and thus less rooting depth. Additionally, such clearings are hotter and drier than forests (Camargo & Kapos 1995). Field observations and heat-flux simulations suggest that desiccating conditions can penetrate up to 100–200 m into fragments from adjoining clearings (Malcolm 1998; Didham and Lawton 1999). Further, streams in fragmented landscapes experience greater temporal variation in flows than do those in forests, because clearings surrounding fragments have less evapotranspiration and rainfall interception by vegetation (Trancoso 2008). This promotes localized flooding in the wet season and stream failure in the dry season, with potentially important impacts on aquatic invertebrates (Nessimian et al. 2008) and other organisms. Forest fragmentation also can alter low-level atmospheric circulation, which in turn affects local cloudiness and rainfall.

The warm, dry air over clearings tends to rise, creating zones of low air pressure. The relatively cool, moist air over forests is drawn into this vacuum (Avissar and Schmidt, 1998). As it warms it also rises and forms convectional clouds over the clearing, which can lead to localized thunderstorms (Avissar and Liu 1996). In this way, clearings of a few hundred hectares or more can draw moisture away from nearby forests (Laurance 2004a, Cochrane and Laurance 2008). In Eastern Amazonia, satellite observations of canopy-water content suggest such desiccating effects typically penetrate 1.0–2.7 km into fragmented forests (Briant et al. 2010). This moisture-robbing function of clearings, in concert with frequent burning in adjoining pastures, could help explain why fragmented forests are so vulnerable to destructive, edge-related fires (Cochrane and Laurance 2002, 2008).

4.2. Edge effects often dominate fragment dynamics

Edge effects are among the most important drivers of ecological change in the BDFFP fragments. The distance to which different edge effects penetrate into fragments varies widely, ranging from <10 to 300 m at the BDFFP (Laurance et al. 2002) and considerably further (at least 2–3 km) in areas of the Amazon where edge-related fires are common (Cochrane and Laurance 2002, 2008; Briant et al. 2010).

Edge phenomena are remarkably diverse. They include increased desiccation stress, wind shear, and wind turbulence that sharply elevate rates of tree mortality and damage (Laurance et al. 1997, 1998a). These in turn cause wide-ranging alterations in the community composition of trees (Laurance et al. 2000, 2006a, 2006b) and lianas (Laurance et al., 2001b). Such stresses may also reduce germination (Bruna 1999) and establishment (Uriarte et al., 2010) of shade-tolerant plant species in fragments, leading to dramatic changes in the composition and abundance of tree seedlings (Benítez-Malvido 1998, Benítez-Malvido and Martinez-Ramos 2003a).

Many animal groups, such as numerous bees, wasps, flies (Fowler et al. 1993), beetles (Didham et al. 1998a, 1998b), ants (Carvalho and Vasconcelos 1999), butterflies (Brown and Hutchings 1997), understory birds (Quintela 1985, Laurance 2004b), and gleaning animal-eating bats (Rocha et al. 2013) decline in abundance near fragment edges. Negative edge effects are apparent even along forest roads (20–30 m width) in large forest tracts. Among understory birds, for example, five of eight foraging guilds declined significantly in abundance within 70 m of roads, whereas tree mortality increased and canopy cover declined (Laurance 2004b).

Some groups of organisms remain stable or even increase in abundance near edges. Leaf bryophytes (Zartman and Nascimento 2006), wandering spiders (*Ctenus* spp.; Rego et al. 2007, Mestre and Gasnier 2008), and many frogs (Gascon 1993) show no significant response to edges. Species that favor forest ecotones or disturbances, such as many gap-favoring and frugivorous bird species (Laurance 2004b), hummingbirds (Stouffer and Bierregaard 1995a), frugivorous bats that exploit early successional plant species (Sampaio 2000), light-loving butterflies (Leidner et al. 2010), and fast-growing lianas (Laurance et al. 2001b), increase in abundance near edges, sometimes dramatically.

4.3. Edge effects are cumulative

BDFFP research provides strong support for the idea that two or more nearby edges create more severe edge effects than does just one (Fig. 2). This conclusion is supported by studies of edge-related changes in forest microclimate (Kapos 1989, Malcolm 1998), vegetation structure (Malcolm 1994), tree mortality (Laurance et al. 2006a), abundance and species richness of tree seedlings (Benítez-Malvido 1998, Benítez-Malvido and Martinez-Ramos 2003a), liana abundance (Laurance et al. 2001b), and the density and diversity of disturbance-loving pioneer trees (Laurance et al. 2006a, 2006b, 2007). The additive effects of nearby edges could help to explain why small (<10 ha) or irregularly shaped forest remnants are often so severely altered by forest fragmentation (Zartman 2003, Laurance et al. 2006a).

4.4. Edge age, structure, and adjoining vegetation influence edge effects

When a forest edge is newly created it is open to fluxes of wind, heat, and light, creating sharp edge-interior gradients in forest microclimate that stress or kill many rainforest trees (Lovejoy et al. 1986, Sizer and Tanner 1999). As the edge ages, however, proliferating vines and lateral branch growth tend to ‘seal’ the edge, making it less permeable to microclimatic changes (Camargo and Kapos 1995, Didham and Lawton 1999). Tree death from microclimatic stress is likely to decline over the first few years after edge creation (D’Angelo et al. 2004) because the edge becomes less permeable, because many drought-sensitive individuals die immediately, and because surviving trees may acclimate to drier, hotter conditions near the edge (Laurance et al. 2006a). Tree mortality from wind turbulence, however, probably increases as the edge ages and becomes more closed. This is because, as suggested by wind-tunnel models, downwind turbulence increases when edges are less permeable (Laurance 2004a).

Regrowth forest adjoining fragment edges can also lessen edge-effect intensity.

Microclimatic alterations (Didham and Lawton 1999), tree mortality (Mesquita et al. 1999), and edge avoidance by understory birds (Develey and Stouffer 2001, Laurance 2004b; Laurance et al. 2004) and gleaning animal-eating bats (Meyer et al., 2013) are all reduced substantially when forest edges are buffered by adjoining regrowth forest, relative to edges adjoined by cattle pastures.

5. Isolation and matrix effects

5.1. Matrix structure and composition affect fragments

Secondary forests have gradually overtaken most pastures in the BDFFP landscape. This lessens the effects of fragmentation for some taxa as the matrix becomes less hostile to faunal use and movements. Several species of insectivorous birds that had formerly disappeared have recolonized fragments as the surrounding secondary forest grew back (Stouffer and Bierregaard 1995b). The rate of bird extinction has also declined (Stouffer et al. 2008). Similarly, gleaning animal-eating bats, which occurred at low abundances in fragments (Sampaio 2000) and in secondary regrowth (Bobrowiec and Gribel 2010) 10-15 years ago, have since increased in response to matrix regeneration (Meyer et al. 2013). A number of other species, including certain forest spiders (Mestre and Gasnier 2008), dung beetles (Quintero and Roslin 2005), euglossine bees (Becker et al. 1991), and monkeys such as red howlers, bearded sakis, and brown capuchins (Boyle and Smith 2010a) have recolonized some fragments.

The surrounding matrix also has a strong effect on plant communities in fragments by mediating certain edge effects (see above), influencing the movements of pollinators (Dick 2001, Dick et al. 2003) and seed dispersers (Jorge 2008, Bobrowiec and Gribel 2010, Boyle and Smith 2010a), and strongly affecting the seed rain that arrives in fragments. For instance, pioneer trees regenerating in fragments differed strikingly in composition between fragments surrounded by *Cecropia*-dominated regrowth and those encircled by *Vismia*-dominated regrowth (Nascimento et al. 2006). In this way plant and animal communities in fragments could come to mirror to some extent the composition of the surrounding matrix (Laurance et al. 2006a, 2006b), a phenomenon observed elsewhere in the tropics (e.g. Janzen 1983, Diamond et al. 1987).

5.2 Matrix is affected by history and forest proximity

Land-use history is a primary driver of secondary succession in the Central Amazon, resulting in the establishment of distinct trajectories differing in structure, composition, biomass, and dynamics (Mesquita et al. 1999, Williamson et al. 2014). Intensive use with prescribed fire to maintain pastures compromises the regenerative potential of land which, once abandoned, is colonized by few species and dominated by the genus *Vismia*, resulting in secondary forests that are depauperate in richness and stalled in succession. Where land use has been less intensive, a more diverse vegetation, dominated by the genus *Cecropia* colonizes, fostering relatively rapid plant succession.

Plant density and species diversity in secondary forests decrease with distance from forest edge, and are significantly different comparing *Vismia* and *Cecropia* dominated secondary forests. These differences were initially attributed to differential seed dispersal limitations (Mesquita et al. 2001, Puerta, 2002). Wieland et al. (2011), however, showed that the seed rain was similar for both types of second-growth and dominated by pioneer species, with only the occasional presence of mature forest species, even very close to forest edges. These results point to other relevant processes affecting plant establishment, such as seed consumption, germination success, and seedling herbivory (Wieland et al. 2011, Massoca et al. 2013)

5.3 Even narrow clearings are harmful

Many Amazonian species avoid clearings, and even a forest road can be an insurmountable barrier for some. A number of understory insectivorous birds exhibit depressed abundances near forest roads (20–40 m width) (Laurance 2004b) and strongly inhibited movements across those roads (Laurance et al. 2004). Experimental translocations of resident adult birds reveal such bird species will cross a highway (50–75 m width) but not a small pasture (250 m width) to return to their territory (Laurance and Gomez 2005). Individuals of other vulnerable species, however, have traversed clearings to escape from small fragments to larger forest areas (Harper 1989, Van Houtan et al. 2007). Captures of understory birds declined dramatically in fragments when a 100 m-wide swath of regrowth forest was cleared around them, suggesting that species willing to traverse regrowth would not cross clearings (Stouffer et al. 2006).

Aside from birds, clearings of just 100–200 m width can evidently reduce or halt the movements of many forest-dependent organisms (Laurance et al. 2009b), ranging from herbivorous insects (Fáveri et al. 2008), euglossine bees (Powell and Powell 1987), and dung beetles (Klein 1989) to the spores of epiphyllous lichens (Zartman and Nascimento 2006, Zartman and Shaw 2006). Narrow clearings can also provide invasion corridors into forests for exotic and nonforest species (Gascon et al. 1999; Laurance et al. 2009b).

6. Landscape dynamics

6.1. Rare disturbances can leave lasting legacies

Rare events such as windstorms and droughts have strongly influenced the ecology of fragments. Rates of tree mortality rose abruptly in fragmented (Laurance et al., 2001c) and intact forests (Williamson et al. 2000, Laurance et al. 2009a) in the year after the intense 1997 El Niño drought. Such pulses of tree death help drive changes in the floristic composition and carbon storage of fragments (Laurance et al. 2007). Leaf-shedding by drought-stressed trees also increases markedly during droughts, especially within ~60 m of forest edges (Laurance and Williamson 2001). This increases the susceptibility of fragments to destructive surface fires (Cochrane and Laurance 2002, 2008).

Intense windblasts from convectional thunderstorms have occasionally strafed parts of the BDFFP landscape and caused intense forest damage and tree mortality, especially in the fragments. Fragments in the easternmost cattle ranch at the BDFFP have had substantially lower rates of tree mortality than did those in the other two ranches, because the former have so far escaped windstorms (Laurance et al. 2007). These differences have strongly influenced the rate and trajectory of change in tree-community composition in fragments (Laurance et al. 2006b). Hence, by altering forest dynamics, composition, structure, and carbon storage, rare disturbances have left an enduring imprint on the ecology of fragmented forests.

6.2. Fragments are hyperdynamic

The BDFFP fragments experience exceptionally large variability in population and community dynamics, relative to intact forest, despite being largely protected from ancillary human threats such as fires, logging, and overhunting. Being a small resource base, a habitat fragment is inherently vulnerable to stochastic effects and external vicissitudes. Species abundances can fluctuate dramatically in small communities, especially when immigration is low and disturbances are frequent (Hubbell 2001). Edge effects, reduced dispersal, external disturbances, and changing herbivore or predation pressure can all elevate the dynamics of plant and animal populations in fragments (Laurance 2002, 2008).

Many examples of hyperdynamism have been observed in the BDFFP fragments. Some butterfly species have experienced dramatic population irruptions in response to a proliferation of their favored host plants along fragment margins (Brown and Hutchings

1997), and butterfly communities in general are hyperdynamic in fragments (Leidner et al. 2010). Bat assemblages also show pronounced species turnover, particularly in 1-ha fragments (Meyer et al. 2013). Streamflows are far more variable in fragmented than forested watersheds (Trancoso 2008). Rates of tree mortality and recruitment are chronically elevated in fragments (Laurance et al. 1998a, b), with major pulses associated with rare disturbances (see above). Further, tree species disappear and turn over far more rapidly in fragments than intact forest, especially within ~100 m of forest margins (Laurance et al. 2006b). These and many other instabilities plague small, dwindling populations in the BDFFP fragments.

6.3. Fragments in different landscapes diverge

An important insight is that different fragmented landscapes— even those as alike as the three large cattle ranches in the BDFFP, which have very similar forests, soils, climate, fragment ages, and land-use histories—can diverge to a surprising degree in species composition and dynamics. Although spanning just a few dozen kilometers, the three ranches are following unexpectedly different trajectories of change.

At the outset, small initial differences among the ranches multiplied into much bigger differences. Parts of the western and eastern ranches were cleared in 1983, when an early wet season prevented burning of the felled forest. Tall, floristically diverse *Cecropia*-dominated regrowth quickly developed in these areas, whereas areas cleared in the years just before or after became cattle pastures or, eventually, scrubby *Vismia*-dominated regrowth (Williamson and Mesquita 2001). These different successional trajectories manifested, for instance, as distinct differences in bat assemblage composition, whereby *Cecropia*-dominated regrowth retained a considerable fraction of forest-specialist bat species found in continuous forest compared to *Vismia* regrowth (Bobrowiec and Gribel 2010). As discussed above, the differing matrix vegetation strongly affected the dynamics of plant and animal communities in the nearby fragments. These differences were magnified by subsequent windstorms, which heavily damaged most fragments in the central and western ranches, yet left fragments in the eastern ranch unscathed. Even identically sized fragments in the three ranches have had remarkably different dynamics and vectors of compositional change (Laurance et al. 2007).

The apparently acute sensitivity of fragments to local landscape and weather dynamics—even within a study area as initially homogeneous as ours—prompted us to propose a ‘landscape-divergence hypothesis’ (Laurance et al. 2007). We argue that fragments within the same landscape tend to have similar dynamics and trajectories of change in species composition, which will often differ from those in other landscapes. Over time, this process will tend to homogenize fragments in the same landscape, and promote ecological divergence among fragments in different landscapes. Evidence for this hypothesis is provided by tree communities in our fragments, which appear to be diverging in composition among the three cattle ranches (Fig. 3). Pioneer and weedy trees are increasing in all fragments, but the composition of these generalist plants and their rate of increase differ markedly among the three ranches (Scariot 2001, Laurance et al. 2006a, 2007, Nascimento et al. 2006). This same pattern of landscape homogenization within ranches can also be seen for bat assemblages in the secondary forest matrix (Bobrowiec and Gribel, 2010).

7. Broader consequences of fragmentation

7.1. Ecological distortions are common

Many ecological interactions are altered in fragmented forests. Fragmented communities can pass through unstable transitional states that may not otherwise occur in nature (Terborgh et al. 2001). Moreover, species at higher trophic levels, such as predators and parasites, are often more vulnerable to fragmentation than are herbivores, thereby altering the structure and functioning of food webs (Didham et al. 1998b, Terborgh et al. 2001).

BDFFP findings suggest that even unhunted forest fragments have reduced densities of key mammalian seed dispersers. As a result, seed dispersal for an endemic, mammal-dispersed tree (*Duckeodendron cestroides*) was far lower in fragments, with just ~5% of the number of seeds being dispersed >10 m away from parent trees than in intact forest (Cramer et al. 2007a). Leaf herbivory appears reduced in fragments, possibly because of lower immigration of insect herbivores (Fáveri et al. 2008). Dung beetles exhibit changes in biomass and guild structure in fragments (Radtke et al. 2008) that could alter rates of forest nutrient cycling and secondary seed dispersal (Klein 1989, Andresen 2003). Exotic Africanized honeybees, a generalist pollinator, are abundant in matrix and edge habitats and can alter pollination distances and gene flow for some tree species (Dick 2001, Dick et al. 2003). A bewildering variety of ecological distortions can pervade fragmented habitats, and a challenge for conservation biologists is to identify those of greatest importance and generality.

7.2. Fragmentation affects much more than biodiversity

Habitat fragmentation affects far more than biodiversity and interactions among species; many ecosystem functions, including hydrology (see above) and biochemical cycling, are also being altered. Among the most important of these are fundamental changes in forest biomass and carbon storage.

Carbon storage in fragmented forests is affected by a suite of interrelated changes. Many trees die near forest edges (Laurance et al. 1997, 1998a), including an alarmingly high proportion of large (≥60 cm dbh) canopy and emergent trees that store much forest carbon (Laurance et al. 2000). Fast-growing pioneer trees and lianas that proliferate in fragments are smaller and have lower wood density, and thereby sequester much less carbon, than do the mature-phase trees they replace (Laurance et al. 2001b, 2006a). Based on current rates of forest fragmentation, the edge-related loss of forest carbon storage might produce up to 150 million tons of atmospheric carbon emissions annually, above and beyond that from tropical deforestation per se (Laurance et al. 1998c). This would exceed the yearly carbon emissions of the entire United Kingdom. Note, however, that most of this emission is already counted in the existing estimates of the impact of Amazonian land-use change because the deforestation emission estimates use forest biomass values for undegraded forest (Fearnside 2000). Because most deforestation occurs by expansion of already-existing clearings, forest edges (with reduced biomass) are the first areas to be cleared. Only the annual increase in the total length of forest edges represents an addition. Improved emissions estimates, with accounting for degradation by logging, fire and fragmentation, are a high priority.

In addition, biomass is being redistributed in fragmented forests. Less biomass is stored in large, densely wooded old-growth trees and more in fast-growing pioneer trees, disturbance-loving lianas, woody debris, and leaf litter (Sizer et al. 2000, Nascimento and Laurance 2004, Vasconcelos and Luizão 2004). Finally, carbon cycling accelerates. The large, mature-phase trees that predominate in intact forests can live for many centuries or even millennia (Chambers et al. 1998, Laurance et al. 2004), sequestering carbon for long periods of time. However, the residence time of carbon in early successional trees, vines, and necromass (wood debris, litter), which proliferate in fragments, is far shorter (Nascimento and Laurance 2004). Other biochemical cycles, such as those affecting key nutrients like phosphorus (Sizer et al. 2000) and calcium (Vasconcelos and Luizão 2004), may also be altered in fragmented forests, given the striking changes in biomass dynamics, hydrology, and thermal regimes they experience.

8. Predicting species responses to fragmentation

8.1. Species losses are highly nonrandom

Species extinctions in the BDFFP fragments have occurred in a largely predictable sequence, with certain species being consistently more vulnerable than others. Among birds, a number of understory insectivores, including army ant-followers, solitary species, terrestrial foragers, and obligate mixed-flock members, are most susceptible to fragmentation. Others, including edge/ gap species, insectivores that use mixed flocks facultatively, hummingbirds, and many frugivores, are far less vulnerable (Antongiovanni and Metzger 2005, Stouffer et al. 2006, 2008). In a similar vein, among bats, gleaning animalivores are consistently the most vulnerable species whereas many frugivores respond positively to fragmentation and disturbance (Sampaio 2000, Bobrowiec and Gribel 2010, Rocha et al. 2013). Primates exhibit similarly predictable patterns of species loss, with wide-ranging frugivores, especially the black spider-monkey, being most vulnerable (Boyle and Smith 2010a). Local extinctions in fragments follow a foreseeable pattern, with species assemblages in smaller fragments rapidly forming a nested subset of those in larger fragments (Stouffer et al. 2008). Random demographic and genetic processes may help to drive tiny populations into oblivion, but the species that reach this precarious threshold are far from random.

8.2. Fragmented communities are not neutral

An important corollary of nonrandom species loss is that fragmented forests are not neutral. Neutral theory (Hubbell 2001) assumes that species in diverse, space-limited communities, such as tropical trees, are competitively equivalent in order to make predictions about phenomena such as species-area curves, the relative abundances of species in communities, and the rate of species turnover in space. Hubbell (2001) emphasizes the potential relevance of neutral theory for predicting community responses to habitat fragmentation: for isolated communities, locally abundant species should be least extinction prone, with rare species being lost more frequently from random demographic processes. Over time, fragments should become dominated by initially abundant species, with rare species gradually vanishing; other ecological traits of species are considered unimportant.

Gilbert et al. (2006) tested the efficacy of neutral theory for predicting changes in tree communities at the BDFFP. Neutral theory effectively predicted the rate of species extinction from plots in fragmented and intact forest as a function of the local diversity and the mortality rate of trees. However, in most fragments, the observed rate of change in species composition was 2–6 times faster than predicted by the theory. Moreover, the theory was wildly erroneous in predicting which species are most prone to extinction. Rather than becoming increasingly dominated by initially common species, fragments in the BDFFP landscape have experienced striking increases in disturbance-loving pioneer species (Laurance et al. 2006a), which were initially rare when the fragments were created. As a model for predicting community responses to habitat fragmentation, neutral theory clearly failed, demonstrating that ecological differences among species strongly influence their responses to fragmentation.

8.3. Matrix use and area needs determine animal vulnerability

The responses of animal species to fragmentation appear largely governed by two key sets of traits. The first is their spatial requirements for forest habitat. In birds (Van Houtan et al. 2007) and mammals (Timo 2003), wide-ranging forest species are more vulnerable than are those with localized ranges and movements. Species with limited spatial needs, such as many small mammals (Malcolm 1997), hummingbirds (Stouffer et al. 2008), frogs (Tocher et al. 1997), and ants (Carvalho and Vasconcelos 1999), are generally less susceptible to fragmentation.

The second key trait for fauna is their tolerance of matrix habitats (Gascon et al. 1999), which comprises cattle pastures and regrowth forest in the BDFFP landscape. Populations of species that avoid the matrix will be entirely isolated in fragments, and therefore vulnerable to local extinction, whereas those that tolerate or exploit the matrix often persist (Laurance 1991, Malcolm 1997, Antongiovanni and Metzger 2005, Ferraz et al. 2007, Bobrowiec and Gribel 2010). At least among terrestrial vertebrates, matrix use is positively associated with tolerance of edge habitats (Laurance 2004b, Farneda 2013), an ability to traverse small clearings (Laurance et al. 2004, Laurance and Gomez 2005), and behavioral flexibility (Neckel-Oliveira and Gascon 2006, Stouffer et al. 2006, Van Houtan et al. 2006, Boyle and Smith 2010b). Within particular animal groups, such as beetles or small mammals, traits such as body size and natural abundance are poor or inconsistent predictors of vulnerability (Laurance 1991, Didham et al. 1998a, Jorge 2008, Boyle and Smith 2010a). Natural abundance, however, is an important predictor of sensitivity to fragmentation for bats at the BDFFP (Farneda, 2013).

8.4. Disturbance tolerance and mutualisms affect plant vulnerability

Among plants, a different suite of factors is associated with vulnerability to fragmentation. Because fragments suffer chronically elevated tree mortality, faster-growing pioneer trees and lianas that favor treefall gaps are favored at the expense of slower-growing mature-phase trees (Laurance et al. 2006a, b). Pioneer species often flourish in the matrix and produce abundant small fruits that are carried into fragments by frugivorous birds and bats that move between the matrix and nearby fragments (Sampaio 2000, Nascimento et al. 2006). Especially vulnerable in fragments are the diverse assemblages of smaller subcanopy trees that are physiologically specialized for growing and reproducing in dark, humid, forest-interior conditions (Laurance et al. 2006b). Tree species that have obligate outbreeding systems, rely on animal seed dispersers, or have relatively large, mammal-dispersed seeds also appear vulnerable (Laurance et al. 2006b, Cramer et al. 2007b).

These combinations of traits suggest that plant communities in fragmented forests are structured primarily by chronic disturbances and microclimatic stresses and possibly also by alterations in animal pollinator and seed-disperser communities. For long-lived plants such as *Heliconia* species and many mature-phase trees, demographic models suggest that factors that reduce adult survival and growth—such as recurring wind disturbance and edge-related microclimatic stresses—exert a strong influence on population growth (Bruna 2003, Bruna and Oli 2005).

Differential tolerance to drought also seems to play a role on secondary forests. We find higher and significant mortality and lower biomass accumulation rates in *Cecropia*-dominated secondary forests, associated with drier years, while *Vismia*-dominated regrowth showed a non-significant, but similar trend. It is likely that different species assemblages account for the differential ability of these successional pathways to support extreme climate events (Mesquita et al. 2012).

9. Broad perspectives

9.1. Long-term research is crucial

Many insights from the BDFFP would have been impossible in a shorter-term study. The exceptional vulnerability of large trees to fragmentation (Laurance et al. 2000) only became apparent after two decades of fragment isolation. Likewise, the importance of ephemeral events such as El Niño droughts (Williamson et al., 2000, Laurance et al. 2001c) and major windstorms (Laurance et al. 2007) would not have been captured in a less-enduring project. Many other key phenomena, such as the kinetics of species loss in fragments (Ferraz et al. 2003), the strong effects of matrix dynamics on fragmented bird and bat assemblages (Antongiovanni and Metzger 2005, Stouffer et al. 2006, Meyer et al. 2013), the divergence of fragments in different landscapes (Laurance et al. 2007), and the effects of fragmentation on rare or long-lived species (Benítez-Malvido and Martinez-Ramos 2003b, Ferraz et al., 2007), are only becoming understood after decades of effort.

Far more remains to be learned. For example, forest-simulation models parameterized with BDFFP data suggest that even small (<10 ha) fragments will require a century or more to stabilize in floristic composition and carbon storage (Groeneveld et al. 2009), given the long-lived nature of many tropical trees. Eventually, these fragments might experience a fundamental reorganization of their plant communities, given striking shifts in the composition of their tree, palm, liana, and herb seedlings (Scariot 2001; Benítez-Malvido and Martinez-Ramos 2003a, Brum et al. 2008). If these newly recruited plants represent the future of the forest, then the BDFFP fragments will eventually experience dramatic changes in floristic composition—comparable to those observed in some other long-fragmented ecosystems (e.g. da Silva and Tabarelli 2000, Girão et al. 2007, Santos et al. 2010).

9.2. The BDFFP is a best-case scenario

Although forest fragments in the BDFFP are experiencing a wide array of ecological changes, it is important to emphasize that it is a controlled experiment. The fragments are square, not irregular, in shape. They are isolated by distances of just 80–650 m from large tracts of surrounding mature forest. They are embedded in a relatively benign matrix increasingly dominated by regrowth forest. And they lack many of the ancillary threats, such as selective logging, wildfires, and overhunting, that plague many fragmented landscapes and wildlife elsewhere in the tropics. Such threats can interact additively or synergistically with fragmentation, creating even greater perils for the rainforest biota (Laurance and Cochrane 2001, Michalski and Peres 2005, Brook et al. 2008). For these reasons, results from the BDFFP are almost certainly optimistic relative to many human-dominated landscapes elsewhere in the tropics.

10. Conservation lessons from the BDFFP

10.1. Amazonian reserves should be large and numerous

A key conclusion from BDFFP research is that nature reserves in Amazonia should ideally be very large—on the order of thousands to tens of thousands of square kilometers (Laurance 2005, Peres 2005). Only at this size will they be likely to maintain natural ecological processes and sustain viable populations of the many rare and patchily distributed species in the region (Ferraz et al. 2007, Radtke et al. 2008); provide resilience from rare calamities such as droughts and intense storms (Laurance et al. 2007); facilitate persistence of terrestrial and aquatic animals that migrate seasonally (Bührnheim and Fernandes 2003); buffer the reserve from large-scale edge effects including fires, forest desiccation, and human encroachment (Cochrane and Laurance 2002, Briant et al. 2010); maximize forest carbon storage (Laurance et al. 1997, 1998c); and provide resilience from future climatic and atmospheric changes—the effects of which are difficult to predict for Amazonia (Laurance and Useche 2009). Further, on the ancient soils of Central and Eastern Amazonia, low plant productivity translates into low population densities of many animals up the food chain, so reserves must be proportionately larger to harbor viable populations (Radtke et al. 2008, Deichmann et al. 2011, 2012).

Nature reserves in Amazonia should also be numerous and stratified across major river basins and climatic and edaphic gradients, in order to preserve locally endemic species (Bierregaard et al. 2001, Laurance, 2007). Further, the core areas of reserves should ideally be free of roads, which can promote human encroachment and hunting, internally fragment wildlife populations, and facilitate invasions of exotic species and fire (Laurance et al. 2009b).

10.2. Protect and reconnect fragments

Few landscapes are as intact as those in the Amazon. Biodiversity hotspots, which sustain the majority of species at risk of extinction, have, by definition, lost over 80% of their natural vegetation and what remains is typically in small fragments (Myers et al. 2000). The BDFFP makes recommendations here, too. Reconnecting isolated fragments by forest restoration will be an effective way of creating areas large enough to slow the rate of species extinctions (Lima and Gascon 1999, Pimm and Jenkins 2005).

In such heavily fragmented landscapes, protecting remaining forest remnants is highly desirable, as they are likely to be key sources of plant propagules and animal seed dispersers and pollinators (Mesquita et al. 2001, Chazdon et al. 2008). They may also act as stepping stones for animal movements (Laurance and Bierregaard 1997, Dick et al. 2003). In regions where forest loss is severe, forest fragments could also sustain the last surviving populations of locally endemic species, thereby underscoring their potential value for nature conservation (Arroyo-Rodríguez et al. 2009).

10.3. Fragmented landscapes can recover

A further lesson is that fragmented landscapes, if protected from fires and other major disturbances, can begin to recover in just a decade or two. Forest edges tend to ‘seal’ themselves, reducing the intensity of deleterious edge effects (Camargo and Kapos 1995, Didham and Lawton 1999, Mesquita et al. 1999). Secondary forests can develop quickly in the surrounding matrix (Mesquita et al. 2001), especially if soils and seedbanks are not depleted by overgrazing or repeated burning (Ribeiro et al. 2009, Norden et al. 2010). Secondary forests facilitate movements of many animal species (Gascon et al. 1999), allowing them to recolonize fragments from which they had formerly disappeared (Becker et al. 1991, Quintero and Roslin 2005, Stouffer et al. 2008, Bobrowiec and Gribel 2010, Boyle and Smith

2010a, Meyer et al. 2013). Species clinging to survival in fragments can also be rescued from local extinction via the genetic and demographic contributions of immigrants (Zartman and Nascimento 2006, Stouffer et al. 2008).

11. The future of the BDFFP

The BDFFP is one of the most enduring and influential ecological research projects in existence today (Gardner et al. 2009, Peres et al. 2010). From the prism of understanding habitat fragmentation, there are vital justifications for continuing it. The project, moreover, is engaged in far more than fragmentation research: it plays a leading role in training Amazonian scientists and decision-makers, and sustains long-term research on global- change phenomena, forest regeneration, and basic ecological studies.

In its 35-year history, the BDFFP has faced myriad challenges. These include, among others, the continuing weakness the US dollar, challenges in obtaining research visas for foreign students and scientists, inadequate core funding from its US and Brazilian sponsors, and the vagaries of finding soft money for long-term research and to hold a minimal number of workers to support infrastructure and logistics. Yet today the BDFFP faces a far more direct threat: encroachment from colonists and hunters. Since the late 1990s, the paving of the 1100-km-long Manaus–Venezuela (BR-174) highway has greatly accelerated forest colonization and logging north of the city. SUFRAMA, a Brazilian federal agency that controls an expanse of land north of Manaus that includes the BDFFP, has begun settling families in farming plots around the immediate periphery of the study area. At least six colonization projects involving 180 families are planned for the area (Laurance and Luizão 2007). This could be the beginning of a dramatic influx into the area, especially if the proposed BR-319 highway between Manaus and Rondônia, a major deforestation hotspot in southern Amazonia, is completed as planned (Fearnside and Graça 2006).

To date, BDFFP staff and supporters have managed to stave off most of the colonization projects—which also threaten to bisect the Central Amazonian Conservation Corridor, a budding network of protected and indigenous lands that is one of the most important conservation areas in the entire Amazon basin (Laurance and Luizão 2007). Yet it is an uphill battle against a government bureaucracy that appears myopically determined to push ahead with colonization at any cost—despite the fact that colonists can barely eke out a living on the region's infamously poor soils (Fearnside and Leal Filho, 2001). That such a globally important research project and conservation area could be lost seems unthinkable. That it could be lost for such a limited gain seems tragic.

Amazon forest is under stress from a variety of global changes that are expected to increase in the coming decades. Beyond the considerable contributions of the BDFFP to date in providing information relevant to understanding these changes, the project is uniquely well placed to track the impacts of these changes as they occur. The BDFFP must continue its role in contributing to the scientific basis for more serious global efforts to contain the current human destruction of the environment at both the global and regional level.

Acknowledgements

We thank [ ] for helpful comments on the manuscript. The National Institute for Amazonian Research (INPA), Smithsonian Institution, US National Science Foundation, Brazilian Science Foundation (CNPq), Amazonian State Science Foundation (FAPEAM), NASA-LBA program, USAID, Mellon Foundation, Blue Moon Fund, Marisla Foundation, and other organizations generously supported the BDFFP. Much of this text is updated from Laurance et al. (2011). This is publication number XXX in the BDFFP technical series.

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FIGURE CAPTIONS

Figure 1. Map of the Biological Dynamics of Forest Fragments Project in central Amazonia.

Figure 2. Forest plots affected by two or more nearby edges (plot center <100 m from edge) suffer greater tree mortality (A) and have a higher density (B) and species richness (C) of disturbance-loving pioneer trees than do plots with just one nearby edge. Values shown are the mean ± SD (after Laurance et al. 2006a).

Figure 3. Increasing divergence of tree-community composition in three fragmented Amazonian landscapes. Tree communities in forest-edge plots (<100 m from the nearest edge) are shown before forest fragmentation and 13–18 years after fragmentation, based on a single ordination of all plots and censuses in the study area. The ordination used importance values for all 267 tree genera found in the plots (after Laurance et al. 2007).

Fig. 1.

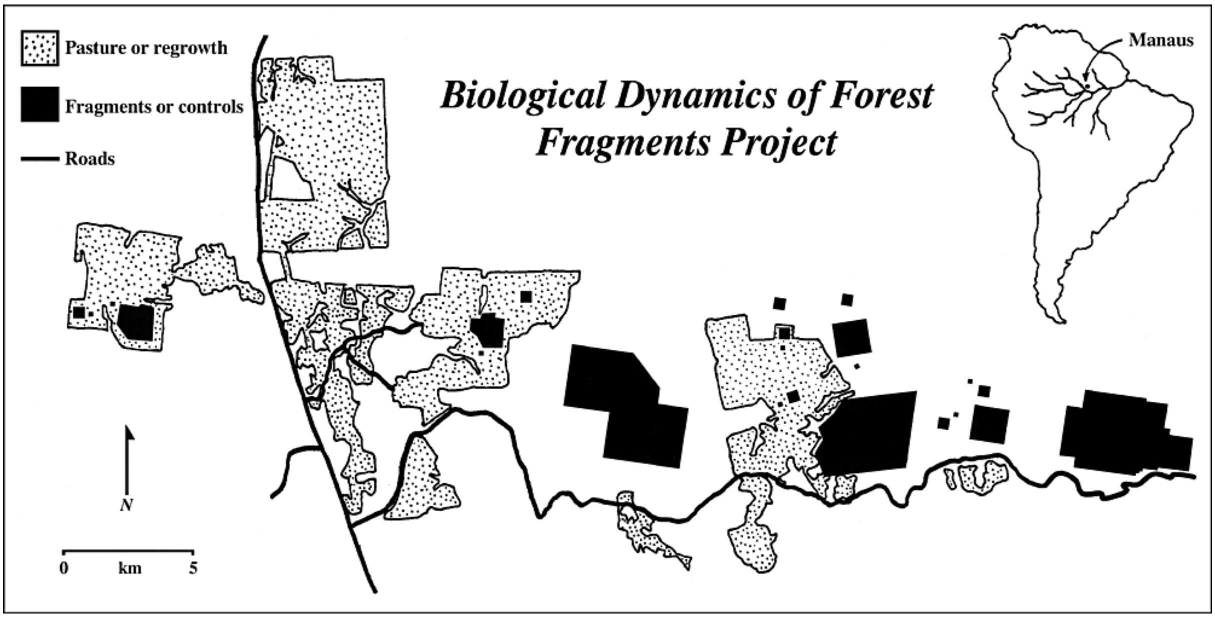
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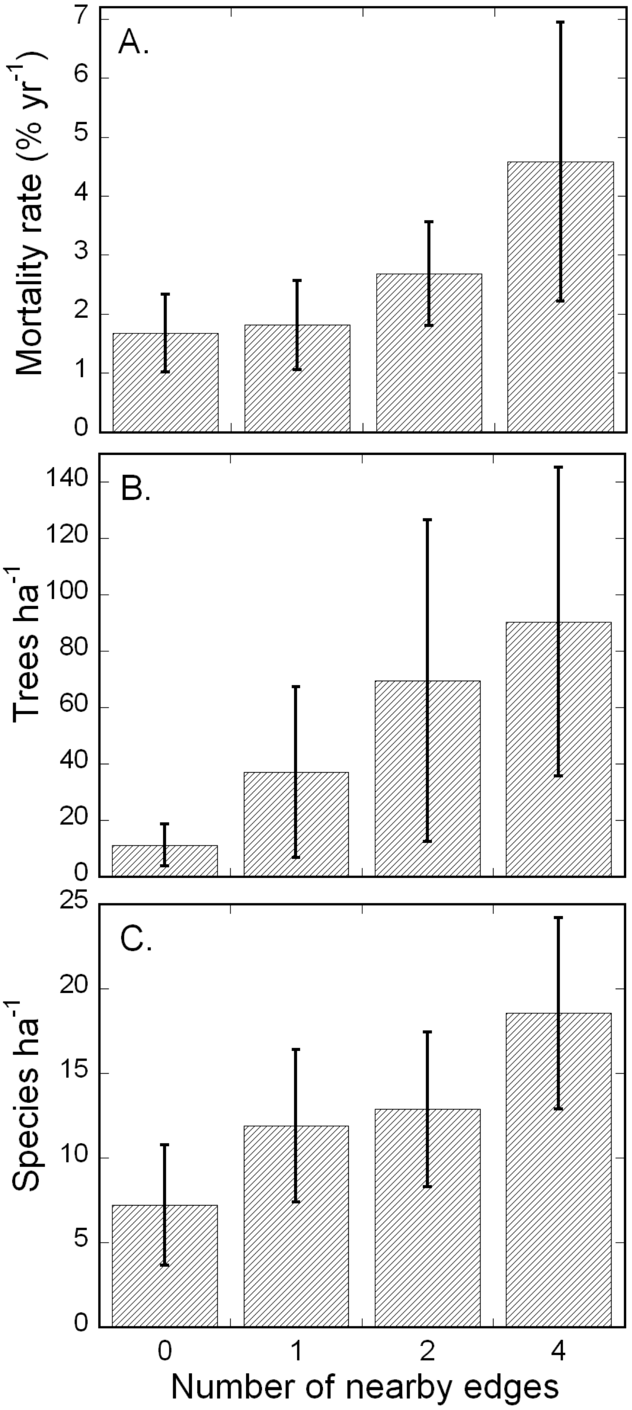
Fig. 2


A.
Mortality rate (% yr-1)
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5
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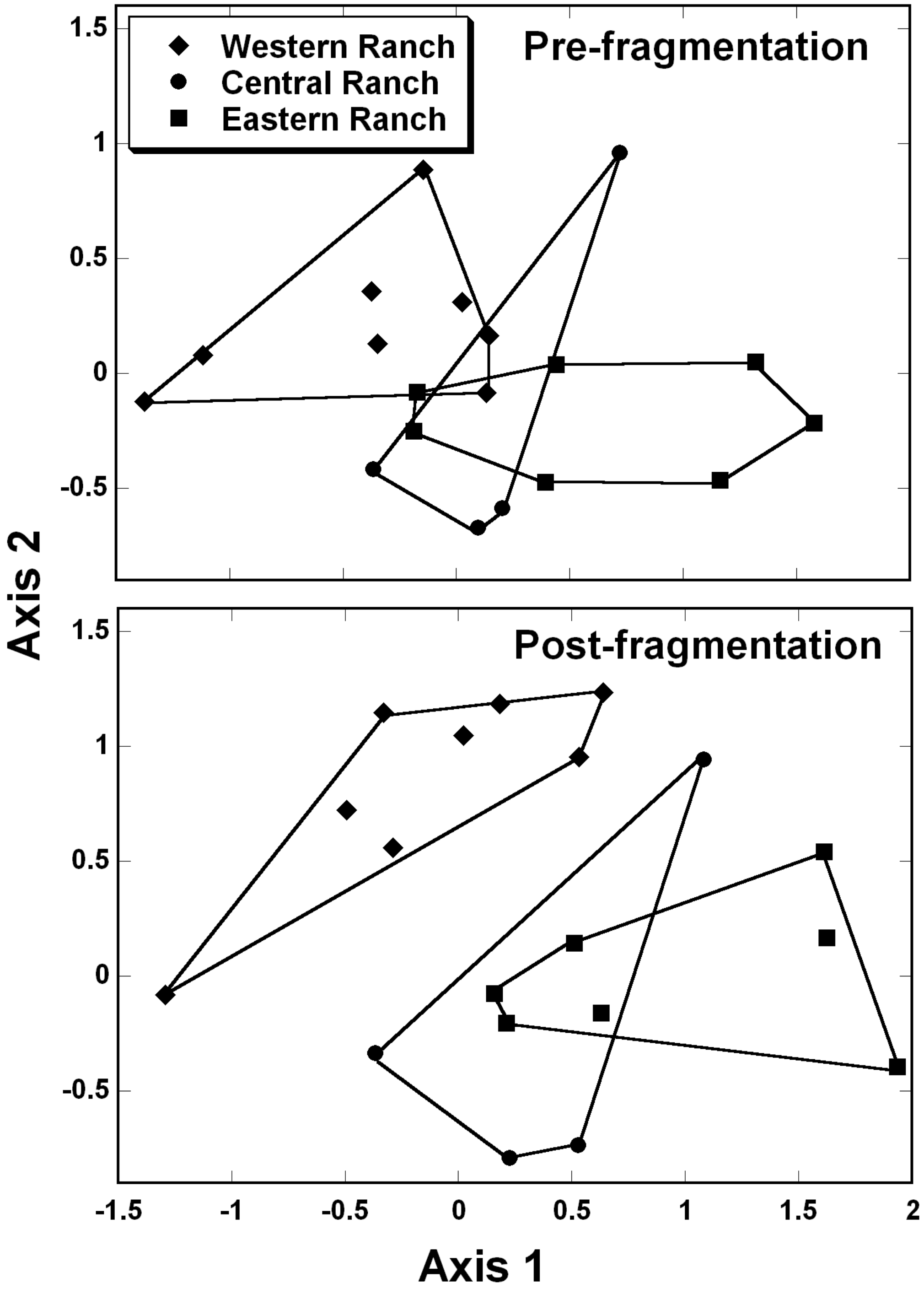
7
B.
Trees ha-1
0
20
40
60
80
100
120
140
C.
Species ha-1
0
5
10
15
20
25
0
1
2
4
Number of nearby edges

1285 Fig. 3



1286