

The text that follows is a PREPRINT
O texto que segue é um PREPRINT.

Please cite as:

Favor citar como:

**Laurance, W.F.; J.L.C. Camargo, P.M.
Fearnside, T.E. Lovejoy, G.B.
Williamson, R.C.G. Mesquita, C.F.J.
Meyer, P.E.D. Bobrowiec, & S.G.W.
Laurance. 2016. An Amazonian forest
and its fragments as a laboratory of
global change. pp. 407-440. In: L. Nagy,
B. Forsberg, P. Artaxo (eds.) *Interactions
Between Biosphere, Atmosphere and
Human Land Use in the Amazon Basin..*
Springer (Ecological Studies 227), Berlin,
Alemanha. 478 pp.**

doi: 10.1007/978-3-662-49902-3_16

ISBN (Hard Cover): 978-3-662-49902-3;

ISBN (Ebook): 978-3-662-49900-9.

Copyright: Springer Science + Business Media

The original publication is available from:

A publicação original está disponível de:

<http://www.springer.com/us/book/9783662499009>

Springer
Tiergartenstraße 17
69121 Heidelberg
Germany

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

William F. Laurance^{1,*}, José L. C. Camargo², Philip M. Fearnside³, Thomas E. Lovejoy^{2,4},
G. Bruce Williamson⁵, Rita C. G. Mesquita⁶, Christoph F. J. Meyer^{2,7}, Paulo E. D.
Bobrowiec^{2,8} & Susan G. W. Laurance^{1,*}

¹Centre for Tropical Environmental and Sustainability Science (TESS) and College of Marine and Environmental Science, James Cook University, Cairns, Queensland 4878, Australia,

*corresponding authors: bill.laurance@jcu.edu.au and susan.laurance@jcu.edu.au

²Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA) and Smithsonian Tropical Research Institute, Manaus, AM 69067-375, Brazil, zeluiscamargo@gmail.com

³Department of Environmental Dynamics, National Institute for Amazonian Research (INPA), Manaus, AM 69067-375, Brazil, phillip.fearnside@gmail.com

⁴Department of Environmental Science and Policy, George Mason University, Fairfax, VA 22030, USA, tlovejoy@unfoundation.org

⁵Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, 70803, USA, btwill@lsu.edu

⁶Long-term Ecological Research (PELD), National Institute for Amazonian Research (INPA), Manaus, AM 69067-375, Brazil, rita@buriti.com.br

⁷Center for Environmental Biology, University of Lisbon, Campo Grande C2, 1749-016 Lisbon, Portugal; E-mail: cmeyer@fc.ul.pt

⁸Coordination of Biodiversity, National Institute for Amazonian Research (INPA), Manaus, AM 69067-375, Brazil, paulobobro@gmail.com

Abstract

We synthesize findings from the world's largest and longest-running experimental study of habitat fragmentation, in central Amazonia. Over the past 36 years, 11 forest fragments ranging from 1-100 ha in size have experienced a wide array of ecological changes. Edge effects have been a dominant driver of fragment dynamics, strongly affecting forest microclimate, tree mortality, carbon storage, and fauna. The matrix of vegetation surrounding fragments has changed markedly over time (evolving from large cattle pastures to mosaics of abandoned pasture and secondary regrowth forest), and this, in turn, has strongly influenced the dynamics of fragments and faunal communities. Both rare weather events and apparent global-change drivers have significantly influenced forest structure and dynamics across the entire study area, both in forest fragments and in nearby intact forest. Such large-scale drivers are likely to interact synergistically with habitat fragmentation.

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

42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91

1. Introduction

The Biological Dynamics of Forest Fragments Project (BDFFP) is the world's largest and longest-running experimental study of habitat fragmentation¹ (Box 1). Located in central Amazonia near the city of Manaus, the BDFFP has evolved since its inception in 1979 into a major epicenter for long-term research. The BDFFP's research mission has gradually broadened to include not only long-term studies of forest fragmentation but also important work on global-change phenomena and a variety of basic research topics.

Here we highlight some key contributions of this singular project to the study of land-use change and regional- and global-scale drivers in central Amazonia, at the heart of the world's largest tropical forest.

1.1 Amazonia and global change

Amazonia stands at the intersection of several key questions for global change, both for study and for action. It is believed to be one of the regions that will be most impacted by projected climate changes (Salazar et al. 2007, Dai 2012, IPCC 2013). It has the potential to contribute significantly to efforts to mitigate climate change during the narrow window of time that we have to avert 'dangerous' global warming (Fearnside 2000, 2012). It is also one of the places where sharply reducing greenhouse-gas emissions—by limiting forest loss and degradation—could deliver the greatest global benefits for humankind (Stickler et al. 2009).

The rapid loss and fragmentation of old-growth forests are among the greatest threats to tropical biodiversity (Lovejoy et al. 1986, Sodhi et al. 2004, Laurance and Peres 2006, Gibson et al. 2011). More than half of all remaining tropical forest occurs in the Amazon Basin, which is being seriously altered by large-scale agriculture (Fearnside, 2001a, Gibbs et al. 2010), industrial logging (Asner et al. 2005), proliferating roads and energy infrastructure (Laurance et al. 2001a, Fearnside 2002, 2007, Killeen 2007), increasing biofuel production (Butler and Laurance 2009), and oil, gas, and mining developments (Finer et al. 2008).

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

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

1.2 Contributions of the BDFFP to global-change research

92 The BDFFP, with 36 years of research in fragmented and continuous forest in central
93 Amazonia (Box 1; Fig. 1), has been contributing to quantifying the interactions of land use
94 and global climate change. BDFFP studies have assessed the vulnerability of the forest to
95 changes in meteorological parameters (Laurance et al. 2009a), including those that are
96 aggravated by fragmentation (Laurance 2004). The long-term monitoring of thousands of
97 individual forest trees, and of populations of various other plant and animal species in the
98 same locations, provides the potential for early detection of global environmental changes.

99 The BDFFP is a source of invaluable long-term datasets. These include high-quality
100 estimates of Amazon forest biomass and carbon stocks (Phillips et al. 1998, Baker et al.
101 2004). The project also contributes greatly to knowledge of the diversity of species and their
102 relationships in an Amazon forest ecosystem (Laurance et al. 2010a, ter Steege et al. 2013).
103 Biodiversity and ecosystem processes represent part of what is lost when the forest is
104 destroyed or degraded, whether by direct human action, by climate change, or by the
105 interaction of both together. Understanding these processes is essential for assessing not only
106 the vulnerability of forests, but also their potential resilience in the face of global change and
107 the rate of recovery following perturbation (Williamson et al. 2014).

108 The BDFFP has made a substantial contribution to debate over climatic influences on
109 the Amazon via its monitoring of lianas and forest dynamics (Laurance et al. 2014a, 2014b).
110 Lianas evidently make better use of rising CO₂ than do trees (e.g., Condon et al. 1992), and
111 contribute significantly to tree damage and mortality (Ingwell et al. 2010). They also form
112 heavily vine-dominated ‘liana forests’ in drier parts of Amazonia (Fearnside 2013). BDFFP
113 plots show a marked increase in liana abundance and biomass between censuses in 1997-99
114 and 2012 (Laurance et al. 2014). Liana increases have also been found in tropical forests in
115 western Amazonia, central America, the Guianas, and elsewhere, with rising CO₂ levels being
116 one of the more likely explanations (see Laurance et al. 2014 and references therein). This
117 negative effect of CO₂ enrichment is not included in the Hadley Centre models, and would
118 likely cancel out some of the benefits indicated in a high-CO₂ future.

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

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

138 One aspect of this discussion to which the BDFFP makes an important contribution is
139 in reducing the uncertainty surrounding biomass and carbon-stock estimates for Amazon
140 forest. The BDFFP tree survey is much more complete than, for example, the 3000 1-ha plots
141 surveyed by the RADAMBRASIL Project (Nogueira et al. 2008). The BDFFP has much

142 better species identifications and includes data on other forest components, such as palms,
143 lianas, strangler figs, understory vegetation, and dead vegetation (necromass). Correct species
144 identification allows better matching with plant functional traits such as wood density and tree
145 form (e.g., Fearnside 1997, Nogueira et al. 2005, 2007, Chave et al. 2006).

146 Crucially, the BDFFP forest data allow one to see the variability in biomass from one
147 hectare to another. The mean aboveground biomass of live trees across 69 1-ha plots was 356
148 ± 47 Mg ha⁻¹ (Laurance et al. 1999). This great variability indicates the need for many plots,
149 rather than relying on only a few plots of 1 ha or less scattered around the region as the basis
150 for calibrating satellite imagery for biomass mapping and for estimating greenhouse-gas
151 emissions from deforestation (see Fearnside 2014).

152

153 2. Long-term studies of forest fragmentation

154 The BDFFP's original mission focuses on assessing the effects of forest fragmentation on
155 Amazonian forests and fauna, and on important ecological and ecosystem processes. Here we
156 summarize some key conservation lessons that have been gleaned to date.

157

158 2.1. Sample effects are important in Amazonia

159 Many species in Amazonian forests are rare or patchily distributed. This phenomenon is
160 especially pronounced in the large expanses of the basin that overlay heavily weathered,
161 nutrient-poor soils (e.g. Radtke et al. 2008), where resources such as fruits, flowers, and
162 nectar are scarce and plants are heavily defended against herbivore attack (Laurance 2001).
163 Herein lies a key implication for understanding forest fragmentation: given their rarity, many
164 species may be absent from fragments not because their populations have vanished, but
165 because they were simply not present at the time of fragment creation—a phenomenon termed
166 the 'sample effect' (Wilcox and Murphy 1985). Such sample effects are the hypothesized
167 explanation for the absence of many rare understory bird species from fragments (Ferraz et al.
168 2007). In addition, many beetles (Didham et al. 1998a), bats (Sampaio et al. 2003), ant-
169 defended plants (Bruna et al. 2005), and trees (Bohlman et al. 2008, Laurance et al. 2010b) at
170 the BDFFP exhibit high levels of habitat specialization or patchiness. In a region where rarity
171 and patchy distributions of species are the norm, sample effects appear to play a major role in
172 structuring fragmented communities. Given these sample effects, nature reserves will have to
173 be especially large to sustain viable populations of rare species (Lovejoy and Oren 1981,
174 Laurance 2005, Peres 2005, Radtke et al. 2008).

175

176 2.2. Fragment size is vital

177 Although fragments range from just 1–100 ha in the BDFFP study area, understanding
178 fragment-area effects has long been a central goal of the project (Lovejoy and Oren 1981,
179 Lovejoy et al. 1984, 1986). The species richness of many organisms declines with fragment
180 area, even with constant sampling effort across all fragments. Such declines are evident in leaf
181 bryophytes (Zartman 2003), tree seedlings (Benítez-Malvido and Martinez-Ramos 2003a),
182 palms (Scariot 1999), understory insectivorous birds (Stratford and Stouffer 1999; Ferraz et
183 al. 2007), gleaning animal-eating bats (Sampaio 2000, Meyer et al. unpublished data),
184 primates (Gilbert and Setz 2001, Boyle and Smith 2010a), and larger herbivorous mammals
185 (Timo 2003), among others. For these groups, smaller fragments are often unable to support
186 viable populations and deleterious edge effects—ecological changes associated with the
187 abrupt, artificial edges of forest fragments— can also rise sharply in intensity (Didham et al.
188 1998a). A few groups, such as ant-defended plants and their ant mutualists, show no
189 significant decline in diversity with fragment area (Bruna et al. 2005).

190 Fragment size also influences the rate of species losses, with smaller fragments losing
191 species more quickly (Lovejoy et al. 1986, Stouffer et al. 2008). Assuming the surrounding

192 matrix is hostile to bird movements and precludes colonization, Ferraz et al. (2003) estimated
193 that a 1000-fold increase in fragment area would be needed to slow the rate of local species
194 extinctions by 10-fold. Even a fragment of 10,000 ha in area would be expected to lose a
195 substantial part of its bird fauna within one century (Ferraz et al. 2003). Similarly, mark-
196 recapture data suggest that very large fragments will be needed to maintain fully intact
197 assemblages of some faunal groups, such as ant-following birds, which forage over large
198 areas of forest (Van Houtan et al. 2007).

200 3. Edge effects

201 3.1. Forest hydrology is disrupted

202 The hydrological regimes of fragmented landscapes differ markedly from those of intact
203 forest (Kapos 1989). Pastures or crops surrounding fragments have much lower rates of
204 evapotranspiration than do forests because they have far lower leaf area and thus less rooting
205 depth. Additionally, such clearings are hotter and drier than forests (Camargo & Kapos 1995).
206 Field observations and heat-flux simulations suggest that desiccating conditions can penetrate
207 up to 100–200 m into fragments from adjoining clearings (Malcolm 1998; Didham and
208 Lawton 1999). Further, streams in fragmented landscapes experience greater temporal
209 variation in flows than do those in forests, because clearings surrounding fragments have less
210 evapotranspiration and rainfall interception by vegetation (Trancoso 2008). Free runoff
211 promotes localized flooding in the wet season and stream failure in the dry season, with
212 potentially important impacts on aquatic invertebrates (Nessimian et al. 2008) and other
213 organisms.

214 Forest fragmentation also can alter low-level atmospheric circulation, which in turn
215 affects local cloudiness and rainfall. The warm, dry air over clearings tends to rise, creating
216 zones of low air pressure. The relatively cool, moist air over forests is drawn into this vacuum
217 (Avisar and Schmidt, 1998). As it warms it also rises and forms convectional clouds over the
218 clearing, which can lead to localized thunderstorms (Avisar and Liu 1996). In this way,
219 clearings of a few hundred hectares or more can draw moisture away from nearby forests
220 (Laurance 2004a, Cochrane and Laurance 2008). In Eastern Amazonia, satellite observations
221 of canopy-water content suggest such desiccating effects typically penetrate 1.0–2.7 km into
222 fragmented forests (Briant et al. 2010). This moisture-robbing function of clearings, in
223 concert with frequent burning in adjoining pastures, could help explain why fragmented
224 forests are so vulnerable to destructive, edge-related fires (Cochrane and Laurance 2002,
225 2008).

227 3.2. Edge effects often dominate fragment dynamics

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

233 Edge phenomena are remarkably diverse (Fig. 2). They include increased desiccation
234 stress, wind shear, and wind turbulence that sharply elevate rates of tree mortality and damage
235 (Laurance et al. 1997, 1998a). These in turn cause wide-ranging alterations in the community
236 composition of trees (Laurance et al. 2000, 2006a, 2006b) and lianas (Laurance et al., 2001b).
237 Such stresses may also reduce germination (Bruna 1999) and establishment (Uriarte et al.,
238 2010) of shade-tolerant plant species in fragments, leading to dramatic changes in the
239 composition and abundance of tree seedlings (Benítez-Malvido 1998, Benítez-Malvido and
240 Martínez-Ramos 2003a).

241 Many animal groups, such as numerous bees, wasps, flies (Fowler et al. 1993), beetles

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

249 Some groups of organisms remain stable or even increase in abundance near edges.
 250 Leaf bryophytes (Zartman and Nascimento 2006), wandering spiders (*Ctenus* spp; Rego et al.
 251 2007, Mestre and Gasnier 2008), and many frogs (Gascon 1993) show no significant response
 252 to edges. Organisms that favor forest ecotones or disturbances, such as many species of gap-
 253 favoring and frugivorous birds (Laurance 2004b), hummingbirds (Stouffer and Bierregaard
 254 1995a), frugivorous bats that exploit early successional plants (Sampaio 2000), light-loving
 255 butterflies (Leidner et al. 2010), and fast-growing lianas (Laurance et al. 2001b), increase in
 256 abundance near edges, sometimes dramatically.

257 3.3. Edge effects are cumulative

258 BDFFP research provides strong support for the idea that two or more nearby edges create
 259 more severe edge effects than does just one (Fig. 3). This conclusion is supported by studies
 260 of edge-related changes in forest microclimate (Kapos 1989, Malcolm 1998), vegetation
 261 structure (Malcolm 1994), tree mortality (Laurance et al. 2006a), abundance and species
 262 richness of tree seedlings (Benítez-Malvido 1998, Benítez-Malvido and Martinez-Ramos
 263 2003a), liana abundance (Laurance et al. 2001b), and the density and diversity of disturbance-
 264 loving pioneer trees (Laurance et al. 2006a, 2006b, 2007). The additive effects of nearby
 265 edges could help to explain why small (<10 ha) or irregularly shaped forest remnants are
 266 often so severely altered by forest fragmentation (Zartman 2003, Laurance et al. 2006a).

267 3.4. Edge age, structure, and adjoining vegetation influence edge effects

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

280 Regrowth forest adjoining fragment edges can also lessen edge-effect intensity.
 281 Microclimatic alterations (Didham and Lawton 1999), tree mortality (Mesquita et al. 1999),
 282 and edge avoidance by understory birds (Develey and Stouffer 2001, Laurance 2004b,
 283 Laurance et al. 2004), and gleaning bats that feed on invertebrates and small vertebrates
 284 (Meyer et al., 2013) are all reduced substantially when forest edges are buffered by adjoining
 285 regrowth forest, relative to edges adjoined by cattle pastures.

286 4. Isolation and matrix effects

287 4.1. Matrix structure and composition affect fragments

288 Secondary forests have gradually overtaken most pastures in the BDFFP landscape. This re-

292 growth lessens the effects of fragmentation for some taxa as the matrix becomes less hostile
 293 to faunal use and movements. Several species of insectivorous birds that had formerly
 294 disappeared have recolonized fragments as the surrounding secondary forest grew back
 295 (Stouffer and Bierregaard 1995b). The rate of local extinctions of birds has also declined
 296 (Stouffer et al. 2008). Similarly, gleaning animal-eating bats, which occurred at low
 297 abundances in fragments (Sampaio 2000) and in secondary regrowth (Bobrowiec and Gribel
 298 2010) 10-15 years ago, have since increased in response to matrix regeneration (Meyer et al.
 299 2013). A number of other species, including certain forest spiders (Mestre and Gasnier 2008),
 300 dung beetles (Quintero and Roslin 2005), euglossine bees (Becker et al. 1991), and monkeys
 301 such as red howlers, bearded sakis, and brown capuchins (Boyle and Smith 2010a) have
 302 recolonized some fragments.

303 The surrounding matrix also has a strong effect on plant communities in fragments by
 304 mediating certain edge effects (see above), influencing the movements of pollinators (Dick
 305 2001, Dick et al. 2003) and seed dispersers (Jorge 2008, Bobrowiec and Gribel 2010, Boyle
 306 and Smith 2010a), and strongly affecting the seed rain that arrives in fragments. For instance,
 307 pioneer trees regenerating in fragments differed strikingly in composition between fragments
 308 surrounded by *Cecropia*-dominated regrowth and those encircled by *Vismia*-dominated
 309 regrowth (Nascimento et al. 2006). In this way plant and animal communities in fragments
 310 could come to mirror to some extent the composition of the surrounding matrix (Laurance et
 311 al. 2006a, 2006b), a phenomenon observed elsewhere in the tropics (e.g. Janzen 1983,
 312 Diamond et al. 1987).

313 314 4.2 Matrix is affected by history and forest proximity

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

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

332 333 4.3 Even narrow clearings are harmful

334 Many Amazonian species avoid clearings, and even a forest road can be an insurmountable
 335 barrier for some. A number of understory insectivorous birds exhibit depressed abundances
 336 near forest roads (20–40 m width) (Laurance 2004b) and strongly inhibited movements across
 337 those roads (Laurance et al. 2004). Experimental translocations of resident adult birds reveal
 338 such bird species will cross a highway (50–75 m width) but not a small pasture (250 m width)
 339 to return to their territory (Laurance and Gomez 2005). Individuals of other vulnerable
 340 species, however, have traversed clearings to escape from small fragments to larger forest
 341 areas (Harper 1989, Van Houtan et al. 2007). Captures of understory birds declined

342 dramatically in fragments when a 100 m-wide swath of regrowth forest was cleared around
 343 them, suggesting that species willing to traverse regrowth would not cross clearings (Stouffer
 344 et al. 2006).

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

351

352 5. Landscape dynamics

353 5.1. Rare disturbances can leave lasting legacies

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

362 Intense windblasts from convectional thunderstorms have occasionally strafed parts of
 363 the BDFFP landscape and caused intense forest damage and tree mortality, especially in the
 364 fragments. Fragments in the easternmost cattle ranch at the BDFFP have had substantially
 365 lower rates of tree mortality than did those in the other two ranches, because the former have
 366 so far escaped windstorms (Laurance et al. 2007). These differences have strongly influenced
 367 the rate and trajectory of change in tree-community composition in fragments (Laurance et al.
 368 2006b). Hence, by altering forest dynamics, composition, structure, and carbon storage, rare
 369 disturbances have left an enduring imprint on the ecology of fragmented forests.

370

371 5.2. Fragments are hyperdynamic

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

380 Many examples of hyperdynamism have been observed in the BDFFP fragments.
 381 Some butterfly species have experienced dramatic population irruptions in response to a
 382 proliferation of their favored host plants along fragment margins (Brown and Hutchings
 383 1997), and butterfly communities in general are hyperdynamic in fragments (Leidner et al.
 384 2010). Bat assemblages also show pronounced species turnover, particularly in 1-ha
 385 fragments (Meyer et al. 2013). Streamflows are far more variable in fragmented than forested
 386 watersheds (Trancoso 2008). Rates of tree mortality and recruitment are chronically elevated
 387 in fragments (Laurance et al. 1998a, b), with major pulses associated with rare disturbances
 388 (see above). Further, tree species disappear and turn over far more rapidly in fragments than
 389 intact forest, especially within ~100 m of forest margins (Laurance et al. 2006b). These and
 390 many other instabilities plague small, dwindling populations in the BDFFP fragments.

391

392 5.3. Fragments in different landscapes diverge

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

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

412 The apparently acute sensitivity of fragments to local landscape and weather
 413 dynamics—even within a study area as initially homogeneous as ours—prompted us to
 414 propose a ‘landscape-divergence hypothesis’ (Laurance et al. 2007). We argue that fragments
 415 within the same landscape tend to have similar dynamics and trajectories of change in species
 416 composition, which will often differ from those in other landscapes. Over time, this process
 417 will tend to homogenize fragments in the same landscape, and promote ecological divergence
 418 among fragments in different landscapes. Evidence for this hypothesis is provided by tree
 419 communities in our fragments, which appear to be diverging in composition among the three
 420 cattle ranches (Fig. 4). Pioneer and weedy trees are increasing in all fragments, but the
 421 composition of these generalist plants and their rate of increase differ markedly among the
 422 three ranches (Scariot 2001, Laurance et al. 2006a, 2007, Nascimento et al. 2006). This same
 423 pattern of landscape homogenization within ranches can also be seen for bat assemblages in
 424 the secondary forest matrix (Bobrowiec and Gribel, 2010).

425

426 6. Broader consequences of fragmentation

427 6.1. Ecological distortions are common

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

433 BDFFP findings suggest that even forest fragments that are un hunted, unlogged, and
 434 unburned have reduced densities of key mammalian seed dispersers. As a result, seed
 435 dispersal for the endemic, mammal-dispersed tree *Duckeodendron cestroides* was far lower in
 436 fragments, with just ~5% of the number of seeds being dispersed >10 m away from parent
 437 trees than in intact forest (Cramer et al. 2007a). Leaf herbivory appears reduced in fragments,
 438 possibly because of lower immigration of insect herbivores (Fáveri et al. 2008). Dung beetles
 439 exhibit changes in biomass and guild structure in fragments (Radtke et al. 2008) that could
 440 alter rates of forest nutrient cycling and secondary seed dispersal (Klein 1989, Andresen
 441 2003). Exotic Africanized honeybees, a generalist pollinator, are abundant in matrix and edge

442 habitats and can alter pollination distances and gene flow for some tree species (Dick 2001,
 443 Dick et al. 2003). A bewildering variety of ecological distortions can pervade fragmented
 444 habitats, and a challenge for conservation biologists is to identify those of greatest importance
 445 and generality.

446

447 6.2. Fragmentation affects much more than biodiversity

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

452 Carbon storage in fragmented forests is affected by a suite of interrelated changes.
 453 Many trees die near forest edges (Laurance et al. 1997, 1998a), including an alarmingly high
 454 proportion of large (≥ 60 cm dbh) canopy and emergent trees that store much forest carbon
 455 (Laurance et al. 2000). Fast-growing pioneer trees and lianas that proliferate in fragments are
 456 smaller and have lower wood density (Fig. 5), and thereby sequester much less carbon, than
 457 do the mature-phase trees they replace (Laurance et al. 2001b, 2006a). Based on current rates
 458 of forest fragmentation, the edge-related loss of forest carbon storage might produce up to 150
 459 million tons of atmospheric carbon emissions annually, above and beyond that from tropical
 460 deforestation per se (Laurance et al. 1998c). Such discharge would exceed the yearly carbon
 461 emissions of the entire United Kingdom. Note, however, that most of this emission is already
 462 counted in the existing estimates of the impact of Amazonian land-use change because the
 463 deforestation emission estimates use forest biomass values for undegraded forest (Fearnside
 464 2000). Because most deforestation occurs by expansion of already-existing clearings, forest
 465 edges (with reduced biomass) are the first areas to be cleared. Only the annual increase in the
 466 total length of forest edges represents an addition. Improved emissions estimates, accounting
 467 for degradation by logging, fire and fragmentation, are a high priority.

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

480

481 7. Predicting species responses to fragmentation

482 7.1. Species losses are highly nonrandom

483 Local extinctions of species in the BDFFP fragments have occurred in a largely predictable
 484 sequence, with certain species being consistently more vulnerable than others. Among birds, a
 485 number of understory insectivores, including army ant-followers, solitary species, terrestrial
 486 foragers, and obligate mixed-flock members, are most susceptible to fragmentation. Others,
 487 including edge/ gap species, insectivores that use mixed flocks facultatively, hummingbirds,
 488 and many frugivores, are far less vulnerable (Antongiovanni and Metzger 2005, Stouffer et al.
 489 2006, 2008). In a similar vein, among bats, gleaning predators are consistently the most
 490 vulnerable species whereas many frugivores respond positively to fragmentation and
 491 disturbance (Sampaio 2000, Bobrowiec and Gribel 2010, Rocha et al. 2013). Primates exhibit

492 similarly predictable patterns of species loss, with wide-ranging frugivores, especially the
 493 black spider-monkey, being most vulnerable (Boyle and Smith 2010a). Local extinctions in
 494 fragments follow a foreseeable pattern, with species assemblages in smaller fragments rapidly
 495 forming a nested subset of those in larger fragments (Stouffer et al. 2008). Random
 496 demographic and genetic processes may help to drive tiny populations into oblivion, but the
 497 species that reach this precarious threshold are far from random.

498
 499

500 7.2. Fragmented communities are not neutral

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

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

523

524 7.3. Matrix use and area needs determine animal vulnerability

525 The responses of animal species to fragmentation appear largely governed by two key sets of
 526 traits. The first is their spatial requirements for forest habitat. In birds (Van Houtan et al.
 527 2007) and mammals (Timo 2003), wide-ranging forest species are more vulnerable than are
 528 those with localized ranges and movements. Species with limited spatial needs, such as many
 529 small mammals (Malcolm 1997), hummingbirds (Stouffer et al. 2008), frogs (Tocher et al.
 530 1997), and ants (Carvalho and Vasconcelos 1999), are generally less susceptible to
 531 fragmentation.

532 The second key trait for fauna is their tolerance of matrix habitats (Gascon et al.
 533 1999), which comprises cattle pastures and regrowth forest in the BDFFP landscape.
 534 Populations of species that avoid the matrix will be entirely isolated in fragments, and
 535 therefore vulnerable to local extinction, whereas those that tolerate or exploit the matrix often
 536 persist (Laurance 1991, Malcolm 1997, Antongiovanni and Metzger 2005, Ferraz et al. 2007,
 537 Bobrowiec and Gribel 2010). At least among terrestrial vertebrates, matrix use is positively
 538 associated with tolerance of edge habitats (Laurance 2004b, Farneda 2013), an ability to
 539 traverse small clearings (Laurance et al. 2004, Laurance and Gomez 2005), and behavioral
 540 flexibility (Neckel-Oliveira and Gascon 2006, Stouffer et al. 2006, Van Houtan et al. 2006,
 541 Boyle and Smith 2010b). Within particular animal groups, such as beetles or small mammals,

542 traits such as body size and natural abundance are poor or inconsistent predictors of
 543 vulnerability (Laurance 1991, Didham et al. 1998a, Jorge 2008, Boyle and Smith 2010a).
 544 Natural abundance, however, is an important predictor of sensitivity to fragmentation for bats
 545 at the BDFFP (Farneda, 2013).

546

547 7.4. Disturbance tolerance and mutualisms affect plant vulnerability

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

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

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

572

573 8. Broad perspectives

574 8.1. Long-term research is crucial

575 Many insights from the BDFFP would have been impossible in a shorter-term study. The
 576 exceptional vulnerability of large trees to fragmentation (Laurance et al. 2000) only became
 577 apparent after two decades of fragment isolation. Likewise, the importance of ephemeral
 578 events such as El Niño droughts (Williamson et al., 2000, Laurance et al. 2001c) and major
 579 windstorms (Laurance et al. 2007) would not have been captured in a less-enduring project.
 580 Many other key phenomena, such as the kinetics of species loss in fragments (Ferraz et al.
 581 2003), the strong effects of matrix dynamics on fragmented bird and bat assemblages
 582 (Antongiovanni and Metzger 2005, Stouffer et al. 2006, Meyer et al. 2013), the divergence of
 583 fragments in different landscapes (Laurance et al. 2007), and the effects of fragmentation on
 584 rare or long-lived species (Benítez-Malvido and Martínez-Ramos 2003b, Ferraz et al., 2007),
 585 are only becoming understood after decades of effort.

586 Far more remains to be learned. For example, forest-simulation models parameterized
 587 with BDFFP data suggest that even small (<10 ha) fragments will require a century or more to
 588 stabilize in floristic composition and carbon storage (Groeneveld et al. 2009), given the long-
 589 lived nature of many tropical trees. Eventually, these fragments might experience a
 590 fundamental reorganization of their plant communities, given striking shifts in the
 591 composition of their tree, palm, liana, and herb seedlings (Scariot 2001; Benítez-Malvido and

592 Martinez-Ramos 2003a, Brum et al. 2008). If these newly recruited plants represent the future
 593 of the forest, then the BDFFP fragments will eventually experience dramatic changes in
 594 floristic composition—comparable to those observed in some other long-fragmented
 595 ecosystems (e.g. da Silva and Tabarelli 2000, Girão et al. 2007, Santos et al. 2010).

596

597 8.2. The BDFFP is a best-case scenario

598 Although forest fragments in the BDFFP are experiencing a wide array of ecological changes,
 599 it is important to emphasize that it is a controlled experiment. The fragments are square, not
 600 irregular, in shape. They are isolated by distances of just 80–650 m from large tracts of
 601 surrounding mature forest. They are embedded in a relatively benign matrix increasingly
 602 dominated by regrowth forest. And they lack many of the ancillary threats, such as selective
 603 logging, wildfires, and overhunting, that plague many fragmented landscapes and wildlife
 604 elsewhere in the tropics (e.g. Moura et al. 2014). Such threats can interact additively or
 605 synergistically with fragmentation, creating even greater perils for the rainforest biota
 606 (Laurance and Cochrane 2001, Michalski and Peres 2005, Brook et al. 2008). For these
 607 reasons, results from the BDFFP are clearly optimistic relative to many human-dominated
 608 landscapes elsewhere in the tropics.

609

610 9. Conservation lessons from the BDFFP

611 9.1. Amazonian reserves should be large and numerous

612 A key conclusion from BDFFP research is that nature reserves in Amazonia should ideally be
 613 very large—on the order of thousands to tens of thousands of square kilometers (Laurance
 614 2005, Peres 2005). Only at this size will they be likely to maintain natural ecological
 615 processes and sustain viable populations of the many rare and patchily distributed species in
 616 the region (Ferraz et al. 2007, Radtke et al. 2008); provide resilience from rare calamities such
 617 as droughts and intense storms (Laurance et al. 2007); facilitate persistence of terrestrial and
 618 aquatic animals that migrate seasonally (Bührnheim and Fernandes 2003); buffer the reserve
 619 from large-scale edge effects including fires, forest desiccation, and human encroachment
 620 (Cochrane and Laurance 2002, Briant et al. 2010); maximize forest carbon storage (Laurance
 621 et al. 1997, 1998c); and provide resilience from future climatic and atmospheric changes—the
 622 effects of which are difficult to predict for Amazonia (Laurance and Useche 2009). Further,
 623 on the ancient soils of Central and Eastern Amazonia, low plant productivity translates into
 624 low population densities of many animals up the food chain, so reserves must be
 625 proportionately larger to harbor viable populations (Radtke et al. 2008, Deichmann et al.
 626 2011, 2012).

627 Nature reserves in Amazonia should also be numerous and stratified across major river
 628 basins and climatic and edaphic gradients, in order to preserve locally endemic species
 629 (Bierregaard et al. 2001, Laurance, 2007). Further, the core areas of reserves should ideally be
 630 free of roads, which can promote human encroachment and hunting, internally fragment
 631 wildlife populations, and facilitate invasions of exotic species and fire (Laurance et al.
 632 2009b).

633

634 9.2. Protect and reconnect fragments

635 Few landscapes are as intact as those in the Amazon. Around the world, biodiversity hotspots,
 636 which sustain the majority of species at risk of extinction, have, by definition, lost over 80%
 637 of their natural vegetation and what remains is typically in small fragments (Myers et al.
 638 2000). The BDFFP makes recommendations here, too. Reconnecting isolated fragments by
 639 forest restoration will be an effective way of creating areas large enough to slow the rate of
 640 local species extinctions (Lima and Gascon 1999, Pimm and Jenkins 2005).

641 In such heavily fragmented landscapes, protecting remaining forest remnants is highly

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

648

649 9.3. Fragmented landscapes can recover

650 A further lesson is that fragmented landscapes, if protected from fires and other major
 651 disturbances, can begin to recover in just a decade or two. Forest edges tend to ‘seal’
 652 themselves, reducing the intensity of deleterious edge effects (Camargo and Kapos 1995,
 653 Didham and Lawton 1999, Mesquita et al. 1999). Secondary forests can develop quickly in
 654 the surrounding matrix (Mesquita et al. 2001), especially if soils and seedbanks are not
 655 depleted by overgrazing or repeated burning (Ribeiro et al. 2009, Norden et al. 2011).
 656 Secondary forests facilitate movements of many animal species (Gascon et al. 1999), allowing
 657 them to recolonize fragments from which they had formerly disappeared (Becker et al. 1991,
 658 Quintero and Roslin 2005, Stouffer et al. 2008, Bobrowiec and Gribel 2010, Boyle and Smith
 659 2010a, Meyer et al. 2013). Species clinging to survival in fragments can also be rescued from
 660 local extinction via the genetic and demographic contributions of immigrants (Zartman and
 661 Nascimento 2006, Stouffer et al. 2008).

662

663 10. The future of the BDFFP

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

670 In its 36-year history, the BDFFP has faced myriad challenges. These include, among
 671 others, the continuing fluctuations in currencies, challenges in obtaining research visas for
 672 foreign students and scientists, inadequate core funding from its US and Brazilian sponsors,
 673 and the vagaries of finding soft money for long-term research and to sustain a minimal
 674 number of workers to support infrastructure and logistics. Yet today the BDFFP faces a far
 675 more direct threat: encroachment from colonists and hunters. Since the late 1990s, the paving
 676 of the 1100-km-long Manaus–Venezuela (BR-174) highway has greatly accelerated forest
 677 colonization and logging north of the city. SUFRAMA, a Brazilian federal agency that
 678 controls an expanse of land north of Manaus that includes the BDFFP, has begun settling
 679 families in farming plots around the immediate periphery of the study area. At least six
 680 colonization projects involving 180 families are planned for the area (Laurance and Luizão
 681 2007). These settlements could be the beginning of a dramatic influx into the area, especially
 682 if the proposed BR-319 highway between Manaus and Rondônia, a major deforestation
 683 hotspot in southern Amazonia, is completed as planned (Fearnside and Graça 2006).

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

692 That it could be lost for such a limited gain seems tragic.

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

699
700

701 Acknowledgements

702 We thank Laszlo Nagy and an anonymous referee for helpful comments on the manuscript.
703 The National Institute for Amazonian Research (INPA), Smithsonian Institution, US National
704 Science Foundation, Brazilian Science Foundation (CNPq), Amazonian State Science
705 Foundation (FAPEAM), NASA-LBA program, USAID, Mellon Foundation, Blue Moon
706 Fund, Marisla Foundation, and other organizations generously supported the BDFFP.
707 Substantial parts of this text are updated from Laurance et al. (2011). This is publication
708 number 640 in the BDFFP technical series.

709

710 Box 1. The Biological Dynamics of Forest Fragments Project

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

720 The BDFFP is located 80 km north of Manaus, Brazil and spans ~1000 km². The
721 topography is relatively flat (80–160 m elevation) but dissected by numerous stream gullies.
722 The heavily weathered, nutrient-poor soils of the study area are typical of large expanses of
723 the Amazon Basin. Rainfall ranges from 1900 to 3500 mm annually with a moderately strong
724 dry season from June to October. The forest canopy is 30–37 m tall, with emergent trees to 55
725 m. Species richness of trees (≥ 10 cm DBH) often exceeds 280 species ha⁻¹ (Oliveira and
726 Mori 1999, Laurance et al. 2010b) with a comparably high level of diversity also evident in
727 many other plant and animal taxa.

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

736 Because of poor soils and low productivity, the ranches surrounding the BDFFP
737 fragments were largely abandoned after government fiscal incentives dried up from 1984
738 onwards. Secondary forests (initially dominated by *Vismia* spp in areas that were cleared and
739 burned, or by *Cecropia* spp in areas that were cleared without fire) proliferated in many
740 formerly forested areas (Mesquita et al. 2001). Some of the regenerating areas initially
741 dominated by *Cecropia* spp later developed into quite mature (>20 m tall), species-rich

742 secondary forests. *Vismia*-dominated regrowth, which is relatively species poor, is changing
 743 far more slowly (Norden et al. 2011, Williamson et al. 2014). To help maintain isolation of
 744 the experimental fragments, 100 m-wide strips of regrowth were cleared and burned around
 745 each fragment on 4–5 occasions, most recently in 2013–2014. Additional human disturbances
 746 that harm many fragmented landscapes in the Amazon, such as major fires and logging, are
 747 largely prevented at the BDFFP. Hunting pressure has been very limited until recently,
 748 following a government decision to increase colonization in the general area (Laurance and
 749 Luizão 2007). Laurance and Bierregaard (1997) and Bierregaard et al. (2001) provide detailed
 750 descriptions of the study area and design.

751

752 References

- 753 Andresen E (2003) Effect of forest fragmentation on dung beetle communities and functional
 754 consequences for plant regeneration. *Ecography* 26:87–97.
- 755 Antongiovanni M, Metzger JP (2005) Influence of matrix habitats on the occurrence of
 756 insectivorous bird species in Amazonian forest fragments. *Biol Conserv* 122:441–451.
- 757 Arroyo-Rodríguez V, Pineda E, Escobar F, Benítez-Malvido J (2009) Conservation value of
 758 small patches to plant species diversity in highly fragmented landscapes. *Conserv Biol*
 759 23:729–739.
- 760 Asner GP, Knapp D, Broadbent E, Oliveira P, Keller M, Silva J (2005) Selective logging in
 761 the Brazilian Amazon. *Science* 310:480–482.
- 762 Avissar R, Liu Y (1996) A three-dimensional numerical study of shallow convective clouds
 763 and precipitation induced by land-surface forcing. *J Geophys Res* 101:7499–7518.
- 764 Avissar R, Schmidt T (1998) An evaluation of the scale at which ground-surface heat flux
 765 patchiness affects the convective boundary layer using a large-eddy simulation model.
 766 *J Atmos Sci* 55:2666–2689.
- 767 Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, et al. (2004) Increasing
 768 biomass in Amazonian forest plots. *Phil Trans Roy Soc B* 359:353–365.
- 769 Barlow J, Peres CA, Henriques L, Stouffer PC, Wunderle J (2006) The responses of
 770 understorey birds to forest fragmentation, logging and wildfires: an Amazonian
 771 synthesis. *Biol Conserv* 128:182–192.
- 772 Becker P, Moure JB, Peralta F (1991) More about euglossine bees in Amazonian forest
 773 fragments. *Biotropica* 23:586–591.
- 774 Benítez-Malvido J (1998) Impact of forest fragmentation on seedling abundance in a tropical
 775 rain forest. *Conserv Biol* 12:380–389.
- 776 Benítez-Malvido J, Martinez-Ramos M (2003a) Influence of edge exposure on tree seedling
 777 species recruitment in tropical rain forest fragments. *Biotropica* 35:530–541.
- 778 Benítez-Malvido J, Martinez-Ramos M (2003b) Impact of forest fragmentation on understory
 779 plant species richness in Amazonia. *Conserv Biol* 17:389–400.
- 780 Bierregaard RO, Lovejoy TE, Kapos V, dos Santos AA, Hutchings RW (1992) The biological
 781 dynamics of tropical rainforest fragments. *Bioscience* 42:859–866.
- 782 Bierregaard R.O., Gascon C., Lovejoy T.E., Mesquita R. (Eds), 2001. *Lessons from*
 783 *Amazonia: Ecology and Conservation of a Fragmented Forest*. Yale University Press,
 784 New Haven, Connecticut.
- 785 Bobrowiec PED, Gribel R (2010) Effects of different secondary vegetation types on bat
 786 community composition in Central Amazonia, Brazil. *Anim Conserv* 13:204–216.
- 787 Bohlman S, Laurance WF, Laurance SG, Nascimento H, Fearnside PM, Andrade A (2008)
 788 Effects of soils, topography, and geographic distance in structuring central Amazonian
 789 tree communities. *J Veg Sci* 19:863–874.
- 790 Boyle SA, Smith AT (2010a) Can landscape and species characteristics predict primate
 791 presence in forest fragments in the Brazilian Amazon? *Biol Conserv* 143:1134–1143.

- 792 Boyle SA, Smith AT (2010b) Behavioral modifications in northern bearded saki monkeys
793 (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. *Primates*
794 51:43–51.
- 795 Brazil, RADAMBRASIL (1973-1983) Levantamento de Recursos Naturais. Ministério das
796 Minas e Energia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.
- 797 Briant G, Gond V, Laurance SGW (2010) Habitat fragmentation and the desiccation of forest
798 canopies: a case study from eastern Amazonia. *Biol Conserv* 143:2763–2769.
- 799 Broadbent E, Asner GP, Keller M, Knapp D, Oliveira P, Silva J (2008) Forest fragmentation
800 and edge effects from deforestation and selective logging in the Brazilian Amazon.
801 *Biol Conserv* 140:142–155.
- 802 Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergisms among extinction drivers under
803 global change. *Trends Ecol Evol* 23:453–460.
- 804 Brown KS, Hutchings RW (1997) Disturbance, fragmentation, and the dynamics of diversity
805 in Amazonian forest butterflies. In: Laurance WF, Bierregaard RO (Eds), *Tropical*
806 *forest remnants: Ecology, management, and conservation of fragmented communities.*
807 University of Chicago Press, Chicago, pp 91–110.
- 808 Brum HD, Nascimento H, Laurance WF, Andrade A, Laurance SGW, Luizão R (2008)
809 Rainforest fragmentation and the demography of the economically important palm
810 *Oenocarpus bacaba* in central Amazonia. *Plant Ecol* 199:209–215.
- 811 Bruna EM (1999) Seed germination in rainforest fragments. *Nature* 402:139.
- 812 Bruna EM (2003) Are plant populations in fragmented habitats recruitment limited? Tests
813 with an Amazonian herb. *Ecology* 84:932–947.
- 814 Bruna E, Oli M (2005) Demographic consequences of habitat fragmentation for an
815 Amazonian understory plant: analysis of life-table response experiments. *Ecology*
816 86:1816–1824.
- 817 Bruna EM, Vasconcelos HL, Heredia S (2005) The effect of habitat fragmentation on
818 communities of mutualists: a test with Amazonian ants and their host plants. *Biol*
819 *Conserv* 124:209–216.
- 820 Bührnheim CM, Fernandes CC (2003) Structure of fish assemblages in Amazonian rainforest
821 streams: effects of habitats and locality. *Copeia* 2003:255–262.
- 822 Butler RA, Laurance WF (2009) Is oil palm the next emerging threat to the Amazon? *Trop*
823 *Cons Sci* 2:1-10.
- 824 Camargo JLC, Kapos V (1995) Complex edge effects on soil moisture and microclimate in
825 central Amazonian forests. *J Trop Ecol* 11:205–211.
- 826 Carvalho KS, Vasconcelos HL (1999) Forest fragmentation in central Amazonia and its
827 effects on litter-dwelling ants. *Biol Conserv* 91:151–158.
- 828 Chambers JQ, Higuchi N, Schimel JP (1998) Ancient trees in Amazonia. *Nature* 391:135–
829 136.
- 830 Chave J, Muller-Landau, HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006)
831 Regional and phylogenetic variation of wood density across 2,456 neotropical tree
832 species. *Ecol Applic* 16:2356-2367.
- 833 Chazdon RL, Harvey CA, Komar O, Griffith DM, Ferguson BG, Martinez- Ramos M,
834 Morales H, Nigh R, Soto-Pinto L, van Breugel M, Philpott SM (2008) Beyond
835 reserves: a research agenda for conserving biodiversity in human-modified tropical
836 landscapes. *Biotropica* 41:142–153.
- 837 Cochrane MA, Laurance WF (2002) Fire as a large-scale edge effect in Amazonian forests. *J*
838 *Trop Ecol* 18:311–325.
- 839 Cochrane MA, Laurance WF (2008) Synergisms among fire, land use, and climate change in
840 the Amazon. *Ambio* 37:522–527.

- 841 Condon MA, Sasek TW, Strain BR (1992) Allocation patterns in two tropical vines in
842 response to increased atmospheric CO₂. *Funct Ecol* 6:680-685.
- 843 Cox PM, Betts RA, Collins M, Harris PP, Huntingford C, Jones CD (2004) Amazonian forest
844 dieback under climate-carbon cycle projections for the 21st century. *Theoret Appl*
845 *Climatol* 78:137-156.
- 846 Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming
847 due to carbon cycle feedbacks in a coupled climate model. *Nature* 408:184–187
- 848 Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CMD
849 (2013) Sensitivity of tropical carbon to climate change constrained by carbon dioxide
850 variability. *Nature* 494:341-344.
- 851 Cramer JM, Mesquita R, Bentos T, Moser B, Williamson GB (2007a) Forest fragmentation
852 reduces seed dispersal of *Duckeodendron cestroides*, a Central Amazon endemic.
853 *Biotropica* 39:709–718.
- 854 Cramer JM, Mesquita R, Williamson GB (2007b) Forest fragmentation differentially affects
855 seed dispersal of large and small-seeded tropical trees. *Biol Conserv* 137:415–423.
- 856 Dai A (2012) Increasing drought under global warming in observations and models. *Nature*
857 *Climate Change* 3:52–58.
- 858 D'Angelo S, Andrade A, Laurance SG, Laurance WF, Mesquita R (2004) Inferred causes of
859 tree mortality in fragmented and intact Amazonian forests. *J Trop Ecol* 20:243–246.
- 860 da Silva JMC, Tabarelli M (2000) Tree species impoverishment and the future flora of the
861 Atlantic forest of northeast Brazil. *Nature* 404:72–74.
- 862 Develey P, Stouffer PC (2001) Roads affect movements by understory mixed-species flocks
863 in central Amazonian Brazil. *Conserv Biol* 15:1416–1422.
- 864 Deichmann JL, Lima A, Williamson GB (2011) Effects of geomorphology and primary
865 productivity on Amazonian leaf litter herpetofauna. *Biotropica* 43:149–156.
- 866 Deichmann JL, Toft CA, Deichmann PM, Lima AP, Williamson GB (2013) Neotropical
867 primary productivity affects biomass of leaf-litter herpetofaunal assemblage. *J Trop*
868 *Ecol* 28:427–435.
- 869 Diamond JM, Bishop KD, Balen SV (1987) Bird survival in an isolated Javan woodland:
870 island or mirror? *Conserv Biol* 1:132–142.
- 871 Dick CW (2001) Genetic rescue of remnant tropical trees by an alien pollinator. *Proc Roy Soc*
872 *B* 268:2391–2396.
- 873 Dick CW, Etchelecu G, Austerlitz F (2003) Pollen dispersal of tropical trees (*Dinizia excelsa*:
874 Fabaceae) by native insects and African honeybees in pristine and fragmented
875 Amazonian rainforest. *Mol Ecol* 12:753–764.
- 876 Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE (1998a) Beetle species
877 responses to tropical forest fragmentation. *Ecol Monogr* 68:295–303.
- 878 Didham RK, Lawton JH (1999) Edge structure determines the magnitude of changes in
879 microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–
880 30.
- 881 Didham RK, Lawton JH, Hammond PM, Eggleton P (1998b) Trophic structure stability and
882 extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Proc Roy Soc*
883 *B* 353:437–451.
- 884 Farneda FZ (2013) Bat species vulnerability to forest fragmentation in the Central Amazon.
885 M.Sc. Thesis. University of Lisbon, Portugal.
- 886 Fáveri SB, Vasconcelos HL, Dirzo R (2008) Effects of Amazonian forest fragmentation on
887 the interaction between plants, insect herbivores, and their natural enemies. *J Trop*
888 *Ecol* 24:57–64.
- 889 Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *For*
890 *Ecol Manage* 90:59-89. |

- 891 Fearnside PM (2000) Global warming and tropical land-use change: Greenhouse gas
 892 emissions from biomass burning, decomposition and soils in forest conversion,
 893 shifting cultivation and secondary vegetation. *Climatic Change* 46:115-158.
- 894 Fearnside PM (2001a) Soybean cultivation as a threat to the environment in Brazil. *Environ*
 895 *Conserv* 28:23–38.
- 896 Fearnside PM (2001b) Saving tropical forests as a global warming countermeasure: An issue
 897 that divides the environmental movement. *Ecol Econ* 39:167-184.
- 898 Fearnside PM (2002) Avança Brasil: Environmental and social consequences of Brazil's
 899 planned infrastructure in Amazonia. *Environ Manage* 30:748-763.
- 900 Fearnside PM (2007) Brazil's Cuiabá-Santarém (BR-163) Highway: The environmental cost
 901 of paving a soybean corridor through the Amazon. *Environ Manage* 39:601-614.
- 902 Fearnside PM (2012) Brazil's Amazon forest in mitigating global warming: Unresolved
 903 controversies. *Climate Policy* 12:70-81.
- 904 Fearnside PM (2013) Vines, CO₂ and Amazon forest dieback. *Nature Online Comment*
 905 (<http://www.nature.com/nature/journal/vaop/ncurrent/full/nature11882.html>).
- 906 Fearnside, PM (2014) The impact of land use on carbon stocks and fluxes. (this volume).
- 907 Fearnside PM, Graça PMLA (2006) BR-319: Brazil's Manaus–Porto Velho highway and the
 908 potential impact of linking the arc of deforestation to central Amazonia. *Environ*
 909 *Manage* 38:705–716.
- 910 Fearnside PM, Leal Filho N (2001) Soil and development in Amazonia: Lessons from the
 911 Biological Dynamics of Forest Fragments Project. In: Bierregaard RO, Gascon C,
 912 Lovejoy TE, Mesquita R (Eds) *Lessons from Amazonia: The ecology and*
 913 *conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut,
 914 USA, pp 291-312.
- 915 Ferraz G, Nichols JD, Hines J, Stouffer PC, Bierregaard RO, Lovejoy TE (2007) A large-
 916 scale deforestation experiment: effects of patch area and isolation on Amazon birds.
 917 *Science* 315:238–241.
- 918 Ferraz G, Russell GJ, Stouffer PC, Bierregaard RO, Pimm SL, Lovejoy TE (2003) Rates of
 919 species loss from Amazonian forest fragments. *Proc Nat Acad Sci USA* 100:14069–
 920 14073.
- 921 Finer M, Jenkins C, Pimm SL, Keane B, Ross C (2008) Oil and gas projects in the western
 922 Amazon: threats to wilderness, biodiversity, and indigenous peoples. *PLoS ONE*
 923 3:e2932.
- 924 Fowler HG, Silva CA, Ventincinque E (1993) Size, taxonomic and biomass distributions of
 925 flying insects in central Amazonia: forest edge vs. understory. *Rev Biol Trop* 41:755–
 926 760.
- 927 Gardner TA, Barlow J, Chazdon R, Ewers R, Harvey C, Peres CA, Sodhi NS (2009)
 928 Prospects for tropical forest biodiversity in a human-modified world. *Ecol Lett*
 929 12:561–582.
- 930 Gascon C (1993) Breeding habitat use by Amazonian primary-forest frog species at the forest
 931 edge. *Biodiv. Conserv.* 2:438–444.
- 932 Gascon C, Lovejoy TE, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos H, Laurance
 933 WF, Zimmerman B, Tocher M, Borges S (1999) Matrix habitat and species
 934 persistence in tropical forest remnants. *Biol Conserv* 91:223–229.
- 935 Gibbs HK, Reusch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010)
 936 Tropical forests were the primary sources of new agricultural lands in the 1980s and
 937 1990s. *Proc Nat Acad Sci USA* 107:16732–16737.
- 938 Gibson L, Lee TM, Koh LP, Brook BW, Gardner, TA, Barlow J, Peres CA, Bradshaw CJA,
 939 Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for
 940 sustaining tropical biodiversity. *Nature* 478:378-381.

- 941 Gilbert B, Laurance WF, Leigh EG, Nascimento H (2006) Can neutral theory predict the
 942 responses of Amazonian tree communities to forest fragmentation? *Am Nat* 168:304–
 943 317.
- 944 Gilbert KA, Setz EZF (2001) Primates in a fragmented landscape: six species in central
 945 Amazonia. In: Laurance WF, Bierregaard RO (Eds) *Tropical forest remnants:
 946 Ecology, management and conservation of fragmented communities*. University of
 947 Chicago Press, Chicago, pp 207–221.
- 948 Girão LC, Lopes AV, Tabarelli M, Bruna EM (2007) Changes in tree reproductive traits
 949 reduce functional diversity in a fragmented Atlantic forest landscape. *PLoS ONE*
 950 2:e908.
- 951 Good P, Jones CD, Lowe JA, Betts RA, Gedney N (2013) Comparing tropical forest
 952 projections from two generations of Hadley Centre Earth System models, HadGEM2-
 953 ES and HadCM3LC. *J. Climate* 26:495–511.
- 954 Groeneveld J, Alves L, Bernacci L, Catharino E, Knogge C, Metzger J, Pütz S, Huth A (2009)
 955 The impact of fragmentation and density regulation on forest succession in the
 956 Atlantic rain forest. *Ecol Model* 220:2450–2459.
- 957 Harper LH (1989) The persistence of ant-following birds in small Amazonian forest
 958 fragments. *Acta Amazonica* 19:249–263.
- 959 Hubbell SP (2001) *The Neutral Theory of Biodiversity and Biogeography*. Princeton
 960 University Press, Princeton, New Jersey.
- 961 Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, Fisher R, Lomas M,
 962 Walker AP, Jones CD, Booth BB, Malhi Y, Hemming D, Kay G, Good P, Lewis SL,
 963 Phillips OL, Atkin OK, Lloyd J, Gloor E, Zaragoza-Castells J, Meir P, Betts R, Harris
 964 PP, Nobre C, Marengo J, Cox PM (2013) Simulated resilience of tropical rainforests
 965 to CO₂-induced climate change. *Nature Geosci.* 6:268–273.
- 966 Ingwell LL, Wright SJ, Becklund KK, Hubbell SP, Schnitzer SA (2010) The impact of lianas
 967 on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *J Ecol*
 968 98:879–887.
- 969 IPCC (2013) Summary for policymakers. In: Stocker T F et al. (Eds) *Climate change 2013:
 970 The physical science basis*. Intergovernmental Panel on Climate Change, Cambridge
 971 University Press, Cambridge, UK.
- 972 Janzen DH (1983) No park is an island: Increase in interference from outside as park size
 973 increases. *Oikos* 41:402–410.
- 974 Jorge ML (2008) Effects of forest fragmentation on two sister genera of Amazonian rodents
 975 (*Myoprocta acouchy* and *Dasyprocta leporina*). *Biol Conserv* 141:617– 623.
- 976 Kapos V (1989) Effects of isolation on the water status of forest patches in the Brazilian
 977 Amazon. *J Trop Ecol* 5:173–185.
- 978 Kapos V, Ganade G, Matusi E, Victoria RL (1993) Delta 13C as an indicator of edge effects
 979 in tropical rainforest reserves. *J Ecol* 81:425–432.
- 980 Killeen TJ (2007) *A Perfect Storm in the Amazon Wilderness: Development and
 981 Conservation in the Context of the Initiative for the Integration of the Regional
 982 Infrastructure of South America (IIRSA)*. Conservation International, Washington,
 983 DC.
- 984 Klein BC (1989) Effects of forest fragmentation on dung and carrion beetle communities in
 985 central Amazonia. *Ecology* 70:1715–1725.
- 986 Laurance SGW (2004b) Responses of understory rain forest birds to road edges in central
 987 Amazonia. *Ecol Applic* 14:1344–1357.
- 988 Laurance SGW, Andrade A, Laurance WF (2010a) Unanticipated effects of stand dynamism
 989 on Amazonian tree diversity. *Biotropica* 42:429–434.
- 990 Laurance SGW, Gomez MS (2005) Clearing width and movements of understory rainforest

- 991 birds. *Biotropica* 37:149–152.
- 992 Laurance SGW, Laurance WF, Andrade A, Fearnside PM, Harms K, Luizão R, (2010b)
- 993 Influence of soils and topography on Amazonian tree diversity: a landscape-scale
- 994 study. *J Veg Sci* 21:96–106.
- 995 Laurance SGW, Laurance WF, Nascimento H, Andrade A, Fearnside PM, Rebello E, Condit
- 996 R (2009a) Long-term variation in Amazon forest dynamics. *J Veg Sci* 20:323–333.
- 997 Laurance SGW, Stouffer PC, Laurance WF (2004) Effects of road clearings on movement
- 998 patterns of understory rainforest birds in central Amazonia. *Conserv Biol* 18:1099–
- 999 1109.
- 1000 Laurance WF (1991) Ecological correlates of extinction proneness in Australian tropical
- 1001 rainforest mammals. *Conserv Biol* 5:79–89.
- 1002 Laurance WF (2001) The hyper-diverse flora of the central Amazon: an overview. In:
- 1003 Bierregaard RO, Gascon C, Lovejoy TE, Mesquita R (Eds), *Lessons from Amazonia:*
- 1004 *Ecology and conservation of a fragmented forest.* Yale University Press, New Haven,
- 1005 Connecticut, pp 47–53.
- 1006 Laurance WF (2002) Hyperdynamism in fragmented habitats. *J Veg Sci* 13:595–602.
- 1007 Laurance WF (2004a) Forest–climate interactions in fragmented tropical landscapes. *Phil.*
- 1008 *Trans. Roy. Soc. B* 359:345–352.
- 1009 Laurance WF (2005) When bigger is better: the need for Amazonian megareserves. *Trends*
- 1010 *Ecol Evol* 20:645–648.
- 1011 Laurance WF (2007) Have we overstated the tropical biodiversity crisis? *Trends Ecol Evol*
- 1012 22:65–70.
- 1013 Laurance WF (2008) Theory meets reality: how habitat fragmentation research has
- 1014 transcended island biogeographic theory. *Biol Conserv* 141:1731–1744.
- 1015 Laurance WF, Andrade A, Magrach, A, Camargo JLC, Valsko J, Campbell M, Fearnside PM,
- 1016 Edwards W, Lovejoy TE, Laurance SGW (2014a) Long-term changes in liana
- 1017 abundance and forest dynamics in undisturbed Amazonian forests. *Ecology* 95:1604–
- 1018 1611.
- 1019 Laurance WF, Andrade A, Magrach A, Camargo JLC, Campbell M, Fearnside PM, Edwards
- 1020 W, Valsko J, Lovejoy TE, Laurance SGW (2014b) Apparent environmental synergism
- 1021 drives the dynamics of Amazonian forest fragments. *Ecology* 95: 3018–3026.
- 1022 Laurance WF, Bierregaard RO (Eds) (1997) *Tropical forest remnants: Ecology, management,*
- 1023 *and conservation of fragmented communities.* University of Chicago Press, Chicago.
- 1024 Laurance WF, Camargo J, Luizão RCC, Laurance SGW, Pimm SL, Bruna E, Stouffer PC,
- 1025 Williamson GB, Benitez-Malvido J, Vasconcelos H, Van Houtan K, Zartman CE,
- 1026 Boyle S, Didham RK, Andrade A, Lovejoy TE (2011) The fate of Amazonian forest
- 1027 fragments: A 32-year investigation. *Biol Conserv* 144:56–67.
- 1028 Laurance WF, Cochrane MA (2001) Synergistic effects in fragmented landscapes. *Conserv*
- 1029 *Biol* 15:1488–1489.
- 1030 Laurance WF, Cochrane M, Bergen S, Fearnside PM, Delamonica P, Barber C, D’Angelo S,
- 1031 Fernandes T (2001a) The future of the Brazilian Amazon. *Science* 291:438–439.
- 1032 Laurance WF, Delamonica P, Laurance SGW, Vasconcelos HL, Lovejoy TE (2000)
- 1033 Rainforest fragmentation kills big trees. *Nature* 404:836.
- 1034 Laurance WF, Fearnside PM, Laurance SGW, Delamonica P, Lovejoy TE, Rankin-de Merona
- 1035 JM, Chambers JQ, Gascon C (1999) Relationship between soils and Amazon forest
- 1036 biomass: a landscape-scale study. *For Ecol Manage* 118:127–138.
- 1037 Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998a) Rain forest
- 1038 fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–
- 1039 2040.
- 1040 Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SGW, Hutchings R, Lovejoy

- 1041 TE (1998b) Effects of forest fragmentation on recruitment patterns in Amazonian tree
 1042 communities. *Conserv Biol* 12:460–464.
- 1043 Laurance WF, Goosem M, Laurance SGW (2009b) Impacts of roads and linear clearings on
 1044 tropical forests. *Trends Ecol Evol* 24:659–669.
- 1045 Laurance WF, Laurance SGW, Delamonica P (1998c) Tropical forest fragmentation and
 1046 greenhouse gas emissions. *For Ecol Manage* 110:173–180.
- 1047 Laurance WF, Laurance SGW, Ferreira LV, Rankin-de Merona J, Gascon C, Lovejoy TE
 1048 (1997) Biomass collapse in Amazonian forest fragments. *Science* 278:1117–1118.
- 1049 Laurance WF, Lovejoy TE, Vasconcelos H, Bruna E, Didham R, Stouffer P, Gascon C,
 1050 Bierregaard R, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian
 1051 forest fragments: a 22-year investigation. *Conserv Biol* 16:605–618.
- 1052 Laurance WF, Luizão RCC (2007) Driving a wedge into the Amazon. *Nature* 448:409–410.
- 1053 Laurance WF, Nascimento H, Laurance SG, Andrade A, Ewers R, Harms K, Luizão R,
 1054 Ribeiro J (2007) Habitat fragmentation, variable edge effects, and the landscape-
 1055 divergence hypothesis. *PLoS ONE* 2:e1017.
- 1056 Laurance WF, Nascimento H, Laurance SG, Andrade A, Fearnside PM, Ribeiro J (2006a)
 1057 Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87:469–
 1058 482.
- 1059 Laurance WF, Nascimento H, Laurance SG, Andrade A, Ribeiro J, Giraldo JP, Lovejoy TE,
 1060 Condit R, Chave J, D'Angelo S (2006b) Rapid decay of tree community composition
 1061 in Amazonian forest fragments. *Proc Nat Acad Sci USA* 103:19010–19014.
- 1062 Laurance WF, Nascimento H, Laurance SG, Condit R, D'Angelo S, Andrade A (2004)
 1063 Inferred longevity of Amazonian rainforest trees based on a long-term demographic
 1064 study. *For Ecol Manage* 190:131–143.
- 1065 Laurance WF, Peres CA (Eds) (2006) *Emerging Threats to Tropical Forests*. University of
 1066 Chicago Press, Chicago, USA.
- 1067 Laurance WF, Perez-Saliciprup D, Delamonica P, Fearnside PM, D'Angelo S, Jerozolinski A,
 1068 Pohl L, Lovejoy TE (2001b) Rain forest fragmentation and the structure of
 1069 Amazonian liana communities. *Ecology* 82:105–116.
- 1070 Laurance WF, Useche DC (2009) Environmental synergisms and extinctions of tropical
 1071 species. *Conserv Biol* 23:1427–1437.
- 1072 Laurance WF, Williamson GB (2001) Positive feedbacks among forest fragmentation,
 1073 drought, and climate change in the Amazon. *Conserv Biol* 15:1529–1535.
- 1074 Laurance WF, Williamson GB, Delamonica P, Olivera A, Gascon C, Lovejoy TE, Pohl L
 1075 (2001c) Effects of a strong drought on Amazonian forest fragments and edges. *J Trop*
 1076 *Ecol* 17:771–785.
- 1077 Leidner AK, Haddad NM, Lovejoy TE (2010) Does tropical forest fragmentation increase
 1078 long-term variability of butterfly communities? *PLoS ONE* 5:e9534.
- 1079 Lima M, Gascon C (1999) The conservation value of linear forest remnants in central
 1080 Amazonia. *Biol Conserv* 91:241–247.
- 1081 Lovejoy TE, Bierregaard RO, Rylands AB, Malcolm JR, Quintela C, Harper L, Brown K,
 1082 Powell A, Powell G, Schubart H, Hays M (1986) Edge and other effects of isolation
 1083 on Amazon forest fragments. In: Soulé ME (Ed), *Conservation biology: The science*
 1084 *of scarcity and diversity*. Sinauer, Sunderland, Massachusetts, pp 257–285.
- 1085 Lovejoy TE, Oren DC (1981) Minimum critical size of ecosystems. In: Burgess RL, Sharp
 1086 DM (Eds), *Forest-island dynamics in man-dominated landscapes*. Springer-Verlag,
 1087 New York, pp 7–12.
- 1088 Lovejoy TE, Rankin JM, Bierregaard RO, Brown KS, Emmons LH, Van der Voort ME
 1089 (1984) Ecosystem decay of Amazon forest fragments. In: Nitecki MH (Ed),
 1090 *Extinctions*. University of Chicago Press, Chicago, pp 295–325.

- 1091 Malcolm JR (1994) Edge effects in central Amazonian forest fragments. *Ecology* 75:2438–
1092 2445.
- 1093 Malcolm JR (1997) Biomass and diversity of small mammals in Amazonian forest fragments.
1094 In: Laurance WF, Bierregaard RO (Eds) *Tropical forest remnants: Ecology,*
1095 *management, and conservation of fragmented communities.* University of Chicago
1096 Press, Chicago, pp 207–221.
- 1097 Malcolm JR (1998) A model of conductive heat flow in forest edges and fragmented
1098 landscapes. *Clim Change* 39:487–502.
- 1099 Massoca PES, Jakovac ACC, Vizcarra TB, Williamson GB, Mesquita RCG (2012)
1100 Dinâmica e trajetórias da sucessão secundária na Amazônia central. *Bol Mus Para*
1101 *Emílio Goeldi Cienc Nat Belém* 7:235-250.
- 1102 Mesquita R, Delamônica P, Laurance WF (1999) Effects of surrounding vegetation on edge-
1103 related tree mortality in Amazonian forest fragments. *Biol Conserv* 91:129–134.
- 1104 Mesquita RCC, Bentos TV, Jakovac ACC, Massoca P, Williamson GB (2012) Amazonian
1105 secondary forests respond to climatic variation: biomass dynamics. 49th Annual
1106 Meeting of the Association for Tropical Biology and Conservation, Bonito, MS,
1107 Brazil.
- 1108 Mesquita R, Ickes K, Ganade G, Williamson GB (2001) Alternative successional pathways in
1109 the Amazon basin. *J Ecol* 89:528–537.
- 1110 Mestre LAM, Gasnier TR (2008) Populações de aranhas errantes do gênero *Ctenus* em
1111 fragmentos florestais na Amazônia Central. *Acta Amazonica* 38:159–164.
- 1112 Michalski F, Peres CA (2005) Anthropogenic determinants of primate and carnivore local
1113 extinctions in a fragmented forest landscape of Southern Amazonia. *Biol Conserv*
1114 124:383–396.
- 1115 Moura NG, Lees AC, Andretti CB, Davis BJW, Solar RRC, Aleixo A, Barlow J, Ferreira J,
1116 Gardner TA (2014) Avian biodiversity in multiple-use landscapes of the Brazilian
1117 Amazon. *Biol Conserv* 167:339-348.
- 1118 Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity
1119 hotspots for conservation priorities. *Nature* 403:853–858.
- 1120 Nascimento H, Andrade A, Camargo J, Laurance WF, Laurance SG, Ribeiro J (2006) Effects
1121 of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conserv*
1122 *Biol* 20:853–860.
- 1123 Nascimento H, Laurance WF (2004) Biomass dynamics in Amazonian forest fragments. *Ecol*
1124 *Appl* 14:S127–S138.
- 1125 Neckel-Oliveira S, Gascon C (2006) Abundance, body size and movement patterns of a
1126 tropical tree frog in continuous and fragmented forests of the Brazilian Amazon. *Biol*
1127 *Conserv* 128:308–315.
- 1128 Nessimian JL, Venticinque EM, Zuanon J, De Marco P, Gordo M, Fidelis L, Batista J, Juen L
1129 (2008) Land use, habitat integrity, and aquatic insect assemblages in central
1130 Amazonian streams. *Hydrobiol* 614:117–131.
- 1131 Nogueira EM, Fearnside PM, Nelson BW, Barbosa RI, Keizer EWH (2008) Estimates of
1132 forest biomass in the Brazilian Amazon: New allometric equations and adjustments to
1133 biomass from wood-volume inventories. *For Ecol Manage* 256:1853-1857.
- 1134 Nogueira EM, Fearnside PM, Nelson BW, França MB (2007) Wood density in forests of
1135 Brazil's 'arc of deforestation': Implications for biomass and flux of carbon from land-
1136 use change in Amazonia. *For Ecol Manage* 248:119-135.
- 1137 Nogueira EM, Nelson BW, Fearnside PM (2005) Wood density in dense forest in central
1138 Amazonia, Brazil. *For Ecol Manage* 208:261-286.
- 1139 Norden N, Mesquita R, Bentos T, Chazdon R, Williamson GB (2011) Contrasting community
1140 compensatory trends in alternative successional pathways in central Amazonia. *Oikos*

- 1141 120:143-151
- 1142 Oliveira de AA, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species
1143 richness on poor soils. *Biodiv Conserv* 8:1219–1244.
- 1144 Peres CA (2005) Why we need megareserves in Amazonia. *Conserv Biol* 19, 728–733.
- 1145 Peres CA, Gardner TA, Barlow J, Zuanon J, Michalski F, Lees A, Vieira I, Moreira F, Feeley
1146 KJ (2010) Biodiversity conservation in human-modified Amazonian forest landscapes.
1147 *Biol Conserv* 143:2314–2327.
- 1148 Phillips OL, Malhi Y, Higuchi N, Laurance WF, Nunez PV, Vasquez RM, et al. (1998)
1149 Changes in the carbon balance of tropical forests: Evidence from long-term plots.
1150 *Science* 282:439-442.
- 1151 Pimm SL (1998) The forest fragment classic. *Nature* 393:23–24.
- 1152 Pimm SL, Jenkins C (2005) Sustaining the variety of life. *Sci Amer* September:66–73.
- 1153 Powell AH, Powell GVN (1987) Population dynamics of male euglossine bees in Amazonian
1154 forest fragments. *Biotropica* 19:176–179.
- 1155 Puerta R (2002) Regeneração arbórea em pastagens abandonadas na região de Manaus em
1156 função da distância da floresta contínua. *Scientia Forestalis* 62:32–39.
- 1157 Quintela CE (1985) Forest Fragmentation and Differential Use of Natural and Man-made
1158 Edges by Understory Birds in Central Amazonia. M.Sc. Thesis, University of Illinois,
1159 Chicago.
- 1160 Quintero I, Roslin T (2005) Rapid recovery of dung beetle communities following habitat
1161 fragmentation in Central Amazonia. *Ecology* 86:3303–3311.
- 1162 Radtke MG, da Fonseca C, Williamson GB (2008) Forest fragment size effects on dung
1163 beetle communities. *Biol Conserv* 141:613–614.
- 1164 Rego F, Venticinque EM, Brescovit A (2007) Effects of forest fragmentation on four *Ctenus*
1165 spider populations (Araneae, Ctenidae) in central Amazonia, Brazil. *Stud Neotrop*
1166 *Fauna Environ* 42:137–144.
- 1167 Ribeiro MBN, Bruna EM, Mantovani W (2009) Influence of post-clearing treatment on the
1168 recovery of herbaceous plant communities in Amazonian secondary forests. *Restor*
1169 *Ecol* 18:50–58.
- 1170 Rocha R, López-Baucells A, Groenenberg M, Silva I, Farneda F, Bobrowiec P, Palmeirim
1171 JM, Meyer CFJ (2013) Effects of forest fragmentation on central Amazonian bats.
1172 Paper presented at the 16th International Bat Research Conference & 43rd North
1173 American Symposium on Bat Research, San José, Costa Rica.
- 1174 Salazar LF, Nobre CA, Oyama MD (2007) Climate change consequences on the biome
1175 distribution in South America. *Geophys Res Lett* 34:L09708.
- 1176 Sampaio EM, 2000. Effects of Forest Fragmentation on the Diversity and Abundance Patterns
1177 of Central Amazonian Bats. Ph.D. Dissertation, University of Tübingen, Germany.
- 1178 Sampaio EM, Kalko E, Bernard E, Rodriguez-Herrera B, Handley C, (2003) A biodiversity
1179 assessment of bats (Chiroptera) in a tropical lowland forest of central Amazonia,
1180 including methodological and conservation considerations. *Stud Neotrop Fauna*
1181 *Environ* 28:17–31.
- 1182 Santos BA, Arroyo-Rodríguez V, Moreno CE, Tabarelli M (2010) Edge-related loss of tree
1183 phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PLoS ONE*
1184 5:e12625.
- 1185 Scariot A (1999) Forest fragmentation effects on diversity of the palm community in central
1186 Amazonia. *J Ecol* 87:66–76.
- 1187 Scariot A (2001) Weedy and secondary palm species in central Amazonian forest fragments.
1188 *Rev Bot Brasil* 15:271–280.
- 1189 Sizer N, Tanner EVJ (1999) Responses of woody plant seedlings to edge formation in a
1190 lowland tropical rainforest. Amazonia. *Biol Conserv* 91:135–142.

- 1191 Sizer N, Tanner EVJ, Kossman-Ferraz I (2000) Edge effects on litterfall mass and nutrient
1192 concentrations in forest fragments in central Amazonia. *J Trop Ecol* 16:853–863.
- 1193 Skole DS, Tucker CJ (1993) Tropical deforestation and habitat fragmentation in the Amazon:
1194 satellite data from 1978 to 1988. *Science* 260:1905–1910.
- 1195 Sodhi NS, Koh LP, Brook BW, Ng P (2004) Southeast Asian biodiversity: an impending
1196 disaster. *Trends Ecol Evol* 19:654–660.
- 1197 Stickler CM et al. (2009) The potential ecological costs and cobenefits of REDD: A critical
1198 review and case study from the Amazon region. *Glob Change Biol* 15:2803–2824.
- 1199 Stouffer PC, Bierregaard RO (1995a) Effects of forest fragmentation on understory
1200 hummingbirds in Amazonian Brazil. *Conserv Biol* 9:1085–1094.
- 1201 Stouffer PC, Bierregaard RO (1995b) Use of Amazonian forest fragments by understory
1202 insectivorous birds. *Ecology* 76:2429–2445.
- 1203 Stouffer PC, Bierregaard RO, Strong C, Lovejoy TE (2006) Long-term landscape change and
1204 bird abundance in Amazonian rainforest fragments. *Conserv Biol* 20:1212–1223.
- 1205 Stouffer PC, Strong C, Naka LN (2008) Twenty years of understory bird extinctions from
1206 Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics.
1207 *Divers Distrib* 15:88–97.
- 1208 Stratford JA, Stouffer PC (1999) Local extinctions of terrestrial insectivorous birds in
1209 Amazonian forest fragments. *Conserv Biol* 13:1416–1423.
- 1210 Terborgh J, Lopez L, Nuñez VP, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R,
1211 Adler G, Lambert T, Balbas L (2001) Ecological meltdown in predator-free forest
1212 fragments. *Science* 294:1923–1926.
- 1213 Ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomao RP, Ernesto Guevara J, Phillips
1214 OL et al. (2013) Hyperdominance in the Amazonia flora. *Science* 342:326–334.
- 1215 Timo TPC (2003) Influência de fragmentação e matriz sobre a comunidade de mamíferos de
1216 médio e grande porte em uma floresta de terra firme na Amazônia central. M.Sc.
1217 Thesis, National Institute for Amazonian Research (INPA), Manaus, Brazil.
- 1218 Tocher M, Gascon C, Zimmerman BL (1997) Fragmentation effects on a central Amazonian
1219 frog community: a ten-year study. In: Laurance WF, Bierregaard RO (Eds), *Tropical
1220 forest remnants: Ecology, management, and conservation of fragmented communities.*
1221 University of Chicago Press, Chicago, pp 124–137.
- 1222 Trancoso R (2008) Hydrological Impacts of Deforestation in Small Catchments in Brazilian
1223 Amazonia. M.Sc. Thesis, National Institute for Amazonian Research (INPA), Manaus,
1224 Brazil.
- 1225 Uriarte M, Bruna EM, Rubim P, Anciães M, Jonckheere I (2010) Effects of forest
1226 fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-
1227 site limitation. *Ecology* 91:1317–1328.
- 1228 Van Houtan KS, Pimm SL, Bierregaard RO, Lovejoy TE, Stouffer PC (2006) Local
1229 extinctions in Amazonian forest fragments. *Ecol Res* 8:129–148.
- 1230 Van Houtan KS, Pimm SL, Halley J, Bierregaard RO, Lovejoy TE (2007) Dispersal of
1231 Amazonian birds in continuous and fragmented forest. *Ecol Lett* 10:219–229.
- 1232 Vasconcelos HL, Luizão FJ (2004) Litter production and litter nutrient concentrations in a
1233 fragmented Amazonian landscape: edge and soil effects. *Ecol Applic* 14:884–892.
- 1234 Wilcox BA, Murphy DD (1985) Conservation strategy: the effects of fragmentation on
1235 extinction. *Am Nat* 125:879–887.
- 1236 Wieland LM, Mesquita RC, Bobrowiec PED, Bentos TV, Williamson GB (2011) Seed rain
1237 and advance regeneration in secondary succession in the Brazilian Amazon. *Trop
1238 Conserv Sci* 4:300–316.
- 1239 Williamson GB, Laurance WF, Oliveira A, Delamonica P, Gascon C, Lovejoy TE, Pohl L
1240 (2000) Amazonian wet forest resistance to the 1997–98 El Niño drought. *Conserv Biol*

- 1241 14:1538–1542.
- 1242 Williamson GB, Longworth JB, Bentos TV, Mesquita RC (2014) Convergence and
1243 divergence in alternative successional pathways in Central Amazonia. *Plant Ecol*
1244 *Diversity* 7:341-348.
- 1245 Williamson GB, Mesquita R (2001) Effects of fire on rain forest regeneration in the Amazon
1246 Basin. In: Laurance WF, Bierregaard RO (Eds), *Tropical forest remnants: Ecology,*
1247 *management, and conservation of fragmented communities.* University of Chicago
1248 Press, Chicago, pp 325–334.
- 1249 Zartman CE (2003) Forest fragmentation effects on epiphyllous bryophyte communities in
1250 central Amazonia. *Ecology* 84:948–954.
- 1251 Zartman CE, Nascimento HEM (2006) Are patch-tracking metacommunities dispersal
1252 limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian
1253 forest fragments. *Biol Conserv* 127:46–54.
- 1254 Zartman CE, Shaw AJ (2006) Metapopulation extinction thresholds in rainforest remnants.
1255 *Am Nat* 167:177–189.
- 1256
- 1257
- 1258

FIGURE CAPTIONS

1259
1260
1261
1262
1263
1264
1265
1266
1267
1268
1269
1270
1271
1272
1273
1274
1275
1276
1277
1278
1279
1280
1281
1282
1283

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

Figure 2. The diversity of edge-effect phenomena studied at the BDFFP and the distance to which each was found to penetrate into fragment interiors (after Laurance et al. 2002).

Figure 3. Forest plots affected by two or more nearby edges (plot center <100 m from edge) suffer greater tree mortality (A) and have a higher density (B) and species richness (C) of disturbance-loving pioneer trees than do plots with just one nearby edge. Values shown are the mean \pm SD (after Laurance et al. 2006a).

Figure 4. Increasing divergence of tree-community composition in three fragmented Amazonian landscapes. Tree communities in forest-edge plots (<100 m from the nearest edge) are shown before forest fragmentation and 13–18 years after fragmentation, based on a single ordination of all plots and censuses in the study area. The ordination used importance values for all 267 tree genera found in the plots (after Laurance et al. 2007).

Fig. 5. Tree genera that increase in forest fragments (those with positive values on the X axis) tend to have lower wood density than do those that decline in fragments (those with negative values on the X axis)(after Laurance et al. 2006b).

Fig. 6. Striking increases in the density of 52 species in nine pioneer or early successional genera (*Annona*, *Bellucia*, *Cecropia*, *Croton*, *Goupia*, *Jacaranda*, *Miconia*, *Pourouma*, *Vismia*) near forest edges in the BDFFP study area (after Laurance et al. 2006a).