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

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ABSTRACT

We synthesize findings from one of the world's largest and longest-running experimental investigations, the Biological Dynamics of Forest Fragments Project (BDFFP). Spanning an area of ~1000 km^2 in central Amazonia, the BDFFP was initially designed to evaluate the effects of fragment area on rainforest biodiversity and ecological processes. However, over its 38-year history to date the project has far transcended its original mission, and now focuses more broadly on landscape dynamics, forest regeneration, regional- and global-change phenomena, and their potential interactions and implications for Amazonian forest conservation. The project has yielded a wealth of insights into the ecological and environmental changes in fragmented forests. For instance, many rainforest species are naturally rare and hence are either missing entirely from many fragments or so sparsely represented as to have little chance of long-term survival. Additionally, edge effects are a prominent driver of fragment dynamics, strongly affecting forest microclimate, tree mortality, carbon storage and a diversity of fauna.

Even within our controlled study area, the landscape has been highly dynamic: for example, the matrix of vegetation surrounding fragments has changed markedly over time, succeeding from large cattle pastures or forest clearcuts to secondary regrowth forest. This, in turn, has influenced the dynamics of plant and animal communities and their trajectories of change over time. In general, fauna and flora have responded differently to fragmentation: the most locally extinction-prone animal species are those that have both large area requirements and low tolerance of the modified habitats surrounding fragments, whereas the most vulnerable plants are those that respond poorly to edge effects or chronic forest disturbances, and that rely on vulnerable animals for seed dispersal or pollination.

Relative to intact forests, most fragments are hyperdynamic, with unstable or fluctuating populations of species in response to a variety of external vicissitudes. Rare weather events such as droughts, windstorms and floods have had strong impacts on fragments and left lasting legacies of change. Both forest fragments and the intact forests in our study area appear to be influenced by larger-scale environmental drivers operating at regional or global scales. These drivers are apparently increasing forest productivity and have led to concerted, widespread increases in forest dynamics and plant growth, shifts in tree-community composition, and increases in liana (woody vine) abundance.

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Such large-scale drivers are likely to interact synergistically with habitat fragmentation, exacerbating its effects for some species and ecological phenomena. Hence, the impacts of fragmentation on Amazonian biodiversity and ecosystem processes appear to be a consequence not only of local site features but also of broader changes occurring at landscape, regional and even global scales.

Key words: Amazonia, biodiversity, carbon storage, climate change, drought, ecosystem services, edge effects, environmental synergisms, habitat fragmentation, nature reserves.

CONTENTS

I. INTRODUCTION

The Biological Dynamics of Forest Fragments Project (BDFFP) is the world's largest and longest-running experimental study of habitat fragmentation (Lovejoy *et al.*, 1986; Bierregaard *et al.*, 1992; Laurance *et al.*, 2002, 2011). Located in central Amazonia (Fig. 1), the BDFFP has evolved since its inception in 1979 into an epicentre for long-term research. Beyond this, its research mission has gradually broadened to include not only forest fragmentation but also studies of forest regeneration, landscape dynamics, climatic variation, regional- and global-change phenomena and a variety of interdisciplinary research topics.

The BDFFP is strategically located at the heart of the Amazon, the world's largest tropical forest. The Amazon itself lies at the intersection of key questions in global change, both for research and for action. It is believed to be one of the major regions that will be most impacted by projected climatic change (Salazar, Nobre & Oyama, 2007; Dai, 2012; IPCC, 2013; Nobre *et al.*, 2016). If effectively conserved and managed, the Amazon has the potential to contribute markedly to efforts to limit climate change during the narrow window of time we have remaining to avert 'dangerous' global warming (Fearnside, 2000, 2016*a*; Houghton, Byers & Nassikas, 2015). Because of its enormous carbon-storage capacity, it is also one of the places on Earth where sharply reducing greenhouse-gas emissions could be achieved by limiting forest loss and degradation, thereby delivering great global benefits for humankind (Stickler *et al.*, 2009).

Today, the BDFFP is one of the most enduring, influential and highly cited environmental investigations in the world (Gardner *et al.*, 2009; Peres *et al.*, 2010; Pitman *et al.*, 2011). Its wide-ranging research has involved hundreds of Brazilian and international investigators and thousands of students and other trainees. Here we synthesize the contributions of this singular project to the study of habitat fragmentation, including its broader consequences for Amazonian ecosystems and biota. We emphasize that many of the local impacts of fragmentation in the Amazon are being modified or exacerbated by environmental changes occurring at wider landscape, regional and even global scales. We assert that the effects of fragmentation cannot be fully understood without considering the influence of these larger-scale phenomena.

II. LARGER-SCALE DRIVERS

(1) Landscape-scale phenomena

The correlated processes of forest loss and fragmentation are among the greatest threats to tropical biodiversity (Lovejoy *et al.*, 1986; Ewers & Didham, 2006; Laurance & Peres, 2006; Gibson *et al.*, 2011). Amazonia harbours more than half of the world's surviving tropical forest, and is currently being altered by large-scale agriculture (Fearnside, 2001; Gibbs *et al.*, 2010), industrial logging (Asner *et al.*, 2005), proliferating roads (Laurance *et al.*, 2001*a*; Fearnside, 2002, 2007; Killeen, 2007), increasing biofuel production (Butler & Laurance, 2009), hydroelectric dams (Fearnside, 2016*b*) and oil, gas and mining developments (Finer *et al.*, 2008).

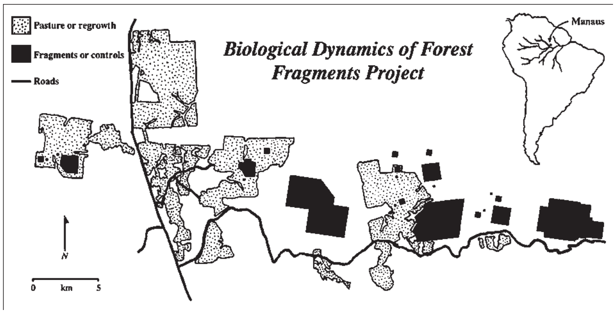

Fig. 1. Map of the Biological Dynamics of Forest Fragments Project in central Amazonia.

Large expanses of the Amazon have already been cleared, resulting in considerable fragmentation. By the early 1990s, the area of forest that was fragmented ($<100\,\mathrm{km}^2$) or vulnerable to edge effects (<1 km from edge) was over 150% greater than the area that had been deforested (Skole & Tucker, 1993). From 1999 to 2002, deforestation and industrial selective logging in Brazilian Amazonia, respectively, created ~32000 and ~38000 km of new forest edge annually (Broadbent *et al.*, 2008). Prevailing land uses in Amazonia, such as cattle ranching and small-scale farming, typically produce landscapes dominated by small (<400 ha) and irregularly shaped forest fragments (Fig. 2) (Cochrane & Laurance, 2002; Broadbent *et al.*, 2008). Such fragments are especially vulnerable to a wide array of edge effects and other external vicissitudes (Bierregaard *et al.*, 1992; Laurance *et al.*, 2002, 2011).

Changes in forest cover can have important effects on local climate and vegetation. Habitat fragmentation can promote forest desiccation *via* phenomena such as the 'vegetation breeze' (Fig. 3). This occurs because fragmentation leads to the juxtaposition of cleared and forested lands, which differ greatly in their physical characteristics. Air above forests is cooled by evaporation and especially plant evapotranspiration, but such cooling is greatly reduced above clearings (Avissar & Schmidt, 1998). As a result, the air above clearings heats up and rises, reducing local air pressure and drawing moist air from the surrounding forests into the clearing. As the rising air cools, its moisture condenses into convective clouds that can produce rainfall over the clearing (Avissar & Liu, 1996). The air is then recycled as cool, dry air back over the forest. In this way, clearings of a few hundred hectares or more can draw moisture away from nearby forests (W.F. Laurance, 2004*b*; Cochrane & Laurance, 2008; Nobre *et al.*, 2016). In eastern Amazonia, satellite observations of canopy water content suggest such desiccating effects

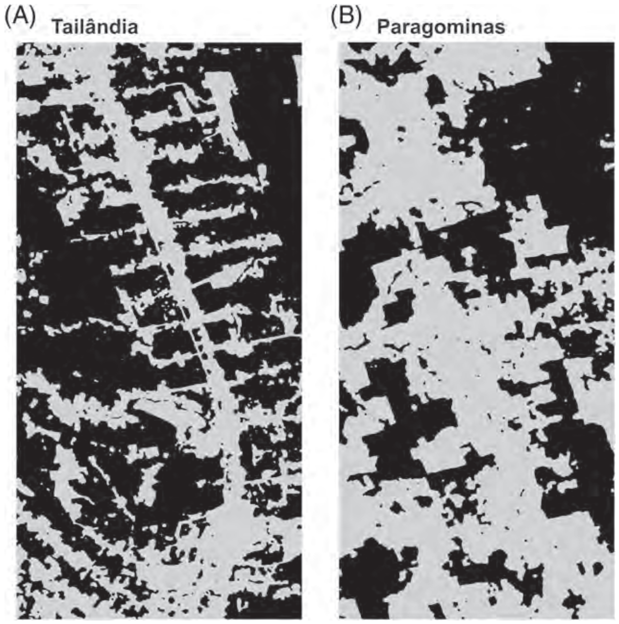

Fig. 2. Habitat fragmentation in eastern Amazonia caused by a (A) forest-colonization project (Tailândia) and (B) cattle ranching (Paragominas). Forests are black and cleared areas are grey. Each image shows an area of about 600 km^2 (adapted from Cochrane & Laurance, 2002).

can penetrate 1.0–2.7 km into fragmented forests (Briant, Gond & Laurance, 2010). This moisture-robbing function of clearings, in concert with frequent burning in adjoining pastures, could help to explain why fragmented forests are so vulnerable to destructive, edge-related fires (Cochrane & Laurance, 2002, 2008; Barlow *et al.,* 2006).

(2) Regional-scale phenomena

Extensive forest clearing reduces the rate of evapotranspiration because pasture grasses and croplands have far less leaf area and shallower roots than do rainforests (Jipp *et al.,* 1998). At regional scales, declining evapotranspiration could reduce rainfall and cloud cover and increase albedo and soil-surface temperatures. Moisture recycling *via* evapotranspiration is exceptionally important in the hydrological regime of the Amazon (Salati & Vose, 1984; Eltahir & Bras, 1994), especially during the dry season (Malhi *et al.,* 2008), because the forest is both vast and far from the nearest ocean.

However, the regional consequences of large-scale deforestation are far from fully understood. Some modelling studies suggest that Amazonian deforestation could reduce basin-wide precipitation by roughly 20–30%, but these estimates rely on a simplistic assumption of complete, uniform forest clearing (e.g. Nobre, Sellers & Shukla, 1991; Dickinson & Kennedy, 1992; Lean & Rowntree, 1993). Model results based on actual (*circa* 1988) deforestation patterns in Brazilian Amazonia have been less dramatic, with deforested regions predicted to experience modest (6–8%) declines in rainfall, moderate (18–33%) reductions in evapotranspiration, higher soil-surface temperatures and greater windspeeds (from reduced surface drag), which could affect moisture convergence and circulation (Walker, Sud & Atlas, 1995; Sud, Yang & Walker, 1996). It is even possible that moderate forest loss and fragmentation could *increase* net regional precipitation in the near term, as a result of increasing convectional storms driven by vegetation breezes, although the main effect would be to remove moisture from forests and redistribute it over adjoining clearings. The greatest concern is that if deforestation reaches some critical threshold, Amazonian rainfall might decline abruptly as the regional hydrological system collapses (Avissar *et al.,* 2002; Nobre *et al.,* 2016).

Massive smoke plumes produced by forest and pasture fires cause two additional effects of forest loss. Smoke hypersaturates the atmosphere with cloud condensation nuclei (microscopic particles in aerosol form) that bind with airborne water molecules and thereby inhibit the formation of raindrops (Rosenfeld, 1999). In addition, by absorbing solar radiation, smoke plumes warm the atmosphere, inhibiting cloud formation. As a result of these two effects, large fires can create rain shadows that extend for hundreds or even thousands of kilometers downwind (Freitas, Silva Dias & Silva Dias, 2000). This can be a serious threat to forests because tropical fires are lit during the critical dry-season months, when plants are already moisture stressed and most vulnerable to fire.

(3) Global-scale phenomena

How will global-change drivers affect the Amazon? Although model predictions for future climates in Amazonia vary considerably, it is generally expected that parts of the basin will become hotter and drier under projected global warming (IPCC, 2013; Nobre *et al.,* 2016). What this portends for the Amazon is a matter of some controversy. Earlier studies assuming CO_2 concentrations about twice those in the pre-industrial atmosphere, notably by the UK Hadley Centre, projected disastrous forest die-offs (Cox *et al.,* 2000, 2004). However, this conclusion has been countered by new models from the same research group, suggesting the Amazon forest will remain almost entirely intact at up to four times pre-industrial CO_2 levels (Cox *et al.,* 2013; Good *et al.,* 2013; Huntingford *et al.,* 2013). The main difference is that the newer models include CO_2-fertilization effects (Kimball *et al.,* 1993), which are assumed to increase plant growth and water-use efficiency. This is because the higher atmospheric CO_2 concentration should allow plants to conserve water by decreasing the duration of stomatal-opening periods while still taking in adequate CO_2 for photosynthesis.

Other global-change phenomena, such as extreme climatic events, could also potentially have important impacts. For instance, droughts in the Amazon are normally associated with El Niño events and are strongest in the southern, eastern and north-central Amazon – areas of the basin that already experience pronounced dry seasons. However, severe droughts in 2005 and 2010 arose from a completely different cause – exceptionally high Atlantic sea-surface temperatures, which caused the rain-bearing

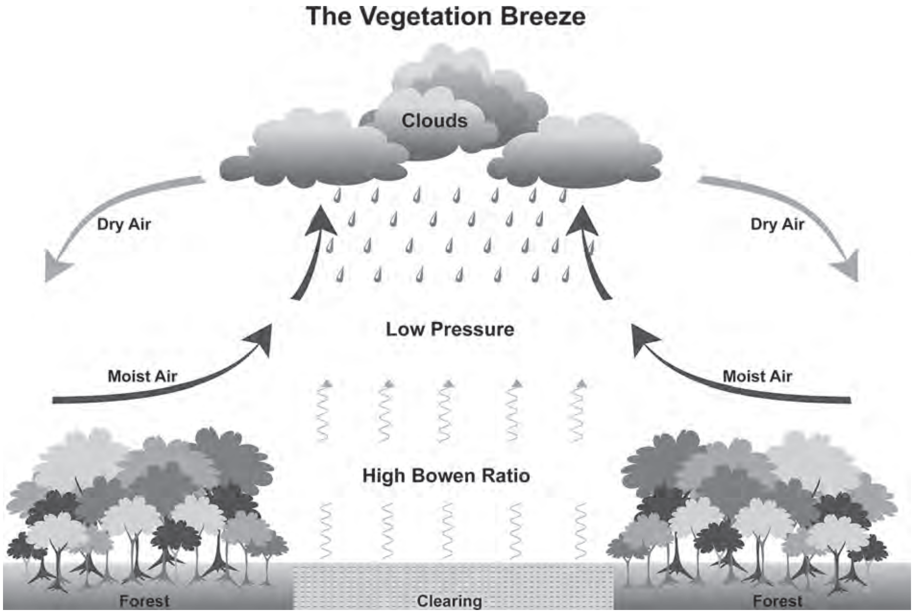

Fig. 3. The vegetation-breeze phenomenon, which can promote forest desiccation in the general vicinity of pastures and clearings (from Cochrane & Laurance, 2008).

inter-tropical convergence zone to shift northward (Lewis *et al.,* 2011). The resulting droughts affected not just the drier, more seasonal parts of the basin but also its wettest areas in central and western Amazonia. Because plant species in these wet areas are adapted to perennially humid conditions, the new droughts caused massive plant mortality, killing tens of millions of trees while releasing several billion tonnes of atmospheric carbon emissions (Lewis *et al.,* 2011; Marengo *et al.,* 2012). With mounting evidence that climatic extremes could become more frequent and intense in a warming world (Vera *et al.,* 2006; Herring *et al.,* 2015; Jiménez-Muñoz *et al.,* 2016), could the Amazon be driven into a new kind of climatic dynamic – one for which its ecosystems and biodiversity are poorly adapted?

III. STUDY AREA AND KEY DATA SETS

(1) Study area

The experimental landscape of the BDFFP spans ~1000 km^2 in area and is located 80 km north of Manaus, Brazil. 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 [$\geq$10 cm diameter at breast height (dbh)] often exceeds 280 species ha^{-1}, which is among the highest known tree diversity in the world (De Oliveira & Mori, 1999; Laurance *et al.,* 2010*b*). Comparably high levels of diversity are seen in many other plant and animal taxa.

The study area includes three large cattle ranches (~5000 ha each) containing 11 forest fragments (five of 1 ha, four of 10 ha and two of 100 ha), and large expanses of nearby continuous forest that serve as experimental controls (Fig. 1). In the early 1980s, the fragments were isolated from nearby intact forest by distances of 80–650 m through clearing and burning of the surrounding forest. A key advantage was that pre-fragmentation censuses were conducted for many animal and plant groups (e.g. trees, understorey 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, especially after government fiscal incentives dried up from 1988 onwards. Secondary forests – initially dominated by *Vismia* spp. in areas that were cleared and burned, and by *Cecropia* spp. in areas that were cleared without fire – proliferated in many formerly forested areas (Mesquita *et al.,* 2001). Some regenerating areas initially dominated by *Cecropia* later grew into structurally well-developed (>20 m tall), species-rich secondary forests (Longworth *et al.,* 2014). *Vismia*-dominated regrowth, however, which is relatively species poor, is maturing far more slowly (Norden *et al.,* 2011; Williamson *et al.,* 2014).

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. However, human disturbances that affect many fragmented landscapes in the Amazon, such as major fires, logging and hunting (Michalski & Peres, 2005), are largely prevented at the BDFFP.

(2) Unique data sets

The BDFFP sustains some of the longest-running and highest-quality environmental data sets in the Amazon. This includes a network of 69 1-ha forest-dynamics plots arrayed across intact and fragmented forests in the study area, which has been monitored since the early 1980s, and a permanent 25-ha plot in intact forest established in 2005. These plots have made important contributions to reducing uncertainties in biomass and carbon-storage estimates for the Amazon (e.g. Phillips *et al.,* 1998; Nascimento & Laurance, 2002; Baker *et al.,* 2004). For example, in comparison to the 3000 1-ha plots surveyed by the RADAMBRASIL Project (Nogueira *et al.,* 2008, 2015), the BDFFP plots include data on nearly all other forest components such as smaller (1–30 cm diameter) trees, palms, lianas, strangler figs, understorey vegetation and dead biomass (Nascimento & Laurance, 2002, 2004). These data allow assessment of spatial variability in aboveground biomass with a high degree of confidence. For example, the aboveground biomass of trees varies considerably among the 69 1-ha plots in the BDFFP landscape (mean ± S.D. = 356 ± 47 Mg ha^{-1}; Laurance *et al.,* 1999). This high variability demonstrates a need for many plots that are spatially stratified, rather than only a few plots of 1 ha or smaller scattered irregularly around the Amazon, for calibrating satellite imagery for biomass mapping, and for estimating greenhouse-gas emissions from ongoing deforestation (see Fearnside, 2016*a*).

Floristic data from the BDFFP are exceptional for their high quality of species identification, allowing better matching with plant functional and phylogenetic traits such as wood density and tree form (e.g. Fearnside, 1997; Nogueira, Nelson & Fearnside, 2005; Chave *et al.,* 2006; Nogueira *et al.,* 2007; Souza *et al.,* 2016). Given their broad spatial extent and temporal depth, these data have also contributed to knowledge of the diversity of Amazonian plant species and their relationships to soil texture and chemistry, topography, forest dynamics and climatic variables at both landscape and regional scales (e.g. Bohlman *et al.,* 2008; S.G. Laurance *et al.,* 2009; Laurance, Andrade & Laurance, 2010*a*; Laurance *et al.,* 2010*b*; ter Steege *et al.,* 2013). Biodiversity and ecosystem processes represent part of what is lost when the forest is destroyed or degraded. Understanding these processes is essential for assessing not only the vulnerability of forests, but also their potential resilience in the face of global change and their rates of recovery following various perturbations (Williamson *et al.,* 2014; Souza *et al.,* 2016). Data sets for a number of faunal groups, such as birds, amphibians, primates and major invertebrate taxa, are of comparable quality and duration.

IV. CHANGES IN INTACT FORESTS

(1) Unexpected trends

As part of its original mission to assess long-term changes in fragmented forests, the BDFFP has two types of experimental controls (Lovejoy *et al.,* 1986; Bierregaard *et al.,* 1992). The first is that standardized censuses of many plant and animal taxa were conducted in each experimental fragment before it was isolated from the surrounding forest. The second is that dozens of 'control' sites in nearby intact forests have been monitored for up to 38 years, to assess the temporal dynamics of these sites. The intact-forest sites were expected to vary randomly over time or respond to occasional vicissitudes such as droughts, but not to change over time in a directional manner.

A major surprise, however, is that the BDFFP controls have changed in several concerted ways (Laurance *et al.,* 2014*a*). Before interpreting how fragmentation has altered ecological communities in the BDFFP, it is first important to identify how the intact-forest sites have changed, as these widespread effects are presumably altering the forest fragments as well. The long-term monitoring of tens of thousands of trees and populations of many other plant and animal groups has allowed researchers to identify synchronous changes in the undisturbed forests at the intact sites, and to attempt to infer their environmental causes.

How have the intact forests changed? Over the past 2–3 decades, we have found that (*i*) forest dynamics (tree mortality and recruitment) have accelerated significantly over time (W.F. Laurance *et al.,* 2004*b*, 2014*a*; S.G. Laurance *et al.,* 2009); (*ii*) tree-community composition has shifted, generally in favour of faster-growing canopy trees and against shade-tolerant subcanopy trees (W.F. Laurance *et al.,* 2004*b*, 2005); (*iii*) growth rates have increased for the large majority (84%) of tree genera in our study area (Fig. 4) (W.F. Laurance *et al.,* 2004*b*); (*iv*) aboveground tree biomass has increased significantly over time (although tree-stem numbers have not changed significantly; S.G. Laurance *et al.,* 2009); and (*v*) lianas have increased markedly in abundance (Fig. 5) (Laurance *et al.,* 2014*a*,*b*).

(2) Potential environmental drivers

Why are the intact forests changing? The causes of such changes are incompletely understood (Lewis, Malhi & Phillips, 2004*a*; Lewis *et al.,* 2009*b*) and often controversial (Clark, 2004; Fearnside, 2004). Nonetheless, the trends we detected appear broadly consistent with those observed elsewhere in many Amazonian (Phillips & Gentry, 1994; Phillips *et al.,* 1998, 2002; Baker *et al.,* 2004; Lewis *et al.,* 2004*b*; Schnitzer & Bongers, 2011) and African (Lewis *et al.,* 2009*b*) tropical forests. These trends are consistent with ecological patterns expected from rising forest productivity, including faster plant growth, increasing forest biomass, intensifying competition leading to greater plant mortality and turnover, and increasing abundances of plant species that can attain high growth rates or are advantaged in dynamic forests (W.F. Laurance *et al.,* 2004*b*; Lewis *et al.,* 2004*b*, 2009*b*).

The most frequently invoked driver of rising tropical forest productivity is CO_2 fertilization (e.g. Lewis *et al.,* 2004*a*, 2009*a*). This is because many plants show faster growth under enriched CO_2 (Oberbauer, Strain & Fletcher, 1985; Granados & Körner, 2002; Körner, 2004) and because

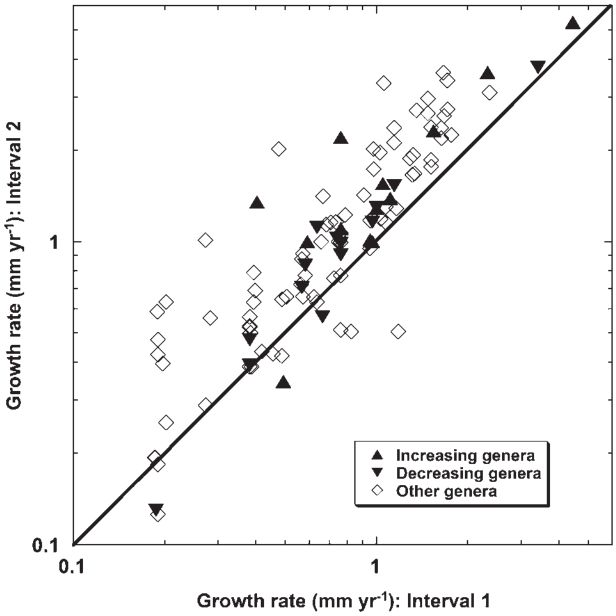

Fig. 4. Rates of tree growth in intact forests of the Biological Dynamics of Forest Fragments Project (BDFFP) have accelerated over time for the large majority (84%) of tree genera (from W.F. Laurance *et al.*, 2004*b*). Data shown are mean rates of trunk-diameter growth for genera that increased or decreased significantly in abundance over time in the plots, as well as those that showed no significant trend. Interval 1 is 1984–1991, and interval 2 is 1992–1999.

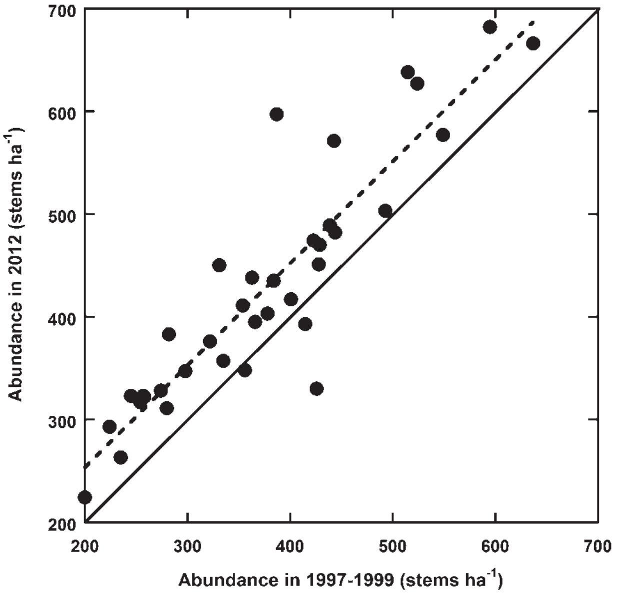

Fig. 5. Increase in abundance of lianas in intact-forest plots of the Biological Dynamics of Forest Fragments Project (BDFFP) (from Laurance *et al.*, 2014*b*). The solid line shows $y = x$ whereas the dotted line is a linear regression fitted to the data.

atmospheric CO_2 levels have risen rapidly, especially in recent decades. This view is supported by compelling evidence of a large carbon sink in the biosphere (Ballantyne *et al.*, 2013), a substantial part of which appears to be on land (Sarmiento *et al.*, 2010) and in the tropics (Lewis *et al.*, 2009*a*; Huntingford *et al.*, 2013).

Other explanations for the rising productivity, however, are not implausible. For instance, droughts can influence forest dynamics and composition and appear to be increasing in parts of the Amazon (Lewis *et al.*, 2009*a*; Marengo *et al.*, 2011; Chou *et al.*, 2013; Fu *et al.*, 2013). The increase in forest dynamics we observed in intact forests appears to be driven primarily by rising tree mortality, with recruitment and growth often lagging behind periods of high mortality. These mortality pulses are positively associated with several factors, including El Niño droughts and increasing rainfall seasonality (S.G. Laurance *et al.*, 2009).

Additionally, multi-decadal shifts in solar radiation or cloudiness could potentially increase forest productivity, although evidence for such shifts in the tropics is limited (Lewis *et al.*, 2009*a*). Recovery from past disturbance has also been hypothesized to underlie changes at some tropical forest sites, but there is no evidence of widespread disturbance in our study area (W.F. Laurance *et al.*, 2004*b*, 2005) aside from charcoal fragments that are at least four centuries old (Bassini & Becker, 1990; Fearnside & Leal Filho, 2001), possibly indicating major fires during past mega-El Niño events (Meggers, 1994).

The notable increases in liana abundance in our intact forests (Laurance *et al.*, 2014*b*) might arise because lianas appear to exploit rising CO_2 concentrations and drier conditions more effectively than do trees (Condon, Sasek & Strain, 1992; Granados & Körner, 2002; but see Marvin *et al.*, 2015). Trees with heavy liana infestations are known to exhibit elevated mortality and reduced growth (Ingwell *et al.*, 2010). Notably, in our study area, liana abundance is strongly and negatively correlated with live tree biomass (Fig. 6) (Laurance *et al.*, 2001*b*). Liana increases over time have also been observed in tropical forests in western Amazonia, the Guianas, Central America and elsewhere (Schnitzer & Bongers, 2011), with rising atmospheric CO_2 and possibly increasing drought being the most frequent explanations (see Laurance *et al.*, 2014*b* and references therein). This potentially negative effect of CO_2 enrichment on forest biomass *via* increasing liana infestations is not included in the latest Hadley Centre models (Cox *et al.*, 2013; Good *et al.*, 2013; Huntingford *et al.*, 2013), and could cancel out some of the carbon-storage benefits suggested for a high-CO_2 future (Körner, 2004, 2017).

Hence, for whatever the reason or reasons, it is apparent that the intact forests in our study area are changing in a variety of ways. Such changes are likely to interact with, and potentially complicate or amplify, the impacts of fragmentation on tropical forest communities.

V. CONSEQUENCES OF FRAGMENT SIZE

The BDFFP's original mission focuses on assessing the effects of fragment area on Amazonian forests and fauna, and on

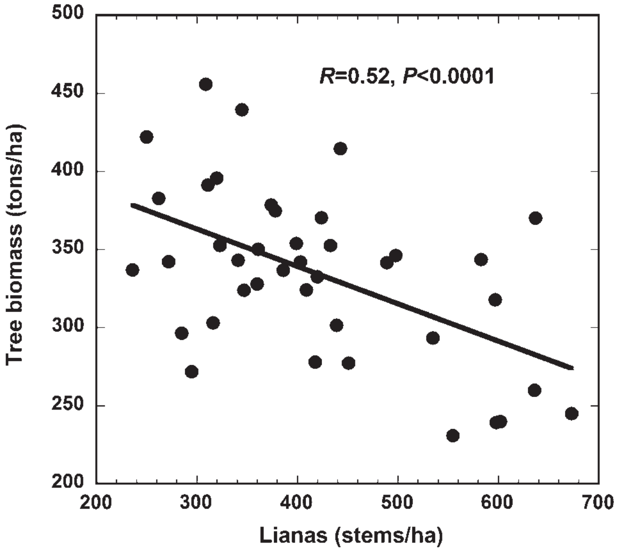

Fig. 6. Negative association between liana abundance and the aboveground biomass of live trees in Biological Dynamics of Forest Fragments Project (BDFFP) forest-dynamics plots (from Laurance *et al.,* 2001*b*).

key ecological and ecosystem processes. Here we summarize major findings and conservation lessons that have been gleaned to date.

(1) Sample effects

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, da Fonseca & Williamson, 2008). In these areas resources such as fruits, flowers and nectar are typically scarce and plants are heavily defended against herbivore attack (Laurance, 2001).

Herein lies 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 & Murphy, 1985). Such sample effects are the hypothesized explanation for the absence of many rare understorey bird species from fragments (Ferraz *et al.,* 2007). In addition, many beetles (Didham *et al.,* 1998*a*), bats (Sampaio *et al.,* 2003; Farneda *et al.,* 2015; Meyer *et al.,* 2015; Rocha *et al.,* 2017), ant-defended plants (Bruna, Vasconcelos & Heredia, 2005) and trees (Bohlman *et al.,* 2008; Laurance *et al.,* 2010*b*) at the BDFFP exhibit high levels of rarity, habitat specialization or patchiness.

(2) Area effects

Understanding fragment-area effects has long been a central goal of the BDFFP (Lovejoy & Oren, 1981; Lovejoy *et al.,* 1984, 1986; Pimm, 1998). The species richness of many organisms declines with decreasing fragment area, even with constant sampling effort across all fragments. Such declines are evident in leaf bryophytes (Zartman, 2003), tree seedlings (Benítez-Malvido & Martinez-Ramos, 2003*b*), palms (Scariot, 1999), understorey insectivorous birds (Stratford & Stouffer, 1999; Ferraz *et al.,* 2007), bats (Sampaio, 2000; Rocha *et al.,* 2017), primates (Gilbert & Setz, 2001; Boyle & Smith, 2010*b*) and larger herbivorous mammals (Timo, 2003), among others. For such groups, smaller fragments (<100 ha) are often unable to support viable populations. 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, Strong & Naka, 2008). Assuming that 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 10000 ha in area would be expected to lose a substantial part of its bird fauna within one century (Ferraz *et al.,* 2003). Similarly, long-term mark–recapture studies suggest that very large fragments will be needed to maintain fully intact assemblages of certain faunal groups, such as ant-following birds, which forage over large areas of forest (Van Houtan *et al.,* 2007).

VI. EDGE EFFECTS

An important insight from the BDFFP is the extent to which edge effects – physical and biotic changes associated with the abrupt, artificial margins of habitat fragments – influence the dynamics and composition of plant and animal communities. Here we summarize key findings from this work.

(1) Forest hydrology

The hydrological regimes of fragmented landscapes differ markedly from those of intact forest (Kapos, 1989; Kapos *et al.,* 1993). Pastures or crops surrounding fragments have much lower rates of evapotranspiration than do forests, causing such areas to be 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 & Lawton, 1999). Further, streams in fragmented landscapes experience greater temporal variation in flow rate than do those in forests, because clearings surrounding fragments have less evapotranspiration and rainfall interception and absorption by vegetation (Trancoso, 2008). Rapid runoff 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 fish assemblages.

(2) Striking diversity of edge effects

At least over the first 3–4 decades after isolation, edge effects have been 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 & Laurance, 2002, 2008; Briant *et al.,* 2010).

Edge phenomena are remarkably diverse (Fig. 7). They include increased desiccation stress, wind shear and wind turbulence that sharply elevate rates of tree mortality and damage (Laurance *et al.,* 1997, 1998*a*). These in turn cause wide-ranging alterations in the community composition of trees (Laurance *et al.,* 2000, 2006*a,b*) and lianas (Laurance *et al.,* 2001*b*). 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 & Martinez-Ramos, 2003*b*).

Many animal groups, such as numerous bees, wasps, flies (Fowler, Silva & Venticinque, 1993), beetles (Didham *et al.,* 1998*a,b*), ants (Carvalho & Vasconcelos, 1999), butterflies (Brown & Hutchings, 1997), understorey birds (Quintela, 1985; S.G. Laurance, 2004*a*) and gleaning predatory bats (Rocha, 2016; Rocha *et al.,* 2017), decline in abundance near forest edges. Edge habitats of continuous forest and larger fragments (100 ha) have fewer species of bats and higher levels of dominance by a few common species (Rocha, 2016; Rocha *et al.,* 2017). Negative edge effects are apparent even along narrow forest roads (20–30 m width). Among understorey birds, for example, five of eight foraging guilds declined significantly in abundance within 70 m of narrow roads, evidently in response to increased light and forest disturbance near road edges (S.G. Laurance, 2004*a*).

Some groups of organisms remain stable or even increase in abundance near edges. Leaf bryophytes (Zartman & Nascimento, 2006), wandering spiders (*Ctenus* spp.; Rego, Venticinque & Brescovit, 2007; Mestre & Gasnier, 2008) and many frogs (Gascon, 1993) displayed no significant response to edges. Organisms that favour forest ecotones or disturbances, such as many species of gap-favouring and frugivorous birds (S.G. Laurance, 2004*a*), hummingbirds (Stouffer & Bierregaard, 1995*a*), frugivorous bats that exploit early successional plants (Sampaio, 2000; Rocha *et al.,* 2017), light-loving butterflies (Leidner, Haddad & Lovejoy, 2010) and fast-growing lianas (Laurance *et al.,* 2001*b*), increase in abundance near edges, sometimes dramatically.

(3) Impacts of multiple edges

BDFFP research demonstrates that plots near two or more edges suffer more severe edge effects than do those near just one edge (Fig. 8). 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.,* 2006*a*), abundance and species richness of tree seedlings (Benítez-Malvido, 1998; Benítez-Malvido & Martinez-Ramos, 2003*b*), liana abundance (Laurance *et al.,* 2001*b*) and the density and diversity of disturbance-loving pioneer trees (Laurance *et al.,* 2006*a,b*, 2007). The additive effects of nearby edges probably 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.,* 2006*a*). Some fauna are likewise sensitive to multiple edges. For instance, the number of nearby forest edges was found to be an important predictor of local bat abundance (Rocha *et al.,* 2017).

(4) Effects of edge age and adjoining vegetation

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 & 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 & Kapos, 1995; Didham & Lawton, 1999). Tree death from microclimatic stress is likely to decline over the first few years after edge creation (D'Angelo *et al.,* 2004) as 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.,* 2006*a*). Tree mortality from wind turbulence, however, probably increases as the edge ages and becomes more closed because, as suggested by wind-tunnel models, downwind turbulence increases if edges are less permeable (W.F. Laurance, 2004*b*).

Regrowth forest adjoining fragment edges can also lessen edge-effect intensity. Microclimatic changes (Didham & Lawton, 1999), tree mortality (Mesquita, Delamônica & Laurance, 1999) and edge avoidance by understorey birds (Develey & Stouffer, 2001; S.G. Laurance, Stouffer & Laurance, 2004; S.G. Laurance, 2004*a*) and gleaning animal-eating bats (Sampaio, 2000; Meyer, Struebig & Willig, 2016; Rocha, 2016; Rocha *et al.,* 2017) are all reduced when forest edges are buffered by adjoining regrowth forest, relative to edges bordered by cattle pastures. Mature regrowth can be particularly benign for some fauna; for example, diverse assemblages of aerial-feeding insectivorous bats showed similar activity patterns in primary forest and in adjoining 30-year-old secondary forests (Navarro, 2014).

VII. FOREST ISOLATION AND THE MATRIX

Unlike true islands encircled by water, habitat fragments are surrounded by a matrix of modified vegetation that can be highly variable in space and time. Here we highlight key factors that can influence the matrix and how, in turn, the matrix influences fragment dynamics and composition.

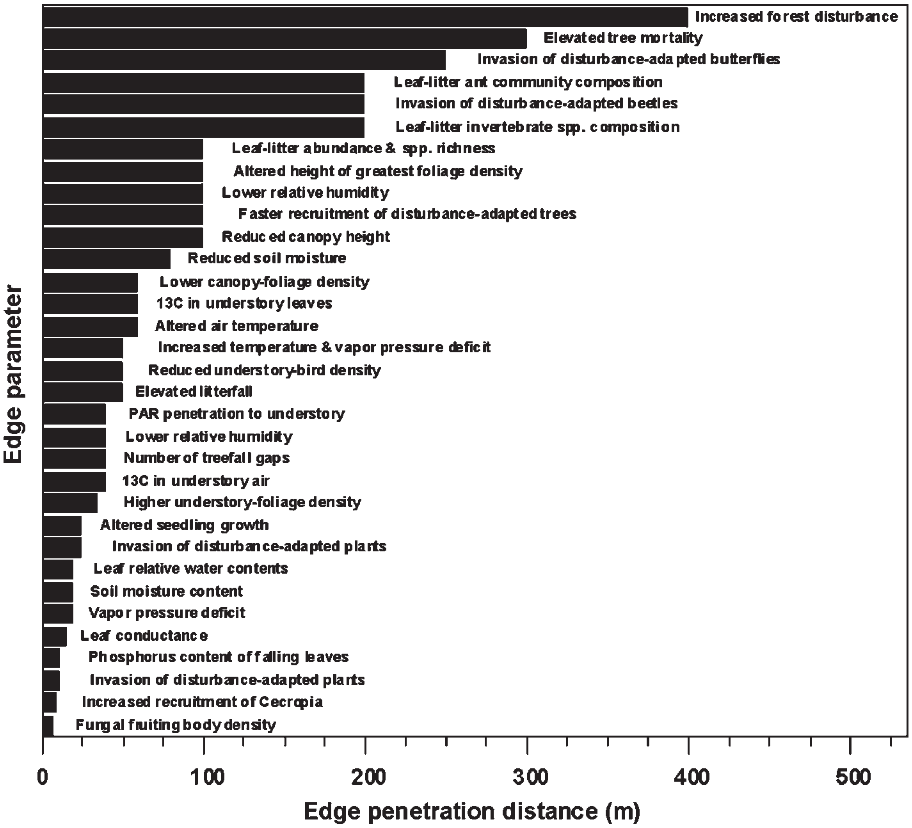

Fig. 7. The diversity of edge-effect phenomena studied at the Biological Dynamics of Forest Fragments Project (BDFFP) and the distance to which each was found to penetrate into fragment interiors (adapted from Laurance *et al.*, 2002). PAR, photosynthetically active radiation. Some environmental phenomena (e.g. relative humidity, soil moisture) appear more than once because they were measured by different investigators using varying methods, times, and/or study locations.

(1) Matrix structure and composition

The BDFFP landscape has experienced considerable dynamism over time. In particular, secondary forests have gradually overgrown most pastures in the study area. This regrowth lessens the effects of fragmentation for some species, with the matrix becoming less hostile to faunal use and movements. Several species of insectivorous birds that had formerly disappeared from fragments have recolonized them as surrounding secondary forests regenerated (Stouffer & Bierregaard, 1995*b*; Stouffer *et al.*, 2011). The rate of local extinctions of birds has also declined (Stouffer *et al.*, 2008).

The regenerating forest in the matrix now permits fragments as small as 100 ha to support bird and bat assemblages similar to those in continuous forest (Wolfe *et al.*, 2015; Rocha *et al.*, 2017). For bats, matrix recovery has resulted in marked compositional changes in fragments and shifts in the rank order of the most abundant species (Meyer *et al.*, 2016; Rocha, 2016). Gleaning animal-eating bats, which formerly occurred at low abundances in fragments (Sampaio, 2000) and young regrowth (Bobrowiec & Gribel, 2010), have increased over the past 10–15 years as the surrounding regrowth has expanded and matured (Meyer *et al.*, 2016; Rocha, 2016; Rocha *et al.*, 2017). A number of other species, including certain forest spiders (Mestre & Gasnier, 2008), dung beetles (Quintero & Roslin, 2005), euglossine bees (Becker, Moure & Peralta, 1991) and monkeys such as red howlers *Alouatta seniculus*, bearded sakis *Chiropotes satanas* and brown capuchins *Cebus apella* (Boyle & Smith, 2010*b*), have also recolonized some of the fragments.

The surrounding matrix also has a strong effect on plant communities in fragments by reducing edge effects (see Section VI), influencing the movements of pollinators (Dick, 2001; Dick, Etchelecu & Austerlitz, 2003) and seed dispersers (Jorge, 2008; Bobrowiec & Gribel, 2010; Boyle & Smith, 2010*b*) and strongly influencing 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 may increasingly tend to mirror the composition of the surrounding matrix (Laurance *et al.*, 2006*a*,*b*), a phenomenon observed elsewhere in the tropics (Janzen, 1983; Diamond, Bishop & Balen, 1987; Laurance, 1991).

(2) Factors influencing the matrix

Land-use history is a key driver of secondary succession in Amazonia, resulting in distinct trajectories of regeneration

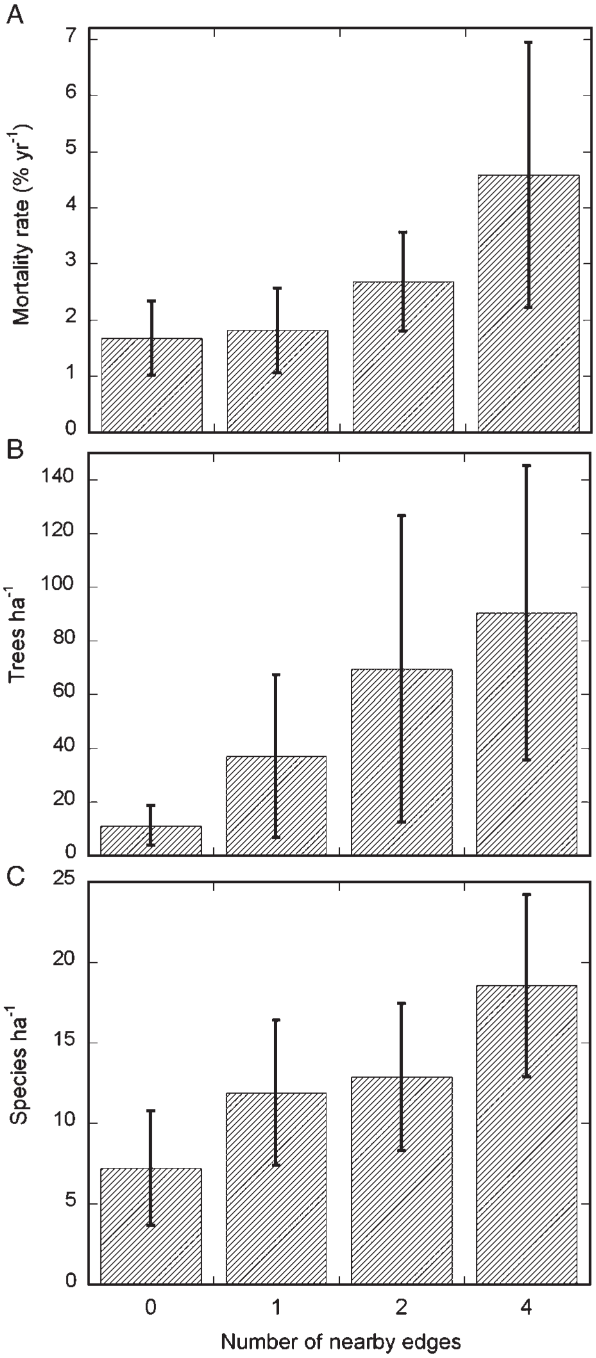

Fig. 8. The effects of single *versus* multiple nearby forest edges on (A) stand-level tree mortality, and (B) density and (C) species richness of disturbance-loving pioneer tree species. Values shown are means ± S.D. (from Laurance *et al.,* 2006*a*).

that differ in structure, composition, biomass and dynamics (Mesquita *et al.,* 1999; Williamson *et al.,* 2014). The recurring use of fire to maintain pastures reduces regenerative potential, leaving lands dominated by scrubby trees in the genus *Vismia,* which are prodigious resprouters that stall succession by inhibiting growth of other tree species (Jakovac *et al.,* 2015). Compared to slash-and-burn agriculture, vegetation biomass recovers much more slowly in lands previously used as pasture, which is currently the predominant land use in Amazonia (Wandelli & Fearnside, 2015). However, where land and fire use has been less intensive, a more diverse vegetation dominated by the genus *Cecropia* fosters relatively rapid plant succession (Longworth *et al.,* 2014).

In regenerating forests, plant density and species diversity both decline with distance from primary forest, and also differ between *Vismia*- and *Cecropia*-dominated regrowth. These differences were initially attributed to differential seed-dispersal limitations (Mesquita *et al.,* 2001; Puerta, 2002). However, it now appears that the seed rains are similar in both types of regrowth and are strongly dominated by pioneer species (Wieland *et al.,* 2011). This suggests that birds and bats, the primary seed dispersers, are feeding mainly in regrowth and rarely transporting primary-forest seeds into the regrowth. Instead, the legacy of past land use endures as abandoned pastures – especially those dominated by *Vismia* – remain depauperate for at least a quarter of a century (Massoca *et al.,* 2012; Mesquita *et al.,* 2015).

(3) Narrow forest clearings

Many Amazonian species avoid forest clearings, even those that are surprisingly narrow. A number of understorey insectivorous birds exhibit depressed abundances near roads of just 20–40 m width (S.G. Laurance, 2004*a*) and their rate of movements across those roads is strongly reduced (S.G. Laurance *et al.,* 2004*a*). Experimental translocations of resident adult birds reveal that such species can be compelled to cross a highway (50–75 m width) but not a small pasture (250 m width) to return to their territory (Laurance & Gomez, 2005). Individuals of some other vulnerable bird species, however, have traversed clearings to escape from small fragments to larger forest areas (Harper, 1989; Van Houtan *et al.,* 2007). Captures of understorey birds declined dramatically in fragments when a 100 m-wide swathe of regrowth forest was cleared around them, suggesting that species willing to traverse regrowth had a strong aversion to such 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.,* 2009), ranging from herbivorous insects (Fáveri, Vasconcelos & Dirzo, 2008), euglossine bees (Powell & Powell, 1987) and dung beetles (Klein, 1989) to the spores of epiphyllous lichens (Zartman & Nascimento, 2006; Zartman & Shaw, 2006). Narrow clearings can also provide invasion corridors into forests for exotic and non-forest species (Gascon *et al.,* 1999; W.F. Laurance, Goosem & Laurance, 2009).

VIII. DYNAMICS OF FOREST FRAGMENTS

Here we highlight some factors that can influence the dynamics of Amazonian forest fragments and the unusual ecological communities than can arise as a consequence.

(1) Rare disturbances

Rare events such as droughts, local flooding and windstorms have strongly influenced the ecology of BDFFP fragments. Rates of tree mortality rose abruptly in both fragmented (Laurance *et al.,* 2001*c*) and intact forests (Williamson *et al.,* 2000) in the year after the intense 1997 El Niño drought and heavy 1998 La Niña rains. Such pulses of tree death can drive changes in 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, increasing the quantity of leaf litter on the forest floor (Laurance & Williamson, 2001). Such dense litter elevates the susceptibility of fragments to intrusion by destructive surface fires (Cochrane & Laurance, 2002, 2008) and can slow forest regeneration by suppressing seed germination and seedling establishment (Bentos, Nascimento & Williamson, 2013). Local flooding caused tree mortality in one of our plots to rise fivefold (S.G. Laurance *et al.,* 2009), a pattern also observed in other low-lying plateaus and microsites in the BDFFP study area (Mori & Becker, 1991).

Intense windblasts from convectional thunderstorms have occasionally flattened 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 those in the other two ranches (Fig. 1), because the former have so far escaped major 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.,* 2006*b*). Hence, by altering forest dynamics, composition, structure and carbon storage, rare disturbances have left an enduring imprint on the ecology of fragmented forests.

(2) Hyperdynamism

Relative to intact forest, the BDFFP fragments experience exceptional variability in population and community dynamics, despite being largely protected from ancillary human threats such as fires, logging and overhunting. Having a small resource base, a habitat fragment is inherently vulnerable to stochastic effects and external vicissitudes. Species abundances can thus 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 favoured host plants along fragment margins (Brown & Hutchings, 1997), and butterfly communities in general are hyperdynamic in fragments (Fig. 9) (Leidner *et al.,* 2010). Bat assemblages also show atypically high species turnover (Meyer *et al.,* 2016), as do understorey birds (Stouffer *et al.,* 2008, 2011), especially in smaller fragments. 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.,* 1998*a,b*), with major mortality pulses associated with rare disturbances (see Section VIII.1). These pulses of tree death followed by accelerated recruitment of young trees lead to large fluctuations in the number of trees per plot (Fig. 10). 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.,* 2006*b*). These and many other instabilities plague small, dwindling populations in the BDFFP fragments.

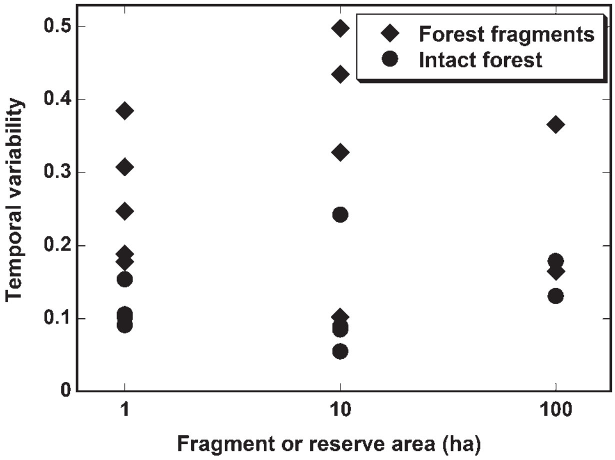

Fig. 9. Elevated temporal variation in butterfly species richness in fragmented forests shown by an index of variability in species richness for fragmented and intact sites sampled in consecutive years (adapted from Leidner *et al.,* 2010).

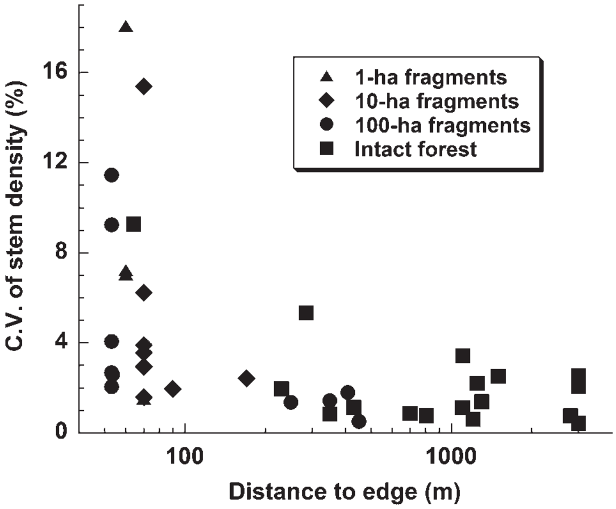

Fig. 10. Elevated temporal variation (C.V., coefficient of variation) in the number of tree stems per plot, shown as a function of distance from the nearest forest edge.

(3) Diverging trajectories of fragments

A key insight from our long-term experiment 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 with fire in the years just before or after became cattle pastures or, eventually, scrubby *Vismia*-dominated regrowth (Williamson & Mesquita, 2001). For example, these different successional trajectories led to distinct bat assemblages: *Cecropia*-dominated regrowth retained a considerably higher fraction of the forest-specialist bat species found in continuous forest, compared to *Vismia* regrowth (Bobrowiec & Gribel, 2010). As discussed above (Section VI), 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 trajectories 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 will 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 within 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. 11). Pioneer and opportunistic trees are increasing in all fragments, but the composition of these secondary plant species and their rates of increase differ markedly among the three ranches (Scariot, 2001; Laurance *et al.*, 2006*a*, 2007; Nascimento *et al.*, 2006). A similar pattern of biotic divergence is evident in the secondary-forest bat assemblages found at the different ranches (Bobrowiec & Gribel, 2010)

(4) Ecological distortions

Many ecological interactions are altered in fragmented landscapes. For instance, in mixed-species bird flocks, interspecific interactions are lower, both in number and frequency, in 10-ha fragments and the secondary forest matrix than in more preserved habitats (continuous forest and 100-ha fragments), resulting in reduced flock cohesion and stability (Mokross *et al.*, 2014). Fragmented communities can pass through unstable transitional states that may not otherwise occur in nature (Terborgh *et al.*, 2001; Gibson *et al.*, 2013). 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.*, 1998*b*; Terborgh *et al.*, 2001).

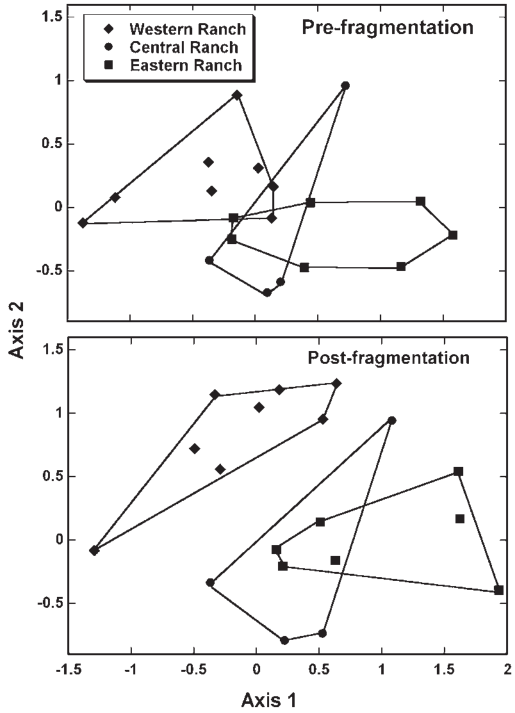

Fig. 11. Increasing divergence over time of tree-community composition in three fragmented landscapes at the Biological Dynamics of Forest Fragments Project (BDFFP). Tree communities in forest-edge plots (<100 m from the nearest edge) are shown before forest fragmentation and 13–18 years after fragmentation, based on an ordination analysis. The ordination used importance values for all 267 tree genera found in the study plots (from Laurance *et al.*, 2007).

BDFFP findings suggest that even forest fragments that are unhunted, unlogged and unburned have reduced densities of key mammalian seed dispersers. As a result, seed dispersal for the 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.*, 2007*a*). 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 *Apis mellifera*, a generalist pollinator, are abundant in matrix and edge habitats and can alter pollination success 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.

(5) Forest carbon dynamics

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

A suite of interrelated changes affects carbon stocks in fragmented forests. Many trees die near forest edges (Laurance *et al.,* 1997, 1998*a*), including an alarmingly high proportion of large ($\geq$60 cm dbh) canopy and emergent trees that store a large fraction of the total forest carbon (Laurance *et al.,* 2000). Compared to the mature-phase trees they replace, fast-growing pioneer trees and lianas that proliferate in fragments are smaller and have lower wood density and thereby sequester much less carbon (Laurance *et al.,* 2001*b*, 2006*a*). Based on current rates of forest fragmentation, the edge-related loss of carbon storage in the tropics could produce tens of millions of tons of atmospheric carbon emissions annually, above and beyond that caused by deforestation *per se* (Laurance, Laurance & Delamonica, 1998*c*; Groeneveld *et al.,* 2009).

In addition, biomass is being fundamentally redistributed in fragmented forests (Fig. 12). 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, Tanner & Kossman-Ferraz, 2000; Nascimento & Laurance, 2004; Vasconcelos & Luizão, 2004). Soil carbon also increases as the abundant dead biomass in fragments decomposes (Barros & Fearnside, 2016). Finally, carbon cycling accelerates. The large, old-growth trees that predominate in intact forests can live for many centuries or even millennia (Chambers, Higuchi & Schimel, 1998; W.F. Laurance *et al.,* 2004*a*), 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 & Laurance, 2004). Other biochemical cycles, such as those affecting key nutrients such as phosphorus (Sizer *et al.,* 2000) and calcium (Vasconcelos & Luizão, 2004), might also be altered in fragmented forests, given the striking changes in biomass dynamics, hydrology and thermal regimes they experience there.

IX. SPECIES RESPONSES TO FRAGMENTATION

Individual species and ecological groups can differ greatly in their responses to habitat fragmentation. Some decline or disappear, others remain roughly stable and yet others increase, sometimes dramatically. Understanding how and why different species vary so dramatically in their responses has been a major goal of conservation researchers. Here we underscore key conclusions from the BDFFP.

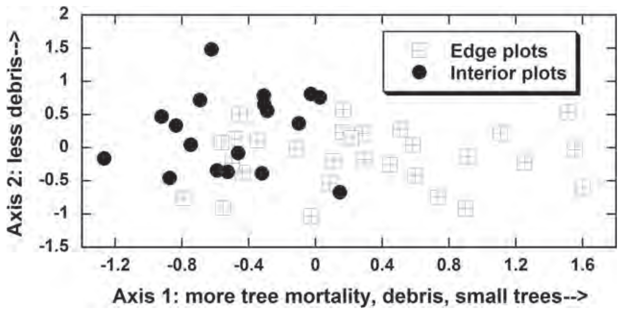

Fig. 12. Plots near forest edges ($<$100 m from edge) generally have higher tree mortality, more small trees, and more woody debris, relative to plots in forest interiors. Data shown are from an ordination analysis of 14 forest-biomass and necromass variables from 50 Biological Dynamics of Forest Fragments Project (BDFFP) plots (from Nascimento & Laurance, 2004).

(1) Non-random extinctions

Local extinctions of species in the BDFFP fragments have occurred in a largely predictable sequence, with certain species being consistently more vulnerable than others. Among birds, various species of understorey 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 & Metzger, 2005; Stouffer *et al.,* 2006, 2008, 2011).

In a similar vein, among bats, gleaning predators are consistently the most vulnerable species whereas many frugivores respond positively to fragmentation and other types of forest disturbance (Sampaio, 2000; Bobrowiec & Gribel, 2010; Farneda *et al.,* 2015; Rocha, 2016; Rocha *et al.,* 2017). Many animal-eating bat species rarely persist in small ($<$100 ha) fragments and in the secondary-forest matrix, reflecting trait-mediated environmental filters that selectively benefit smaller fruit- and nectar-feeding species (Farneda *et al.,* 2015). Primates exhibit similarly predictable patterns of species loss, with wide-ranging frugivores, especially the black spider-monkey *Ateles paniscus*, being most vulnerable (Boyle & Smith, 2010*b*). Hence, 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.

(2) Non-neutral extinctions

An important corollary of non-random 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 roughly equivalent in competitive and demographic terms. Making these assumptions allows one 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 utility 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 the 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 local extinctions of species from plots in fragmented and intact forest, as a function of the local diversity and 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 local extinction. Rather than becoming increasingly dominated by initially common species, fragments in the BDFFP landscape have experienced striking increases over time in disturbance-loving pioneer species (Fig. 13) (Laurance *et al.*, 2006*a*), 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.

(3) Key correlates of animal vulnerability

In the BDFFP landscape, 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. Among birds (Van Houtan *et al.*, 2007) and mammals (Timo, 2003), wide-ranging forest species are more vulnerable than 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, Gascon & Zimmerman, 1997) and ants (Carvalho & 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 regrowth forest and cattle pastures in the BDFFP landscape. Populations of species that entirely avoid the matrix will be demographically and genetically isolated in fragments, and therefore vulnerable to local extinction, whereas those that tolerate or exploit the matrix often persist (Laurance, 1991; Malcolm, 1997; Antongiovanni & Metzger, 2005; Ferraz *et al.*, 2007; Bobrowiec & Gribel, 2010).

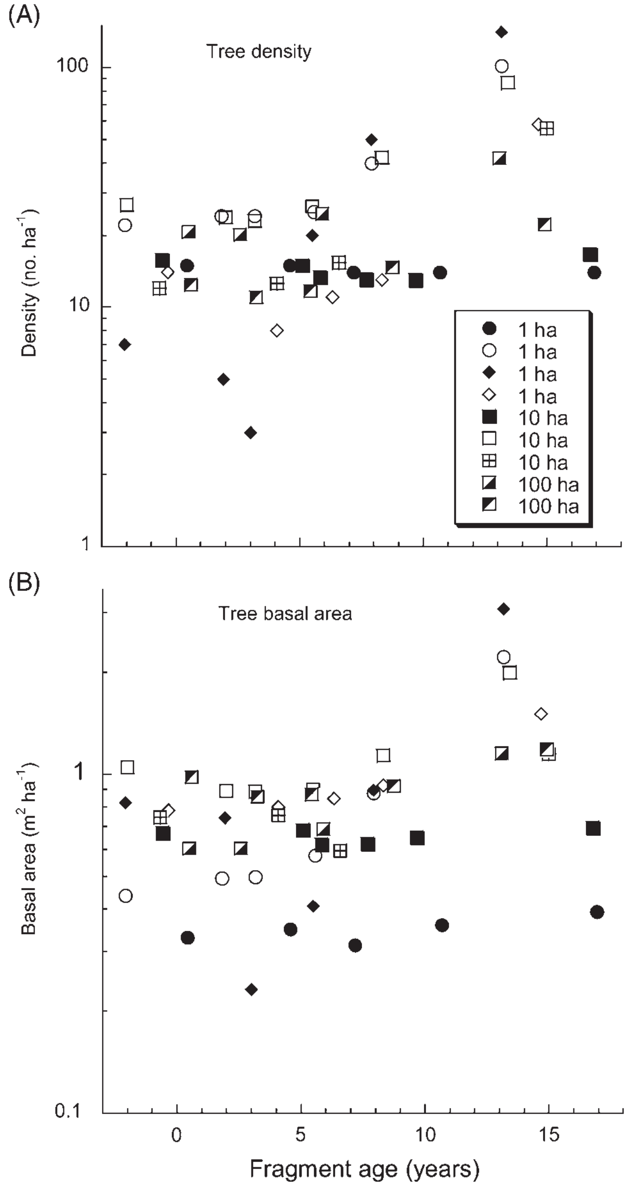

Fig. 13. Striking increases over time in the density (A) and basal area (B) of 52 species of early successional trees in forest fragments in the Biological Dynamics of Forest Fragments Project (BDFFP) study area. Note that vertical axes are $\log_{10}$-transformed (after Laurance *et al.*, 2006*a*).

At least among terrestrial vertebrates, matrix use is positively associated with tolerance of edge habitats (S.G. Laurance, 2004*a*; Farneda *et al.*, 2015), an ability to traverse small clearings (S.G. Laurance *et al.*, 2004; Laurance & Gomez, 2005), behavioural flexibility (Neckel-Oliveira & Gascon, 2006; Stouffer *et al.*, 2006; Van Houtan *et al.*, 2006; Boyle & Smith, 2010*a*) and a capacity to feed on early successional plants that thrive in the matrix (Farneda *et al.*, 2015; Meyer *et al.*, 2016; Rocha *et al.*, 2017). Within particular animal groups, such as beetles or small mammals, traits such as body size and natural abundance are generally poor or inconsistent predictors of vulnerability

(Laurance, 1991; Didham *et al.*, 1998*a*; Jorge, 2008; Boyle & Smith, 2010*b*).

(4) Key correlates of 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 colonize treefall gaps are favoured at the expense of slower-growing old-growth trees (Laurance *et al.*, 2006*a,b*). Pioneer species often flourish in the matrix and produce abundant small fruits that can be carried into fragments by frugivorous birds and bats that move between the matrix and nearby fragments (Sampaio, 2000; Nascimento *et al.*, 2006; Rocha *et al.*, 2017). Especially vulnerable in fragments are the diverse assemblages of smaller subcanopy trees that are physiologically specialized for growth and reproduction in dark, humid, forest-interior conditions (Laurance *et al.*, 2006*b*). 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.*, 2006*b*; Cramer, Mesquita & Williamson, 2007*b*).

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 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, have a strong negative influence on population growth (Lindenmayer & Laurance, 2016).

X. HORIZONS FOR NEW RESEARCH

Although BDFFP researchers have embraced a diversity of research themes, some topics remain poorly explored or enigmatic. For instance, there has been relatively little work to date on the effects of fragmentation on the phylogenetic and functional composition of forests and animal assemblages (but see Didham *et al.*, 1998*b*; Andresen, 2003). A study that examined changes in the phylogenetic structure of trees at the BDFFP concluded that most study sites, including small and large fragments as well as intact-forest plots, exhibited a progressive decline over time in phylogenetic diversity (Fig. 14) (Santos *et al.*, 2014). This evidently occurred because tree genera that have increased in abundance across the study area are more closely related phylogenetically than are those that have declined. Do such changes reflect community-wide responses to large-scale drivers, such as global-change phenomena (W.F. Laurance *et al.*, 2004*a*), shifts in regional rainfall (S.G. Laurance *et al.*, 2009), or some other widespread event? Further study is needed.

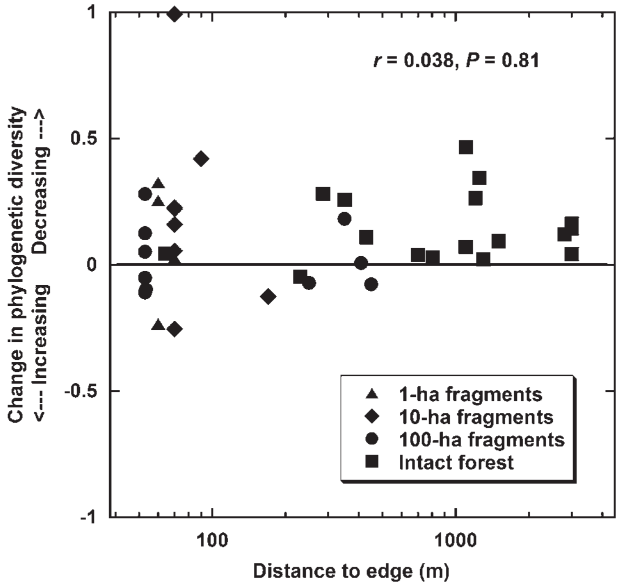

Fig. 14. Changes over time in the phylogenetic diversity of tree communities in 1-ha plots in the Biological Dynamics of Forest Fragments Project (BDFFP) study area (adapted from Santos *et al.*, 2014). Points with positive values (above the horizontal line) exhibited declining phylogenetic diversity over time, whereas those with negative values had opposite trends.

Similarly, ecological interactions such as pollination and seed dispersal have been poorly studied at the BDFFP. Changes in pollinator assemblages (Dick, 2001; Dick *et al.*, 2003) might be expected to alter plant pollination, seed set, and gene flow among plants, but such effects are largely unknown. Could shifts in the abundance of old-growth tree species, such the decline of obligate outbreeders and species that require animal seed dispersers (Laurance *et al.*, 2006*b*), reflect losses of key fauna in fragmented forests? Other ecological interactions, such as predator–prey, host–pathogen, and plant–mycorrhizal relationships, are virtually unstudied (but see Benitez-Malvido, Garcia-Guzman & Kossman-Ferraz, 1999).

Species invasions are also poorly understood in the BDFFP landscape. Taxon-specific studies suggest that the matrix supports a variety of plant, vertebrate, and invertebrate species that are foreign to Amazon rainforests, many of which are also detected in forest fragments (e.g. Brown & Hutchings, 1997; Tocher *et al.*, 1997; Dick, 2001; Scariot, 2001; Laurance *et al.*, 2002, 2011). Do such invaders have significant ecological effects? Are they increasing in diversity or abundance over time, as might be expected as new invasive species colonize the study area? Are expanding roads and powerline clearings providing avenues for species invasions (W.F. Laurance *et al.*, 2009)? Are some species capable of invading intact forests? Are foreign pathogens arriving? An array of such questions remains unanswered.

Finally, there is considerable scope to use modelling approaches with BDFFP data to generate long-term ($\geq$100-year) projections about the fate of fragmented forests. One such study, using a novel neural-network approach, suggested that tree communities in forest fragments will become increasingly dominated by early successional species but that seed rain from forest interiors will continue to maintain a mix of pioneer and old-growth species, even near heavily disturbed forest edges (Ewers *et al.,* 2017). Another modelling study used data on elevated tree mortality and floristic changes from the BDFFP to make projections of long-term carbon-storage declines and shifts in plant functional groups in fragmented forests (Groeneveld *et al.,* 2009).

XI. GENERAL LESSONS

The BDFFP provides a number of valuable lessons for environmental researchers and those working in developing nations. Here we highlight two conclusions of particular relevance.

(1) Values of long-term research

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.,* 2001*c*) 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 & Metzger, 2005; Stouffer *et al.,* 2006, 2011; Meyer *et al.,* 2016; Rocha, 2016), the divergence of fragments in different landscapes (Laurance *et al.,* 2007) and the effects of fragmentation on rare or long-lived species (Benítez-Malvido & Martinez-Ramos, 2003*a*; Ferraz *et al.,* 2007) and alternative successional pathways (Mesquita *et al.,* 2015), 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 major shifts in the composition of their tree, palm, liana and herb seedlings (Scariot, 2001; Benítez-Malvido & Martinez-Ramos, 2003*b*; Brum *et al.,* 2008) relative to those in intact forest. If these newly recruited plants represent the future of the forest, then the BDFFP fragments could eventually experience dramatic changes in floristic composition, comparable to those observed in some other tropical forests that have long been fragmented (e.g. da Silva & Tabarelli, 2000; Girão *et al.,* 2007; Santos *et al.,* 2010).

(2) Training is vital

Among the most enduring legacies of the BDFFP has been its leading role in training students and environmental decision-makers. To date, the project has yielded over 700 technical publications (http://pdbff.inpa.gov.br) and more than 200 Ph.D. and M.Sc. theses. It has also trained more than 700 graduate students and conservation professionals in sponsored courses, and hosted over 1000 student interns to date. Many of those who have benefited from BDFFP training are from Brazil or other Latin American nations. Among these are numerous individuals who have now advanced professionally to hold positions in government agencies, universities and non-governmental conservation organizations.

These training programs have had manifold benefits. For example, former BDFFP students and researchers have led opposition to a Brazilian government scheme to settle colonists in and around the BDFFP study area – an initiative that could bisect the Central Amazonian Conservation Corridor, a complex of protected and indigenous lands that is one of the most important conservation networks in Amazonia (Laurance & Luizão, 2007). BDFFP trainees have also been leaders in documenting the impacts of major highways and infrastructure projects that are crisscrossing the Amazon (e.g. Laurance *et al.,* 2001*a*; Fearnside & Graça, 2006) and that could promote large-scale human migration and forest disruption (Barni, Fearnside & Graça, 2015). A near-term threat to the BDFFP is a nearly completed highway (BR-319) that will link the 'arc of deforestation' in southern Amazonia to Manaus and the BDFFP, potentially promoting large-scale invasions or settlement of the study area (Fearnside, 2015).

XII. LESSONS FOR CONSERVATION

We conclude by highlighting some important general lessons from the BDFFP for conserving the Amazon and other tropical forests.

(1) The BDFFP is a best-case scenario

Although the BDFFP's forest fragments are experiencing a wide array of ecological alterations, it is important to emphasize that it is a controlled experiment. The fragments are square, not irregular, in shape. They are isolated by clearings of only 80–650 m width from large tracts of surrounding mature forest. They are embedded within a relatively benign matrix dominated by forest regrowth, not harsher anthropogenic habitats. In addition, these fragments are largely free from ancillary threats, such as selective logging, wildfires and overhunting, which plague many fragmented landscapes and wildlife populations elsewhere in the tropics (e.g. Moura *et al.,* 2014). Such threats can interact additively or synergistically with fragmentation, creating even greater perils for the rainforest biota (Laurance &

Cochrane, 2001; Michalski & Peres, 2005; Brook, Sodhi & Bradshaw, 2008). For these reasons, the effects of fragmentation at the BDFFP are clearly modest, relative to many human-dominated landscapes elsewhere in the tropics.

(2) 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 in area (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). Such large reserves will also provide greater resilience from rare calamities such as droughts (Feldpausch *et al.,* 2016) and intense storms (Laurance *et al.,* 2007), facilitate persistence of terrestrial and aquatic animals that migrate seasonally (Bührnheim & Fernandes, 2003) and buffer the reserve from external threats such as fires, large-scale forest desiccation and human encroachment (Cochrane & Laurance, 2002; Briant *et al.,* 2010).

Large reserves will also maximize forest carbon storage (Laurance *et al.,* 1997, 1998*c*) and provide greater resilience to future climatic and atmospheric changes (Laurance, 2005, 2016; Peres, 2005). Further, on the ancient, nutrient-starved soils of central and eastern Amazonia, low plant productivity translates into low population densities of many animals, especially as one moves up the food chain, so reserves must be proportionately larger to harbour viable populations of these species (Radtke *et al.,* 2008; Deichmann, Lima & Williamson, 2011; Deichmann *et al.,* 2012). The recent observation that within-species genetic variation of terrestrial vertebrates is higher in wilderness areas than in human-disturbed habitats further underscores the value of large nature reserves for sustaining biological diversity and the capacity of species to adapt to future environmental insults (Miraldo *et al.,* 2016).

Beyond large size, nature reserves in Amazonia should also be numerous and stratified across major river basins and climatic and edaphic gradients in order to preserve biophysically distinctive ecoregions (Olson *et al.,* 2001; Tscharntke *et al.,* 2012) and locally endemic species (Bierregaard *et al.,* 2001; Laurance, 2007). In addition, the core areas of nature reserves should ideally be free of roads, which facilitate human encroachment and hunting, internally fragment wildlife populations and promote invasions of exotic species (W.F. Laurance *et al.,* 2009).

(3) No fragment is unimportant

Tropical forests are being rapidly lost and fragmented (e.g. Myers *et al.,* 2000; Sloan *et al.,* 2014), and a key question is whether smaller (e.g. <10 ha) forest fragments have much value for nature conservation. We assert that there is no such thing as an 'unimportant' forest fragment. In 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 in human-dominated lands (Laurance & Bierregaard, 1997; Lima & Gascon, 1999; Dick *et al.,* 2003). In regions where forest loss is severe, forest fragments could sustain the last surviving populations of locally endemic species, underscoring their potential value for nature conservation (Arroyo-Rodríguez *et al.,* 2009). Finally, the observation that regenerating forests recover floristic diversity far faster in regions where small fragments of primary forest remain than in those lacking such fragments underscores the vital role of retaining even tiny fragments of the original forest (Van Breugel *et al.,* 2013).

(4) Wounded 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. Newly created forest edges tend to 'seal' themselves in a few years, reducing the intensity of deleterious edge effects (Camargo & Kapos, 1995; Didham & Lawton, 1999; Mesquita *et al.,* 1999). Secondary forests can develop quite rapidly in the surrounding matrix (Mesquita *et al.,* 2001), especially if soils and their seedbanks are not depleted by repeated burning and grazing (Ribeiro, Bruna & Mantovani, 2009; Norden *et al.,* 2011). Secondary forests facilitate movements of many animal species (Gascon *et al.,* 1999; Powell, Stouffer & Johnson, 2013), allowing them to recolonize fragments from which they had formerly disappeared (Becker *et al.,* 1991; Quintero & Roslin, 2005; Stouffer *et al.,* 2008; Bobrowiec & Gribel, 2010; Boyle & Smith, 2010*b*; Rocha, 2016; Rocha *et al.,* 2017). Species clinging to survival in fragments can also be rescued from local extinction *via* the genetic and demographic contributions of immigrants (Pimm & Jenkins, 2005; Zartman & Nascimento, 2006; Stouffer *et al.,* 2008). Compared to the BDFFP landscape, rates of forest recovery are probably slower in localities with severe forest loss, but such regions are likely to be of particular conservation significance and thereby worthy of efforts to reduce their recurring threats.

XIII. FRAGMENTATION AND LARGER-SCALE DRIVERS

(1) Interacting drivers

Taken in its entirety, it seems apparent from the large-scale, long-term research effort at the BDFFP that forest fragments and their biodiversity are influenced by a variety of local and larger-scale factors. The intrinsic attributes of a fragment, such as its size, shape and degree of isolation from intact forest, are unquestionably important. However, these attributes are clearly modified by the features of the surrounding landscape and its dynamics over time. Such landscape features can influence the nature and magnitude of edge effects in fragments (Fig. 7), the permeability of the matrix for faunal movements, the composition of the seed rain entering fragments, the likelihood of destructive surface fires penetrating into fragments, and the intensity of abiotic forces such as microclimatic changes, wind turbulence and vegetation breezes (Fig. 3) that in turn can strongly influence fragment biodiversity and ecosystem processes.

External vicissitudes, such as rare droughts, windstorms and intense rainfall events, can also leave a lasting imprint. Such phenomena might be influenced both by landscape-scale features as well as regional and possibly global climatic drivers. More generally, it is apparent that even intact forests in the BDFFP are experiencing concerted long-term changes in their composition and dynamics, which seem to reflect increasing forest productivity. These changes appear broadly consistent with those expected from increasing CO_2 fertilization, although other environmental causes, such as declining cloudiness and increasing forest insolation, are also plausible. Whatever their causes, it is likely that the suite of changes observed in Amazonian forest fragments are partly a consequence of drivers operating at much larger spatial scales.

In some cases, large-scale drivers could exacerbate ecological changes in forest fragments. For instance, elevated forest dynamics and proliferating lianas could result both from edge effects in fragments (microclimatic stresses and elevated wind turbulence that kill many trees) as well as from larger-scale drivers that increase forest productivity and dynamism while favouring fast-growing plant species (Laurance *et al.,* 2014*a*). In other cases, the larger-scale drivers might operate in opposition to local fragmentation effects. For example, the dramatic 'biomass collapse' observed in fragments resulting from the mortality of many trees (Laurance *et al.,* 1997, 2000) might be partially countered by increasing forest productivity that in turn promotes faster tree growth – although this is likely to have only a modest effect given the pronounced loss of large, old-growth trees in fragments and their replacement by smaller, lighter-wooded trees and vines (Fig. 6) that store much less carbon (Laurance *et al.,* 2006*a,b*).

That fragments are being influenced by multiple drivers operating at widely varying spatial scales underscores serious complications for those seeking to understand and predict the effects of habitat fragmentation. Such drivers could interact in complex and potentially synergistic ways (Laurance & Useche, 2009), and it is virtually impossible to establish reliable experimental controls for global phenomena that may be operating everywhere (Laurance *et al.,* 2014*a*). Indeed, it is quite possible that even the most remote and seemingly pristine regions of the Earth are being influenced by certain global-change phenomena.

A further complicating matter is that even relatively modest differences between landscapes, such as rare weather events or subtle differences in land-use practices, could potentially multiply over time into far more pervasive changes. This idea is supported by the marked differences in trajectories of floristic change in forest fragments in the different cattle ranches (Fig. 11), even in a landscape as nearly uniform in its soils, climate, vegetation and land-use history as the BDFFP. This observation leads to the prediction that fragments within the same landscape will tend to converge in composition and dynamics over time, whereas those in different landscapes will tend to diverge. That such minor differences can seemingly provoke large consequences sends a strong note of caution for conservation biologists: it may be possible to make general predictions about the consequences of habitat fragmentation, but the interplay of local and larger-scale phenomena could render efforts to make precise local predictions or draw broad generalizations virtually impossible.

(2) The Amazon and climate change

Amazonian forests store roughly 150–200 billion tonnes of carbon in their live biomass (Malhi *et al.,* 2006; Feldpausch *et al.,* 2012), the release of which could seriously hinder efforts to limit harmful climate change. Beyond this, Amazonian forests play vital roles in regional and global hydrological regimes, transporting massive quantities of moisture and heat to higher latitudes (Avissar & Werth, 2005; Nobre *et al.,* 2016). For such reasons, conserving tropical forests such as the Amazon is likely to have markedly greater benefits for limiting global warming than would protecting higher-latitude forests (Bala *et al.,* 2007).

Efforts to sustain the Amazon as a viable biophysical system can be guided by current research, which while constrained by uncertainties provides provisional guidelines for conserving the basin's forests (Nagy, Forsberg & Artaxo, 2016). The best available information suggests that the destruction of more than 30–40% of all Amazonian forests could sharply increase the chances of a collapse of the crucial water-recycling functions that help to sustain Amazonian rainfall, especially during the critical dry-season months when forests are most susceptible to fire (Malhi *et al.,* 2008; Nobre *et al.,* 2016). With current Amazon deforestation levels at about 20% and large areas of additional forest being degraded by logging and surface fires and penetrated by new roads, hydroelectric dams, mining and other developments, there is clearly a real potential for further large-scale forest loss (Laurance *et al.,* 2001*a*; Fearnside, 2002, 2007, 2016*b*).

The ongoing fragmentation of the Amazon at a large spatial scale will clearly increase the chances of both planned and unplanned forest destruction, because fragmented forest tracts are far more vulnerable than intact forests to predatory logging, wildfires, climate change and other anthropogenic impacts (Cochrane & Laurance, 2002, 2008). Hence, a blueprint for conserving the Amazon and thereby reaping its bioclimatic benefits for humanity and the global ecosystem would be to greatly discourage further large-scale fragmentation while maintaining large, intact forest blocks that could potentially persist in perpetuity.

XIV. CONCLUSIONS

(1) In the heart of the Amazon, a large-scale, 38-year research project has revealed that the dynamics and community composition of fragmented rainforests cannot be understood simply as a consequence of local site attributes, such as fragment size or the surrounding topography. Rather, at least some ecological changes appear to result from interactions among local features and larger-scale changes occurring at landscape, regional and even global scales.

(2) In undisturbed forests, observed changes are consistent with those expected from rising forest productivity, and include accelerating forest dynamics, concerted shifts in tree-community composition, elevated growth rates for most tree species, and increasing abundances of disturbance-loving lianas. Plant fertilization from rising atmospheric CO_2 levels might explain these trends, although other causes are not implausible.

(3) In general, ecological changes in forest fragments are strongly influenced by edge and sample effects, the dynamics of the surrounding matrix of modified vegetation, and rare disturbances such as droughts and windstorms. Because of their high sensitivity to local vicissitudes, forest fragments in different landscapes are predicted to diverge over time in dynamics and community composition, whereas those in the same landscape may converge.

(4) Different species vary markedly in their vulnerability to forest fragmentation. Animal species that decline in abundance or disappear in forest fragments frequently have large area requirements and avoid the surrounding matrix, whereas susceptible plant species fare poorly in disturbed or edge-altered forests and often require vulnerable animal species for seed dispersal or pollination.

(5) Much of the Amazon overlays nutrient-starved soils where most plant and animal species are both rare and patchily distributed. This, combined with the increased vulnerability of fragmented forests to various human disturbances, suggests that Amazonian nature reserves should be large (ideally $>10^4\,\text{km}^2$) and numerous to ensure their long-term viability. Larger reserves will also be more resilient to future climatic change and extreme weather events.

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