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

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28

29 Abstract

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

42

43 Keywords: Amazonia, Biodiversity, Climate change, Edge effects, Ecosystem services,

44 Environmental synergisms, Global change, Habitat fragmentation, Rainforest

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49 1. Introduction

50 1.1 Amazonia and global change

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

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

65 The BDFFP is a source of invaluable long-term datasets. These include high-quality
66 estimates of Amazon forest biomass and carbon stocks (Phillips et al. 1998, Baker et al.
67 2004)—needed to reduce uncertainties in estimating the climatic impact of destroying the
68 forest and the consequent benefit of avoiding this destruction. The project also contributes
69 greatly to knowledge of the diversity of species and their relationships in an Amazon forest
70 ecosystem (Laurance et al. 2010a, ter Steege et al. 2013). Biodiversity and ecosystem
71 processes represent part of what is lost when the forest is destroyed or degraded, whether by
72 direct human action, by climate change, or by the interaction of both together. Understanding

73 these processes is also essential for assessing not only the vulnerability of forests, but also
74 their potential resilience in the face of global change.

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

81 The exploitation of Amazonia is driving forest fragmentation on a vast spatial scale.
82 By the early 1990s, the area of Amazonian forest that was fragmented (<100 km²) or
83 vulnerable to edge effects (<1 km from edge) was over 150% greater than the area that had
84 been deforested (Skole and Tucker 1993). From 1999 to 2002, deforestation and logging in
85 Brazilian Amazonia respectively created ~32,000 and ~38,000 km of new forest edge
86 annually (Broadbent et al. 2008). Prevailing land uses in Amazonia, such as cattle ranching
87 and small-scale farming, produce landscapes dominated by small (<400 ha) and irregularly
88 shaped forest fragments (Cochrane and Laurance 2002, Broadbent et al. 2008). Such
89 fragments are highly vulnerable to edge effects, fires, and other deleterious consequences of
90 forest fragmentation (Laurance et al. 2002, Barlow et al. 2006, Cochrane and Laurance 2008).

91 While model predictions for future climate in Amazonia vary considerably, there is
92 broad agreement that the region will be hotter and drier under expected global warming (Dai
93 2012, IPCC 2013). What this portends for Amazonian forest is a matter of some controversy.
94 Disastrous die-off projected by the UK Meteorological Office Hadley Centre at atmospheric
95 CO₂ concentrations approximately two times those in the pre-industrial atmosphere (Cox et al.
96 2000, 2004) have now been countered by a new model version from the same group
97 indicating the Amazon forest almost entirely intact, even with up to four times the pre-

98 industrial CO₂ concentration (Cox et al. 2013, Good et al. 2013, Huntingford et al. 2013). The
99 main difference is inclusion of CO₂-fertilization effects, making the trees grow faster, resist
100 stress better, and close their stomata more frequently such that they use and need less water.

101 The BDFFP has made a significant contribution to debate over climatic influences on
102 the Amazon via its monitoring of lianas (Laurance et al. 2014). Lianas evidently make better
103 use of rising CO₂ than do trees (e.g., Condon et al. 1992), and contribute significantly to tree
104 damage and mortality (Ingwell et al. 2010). They also are most prone to form heavily vine-
105 dominated “liana forests” in drier parts of Amazonia, where climate is similar to that expected
106 over much wider areas of the region in the future (Fearnside 2013). BDFFP plots show a
107 marked increase in liana abundance and biomass between censuses in 1997-99 and 2012.
108 Since liana increases have also been found in tropical forests in Western Amazonia, Central
109 America, the Guianas, and elsewhere, with rising CO₂ levels being one of the more likely
110 explanations. This negative effect of CO₂ enrichment is not included in the Hadley Centre
111 models, and would likely cancel out some of the benefits indicated in a high-CO₂ future.

112 BDFFP data also help reveal the direct effects of a warmer, drier climate on the forest.
113 The microclimate on forest edges is significantly hotter and drier than that in the continuous
114 forest (Kapos 1989, Kapos et al. 1993, Camargo and Kapos 1995). Canopy trees are
115 vulnerable to changing microclimates on forest edges during the dry season, with desiccation
116 detected up to 2 km from clearings (Briant et al. 2010). At the BDFFP, edge-associated tree
117 mortality and “biomass collapse” have been extensively documented (Laurance et al. 1997,
118 1998, 2000, Nascimento and Laurance 2004). Because the entire forest can be expected to
119 face comparable conditions under projected climate change, the dead trees in the BDFFP
120 fragment edges stand as a clear warning of the power of these changes.

121 Better estimates of how the forest will fare under changed climate are essential for
122 many reasons, including providing the scientific basis needed to convince both world leaders

123 and the general public that containing climate change is worth the cost. But just as basic is the
124 question of what to do about climate change once the world finally decides that it is time to
125 act. The role of tropical forests is critical to this debate, as they contain a large stock of carbon
126 that could either be released by deforestation, logging, and fire, or conserved for their crucial
127 environmental values. The ways that avoiding these emissions could be incorporated into
128 global mitigation efforts, how carbon benefits would be rewarded, and how they should be
129 calculated have been the subject of longstanding controversy dividing environmental groups,
130 national governments, and scientists (see Fearnside 2001b, 2012a,b).

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

143 Crucially, the BDFFP forest data allow one to see the variability in biomass from one
144 hectare to another. The mean aboveground biomass of live trees across 69 1-ha plots was
145 355.8 ± 47 tons per ha (Mg ha^{-1}), ranging from 230.7 to 491.6 Mg ha^{-1} for individual plots
146 (Laurance et al. 1999). This great variability indicates the need for many plots, rather than
147 relying on only a few plots of 1 ha or less scattered around the region as the basis for

148 calibrating satellite imagery for biomass mapping and for estimating greenhouse-gas
149 emissions from deforestation (see Fearnside 2014). The relationships of biomass with soil
150 characters in the BDFFP (Laurance et al. 1999), and the corresponding relationships with
151 topography and distance above the water table found in other studies in the state of Amazonas
152 (de Castilho et al. 2006, Schiatti et al. 2013), are essential to future improvement in biomass
153 estimates across the region. These estimates form the basis of any form of reward for
154 maintaining Amazonian forest as a global-warming mitigation measure.

155

156 1.2. The Biological Dynamics of Forest Fragments Project

157 Starting in 1979, the Biological Dynamics of Forest Fragments Project (BDFFP) has been
158 assessing the impacts of fragmentation on the Amazon rainforest and biota (Lovejoy et al.
159 1986, Bierregaard et al. 1992, Pimm 1998, Laurance et al. 2002, 2011). Today, 35 years later,
160 it is the world's largest and longest-running experimental study of habitat fragmentation, as
161 well as one of the most highly cited ecological investigations ever conducted (Gardner et al.
162 2009, Peres et al. 2010, Pitman et al. 2011). The BDFFP has also been a global leader in
163 research, training, and capacity development, with over 640 publications
164 (<http://pdbff.inpa.gov.br>), more than 180 student theses, over 700 graduate students and
165 conservation professionals participating in sponsored courses, and over 1000 student interns
166 to date.

167 The BDFFP is located 80 km north of Manaus, Brazil and spans ~1000 km². The
168 topography is relatively flat (80–160 m elevation) but dissected by numerous stream gullies.
169 The heavily weathered, nutrient-poor soils of the study area are typical of large expanses of
170 the Amazon Basin. Rainfall ranges from 1900 to 3500 mm annually with a moderately strong
171 dry season from June to October. The forest canopy is 30–37 m tall, with emergent trees to 55
172 m. Species richness of trees (≥ 10 cm DBH) often exceeds 280 species ha⁻¹ (Oliveira and

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

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

183 Because of poor soils and low productivity, the ranches surrounding the BDFFP
184 fragments were largely abandoned after government fiscal incentives dried up from 1984
185 onwards. Secondary forests (initially dominated by *Vismia* spp. in areas that were cleared and
186 burned, or by *Cecropia* spp. in areas that were cleared without fire) proliferated in many
187 formerly cleared areas (Mesquita et al. 2001). Some of the regenerating areas initially
188 dominated by *Cecropia* spp. later developed into quite mature (>20 m tall), species-rich
189 secondary forests. *Vismia*-dominated regrowth, which is relatively species poor, is changing
190 far more slowly (Norden et al. 2010). To help maintain isolation of the experimental
191 fragments, 100 m-wide strips of regrowth were cleared and burned around each fragment on
192 4–5 occasions, most recently in 2013–2014. Additional human disturbances that harm many
193 fragmented landscapes in the Amazon, such as major fires and logging, are largely prevented
194 at the BDFFP. Hunting pressure has been very limited until recently. Laurance and
195 Bierregaard (1997) and Bierregaard et al. (2001) provide detailed descriptions of the study
196 area and design.

197

198 3. Sample and area effects

199 3.1. Sample effects are important in Amazonia

200 Many species in Amazonian forests are rare or patchily distributed. This phenomenon is
201 especially pronounced in the large expanses of the basin that overlay heavily weathered,
202 nutrient-poor soils (e.g. Radtke et al. 2008), where resources such as fruits, flowers, and
203 nectar are scarce and plants are heavily defended against herbivore attack (Laurance 2001).
204 This has a key implication for understanding forest fragmentation: given their rarity, many
205 species may be absent from fragments not because their populations have vanished, but
206 because they were simply not present at the time of fragment creation—a phenomenon termed
207 the ‘sample effect’ (Wilcox and Murphy 1985). Such sample effects are the hypothesized
208 explanation for the absence of many rare understory bird species from fragments (Ferraz et al.
209 2007). In addition, many beetles (Didham et al. 1998a), bats (Sampaio et al. 2003), ant-
210 defended plants (Bruna et al. 2005), and trees (Bohlman et al. 2008, Laurance et al. 2010b) at
211 the BDFFP exhibit high levels of habitat specialization or patchiness. In a region where rarity
212 and patchy distributions of species are the norm, sample effects appear to play a major role in
213 structuring fragmented communities. Given these sample effects, nature reserves will have to
214 be especially large to sustain viable populations of rare species (Lovejoy and Oren 1981,
215 Laurance 2005, Peres 2005, Radtke et al. 2008).

216

217 3.2. Fragment size is vital

218 Although fragments range from just 1–100 ha in the BDFFP study area, understanding
219 fragment-area effects has long been a central goal of the project (Lovejoy and Oren 1981,
220 Lovejoy et al. 1984, 1986). The species richness of many organisms declines with fragment
221 area, even with constant sampling effort across all fragments. Such declines are evident in leaf
222 bryophytes (Zartman 2003), tree seedlings (Benítez-Malvido and Martinez-Ramos 2003a),

223 palms (Scariot 1999), understory insectivorous birds (Stratford and Stouffer 1999; Ferraz et
224 al. 2007), gleaning animal-eating bats (Sampaio 2000, Rocha et al., 2013), primates (Gilbert
225 and Setz 2001, Boyle and Smith 2010a), and larger herbivorous mammals (Timo 2003),
226 among others. For these groups, smaller fragments are often unable to support viable
227 populations and deleterious edge effects—ecological changes associated with the abrupt,
228 artificial edges of forest fragments— can also rise sharply in intensity (Didham et al. 1998a).
229 A few groups, such as ant-defended plants and their ant mutualists, show no significant
230 decline in diversity with fragment area (Bruna et al. 2005).

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

240

241 4. Edge effects

242 4.1. Forest hydrology is disrupted

243 The hydrological regimes of fragmented landscapes differ markedly from those of intact
244 forest (Kapos 1989). Pastures or crops surrounding fragments have much lower rates of
245 evapotranspiration than do forests because they have far lower leaf area and thus less rooting
246 depth. Additionally, such clearings are hotter and drier than forests (Camargo & Kapos 1995).
247 Field observations and heat-flux simulations suggest that desiccating conditions can penetrate

248 up to 100–200 m into fragments from adjoining clearings (Malcolm 1998; Didham and
249 Lawton 1999). Further, streams in fragmented landscapes experience greater temporal
250 variation in flows than do those in forests, because clearings surrounding fragments have less
251 evapotranspiration and rainfall interception by vegetation (Trancoso 2008). This promotes
252 localized flooding in the wet season and stream failure in the dry season, with potentially
253 important impacts on aquatic invertebrates (Nessimian et al. 2008) and other organisms.
254 Forest fragmentation also can alter low-level atmospheric circulation, which in turn affects
255 local cloudiness and rainfall.

256 The warm, dry air over clearings tends to rise, creating zones of low air pressure. The
257 relatively cool, moist air over forests is drawn into this vacuum (Avissar and Schmidt, 1998).
258 As it warms it also rises and forms convectional clouds over the clearing, which can lead to
259 localized thunderstorms (Avissar and Liu 1996). In this way, clearings of a few hundred
260 hectares or more can draw moisture away from nearby forests (Laurance 2004a, Cochrane and
261 Laurance 2008). In Eastern Amazonia, satellite observations of canopy-water content suggest
262 such desiccating effects typically penetrate 1.0–2.7 km into fragmented forests (Briant et al.
263 2010). This moisture-robbing function of clearings, in concert with frequent burning in
264 adjoining pastures, could help explain why fragmented forests are so vulnerable to
265 destructive, edge-related fires (Cochrane and Laurance 2002, 2008).

266

267 4.2. Edge effects often dominate fragment dynamics

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

273 Edge phenomena are remarkably diverse. They include increased desiccation stress,
274 wind shear, and wind turbulence that sharply elevate rates of tree mortality and damage
275 (Laurance et al. 1997, 1998a). These in turn cause wide-ranging alterations in the community
276 composition of trees (Laurance et al. 2000, 2006a, 2006b) and lianas (Laurance et al., 2001b).
277 Such stresses may also reduce germination (Bruna 1999) and establishment (Uriarte et al.,
278 2010) of shade-tolerant plant species in fragments, leading to dramatic changes in the
279 composition and abundance of tree seedlings (Benítez-Malvido 1998, Benítez-Malvido and
280 Martinez-Ramos 2003a).

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

289 Some groups of organisms remain stable or even increase in abundance near edges.
290 Leaf bryophytes (Zartman and Nascimento 2006), wandering spiders (*Ctenus* spp.; Rego et al.
291 2007, Mestre and Gasnier 2008), and many frogs (Gascon 1993) show no significant response
292 to edges. Species that favor forest ecotones or disturbances, such as many gap-favoring and
293 frugivorous bird species (Laurance 2004b), hummingbirds (Stouffer and Bierregaard 1995a),
294 frugivorous bats that exploit early successional plant species (Sampaio 2000), light-loving
295 butterflies (Leidner et al. 2010), and fast-growing lianas (Laurance et al. 2001b), increase in
296 abundance near edges, sometimes dramatically.

297

298 4.3. Edge effects are cumulative

299 BDFFP research provides strong support for the idea that two or more nearby edges create
300 more severe edge effects than does just one (Fig. 2). This conclusion is supported by studies
301 of edge-related changes in forest microclimate (Kapos 1989, Malcolm 1998), vegetation
302 structure (Malcolm 1994), tree mortality (Laurance et al. 2006a), abundance and species
303 richness of tree seedlings (Benítez-Malvido 1998, Benítez-Malvido and Martinez-Ramos
304 2003a), liana abundance (Laurance et al. 2001b), and the density and diversity of disturbance-
305 loving pioneer trees (Laurance et al. 2006a, 2006b, 2007). The additive effects of nearby
306 edges could help to explain why small (<10 ha) or irregularly shaped forest remnants are
307 often so severely altered by forest fragmentation (Zartman 2003, Laurance et al. 2006a).

308

309 4.4. Edge age, structure, and adjoining vegetation influence edge effects

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

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

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

328

329 5. Isolation and matrix effects

330 5.1. Matrix structure and composition affect fragments

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

343 The surrounding matrix also has a strong effect on plant communities in fragments by
344 mediating certain edge effects (see above), influencing the movements of pollinators (Dick
345 2001, Dick et al. 2003) and seed dispersers (Jorge 2008, Bobrowiec and Gribel 2010, Boyle
346 and Smith 2010a), and strongly affecting the seed rain that arrives in fragments. For instance,
347 pioneer trees regenerating in fragments differed strikingly in composition between fragments

348 surrounded by *Cecropia*-dominated regrowth and those encircled by *Vismia*-dominated
349 regrowth (Nascimento et al. 2006). In this way plant and animal communities in fragments
350 could come to mirror to some extent the composition of the surrounding matrix (Laurance et
351 al. 2006a, 2006b), a phenomenon observed elsewhere in the tropics (e.g. Janzen 1983,
352 Diamond et al. 1987).

353

354 5.2 Matrix is affected by history and forest proximity

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

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

372

373 5.3 Even narrow clearings are harmful

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

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

391

392 6. Landscape dynamics

393 6.1. Rare disturbances can leave lasting legacies

394 Rare events such as windstorms and droughts have strongly influenced the ecology of
395 fragments. Rates of tree mortality rose abruptly in fragmented (Laurance et al., 2001c) and
396 intact forests (Williamson et al. 2000, Laurance et al. 2009a) in the year after the intense 1997
397 El Niño drought. Such pulses of tree death help drive changes in the floristic composition and

398 carbon storage of fragments (Laurance et al. 2007). Leaf-shedding by drought-stressed trees
399 also increases markedly during droughts, especially within ~60 m of forest edges (Laurance
400 and Williamson 2001). This increases the susceptibility of fragments to destructive surface
401 fires (Cochrane and Laurance 2002, 2008).

402 Intense windblasts from convectonal thunderstorms have occasionally strafed parts of
403 the BDFFP landscape and caused intense forest damage and tree mortality, especially in the
404 fragments. Fragments in the easternmost cattle ranch at the BDFFP have had substantially
405 lower rates of tree mortality than did those in the other two ranches, because the former have
406 so far escaped windstorms (Laurance et al. 2007). These differences have strongly influenced
407 the rate and trajectory of change in tree-community composition in fragments (Laurance et al.
408 2006b). Hence, by altering forest dynamics, composition, structure, and carbon storage, rare
409 disturbances have left an enduring imprint on the ecology of fragmented forests.

410

411 6.2. Fragments are hyperdynamic

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

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

423 1997), and butterfly communities in general are hyperdynamic in fragments (Leidner et al.
424 2010). Bat assemblages also show pronounced species turnover, particularly in 1-ha
425 fragments (Meyer et al. 2013). Streamflows are far more variable in fragmented than forested
426 watersheds (Trancoso 2008). Rates of tree mortality and recruitment are chronically elevated
427 in fragments (Laurance et al. 1998a, b), with major pulses associated with rare disturbances
428 (see above). Further, tree species disappear and turn over far more rapidly in fragments than
429 intact forest, especially within ~100 m of forest margins (Laurance et al. 2006b). These and
430 many other instabilities plague small, dwindling populations in the BDFFP fragments.

431

432 6.3. Fragments in different landscapes diverge

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

438 At the outset, small initial differences among the ranches multiplied into much bigger
439 differences. Parts of the western and eastern ranches were cleared in 1983, when an early wet
440 season prevented burning of the felled forest. Tall, floristically diverse *Cecropia*-dominated
441 regrowth quickly developed in these areas, whereas areas cleared in the years just before or
442 after became cattle pastures or, eventually, scrubby *Vismia*-dominated regrowth (Williamson
443 and Mesquita 2001). These different successional trajectories manifested, for instance, as
444 distinct differences in bat assemblage composition, whereby *Cecropia*-dominated regrowth
445 retained a considerable fraction of forest-specialist bat species found in continuous forest
446 compared to *Vismia* regrowth (Bobrowiec and Gribel 2010). As discussed above, the differing
447 matrix vegetation strongly affected the dynamics of plant and animal communities in the

448 nearby fragments. These differences were magnified by subsequent windstorms, which
449 heavily damaged most fragments in the central and western ranches, yet left fragments in the
450 eastern ranch unscathed. Even identically sized fragments in the three ranches have had
451 remarkably different dynamics and vectors of compositional change (Laurance et al. 2007).

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

465

466 7. Broader consequences of fragmentation

467 7.1. Ecological distortions are common

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

473 BDFFP findings suggest that even un hunted forest fragments have reduced densities
474 of key mammalian seed dispersers. As a result, seed dispersal for an endemic, mammal-
475 dispersed tree (*Duckeodendron cestroides*) was far lower in fragments, with just ~5% of the
476 number of seeds being dispersed >10 m away from parent trees than in intact forest (Cramer
477 et al. 2007a). Leaf herbivory appears reduced in fragments, possibly because of lower
478 immigration of insect herbivores (Fáveri et al. 2008). Dung beetles exhibit changes in
479 biomass and guild structure in fragments (Radtke et al. 2008) that could alter rates of forest
480 nutrient cycling and secondary seed dispersal (Klein 1989, Andresen 2003). Exotic
481 Africanized honeybees, a generalist pollinator, are abundant in matrix and edge habitats and
482 can alter pollination distances and gene flow for some tree species (Dick 2001, Dick et al.
483 2003). A bewildering variety of ecological distortions can pervade fragmented habitats, and a
484 challenge for conservation biologists is to identify those of greatest importance and
485 generality.

486

487 7.2. Fragmentation affects much more than biodiversity

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

492 Carbon storage in fragmented forests is affected by a suite of interrelated changes.
493 Many trees die near forest edges (Laurance et al. 1997, 1998a), including an alarmingly high
494 proportion of large (≥ 60 cm dbh) canopy and emergent trees that store much forest carbon
495 (Laurance et al. 2000). Fast-growing pioneer trees and lianas that proliferate in fragments are
496 smaller and have lower wood density, and thereby sequester much less carbon, than do the
497 mature-phase trees they replace (Laurance et al. 2001b, 2006a). Based on current rates of

498 forest fragmentation, the edge-related loss of forest carbon storage might produce up to 150
499 million tons of atmospheric carbon emissions annually, above and beyond that from tropical
500 deforestation per se (Laurance et al. 1998c). This would exceed the yearly carbon emissions
501 of the entire United Kingdom. Note, however, that most of this emission is already counted in
502 the existing estimates of the impact of Amazonian land-use change because the deforestation
503 emission estimates use forest biomass values for undegraded forest (Fearnside 2000). Because
504 most deforestation occurs by expansion of already-existing clearings, forest edges (with
505 reduced biomass) are the first areas to be cleared. Only the annual increase in the total length
506 of forest edges represents an addition. Improved emissions estimates, with accounting for
507 degradation by logging, fire and fragmentation, are a high priority.

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

520

521 8. Predicting species responses to fragmentation

522 8.1. Species losses are highly nonrandom

523 Species extinctions in the BDFFP fragments have occurred in a largely predictable sequence,
524 with certain species being consistently more vulnerable than others. Among birds, a number
525 of understory insectivores, including army ant-followers, solitary species, terrestrial foragers,
526 and obligate mixed-flock members, are most susceptible to fragmentation. Others, including
527 edge/ gap species, insectivores that use mixed flocks facultatively, hummingbirds, and many
528 frugivores, are far less vulnerable (Antongiovanni and Metzger 2005, Stouffer et al. 2006,
529 2008). In a similar vein, among bats, gleaning animalivores are consistently the most
530 vulnerable species whereas many frugivores respond positively to fragmentation and
531 disturbance (Sampaio 2000, Bobrowiec and Gribel 2010, Rocha et al. 2013). Primates exhibit
532 similarly predictable patterns of species loss, with wide-ranging frugivores, especially the
533 black spider-monkey, being most vulnerable (Boyle and Smith 2010a). Local extinctions in
534 fragments follow a foreseeable pattern, with species assemblages in smaller fragments rapidly
535 forming a nested subset of those in larger fragments (Stouffer et al. 2008). Random
536 demographic and genetic processes may help to drive tiny populations into oblivion, but the
537 species that reach this precarious threshold are far from random.

538

539 8.2. Fragmented communities are not neutral

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

548 become dominated by initially abundant species, with rare species gradually vanishing; other
549 ecological traits of species are considered unimportant.

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

561

562 8.3. Matrix use and area needs determine animal vulnerability

563 The responses of animal species to fragmentation appear largely governed by two key sets of
564 traits. The first is their spatial requirements for forest habitat. In birds (Van Houtan et al.
565 2007) and mammals (Timo 2003), wide-ranging forest species are more vulnerable than are
566 those with localized ranges and movements. Species with limited spatial needs, such as many
567 small mammals (Malcolm 1997), hummingbirds (Stouffer et al. 2008), frogs (Tocher et al.
568 1997), and ants (Carvalho and Vasconcelos 1999), are generally less susceptible to
569 fragmentation.

570 The second key trait for fauna is their tolerance of matrix habitats (Gascon et al.
571 1999), which comprises cattle pastures and regrowth forest in the BDFFP landscape.
572 Populations of species that avoid the matrix will be entirely isolated in fragments, and

573 therefore vulnerable to local extinction, whereas those that tolerate or exploit the matrix often
574 persist (Laurance 1991, Malcolm 1997, Antongiovanni and Metzger 2005, Ferraz et al. 2007,
575 Bobrowiec and Gribel 2010). At least among terrestrial vertebrates, matrix use is positively
576 associated with tolerance of edge habitats (Laurance 2004b, Farneda 2013), an ability to
577 traverse small clearings (Laurance et al. 2004, Laurance and Gomez 2005), and behavioral
578 flexibility (Neckel-Oliveira and Gascon 2006, Stouffer et al. 2006, Van Houtan et al. 2006,
579 Boyle and Smith 2010b). Within particular animal groups, such as beetles or small mammals,
580 traits such as body size and natural abundance are poor or inconsistent predictors of
581 vulnerability (Laurance 1991, Didham et al. 1998a, Jorge 2008, Boyle and Smith 2010a).
582 Natural abundance, however, is an important predictor of sensitivity to fragmentation for bats
583 at the BDFFP (Farneda, 2013).

584

585 8.4. Disturbance tolerance and mutualisms affect plant vulnerability

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

597 These combinations of traits suggest that plant communities in fragmented forests are

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

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

610

611 9. Broad perspectives

612 9.1. Long-term research is crucial

613 Many insights from the BDFFP would have been impossible in a shorter-term study. The
614 exceptional vulnerability of large trees to fragmentation (Laurance et al. 2000) only became
615 apparent after two decades of fragment isolation. Likewise, the importance of ephemeral
616 events such as El Niño droughts (Williamson et al., 2000, Laurance et al. 2001c) and major
617 windstorms (Laurance et al. 2007) would not have been captured in a less-enduring project.
618 Many other key phenomena, such as the kinetics of species loss in fragments (Ferraz et al.
619 2003), the strong effects of matrix dynamics on fragmented bird and bat assemblages
620 (Antongiovanni and Metzger 2005, Stouffer et al. 2006, Meyer et al. 2013), the divergence of
621 fragments in different landscapes (Laurance et al. 2007), and the effects of fragmentation on
622 rare or long-lived species (Benítez-Malvido and Martinez-Ramos 2003b, Ferraz et al., 2007),

623 are only becoming understood after decades of effort.

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

634

635 9.2. The BDFFP is a best-case scenario

636 Although forest fragments in the BDFFP are experiencing a wide array of ecological changes,
637 it is important to emphasize that it is a controlled experiment. The fragments are square, not
638 irregular, in shape. They are isolated by distances of just 80–650 m from large tracts of
639 surrounding mature forest. They are embedded in a relatively benign matrix increasingly
640 dominated by regrowth forest. And they lack many of the ancillary threats, such as selective
641 logging, wildfires, and overhunting, that plague many fragmented landscapes and wildlife
642 elsewhere in the tropics. Such threats can interact additively or synergistically with
643 fragmentation, creating even greater perils for the rainforest biota (Laurance and Cochrane
644 2001, Michalski and Peres 2005, Brook et al. 2008). For these reasons, results from the
645 BDFFP are almost certainly optimistic relative to many human-dominated landscapes
646 elsewhere in the tropics.

647

648 10. Conservation lessons from the BDFFP

649 10.1. Amazonian reserves should be large and numerous

650 A key conclusion from BDFFP research is that nature reserves in Amazonia should ideally be
651 very large—on the order of thousands to tens of thousands of square kilometers (Laurance
652 2005, Peres 2005). Only at this size will they be likely to maintain natural ecological
653 processes and sustain viable populations of the many rare and patchily distributed species in
654 the region (Ferraz et al. 2007, Radtke et al. 2008); provide resilience from rare calamities such
655 as droughts and intense storms (Laurance et al. 2007); facilitate persistence of terrestrial and
656 aquatic animals that migrate seasonally (Bührnheim and Fernandes 2003); buffer the reserve
657 from large-scale edge effects including fires, forest desiccation, and human encroachment
658 (Cochrane and Laurance 2002, Briant et al. 2010); maximize forest carbon storage (Laurance
659 et al. 1997, 1998c); and provide resilience from future climatic and atmospheric changes—the
660 effects of which are difficult to predict for Amazonia (Laurance and Useche 2009). Further,
661 on the ancient soils of Central and Eastern Amazonia, low plant productivity translates into
662 low population densities of many animals up the food chain, so reserves must be
663 proportionately larger to harbor viable populations (Radtke et al. 2008, Deichmann et al.
664 2011, 2012).

665 Nature reserves in Amazonia should also be numerous and stratified across major river
666 basins and climatic and edaphic gradients, in order to preserve locally endemic species
667 (Bierregaard et al. 2001, Laurance, 2007). Further, the core areas of reserves should ideally be
668 free of roads, which can promote human encroachment and hunting, internally fragment
669 wildlife populations, and facilitate invasions of exotic species and fire (Laurance et al.
670 2009b).

671

672 10.2. Protect and reconnect fragments

673

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

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

687

688 10.3. Fragmented landscapes can recover

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

698 2010a, Meyer et al. 2013). Species clinging to survival in fragments can also be rescued from
699 local extinction via the genetic and demographic contributions of immigrants (Zartman and
700 Nascimento 2006, Stouffer et al. 2008).

701

702 11. The future of the BDFFP

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

709 In its 35-year history, the BDFFP has faced myriad challenges. These include, among
710 others, the continuing weakness the US dollar, challenges in obtaining research visas for
711 foreign students and scientists, inadequate core funding from its US and Brazilian sponsors,
712 and the vagaries of finding soft money for long-term research and to hold a minimal number
713 of workers to support infrastructure and logistics. Yet today the BDFFP faces a far more
714 direct threat: encroachment from colonists and hunters. Since the late 1990s, the paving of the
715 1100-km-long Manaus–Venezuela (BR-174) highway has greatly accelerated forest
716 colonization and logging north of the city. SUFRAMA, a Brazilian federal agency that
717 controls an expanse of land north of Manaus that includes the BDFFP, has begun settling
718 families in farming plots around the immediate periphery of the study area. At least six
719 colonization projects involving 180 families are planned for the area (Laurance and Luizão
720 2007). This could be the beginning of a dramatic influx into the area, especially if the
721 proposed BR-319 highway between Manaus and Rondônia, a major deforestation hotspot in
722 southern Amazonia, is completed as planned (Fearnside and Graça 2006).

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

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

738

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FIGURE CAPTIONS

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1264

1265 Figure 1. Map of the Biological Dynamics of Forest Fragments Project in central Amazonia.

1266

1267 Figure 2. Forest plots affected by two or more nearby edges (plot center <100 m from edge)

1268 suffer greater tree mortality (A) and have a higher density (B) and species richness (C) of

1269 disturbance-loving pioneer trees than do plots with just one nearby edge. Values shown are

1270 the mean \pm SD (after Laurance et al. 2006a).

1271

1272 Figure 3. Increasing divergence of tree-community composition in three fragmented

1273 Amazonian landscapes. Tree communities in forest-edge plots (<100 m from the nearest

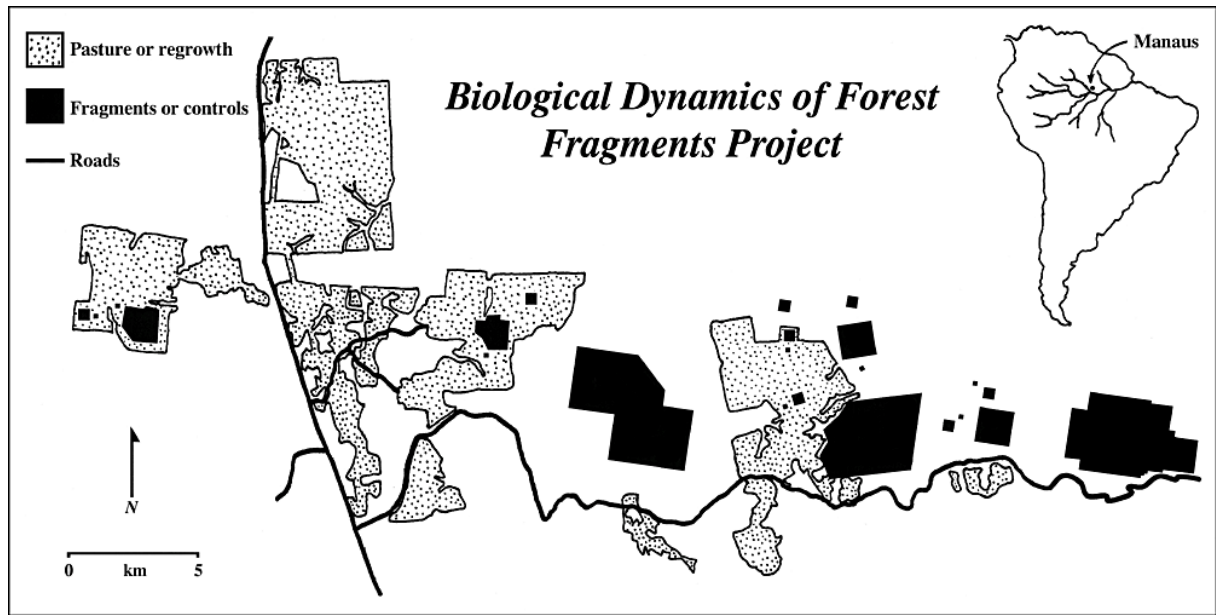
1274 edge) are shown before forest fragmentation and 13–18 years after fragmentation, based on a

1275 single ordination of all plots and censuses in the study area. The ordination used importance

1276 values for all 267 tree genera found in the plots (after Laurance et al. 2007).

1277 Fig. 1.

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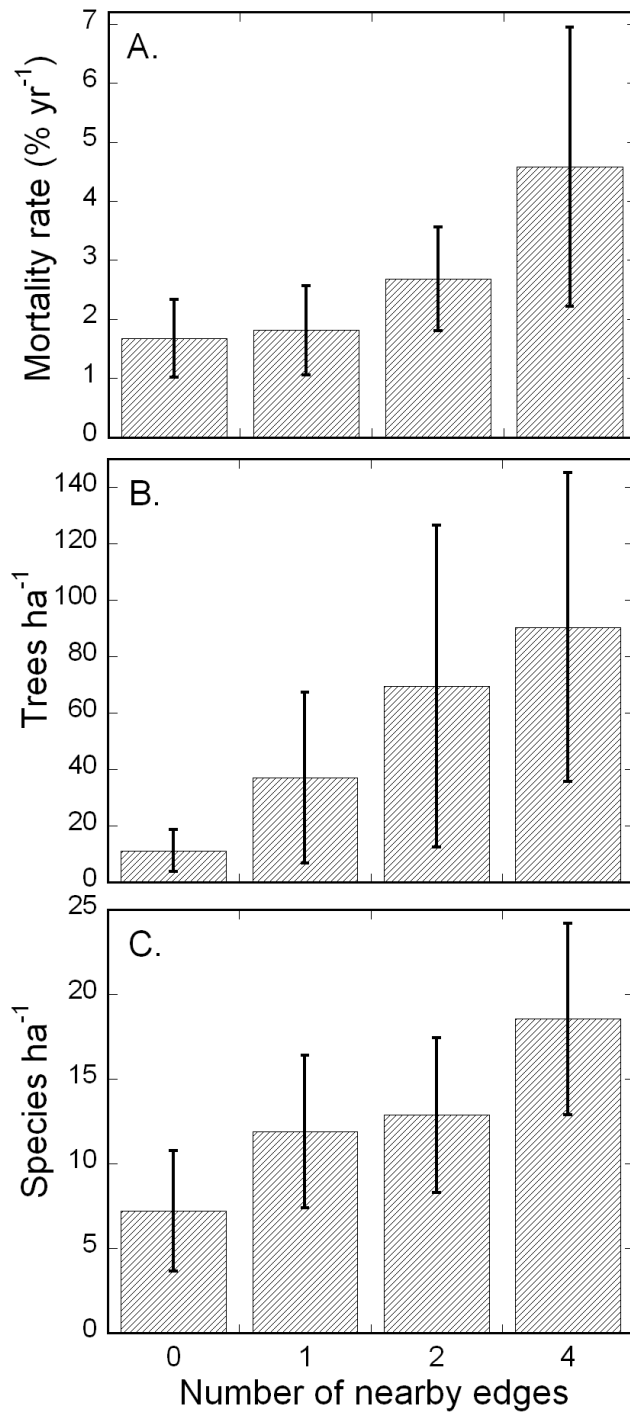


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1281 Fig. 2

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1285 Fig. 3

