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

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Running head: *Amazonian fragments and global change*

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31

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33

34 **ABSTRACT**

35 We synthesize findings from one of the world's largest and longest-running experimental
36 investigations, the Biological Dynamics of Forest Fragments Project (BDFFP). Spanning an
37 area of ~1,000 km² in central Amazonia, the BDFFP was initially designed to evaluate the
38 effects of fragment area on rainforest biodiversity and ecological processes. However, over its
39 38-year history to date the project has far transcended its original mission, and now focuses
40 more broadly on landscape dynamics, forest regeneration, regional- and global-change
41 phenomena, and their potential interactions and implications for Amazonian forest
42 conservation. The project has yielded a wealth of insights into the ecological and
43 environmental changes in fragmented forests. For instance, many rainforest species are
44 naturally rare and hence are either missing entirely from many fragments or so sparsely
45 represented as to have little chance of long-term survival. Additionally, edge effects are a
46 prominent driver of fragment dynamics, strongly affecting forest microclimate, tree mortality,
47 carbon storage and a diversity of fauna.

48 Even within our controlled study area, the landscape has been highly dynamic: for
49 example, the matrix of vegetation surrounding fragments has changed markedly over time,
50 succeeding from large cattle pastures or forest clearcuts to secondary regrowth forest. This, in

51 turn, has influenced the dynamics of plant and animal communities and their trajectories of
52 change over time. In general, fauna and flora have responded differently to fragmentation: the
53 most locally extinction-prone animal species are those that have both large area requirements
54 and low tolerance of the modified habitats surrounding fragments, whereas the most
55 vulnerable plants are those that respond poorly to edge effects or chronic forest disturbances,
56 and that rely on vulnerable animals for seed dispersal or pollination.

57 Relative to intact forests, most fragments are hyperdynamic, with unstable or
58 fluctuating populations of species in response to a variety of external vicissitudes. Rare
59 weather events such as droughts, windstorms and floods have had strong impacts on
60 fragments and left lasting legacies of change. Both forest fragments and the intact forests in
61 our study area appear to be influenced by larger-scale environmental drivers operating at
62 regional or global scales. These drivers are apparently increasing forest productivity and have
63 led to concerted, widespread increases in forest dynamics and plant growth, shifts in tree-
64 community composition, and increases in liana (woody vine) abundance. Such large-scale
65 drivers are likely to interact synergistically with habitat fragmentation, exacerbating its effects
66 for some species and ecological phenomena. Hence, the impacts of fragmentation on
67 Amazonian biodiversity and ecosystem processes appear to be a consequence not only of
68 local site features but also of broader changes occurring at landscape, regional and even
69 global scales.

70

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

73

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125 I. INTRODUCTION

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

133 The BDFFP is strategically located at the heart of the Amazon, the world's largest
134 tropical forest. The Amazon itself lies at the intersection of key questions in global change,
135 both for research and for action. It is believed to be one of the major regions that will be most
136 impacted by projected climatic change (Salazar *et al.*, 2007; Dai, 2012; IPCC, 2013; Nobre *et al.*,
137 2016). If effectively conserved and managed, the Amazon has the potential to contribute
138 markedly to efforts to limit climate change during the narrow window of time we have
139 remaining to avert 'dangerous' global warming (Fearnside, 2000, 2012; Houghton *et al.*,
140 2015). Because of its enormous carbon-storage capacity, it is also one of the places on Earth
141 where sharply reducing greenhouse-gas emissions could be achieved by limiting forest loss
142 and degradation, thereby delivering great global benefits for humankind (Stickler *et al.*,
143 2009).

144 Today, the BDFFP is one of the most enduring, influential and highly cited
145 environmental investigations in the world (Gardner *et al.*, 2009; Peres *et al.*, 2010; Pitman *et al.*,
146 2011). Its wide-ranging research has involved hundreds of Brazilian and international
147 investigators and thousands of students and other trainees. Here we synthesize the
148 contributions of this singular project to the study of habitat fragmentation, including its
149 broader consequences for Amazonian ecosystems and biota. We emphasize that many of the

150 local impacts of fragmentation in the Amazon are being modified or exacerbated by
151 environmental changes occurring at wider landscape, regional and even global scales. We
152 assert that the effects of fragmentation cannot be fully understood without considering the
153 influence of these larger-scale phenomena.

154

155 **II. LARGER-SCALE DRIVERS**

156 **(1) Landscape-scale phenomena**

157 The correlated processes of forest loss and fragmentation are among the greatest threats to
158 tropical biodiversity (Lovejoy *et al.*, 1986; Ewers & Didham, 2006; Laurance & Peres, 2006;
159 Gibson *et al.*, 2011). Amazonia harbors more than half of the world's surviving tropical
160 forest, and is currently being altered by large-scale agriculture (Fearnside, 2001a; Gibbs *et al.*,
161 2010), industrial logging (Asner *et al.*, 2005), proliferating roads (Laurance *et al.*, 2001a;
162 Fearnside, 2002, 2007; Killeen, 2007), increasing biofuel production (Butler & Laurance,
163 2009), hydroelectric dams (Fearnside, 2016a) and oil, gas and mining developments (Finer *et*
164 *al.*, 2008).

165 Large expanses of the Amazon have already been cleared, resulting in considerable
166 fragmentation. By the early 1990s, the area of forest that was fragmented ($<100 \text{ km}^2$) or
167 vulnerable to edge effects ($<1 \text{ km}$ from edge) was over 150% greater than the area that had
168 been deforested (Skole & Tucker, 1993). From 1999 to 2002, deforestation and industrial
169 selective logging in Brazilian Amazonia, respectively, created $\sim 32,000$ and $\sim 38,000 \text{ km}$ of
170 new forest edge annually (Broadbent *et al.*, 2008). Prevailing land uses in Amazonia, such as
171 cattle ranching and small-scale farming, typically produce landscapes dominated by small
172 ($<400 \text{ ha}$) and irregularly shaped forest fragments (Fig. 2)(Cochrane & Laurance, 2002;
173 Broadbent *et al.*, 2008). Such fragments are especially vulnerable to a wide array of edge
174 effects and other external vicissitudes (Bierregaard *et al.*, 1992; Laurance *et al.*, 2002, 2011).

175 Changes in forest cover can have important effects on local climate and vegetation.
176 Habitat fragmentation can promote forest desiccation via phenomena such as the “vegetation
177 breeze” (Fig. 3). This occurs because fragmentation leads to the juxtaposition of cleared and
178 forested lands, which differ greatly in their physical characteristics. Air above forests is
179 cooled by evaporation and especially plant evapotranspiration, but such cooling is greatly
180 reduced above clearings (Avissar & Schmidt, 1998). As a result, the air above clearings heats
181 up and rises, reducing local air pressure and drawing moist air from the surrounding forests
182 into the clearing. As the rising air cools, its moisture condenses into convective clouds that
183 can produce rainfall over the clearing (Avissar & Liu, 1996). The air is then recycled—as
184 cool, dry air—back over the forest. In this way, clearings of a few hundred hectares or more
185 can draw moisture away from nearby forests (Laurance, 2004a; Cochrane & Laurance, 2008;
186 Nobre *et al.*, 2016). In eastern Amazonia, satellite observations of canopy-water content
187 suggest such desiccating effects can penetrate from 1.0-2.7 km into fragmented forests (Briant
188 *et al.*, 2010). This moisture-robbing function of clearings, in concert with frequent burning in
189 adjoining pastures, could help to explain why fragmented forests are so vulnerable to
190 destructive, edge-related fires (Cochrane & Laurance, 2002, 2008; Barlow *et al.*, 2006).

191

192 **(2) Regional-scale phenomena**

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

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

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

224

225 (3) Global-change phenomena

226 How will global-change drivers affect the Amazon? Although model predictions for future
227 climates in Amazonia vary considerably, it is generally expected that parts of the basin will
228 become hotter and drier under projected global warming (IPCC, 2013; Nobre *et al.*, 2016).
229 What this portends for the Amazon is a matter of some controversy. Earlier studies assuming
230 CO₂ concentrations about twice those in the pre-industrial atmosphere, notably by the UK
231 Hadley Centre, projected disastrous forest die-offs (Cox *et al.*, 2000, 2004). However, this
232 conclusion has now been countered by new models from the same research group, suggesting
233 the Amazon forest will remain almost entirely intact at up to four times pre-industrial CO₂
234 levels (Cox *et al.*, 2013; Good *et al.*, 2013; Huntingford *et al.*, 2013). The main difference is
235 that the newer models include CO₂-fertilization effects (Kimball *et al.*, 1993), which are
236 assumed to increase plant growth and water-use efficiency. This is because the higher
237 atmospheric CO₂ concentration should allow plants to conserve water by decreasing the
238 duration of stomatal-opening periods while still taking in adequate CO₂ for photosynthesis.

239 Other global-change phenomena, such as extreme climatic events, could also
240 potentially have important impacts. For instance, droughts in the Amazon are normally
241 associated with El Niño events and are strongest in the southern, eastern and north-central
242 Amazon—areas of the basin that already experience pronounced dry seasons. However,
243 severe droughts in 2005 and 2010 arose from a completely different cause—exceptionally
244 high Atlantic sea-surface temperatures, which caused the rain-bearing inter-tropical
245 convergence zone to shift northward (Lewis *et al.*, 2011). The resulting droughts affected not
246 just the drier, more seasonal parts of the basin but also its wettest areas in central and western
247 Amazonia. Because plant species in these wet areas are adapted to perennially humid
248 conditions, the new droughts caused massive plant mortality, killing tens of millions of trees
249 while releasing several billion tonnes of atmospheric carbon emissions (Lewis *et al.*, 2011;

250 Marengo *et al.*, 2012). With mounting evidence that climatic extremes could become more
251 frequent and intense in a warming world (Vera *et al.*, 2006; Herring *et al.*, 2015; Jiménez-
252 Muñoz *et al.*, 2016), could the Amazon be driven into a new kind of climatic dynamic—one
253 for which its ecosystems and biodiversity are poorly adapted?

254

255 **III. STUDY AREA AND KEY DATASETS**

256 **(1) Study area**

257 The experimental landscape of the BDFFP spans ~1000 km² in area and is located 80 km
258 north of Manaus, Brazil. The topography is relatively flat (80-160 m elevation) but dissected
259 by numerous stream gullies. The heavily weathered, nutrient-poor soils of the study area are
260 typical of large expanses of the Amazon Basin. Rainfall ranges from 1900 to 3500 mm
261 annually with a moderately strong dry season from June to October. The forest canopy is 30-
262 37 m tall, with emergent trees to 55 m. Species richness of trees (≥ 10 cm diameter at breast
263 height) often exceeds 280 species ha⁻¹, which is among the highest known tree diversity in the
264 world (Oliveira & Mori, 1999; S. G. Laurance *et al.*, 2010b). Comparably high levels of
265 diversity are seen in many other plant and animal taxa.

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

274 Because of poor soils and low productivity, the ranches surrounding the BDFFP

275 fragments were largely abandoned, especially after government fiscal incentives dried up
276 from 1988 onwards. Secondary forests—initially dominated by *Vismia* spp. in areas that were
277 cleared and burned, and by *Cecropia* spp. in areas that were cleared without fire—proliferated
278 in many formerly forested areas (Mesquita *et al.*, 2001). Some regenerating areas initially
279 dominated by *Cecropia* later grew into **structurally complex** (>20 m tall), species-rich
280 secondary forests (Longworth *et al.*, 2014). *Vismia*-dominated regrowth, however, which is
281 relatively species poor, is maturing far more slowly (Norden *et al.*, 2011; Williamson *et al.*,
282 2014).

283 To help maintain isolation of the experimental fragments, 100 m-wide strips of
284 regrowth were cleared and burned around each fragment on 4-5 occasions, most recently in
285 2013-2014. However, human disturbances that affect many fragmented landscapes in the
286 Amazon, such as major fires, logging and hunting (Michalski & Peres, 2005), are largely
287 prevented at the BDFFP.

288

289 **(2) Unique datasets**

290 The BDFFP sustains some of the longest-running and highest-quality environmental datasets
291 in the Amazon. This includes a network of 69 1-ha forest-dynamics plots arrayed across intact
292 and fragmented forests in the study area, which has been monitored since the early 1980s, and
293 a permanent 25-ha plot in intact forest established in 2005. These plots have made important
294 contributions to reducing uncertainties in biomass and carbon-storage estimates for the
295 Amazon (e.g. Phillips *et al.*, 1998; Baker *et al.*, 2004; Nascimento & Laurance, 2002). For
296 example, in comparison to the 3000 1-ha plots surveyed by the RADAMBRASIL Project
297 (Nogueira *et al.*, 2008, 2015), the BDFFP plots include data on nearly all other forest
298 components such as smaller (1-30 cm diameter) trees, palms, lianas, strangler figs, understory
299 vegetation and dead biomass (Nascimento & Laurance, 2002, 2004). These data allow one to

300 assess spatial variability in aboveground biomass with a high degree of confidence. For
301 example, the aboveground biomass of trees varies considerably among the 69 1-ha plots in the
302 BDFFP landscape (mean \pm SD = 356 \pm 47 Mg ha⁻¹; Laurance *et al.*, 1999). This high
303 variability demonstrates a need for many plots that are spatially stratified, rather than only a
304 few plots of 1 ha or smaller scattered irregularly around the Amazon, for calibrating satellite
305 imagery for biomass mapping, and for estimating greenhouse-gas emissions from ongoing
306 deforestation (see Fearnside, 2016b).

307 Floristic data from the BDFFP are exceptional for their high quality of species
308 identifications, allowing better matching with plant functional and phylogenetic traits such as
309 wood density and tree form (e.g., Fearnside, 1997; Nogueira *et al.*, 2005, 2007; Chave *et al.*,
310 2006; Souza *et al.*, 2016). Given their broad spatial extent and temporal depth, these data have
311 also contributed to knowledge of the diversity of Amazonian plant species and their
312 relationships to soil texture and chemistry, topography, forest dynamics and climatic variables
313 at both landscape and regional scales (e.g. Bohlman *et al.*, 2008; S. G. Laurance *et al.*, 2009,
314 2010a, 2010b; ter Steege *et al.*, 2013). Biodiversity and ecosystem processes represent part of
315 what is lost when the forest is destroyed or degraded. Understanding these processes is
316 essential for assessing not only the vulnerability of forests, but also their potential resilience
317 in the face of global change and their rates of recovery following various perturbations
318 (Williamson *et al.*, 2014; Souza *et al.*, 2016). Datasets for a number of faunal groups, such as
319 birds, amphibians, primates and major invertebrate taxa, are of comparable quality and
320 duration.

321

322 **IV. CHANGES IN INTACT FORESTS**

323 **(1) Unexpected trends**

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

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

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

348

349 **(2) Potential environmental drivers**

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

360 The most frequently invoked driver of rising tropical forest productivity is CO₂
361 fertilization (e.g. Lewis *et al.*, 2004a, 2009b), presumably because many plants show faster
362 growth under enriched CO₂ (Oberbauer *et al.*, 1985; Granados & Körner, 2002; Körner 2004)
363 and because atmospheric CO₂ levels have risen rapidly, especially in recent decades. This
364 view is supported by compelling evidence of a large carbon sink in the biosphere (Ballantyne
365 *et al.*, 2013), a substantial part of which appears to be on land (Sarmiento *et al.*, 2010) and in
366 the tropics (Lewis *et al.*, 2009b; Huntingford *et al.*, 2013).

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

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

381 The notable increases in liana abundance in our intact forests (Laurance *et al.*, 2014a)
382 might arise because lianas appear to exploit rising CO₂ concentrations and drier conditions
383 more effectively than do trees (Condon *et al.*, 1992; Granados & Körner, 2002; but see
384 Marvin *et al.*, 2015). Trees with heavy liana infestations are known to exhibit elevated
385 mortality and reduced growth (Ingwell *et al.*, 2010). Notably, in our study area, liana
386 abundance is strongly and negatively correlated with live tree biomass (Fig. 6)(Laurance *et*
387 *al.*, 2001b). Liana increases over time have also been observed in tropical forests in western
388 Amazonia, the Guianas, Central America and elsewhere (Schnitzer & Bongers, 2011), with
389 rising atmospheric CO₂ and possibly increasing drought being the most frequent explanations
390 (see Laurance *et al.*, 2014a and references therein). This potentially negative effect of CO₂
391 enrichment on forest biomass via increasing liana infestations is not included in the latest
392 Hadley Centre models (Cox *et al.*, 2013; Good *et al.*, 2013; Huntingford *et al.*, 2013), and
393 could cancel out some of the carbon-storage benefits suggested for a high-CO₂ future (Körner,
394 2004, 2017).

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

399

400 V. CONSEQUENCES OF FRAGMENT SIZE

401 The BDFFP's original mission focuses on assessing the effects of fragment area on
402 Amazonian forests and fauna, and on key ecological and ecosystem processes. Here we
403 summarize major findings and conservation lessons that have been gleaned to date.

404

405 (1) Sample effects

406 Many species in Amazonian forests are rare or patchily distributed. This phenomenon is
407 especially pronounced in the large expanses of the basin that overlay heavily weathered,
408 nutrient-poor soils (e.g. Radtke *et al.*, 2008). In such areas resources such as fruits, flowers
409 and nectar are typically scarce and plants are heavily defended against herbivore attack
410 (Laurance, 2001).

411 Herein lies a key implication for understanding forest fragmentation: given their rarity,
412 many species may be absent from fragments not because their populations have vanished, but
413 because they were simply not present at the time of fragment creation—a phenomenon termed
414 the 'sample effect' (Wilcox & Murphy, 1985). Such sample effects are the hypothesized
415 explanation for the absence of many rare understory bird species from fragments (Ferraz *et*
416 *al.*, 2007). In addition, many beetles (Didham *et al.*, 1998a), bats (Sampaio, *et al.*, 2003;
417 Farneda *et al.*, 2015; Meyer *et al.*, 2015; Rocha *et al.*, 2016), ant-defended plants (Bruna, *et*
418 *al.*, 2005) and trees (Bohlman *et al.*, 2008; Laurance *et al.*, 2010b) at the BDFFP exhibit high
419 levels of rarity, habitat specialization or patchiness.

420

421 (2) Area effects

422 Understanding fragment-area effects has long been a central goal of the BDFFP (Lovejoy &
423 Oren, 1981; Lovejoy *et al.*, 1984, 1986; Pimm, 1998). The species richness of many

424 organisms declines with decreasing fragment area, even with constant sampling effort across
425 all fragments. Such declines are evident in leaf bryophytes (Zartman, 2003), tree seedlings
426 (Benítez-Malvido & Martinez-Ramos, 2003a), palms (Scariot, 1999), understory
427 insectivorous birds (Stratford & Stouffer, 1999; Ferraz *et al.*, 2007), bats (Sampaio, 2000;
428 Rocha *et al.*, 2016), primates (Gilbert & Setz, 2001; Boyle & Smith, 2010a) and larger
429 herbivorous mammals (Timo 2003), among others. For such groups, smaller fragments (<100
430 ha) are often unable to support viable populations. A few groups, such as ant-defended plants
431 and their ant mutualists, show no significant decline in diversity with fragment area (Bruna, *et*
432 *al.*, 2005).

433 Fragment size also influences the rate of species losses, with smaller fragments losing
434 species more quickly (Lovejoy *et al.*, 1986; Stouffer *et al.*, 2008). Assuming that the
435 surrounding matrix is hostile to bird movements and precludes colonization, Ferraz *et al.*
436 (2003) estimated that a 1000-fold increase in fragment area would be needed to slow the rate
437 of local species extinctions by 10-fold. Even a fragment of 10,000 ha in area would be
438 expected to lose a substantial part of its bird fauna within one century (Ferraz *et al.*, 2003).
439 Similarly, long-term mark-recapture studies suggest that very large fragments will be needed
440 to maintain fully intact assemblages of certain faunal groups, such as ant-following birds,
441 which forage over large areas of forest (Van Houtan *et al.*, 2007).

442

443 **VI. EDGE EFFECTS**

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

448

449 **(1) Forest hydrology**

450 The hydrological regimes of fragmented landscapes differ markedly from those of intact
451 forest (Kapos, 1989; Kapos *et al.*, 1993). Pastures or crops surrounding fragments have much
452 lower rates of evapotranspiration than do forests, causing such areas to be hotter and drier
453 than forests (Camargo & Kapos, 1995). Field observations and heat-flux simulations suggest
454 that desiccating conditions can penetrate up to 100-200 m into fragments from adjoining
455 clearings (Malcolm, 1998; Didham & Lawton, 1999). Further, streams in fragmented
456 landscapes experience greater temporal variation in flow rate than do those in forests, because
457 clearings surrounding fragments have less evapotranspiration and rainfall interception and
458 absorption by vegetation (Trancoso, 2008). Rapid runoff promotes localized flooding in the
459 wet season and stream failure in the dry season, with potentially important impacts on aquatic
460 invertebrates (Nessimian *et al.*, 2008) and fish assemblages.

461

462 **(2) Striking diversity of edge effects**

463 At least over the first 3-4 decades after isolation, edge effects have been among the most
464 important drivers of ecological change in the BDFFP fragments. The distance to which
465 different edge effects penetrate into fragments varies widely, ranging from 10-300 m at the
466 BDFFP (Laurance *et al.*, 2002) and considerably further (at least 2-3 km) in areas of the
467 Amazon where edge-related fires are common (Cochrane & Laurance, 2002, 2008; Briant *et*
468 *al.*, 2010).

469 Edge phenomena are remarkably diverse (Fig. 7). They include increased desiccation
470 stress, wind shear and wind turbulence that sharply elevate rates of tree mortality and damage
471 (Laurance *et al.*, 1997, 1998a). These in turn cause wide-ranging alterations in the community
472 composition of trees (Laurance *et al.*, 2000, 2006a, 2006b) and lianas (Laurance *et al.*,
473 2001b). Such stresses may also reduce germination (Bruna 1999) and establishment (Uriarte

474 *et al.*, 2010) of shade-tolerant plant species in fragments, leading to dramatic changes in the
475 composition and abundance of tree seedlings (Benítez-Malvido, 1998; Benítez-Malvido &
476 Martínez-Ramos, 2003a).

477 Many animal groups, such as numerous bees, wasps, flies (Fowler *et al.*, 1993),
478 beetles (Didham *et al.*, 1998a, 1998b), ants (Carvalho & Vasconcelos, 1999), butterflies
479 (Brown & Hutchings, 1997), understory birds (Quintela, 1985; S. G. Laurance, 2004) and
480 gleaning predatory bats (Rocha, 2016; Rocha *et al.*, 2016), decline in abundance near forest
481 edges. Edge habitats of continuous forest and larger fragments (100 ha) have fewer species of
482 bats and higher levels of dominance by a few common species (Rocha, 2016; Rocha *et al.*,
483 2016). Negative edge effects are apparent even along narrow forest roads (20-30 m width).
484 Among understory birds, for example, five of eight foraging guilds declined significantly in
485 abundance within 70 m of narrow roads, evidently in response to increased light and forest
486 disturbance near road edges (Laurance, 2004b).

487 Some groups of organisms remain stable or even increase in abundance near edges.
488 Leaf bryophytes (Zartman & Nascimento, 2006), wandering spiders (*Ctenus* spp; Rego *et al.*,
489 2007; Mestre & Gasnier, 2008) and many frogs (Gascon, 1993) displayed no significant
490 response to edges. Organisms that favor forest ecotones or disturbances, such as many species
491 of gap-favoring and frugivorous birds (Laurance, 2004b), hummingbirds (Stouffer &
492 Bierregaard, 1995a), frugivorous bats that exploit early successional plants (Sampaio, 2000,
493 Rocha *et al.*, 2016), light-loving butterflies (Leidner *et al.*, 2010) and fast-growing lianas
494 (Laurance *et al.*, 2001b), increase in abundance near edges, sometimes dramatically.

495

496 **(3) Impacts of multiple edges**

497 BDFFP research demonstrates that plots near two or more edges suffer more severe edge
498 effects than do those near just one edge (Fig. 8). This conclusion is supported by studies of

499 edge-related changes in forest microclimate (Kapos, 1989; Malcolm, 1998), vegetation
500 structure (Malcolm 1994), tree mortality (Laurance *et al.*, 2006a), abundance and species
501 richness of tree seedlings (Benítez-Malvido, 1998; Benítez-Malvido & Martinez-Ramos,
502 2003a), liana abundance (Laurance *et al.*, 2001b) and the density and diversity of disturbance-
503 loving pioneer trees (Laurance *et al.*, 2006a, 2006b, 2007). The additive effects of nearby
504 edges probably help to explain why small (<10 ha) or irregularly shaped forest remnants are
505 often so severely altered by forest fragmentation (Zartman, 2003; Laurance *et al.*, 2006a).
506 Some fauna are likewise sensitive to multiple edges. For instance, the number of nearby forest
507 edges was found to be an important predictor of local bat abundance (Rocha *et al.*, 2016).

508

509 **(4) Effects of edge age and adjoining vegetation**

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

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

522 Microclimatic changes (Didham & Lawton, 1999), tree mortality (Mesquita *et al.*, 1999) and
523 edge avoidance by understory birds (Develey & Stouffer, 2001; Laurance, 2004b, S. G.

524 Laurance *et al.*, 2004) and gleaning animal-eating bats (Sampaio, 2000; Meyer *et al.*, 2016;
525 Rocha, 2016; Rocha *et al.*, 2016) are all reduced when forest edges are buffered by adjoining
526 regrowth forest, relative to edges bordered by cattle pastures. Mature regrowth can be
527 particularly benign for some fauna; for example, diverse assemblages of aerial-feeding
528 insectivorous bats showed similar activity patterns in primary forest and in adjoining 30-year-
529 old secondary forests (Navarro, 2014).

530

531 **VII. FOREST ISOLATION AND THE MATRIX**

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

536

537 **(1) Matrix structure and composition**

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

545 The regenerating forest in the matrix now permits fragments as small as 100 ha to
546 support bird and bat assemblages similar to those in continuous forest (Wolfe *et al.*, 2015;
547 Rocha *et al.*, 2016). For bats, matrix recovery has resulted in marked compositional changes
548 in fragments and shifts in the rank order of the most abundant species (Meyer *et al.*, 2016;

549 Rocha, 2016). Gleaning animal-eating bats, which formerly occurred at low abundances in
550 fragments (Sampaio, 2000) and young regrowth (Bobrowiec & Gribel, 2010), have increased
551 over the past 10-15 years as the surrounding regrowth has expanded and matured (Meyer *et*
552 *al.*, 2016; Rocha, 2016; Rocha *et al.*, 2016). A number of other species, including certain
553 forest spiders (Mestre & Gasnier, 2008), dung beetles (Quintero & Roslin, 2005), euglossine
554 bees (Becker *et al.*, 1991) and monkeys such as red howlers, bearded sakis and brown
555 capuchins (Boyle & Smith, 2010a), have also recolonized some of the fragments.

556 The surrounding matrix also has a strong effect on plant communities in fragments by
557 reducing edge effects (see above), influencing the movements of pollinators (Dick, 2001;
558 Dick *et al.*, 2003) and seed dispersers (Jorge, 2008; Bobrowiec & Gribel, 2010; Boyle &
559 Smith, 2010a) and strongly influencing the seed rain that arrives in fragments. For instance,
560 pioneer trees regenerating in fragments differed strikingly in composition between fragments
561 surrounded by *Cecropia*-dominated regrowth and those encircled by *Vismia*-dominated
562 regrowth (Nascimento *et al.*, 2006). In this way plant and animal communities in fragments
563 may increasingly tend to mirror the composition of the surrounding matrix (Laurance *et al.*,
564 2006a, 2006b), a phenomenon observed elsewhere in the tropics (Janzen, 1983; Diamond *et*
565 *al.*, 1987; Laurance, 1991).

566

567 **(2) Factors influencing the matrix**

568 Land-use history is a key driver of secondary succession in Amazonia, resulting in distinct
569 trajectories of regeneration that differ in structure, composition, biomass and dynamics
570 (Mesquita *et al.*, 1999; Williamson *et al.*, 2014). The recurring use of fire to maintain pastures
571 reduces regenerative potential, leaving lands dominated by scrubby trees in the genus *Vismia*,
572 which are prodigious resprouters that stall succession by inhibiting growth of other tree
573 species (Jakovac *et al.*, 2015). Compared to slash-and-burn agriculture, vegetation biomass

574 recovers much more slowly in lands previously used as pasture, which is currently the
575 predominant land use in Amazonia (Wandelli & Fearnside, 2015). However, where land and
576 fire use has been less intensive, a more diverse vegetation dominated by the genus *Cecropia*
577 fosters relatively rapid plant succession (Longworth *et al.*, 2014).

578 In regenerating forests, plant density and species diversity both decline with distance
579 from primary forest, and also differ between *Vismia*- and *Cecropia*-dominated regrowth.
580 These differences were initially attributed to differential seed-dispersal limitations (Mesquita
581 *et al.*, 2001; Puerta, 2002). However, it now appears that the seed rains are similar in both
582 types of regrowth and are strongly dominated by pioneer species (Wieland *et al.*, 2011). This
583 suggests that birds and bats, the primary seed dispersers, are feeding mainly in regrowth and
584 rarely transporting primary-forest seeds into the regrowth. Instead, the legacy of past land use
585 endures as abandoned pastures—especially those dominated by *Vismia*—remain depauperate
586 for at least a quarter of a century (Massoca *et al.*, 2013; Mesquita *et al.*, 2015).

587

588 **(3) Narrow forest clearings**

589 Many Amazonian species avoid forest clearings, even those that are surprisingly narrow. A
590 number of understory insectivorous birds exhibit depressed abundances near roads of just 20-
591 40 m width (S. G. Laurance, 2004b) and their rate of movements across those roads is
592 strongly reduced (S. G. Laurance *et al.*, 2004). Experimental translocations of resident adult
593 birds reveal that such species can be compelled to cross a highway (50-75 m width) but not a
594 small pasture (250 m width) to return to their territory (Laurance & Gomez, 2005).

595 Individuals of some other vulnerable bird species, however, have traversed clearings to escape
596 from small fragments to larger forest areas (Harper, 1989; Van Houtan *et al.*, 2007). Captures
597 of understory birds declined dramatically in fragments when a 100 m-wide swath of regrowth
598 forest was cleared around them, suggesting that species willing to traverse regrowth had a

599 strong aversion to such clearings (Stouffer *et al.*, 2006).

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

606

607 **VIII. DYNAMICS OF FOREST FRAGMENTS**

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

610

611 **(1) Rare disturbances**

612 Rare events such as droughts, local flooding and windstorms have strongly influenced the
613 ecology of BDFFP fragments. Rates of tree mortality rose abruptly in both fragmented
614 (Laurance *et al.*, 2001c) and intact forests (Williamson *et al.*, 2000) in the year after the
615 intense 1997 El Niño drought and heavy 1998 La Niña rains. Such pulses of tree death can
616 drive changes in the floristic composition and carbon storage of fragments (Laurance *et al.*,
617 2007). Leaf-shedding by drought-stressed trees also increases markedly during droughts,
618 especially within ~60 m of forest edges, increasing the quantity of leaf litter on the forest floor
619 (Laurance & Williamson, 2001). Such dense litter elevates the susceptibility of fragments to
620 intrusion by destructive surface fires (Cochrane & Laurance, 2002, 2008) and can slow forest
621 regeneration by suppressing seed germination and seedling establishment (Bentos *et al.*,
622 2013). Local flooding caused tree mortality in one of our plots to rise five-fold (S. G.
623 Laurance *et al.*, 2009), a pattern also observed in other low-lying plateaus and microsites in

624 the BDFFP study area (Mori & Becker, 1991).

625 Intense windblasts from convectional thunderstorms have occasionally flattened parts
626 of the BDFFP landscape and caused intense forest damage and tree mortality, especially in
627 the fragments. Fragments in the easternmost cattle ranch at the BDFFP have had substantially
628 lower rates of tree mortality than those in the other two ranches (Fig. 1), because the former
629 have so far escaped major windstorms (Laurance *et al.*, 2007). These differences have
630 strongly influenced the rate and trajectory of change in tree-community composition in
631 fragments (Laurance *et al.*, 2006b). Hence, by altering forest dynamics, composition,
632 structure and carbon storage, rare disturbances have left an enduring imprint on the ecology of
633 fragmented forests.

634

635 **(2) Hyperdynamism**

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

644 Many examples of hyperdynamism have been observed in the BDFFP fragments.
645 Some butterfly species have experienced dramatic population irruptions in response to a
646 proliferation of their favored host plants along fragment margins (Brown & Hutchings, 1997),
647 and butterfly communities in general are hyperdynamic in fragments (Fig. 9)(Leidner *et al.*,
648 2010). Bat assemblages also show atypically high species turnover (Meyer *et al.*, 2016), as do

649 understory birds (Stouffer *et al.*, 2008, 2011), especially in smaller fragments. Streamflows
650 are far more variable in fragmented than forested watersheds (Trancoso, 2008). Rates of tree
651 mortality and recruitment are chronically elevated in fragments (Laurance *et al.*, 1998a,
652 1998b), with major mortality pulses associated with rare disturbances (see above). These
653 pulses of tree death followed by accelerated recruitment of young trees lead to large
654 fluctuations in the number of trees per plot (Fig. 10). Further, tree species disappear and turn
655 over far more rapidly in fragments than intact forest, especially within ~100 m of forest
656 margins (Laurance *et al.*, 2006b). These and many other instabilities plague small, dwindling
657 populations in the BDFFP fragments.

658

659 **(3) Diverging trajectories of fragments**

660 A key insight from our long-term experiment is that different fragmented landscapes— even
661 those as alike as the three large cattle ranches in the BDFFP, which have very similar forests,
662 soils, climate, fragment ages and land-use histories—can diverge to a surprising degree in
663 species composition and dynamics. Although spanning just a few dozen kilometers, the three
664 ranches are following unexpectedly different trajectories of change.

665 At the outset, small initial differences among the ranches multiplied into much bigger
666 differences. Parts of the western and eastern ranches were cleared in 1983, when an early wet
667 season prevented burning of the felled forest. Tall, floristically diverse *Cecropia*-dominated
668 regrowth quickly developed in these areas, whereas areas cleared with fire in the years just
669 before or after became cattle pastures or, eventually, scrubby *Vismia*-dominated regrowth
670 (Williamson & Mesquita, 2001). For example, these different successional trajectories led to
671 distinct bat assemblages: *Cecropia*-dominated regrowth retained a considerably higher
672 fraction of the forest-specialist bat species found in continuous forest, compared to *Vismia*
673 regrowth (Bobrowiec & Gribel, 2010). As discussed above, the differing matrix vegetation

674 strongly affected the dynamics of plant and animal communities in the nearby fragments.
675 These differences were magnified by subsequent windstorms, which heavily damaged most
676 fragments in the central and western ranches, yet left fragments in the eastern ranch
677 unscathed. Even identically sized fragments in the three ranches have had remarkably
678 different dynamics and trajectories of compositional change (Laurance *et al.*, 2007).
679 The apparently acute sensitivity of fragments to local landscape and weather dynamics—even
680 within a study area as initially homogeneous as ours—prompted us to propose a “landscape-
681 divergence hypothesis” (Laurance *et al.*, 2007). We argue that fragments within the same
682 landscape will tend to have similar dynamics and trajectories of change in species
683 composition, which will often differ from those in other landscapes. Over time, this process
684 will tend to homogenize fragments within the same landscape, and promote ecological
685 divergence among fragments in different landscapes. Evidence for this hypothesis is provided
686 by tree communities in our fragments, which appear to be diverging in composition among
687 the three cattle ranches (Fig. 11). Pioneer and opportunistic trees are increasing in all
688 fragments, but the composition of these secondary plant species and their rates of increase
689 differ markedly among the three ranches (Scariot, 2001; Laurance *et al.*, 2006a,
690 2007; Nascimento *et al.*, 2006). A similar pattern of biotic divergence is evident in the
691 secondary-forest bat assemblages found at the different ranches (Bobrowiec & Gribel, 2010).

692

693 **(4) Ecological distortions**

694 Many ecological interactions are altered in fragmented landscapes. For instance, in mixed-
695 species bird flocks, interspecific interactions are lower, both in number and frequency, in 10-
696 ha fragments and the secondary forest matrix than in more preserved habitats (continuous
697 forest and 100-ha fragments), resulting in reduced flock cohesion and stability (Mokross *et*
698 *al.*, 2014). Fragmented communities can pass through unstable transitional states that may not

699 otherwise occur in nature (Terborgh *et al.*, 2001; Gibson *et al.*, 2013). Moreover, species at
700 higher trophic levels, such as predators and parasites, are often more vulnerable to
701 fragmentation than are herbivores, thereby altering the structure and functioning of food webs
702 (Didham *et al.*, 1998b; Terborgh *et al.*, 2001).

703 BDFFP findings suggest that even forest fragments that are un hunted, unlogged and
704 unburned have reduced densities of key mammalian seed dispersers. As a result, seed
705 dispersal for the endemic, mammal-dispersed tree *Duckeodendron cestroides* was far lower in
706 fragments, with just ~5% of the number of seeds being dispersed >10 m away from parent
707 trees than in intact forest (Cramer *et al.*, 2007a). Leaf herbivory appears reduced in fragments,
708 possibly because of lower immigration of insect herbivores (Fáveri *et al.*, 2008). Dung beetles
709 exhibit changes in biomass and guild structure in fragments (Radtke *et al.*, 2008) that could
710 alter rates of forest nutrient cycling and secondary seed dispersal (Klein, 1989; Andresen,
711 2003). Exotic Africanized honeybees, a generalist pollinator, are abundant in matrix and edge
712 habitats and can alter pollination success and gene flow for some tree species (Dick, 2001;
713 Dick *et al.*, 2003). A bewildering variety of ecological distortions can pervade fragmented
714 habitats, and a challenge for conservation biologists is to identify those of greatest importance
715 and generality.

716

717 **(5) Forest-carbon dynamics**

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

722 A suite of interrelated changes affects carbon stocks in fragmented forests. Many trees
723 die near forest edges (Laurance *et al.*, 1997, 1998a), including an alarmingly high proportion

724 of large (≥ 60 cm dbh) canopy and emergent trees that store a large fraction of the total forest
725 carbon (Laurance *et al.*, 2000). Compared to the mature-phase trees they replace, fast-growing
726 pioneer trees and lianas that proliferate in fragments are smaller and have lower wood density
727 and thereby sequester much less carbon (Laurance *et al.*, 2001b, 2006a). Based on current
728 rates of forest fragmentation, the edge-related loss of carbon storage in the tropics could
729 produce tens of millions of tons of atmospheric carbon emissions annually, above and beyond
730 that caused by deforestation per se (Laurance *et al.*, 1998c; Groeneveld *et al.*, 2009).

731 In addition, biomass is being fundamentally redistributed in fragmented forests (Fig.
732 12). Less biomass is stored in large, densely wooded old-growth trees and more in fast-
733 growing pioneer trees, disturbance-loving lianas, woody debris and leaf litter (Sizer *et al.*,
734 2000; Nascimento & Laurance, 2004; Vasconcelos & Luizão, 2004). Soil carbon also
735 increases as the abundant dead biomass in fragments decomposes (Barros & Fearnside, 2016).
736 Finally, carbon cycling accelerates. The large, old-growth trees that predominate in intact
737 forests can live for many centuries or even millennia (Chambers *et al.*, 1998; Laurance *et al.*,
738 2004b), sequestering carbon for long periods of time. However, the residence time of carbon
739 in early successional trees, vines and necromass (wood debris, litter), which proliferate in
740 fragments, is far shorter (Nascimento & Laurance, 2004). Other biochemical cycles, such as
741 those affecting key nutrients such as phosphorus (Sizer *et al.*, 2000) and calcium
742 (Vasconcelos & Luizão, 2004), might also be altered in fragmented forests, given the striking
743 changes in biomass dynamics, hydrology and thermal regimes they experience there.

744

745 **IX. SPECIES RESPONSES TO FRAGMENTATION**

746 Individual species and ecological groups can differ greatly in their responses to habitat
747 fragmentation. Some decline or disappear, others remain roughly stable and yet others
748 increase, sometimes dramatically. Understanding how and why different species vary so

749 dramatically in their responses has been a major goal of conservation researchers. Here we
750 underscore key conclusions from the BDFFP.

751

752 **(1) Non-random extinctions**

753 Local extinctions of species in the BDFFP fragments have occurred in a largely predictable
754 sequence, with certain species being consistently more vulnerable than others. Among birds,
755 various species of understory insectivores, including army ant-followers, solitary species,
756 terrestrial foragers and obligate mixed-flock members, are most susceptible to fragmentation.
757 Others, including edge/gap species, insectivores that use mixed flocks facultatively,
758 hummingbirds and many frugivores, are far less vulnerable (Antongiovanni & Metzger, 2005;
759 Stouffer *et al.*, 2006, 2008, 2011).

760 In a similar vein, among bats, gleaning predators are consistently the most vulnerable
761 species whereas many frugivores respond positively to fragmentation and other types of forest
762 disturbance (Sampaio, 2000; Bobrowiec & Gribel, 2010; Farneda *et al.*, 2015; Rocha, 2016;
763 Rocha *et al.*, 2016). Many animal-eating bat species rarely persist in small (<100 ha)
764 fragments and in the secondary-forest matrix, reflecting trait-mediated environmental filters
765 that selectively benefit smaller fruit- and nectar-feeding species (Farneda *et al.*, 2015).
766 Primates exhibit similarly predictable patterns of species loss, with wide-ranging frugivores,
767 especially the black spider-monkey, being most vulnerable (Boyle & Smith, 2010a). Hence,
768 local extinctions in fragments follow a foreseeable pattern, with species assemblages in
769 smaller fragments rapidly forming a nested subset of those in larger fragments (Stouffer *et al.*,
770 2008). Random demographic and genetic processes may help to drive tiny populations into
771 oblivion, but the species that reach this precarious threshold are far from random.

772

773

774 **(2) Non-neutral extinctions**

775 An important corollary of nonrandom species loss is that fragmented forests are not neutral.
776 Neutral theory (Hubbell, 2001) assumes that species in diverse, space-limited communities,
777 such as tropical trees, are roughly equivalent in competitive and demographic terms. Making
778 these assumptions allows one to make predictions about phenomena such as species-area
779 curves, the relative abundances of species in communities, and the rate of species turnover in
780 space. Hubbell (2001) emphasizes the potential utility of neutral theory for predicting
781 community responses to habitat fragmentation: for isolated communities, locally abundant
782 species should be least extinction prone, with rare species being lost more frequently from
783 random demographic processes. Over time, fragments should become dominated by the
784 initially abundant species, with rare species gradually vanishing; other ecological traits of
785 species are considered unimportant.

786 Gilbert *et al.* (2006) tested the efficacy of neutral theory for predicting changes in tree
787 communities at the BDFFP. Neutral theory effectively predicted the rate of local extinctions
788 of species from plots in fragmented and intact forest, as a function of the local diversity and
789 mortality rate of trees. However, in most fragments, the observed rate of change in species
790 composition was 2-6 times faster than predicted by the theory. Moreover, the theory was
791 wildly erroneous in predicting which species are most prone to local extinction. Rather than
792 becoming increasingly dominated by initially common species, fragments in the BDFFP
793 landscape have experienced striking increases over time in disturbance-loving pioneer species
794 (Fig. 13) (Laurance *et al.*, 2006a), which were initially rare when the fragments were created.
795 As a model for predicting community responses to habitat fragmentation, neutral theory
796 clearly failed, demonstrating that ecological differences among species strongly influence
797 their responses to fragmentation.

798

799 **(3) Key correlates of animal vulnerability**

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

807 The second key trait for fauna is their tolerance of matrix habitats (Gascon *et al.*,
808 1999), which comprises regrowth forest and cattle pastures in the BDFFP landscape.
809 Populations of species that entirely avoid the matrix will be demographically and genetically
810 isolated in fragments, and therefore vulnerable to local extinction, whereas those that tolerate
811 or exploit the matrix often persist (Laurance, 1991; Malcolm, 1997; Antongiovanni &
812 Metzger, 2005; Ferraz *et al.*, 2007; Bobrowiec & Gribel, 2010).

813 At least among terrestrial vertebrates, matrix use is positively associated with
814 tolerance of edge habitats (Laurance, 2004b; Farneda *et al.*, 2015), an ability to traverse small
815 clearings (S. G. Laurance *et al.*, 2004; S. G. Laurance & Gomez, 2005), behavioral flexibility
816 (Neckel-Oliveira & Gascon, 2006; Stouffer *et al.*, 2006; Van Houtan *et al.*, 2006; Boyle &
817 Smith, 2010b) and a capacity to feed on early successional plants that thrive in the matrix
818 (Farneda *et al.*, 2015; Rocha *et al.*, 2016; Meyer *et al.*, 2016). Within particular animal
819 groups, such as beetles or small mammals, traits such as body size and natural abundance are
820 generally poor or inconsistent predictors of vulnerability (Laurance, 1991; Didham *et al.*,
821 1998a; Jorge, 2008; Boyle & Smith, 2010a; but see Jorge *et al.*, 2015).

822

823

824 **(4) Key correlates of plant vulnerability**

825 Among plants, a different suite of factors is associated with vulnerability to fragmentation.
826 Because fragments suffer chronically elevated tree mortality, faster-growing pioneer trees and
827 lianas that favor treefall gaps are favored at the expense of slower-growing old-growth trees
828 (Laurance *et al.*, 2006a, 2006b). Pioneer species often flourish in the matrix and produce
829 abundant small fruits that can be carried into fragments by frugivorous birds and bats that
830 move between the matrix and nearby fragments (Sampaio, 2000; Nascimento *et al.*, 2006;
831 Rocha *et al.*, 2016). Especially vulnerable in fragments are the diverse assemblages of smaller
832 subcanopy trees that are physiologically specialized for growth and reproduction in dark,
833 humid, forest-interior conditions (Laurance *et al.*, 2006b). Tree species that have obligate
834 outbreeding systems, rely on animal seed dispersers or have relatively large, mammal-
835 dispersed seeds also appear vulnerable (Laurance *et al.*, 2006b; Cramer *et al.*, 2007b).

836 These combinations of traits suggest that plant communities in fragmented forests are
837 structured primarily by chronic disturbances and microclimatic stresses, and possibly also by
838 alterations in animal pollinator and seed-disperser communities. For long-lived plants such as
839 many mature-phase trees, demographic models suggest that factors that reduce adult survival
840 and growth—such as recurring wind disturbance and edge-related microclimatic stresses—
841 have a strong negative influence on population growth (Lindenmayer & Laurance, 2016).

842

843 **X. HORIZONS FOR NEW RESEARCH**

844 Although BDFFP researchers have attacked a diversity of research themes, some topics
845 remain poorly explored or enigmatic. For instance, there has been relatively little work to date
846 on the effects of fragmentation on the phylogenetic and functional composition of forests (but
847 see Didham *et al.*, 1998b; Andresen, 2003). A study that examined changes in the
848 phylogenetic structure of trees at the BDFFP concluded that most study sites—including

849 small and large fragments as well as intact-forest plots—exhibited a progressive decline over
850 time in phylogenetic diversity (Fig. 14)(Santos *et al.*, 2014). This evidently occurred because
851 tree genera that have increased in abundance across the study area are more closely related
852 phylogenetically than are those that have declined. Do such changes reflect community-wide
853 responses to large-scale drivers, such as global-change phenomena (Laurance *et al.*, 2004b),
854 shifts in regional rainfall (S. G. Laurance *et al.*, 2009), or some other widespread event?
855 Further study is needed.

856 Similarly, ecological interactions such as pollination and seed dispersal have been
857 poorly studied at the BDFFP. Changes in pollinator assemblages (Dick, 2001; Dick *et al.*,
858 2003) might be expected to alter plant pollination, seed set, and gene flow among plants, but
859 such effects are largely unknown. Could shifts in the abundance of old-growth tree species—
860 such the decline of obligate outbreeders and species that require animal seed dispersers
861 (Laurance *et al.*, 2006b)—reflect losses of key fauna in fragmented forests? Other ecological
862 interactions, such as predator-prey, host-pathogen, and plant-mycorrhizal relationships, are
863 virtually unstudied (but see Benitez-Malvido *et al.*, 1999).

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

873 Finally, there is considerable scope to use modeling approaches with BDFFP data to

874 generate long-term (≥ 100 -year) projections about the fate of fragmented forests. One such
875 study, using a novel neural-network approach, suggested that tree communities in forest
876 fragments will become increasingly dominated by early successional species but that seed rain
877 from forest interiors will continue to maintain a mix of pioneer and old-growth species, even
878 near heavily disturbed forest edges (Ewers *et al.*, 2017). Another modeling study used data on
879 elevated tree mortality and floristic changes from the BDFFP to make projections of long-
880 term carbon-storage declines and shifts in plant-functional groups in fragmented forests
881 (Groeneveld *et al.*, 2009).

882

883 **XI. GENERAL LESSONS**

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

886

887 **(1) Values of long-term research**

888 Many insights from the BDFFP would have been impossible in a shorter-term study. The
889 exceptional vulnerability of large trees to fragmentation (Laurance *et al.*, 2000) only became
890 apparent after two decades of fragment isolation. Likewise, the importance of ephemeral
891 events such as El Niño droughts (Williamson *et al.*, 2000; Laurance *et al.*, 2001c) and major
892 windstorms (Laurance *et al.*, 2007) would not have been captured in a less-enduring project.
893 Many other key phenomena, such as the kinetics of species loss in fragments (Ferraz *et al.*,
894 2003), the strong effects of matrix dynamics on fragmented bird and bat assemblages
895 (Antongiovanni & Metzger, 2005; Stouffer *et al.*, 2006, 2011; Meyer *et al.*, 2016; Rocha,
896 2016), the divergence of fragments in different landscapes (Laurance *et al.*, 2007) and the
897 effects of fragmentation on rare or long-lived species (Benítez-Malvido & Martinez-Ramos,
898 2003b; Ferraz *et al.*, 2007) and alternative successional pathways (Mesquita *et al.*, 2015), are

899 only becoming understood after decades of effort.

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

911

912 **(2) Training is vital**

913 Among the most enduring legacies of the BDFFP has been its leading role in training students
914 and environmental decision-makers. To date, the project has yielded over 700 technical
915 publications (<http://pdbff.inpa.gov.br>) and more than 200 Ph.D. and M.Sc. theses. It has also
916 trained more than 700 graduate students and conservation professionals in sponsored courses,
917 and hosted over 1,000 student interns to date. Many of those who have benefited from BDFFP
918 training are from Brazil or other Latin American nations. Among these are numerous
919 individuals who have now advanced professionally to hold important positions in government
920 agencies, universities and nongovernmental conservation organizations.

921 These training programs have had manifold benefits. For example, former BDFFP
922 students and researchers have led opposition to a Brazilian government scheme to settle
923 colonists in and around the BDFFP study area—an initiative that could bisect the Central

924 Amazonian Conservation Corridor, a complex of protected and indigenous lands that is one of
925 the most important conservation networks in Amazonia (Laurance & Luizão, 2007). BDFFP
926 trainees have also been leaders in documenting the impacts of major highways and
927 infrastructure projects that are crisscrossing the Amazon (e.g. Laurance et al., 2001a;
928 Fearnside & Graça, 2006) and that could promote large-scale human migration and forest
929 disruption (Barni *et al.*, 2015). A near-term threat to the BDFFP is a nearly completed
930 highway (BR-319) that will link the ‘arc of deforestation’ in southern Amazonia to Manaus
931 and the BDFFP, potentially promoting large-scale invasions or settlement of the study area
932 (Fearnside, 2015).

933

934 **XII. LESSONS FOR CONSERVATION**

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

937

938 **(1) The BDFFP is a best-case scenario**

939 Although the BDFFP’s forest fragments are experiencing a wide array of ecological
940 alterations, it is important to emphasize that it is a controlled experiment. The fragments are
941 square, not irregular, in shape. They are isolated by clearings of only 80-650 m width from
942 large tracts of surrounding mature forest. They are embedded within a relatively benign
943 matrix dominated by forest regrowth, not harsher anthropogenic habitats. In addition, these
944 fragments are largely free from ancillary threats, such as selective logging, wildfires and
945 overhunting, which plague many fragmented landscapes and wildlife populations elsewhere
946 in the tropics (e.g. Moura *et al.*, 2014). Such threats can interact additively or synergistically
947 with fragmentation, creating even greater perils for the rainforest biota (Laurance &
948 Cochrane, 2001; Michalski & Peres, 2005; Brook *et al.*, 2008). For these reasons, the effects

949 of fragmentation at the BDFFP are clearly modest, relative to many human-dominated
950 landscapes elsewhere in the tropics.

951

952 **(2) Reserves should be large and numerous**

953 A key conclusion from BDFFP research is that nature reserves in Amazonia should ideally be
954 very large—on the order of thousands to tens of thousands of square kilometers in area
955 (Laurance, 2005; Peres, 2005). Only at this size will they be likely to maintain natural
956 ecological processes and sustain viable populations of the many rare and patchily distributed
957 species in the region (Ferraz *et al.*, 2007; Radtke *et al.*, 2008). Such large reserves will also
958 provide greater resilience from rare calamities such as droughts (Feldpausch *et al.*, 2016) and
959 intense storms (Laurance *et al.*, 2007), facilitate persistence of terrestrial and aquatic animals
960 that migrate seasonally (Bührnheim & Fernandes, 2003) and buffer the reserve from external
961 threats such as fires, large-scale forest desiccation and human encroachment (Cochrane &
962 Laurance, 2002; Briant *et al.*, 2010).

963 Large reserves will also maximize forest carbon storage (Laurance *et al.*, 1997, 1998c)
964 and provide greater resilience to future climatic and atmospheric changes (Laurance, 2005,
965 2016; Peres, 2005). Further, on the ancient, nutrient-starved soils of central and eastern
966 Amazonia, low plant productivity translates into low population densities of many animals,
967 especially as one moves up the food chain, so reserves must be proportionately larger to
968 harbor viable populations of these species (Radtke *et al.*, 2008; Deichmann *et al.*, 2011,
969 2012). The recent observation that within-species genetic variation of terrestrial vertebrates is
970 higher in wilderness areas than in human-disturbed habitats further underscores the value of
971 large nature reserves for sustaining biological diversity and the capacity of species to adapt to
972 future environmental insults (Miraldo *et al.*, 2016).

973 Beyond large size, nature reserves in Amazonia should also be numerous and stratified

974 across major river basins and climatic and edaphic gradients in order to preserve
975 biophysically distinctive ecoregions (Olson *et al.*, 2001; Tscharnke *et al.*, 2012) and locally
976 endemic species (Bierregaard *et al.*, 2001; Laurance, 2007). In addition, the core areas of
977 nature reserves should ideally be free of roads, which facilitate human encroachment and
978 hunting, internally fragment wildlife populations and promote invasions of exotic species
979 (Laurance *et al.*, 2009).

980

981 **(3) No fragment is unimportant**

982 Tropical forests are being rapidly lost and fragmented (e.g. Myers *et al.*, 2000; Sloan *et al.*,
983 2014), and a key question is whether smaller (e.g. <10 ha) forest fragments have much value
984 for nature conservation. We assert that there is no such thing as an ‘unimportant’ forest
985 fragment. In heavily fragmented landscapes, protecting remaining forest remnants is highly
986 desirable, as they are likely to be key sources of plant propagules and animal seed dispersers
987 and pollinators (Mesquita *et al.*, 2001; Chazdon *et al.*, 2008). They may also act as stepping
988 stones for animal movements in human-dominated lands (Laurance & Bierregaard, 1997;
989 Lima & Gascon, 1999; Dick *et al.*, 2003). In regions where forest loss is severe, forest
990 fragments could sustain the last surviving populations of locally endemic species,
991 underscoring their potential value for nature conservation (Arroyo-Rodríguez *et al.*, 2009).
992 Finally, the observation that regenerating forests recover floristic diversity far faster in
993 regions where small fragments of primary forest remain than in those lacking such fragments
994 underscores the vital role of retaining even tiny fragments of the original forest (Van Breugel
995 *et al.*, 2013).

996

997 **(4) Wounded landscapes can recover**

998 A further lesson is that fragmented landscapes, if protected from fires and other major

999 disturbances, can begin to recover in just a decade or two. Newly created forest edges tend to
1000 'seal' themselves in a few years, reducing the intensity of deleterious edge effects (Camargo
1001 & Kapos, 1995; Didham & Lawton, 1999; Mesquita *et al.*, 1999). Secondary forests can
1002 develop quite rapidly in the surrounding matrix (Mesquita *et al.*, 2001), especially if soils and
1003 their seedbanks are not depleted by repeated burning and grazing (Ribeiro *et al.*, 2009;
1004 Norden *et al.*, 2011). Secondary forests facilitate movements of many animal species (Gascon
1005 *et al.*, 1999; Powell *et al.*, 2013), allowing them to recolonize fragments from which they had
1006 formerly disappeared (Becker *et al.*, 1991; Quintero & Roslin, 2005; Stouffer *et al.*, 2008;
1007 Bobrowiec & Gribel, 2010; Boyle & Smith, 2010a; Rocha, 2016; Rocha *et al.*, 2016). Species
1008 clinging to survival in fragments can also be rescued from local extinction via the genetic and
1009 demographic contributions of immigrants (Pimm & Jenkins, 2005; Zartman & Nascimento,
1010 2006; Stouffer *et al.*, 2008). Compared to the BDFFP landscape, rates of forest recovery are
1011 probably slower in localities with severe forest loss, but such regions are likely to be of
1012 particular conservation significance and thereby worthy of efforts to reduce their recurring
1013 threats.

1014

1015 **XIII. FRAGMENTATION AND LARGER-SCALE DRIVERS**

1016 **(1) Interacting drivers**

1017 Taken in its entirety, it seems apparent from the large-scale, long-term research effort at the
1018 BDFFP that forest fragments and their biodiversity are being influenced by a variety of local
1019 and larger-scale factors. The intrinsic attributes of a fragment, such as its size, shape and
1020 degree of isolation from intact forest, are unquestionably important. However, these attributes
1021 are clearly modified by the features of the surrounding landscape and its dynamics over time.
1022 Such landscape features can influence the nature and magnitude of edge effects in fragments
1023 (Fig. 7), the permeability of the matrix for faunal movements, the composition of the seed

1024 rain entering fragments, the likelihood of destructive surface fires penetrating into fragments,
1025 and the intensity of abiotic forces such as microclimatic changes, wind turbulence and
1026 vegetation breezes (Fig. 3) that in turn can strongly influence fragment biodiversity and
1027 ecosystem processes.

1028 External vicissitudes, such as rare droughts, windstorms and intense rainfall events,
1029 can also leave a lasting imprint. Such phenomena might be influenced both by landscape-
1030 scale features as well as regional and possibly global climatic drivers. More generally, it is
1031 apparent that even intact forests in the BDFFP are experiencing concerted long-term changes
1032 in their composition and dynamics, which seem to reflect increasing forest productivity.
1033 These changes appear broadly consistent with those expected from increasing CO₂
1034 fertilization, although other environmental causes, such as declining cloudiness and increasing
1035 forest insolation, are also plausible. Whatever their causes, it is likely that the suite of changes
1036 observed in Amazonian forest fragments are partly a consequence of drivers operating at
1037 much larger spatial scales.

1038 In some cases, large-scale drivers could exacerbate ecological changes in forest
1039 fragments. For instance, elevated forest dynamics and proliferating lianas could result both
1040 from edge effects in fragments (microclimatic stresses and elevated wind turbulence that kill
1041 many trees) as well as from larger-scale drivers that increase forest productivity and
1042 dynamism while favoring fast-growing plant species (Laurance *et al.*, 2014b). In other cases,
1043 the larger-scale drivers might operate in opposition to local fragmentation effects. For
1044 example, the dramatic ‘biomass collapse’ observed in fragments from the mortality of many
1045 trees (Laurance *et al.*, 1997, 2000) might be partially countered by increasing forest
1046 productivity that in turn promotes faster tree growth—although this is likely to have only a
1047 modest effect given the pronounced loss of large, old-growth trees in fragments and their

1048 replacement by smaller, lighter-wooded trees and vines (Fig. 6) that store much less carbon
1049 (Laurance *et al.*, 2006a, 2006b).

1050 That fragments are being influenced by multiple drivers operating at widely varying
1051 spatial scales underscores serious complications for those seeking to understand and predict
1052 the effects of habitat fragmentation. Such drivers could interact in complex and potentially
1053 synergistic ways (Laurance & Useche, 2009), and it is virtually impossible to establish
1054 reliable experimental controls for global phenomena that may be operating everywhere
1055 (Laurance *et al.*, 2014b). Indeed, it is quite possible that even the most remote and seemingly
1056 pristine regions of the Earth are being influenced by certain global-change phenomena.

1057 A further complicating matter is that even relatively modest differences between
1058 landscapes, such as rare weather events or subtle differences in land-use practices, could
1059 potentially multiply over time into far more pervasive changes. This idea is supported by the
1060 marked differences in trajectories of floristic change in forest fragments in the different cattle
1061 ranches (Fig. 11), even in a landscape as nearly uniform in its soils, climate, vegetation and
1062 land-use history as the BDFFP. This observation leads to the prediction that fragments within
1063 the same landscape will tend to converge in composition and dynamics over time, whereas
1064 those in different landscapes will tend to diverge. That such minor differences can seemingly
1065 provoke large consequences sends a strong note of caution for conservation biologists: it may
1066 be possible to make general predictions about the consequences of habitat fragmentation, but
1067 the interplay of local and larger-scale phenomena could render efforts to make precise local
1068 predictions or draw broad generalizations virtually impossible.

1069

1070 **(2) The Amazon and climate change**

1071 Amazonian forests store roughly 150-200 billion tonnes of carbon in their live biomass
1072 (Malhi *et al.*, 2006, Feldpausch *et al.* 2012), the release of which could seriously hinder

1073 efforts to limit harmful climate change. Beyond this, Amazonian forests play vital roles in
1074 regional and global hydrological regimes, transporting massive quantities of moisture and
1075 heat to higher latitudes (Avisar & Worth, 2006; Nobre *et al.*, 2016). For such reasons,
1076 conserving tropical forests such as the Amazon is likely to have markedly greater benefits for
1077 limiting global warming than would protecting higher-latitude forests (Bala *et al.*, 2007).

1078 Efforts to sustain the Amazon as a viable biophysical system can be guided by current
1079 research, which while constrained by uncertainties provides provisional guidelines for
1080 conserving the basin's forests (Nagy *et al.*, 2016). The best available information suggests
1081 that the destruction of more than 30-40% of all Amazonian forests could sharply increase the
1082 chances of a collapse of the crucial water-recycling functions that help to sustain Amazonian
1083 rainfall, especially during the critical dry-season months when forests are most susceptible to
1084 fire (Malhi *et al.*, 2008; Nobre *et al.*, 2016). With current Amazon deforestation levels at
1085 about 20% and large areas of additional forest being degraded by logging and surface fires
1086 and penetrated by new roads, hydroelectric dams, mining and other developments, there is
1087 clearly a real potential for further large-scale forest loss (Laurance *et al.*, 2001a; Fearnside,
1088 2002, 2007, 2016a).

1089 The ongoing fragmentation of the Amazon at a large spatial scale will clearly increase
1090 the chances of both planned and unplanned forest destruction, because fragmented forest
1091 tracts are far more vulnerable than intact forests to predatory logging, wildfires, climate
1092 change and other anthropogenic impacts (Cochrane & Laurance, 2002, 2008). Hence, a
1093 blueprint for conserving the Amazon and thereby reaping its bioclimatic benefits for humanity
1094 and the global ecosystem would be to greatly discourage further large-scale fragmentation
1095 while maintaining large, intact forest blocks that could potentially persist in perpetuity.

1096

1097

1098 **XIV. CONCLUSIONS**

1099 (1) In the heart of the Amazon, a large-scale, 38-year research project has revealed
1100 that the dynamics and community composition of fragmented rainforests cannot be
1101 understood simply as a consequence of local site attributes, such as fragment size or the
1102 surrounding topography. Rather, at least some ecological changes appear to result from
1103 interactions among local features and larger-scale changes occurring at landscape, regional
1104 and even global scales.

1105 (2) In undisturbed forests, observed changes are consistent with those expected from
1106 rising forest productivity, and include accelerating forest dynamics, concerted shifts in tree-
1107 community composition, elevated growth rates for most tree species, and increasing
1108 abundances of disturbance-loving lianas. Plant fertilization from rising atmospheric CO₂
1109 levels might explain these trends, although other causes are not implausible.

1110 (3) In general, ecological changes in forest fragments are strongly influenced by edge
1111 and sample effects, the dynamics of the surrounding matrix of modified vegetation, and rare
1112 disturbances such as droughts and windstorms. Because of their high sensitivity to local
1113 vicissitudes, forest fragments in different landscapes are predicted to diverge over time in
1114 dynamics and community composition, whereas those in the same landscape may converge.

1115 (4) Different species vary markedly in their vulnerability to forest fragmentation.
1116 Animal species that decline in abundance or disappear in forest fragments frequently have
1117 large area requirements and avoid the surrounding matrix, whereas susceptible plant species
1118 fare poorly in disturbed or edge-altered forests and often require vulnerable animal species for
1119 seed dispersal or pollination.

1120 (5) Much of the Amazon overlays nutrient-starved soils where most plant and animal
1121 species are both rare and patchily distributed. This, combined with the increased vulnerability
1122 of fragmented forests to various human disturbances, suggests that Amazonian nature reserves

1123 should be large (ideally $>10^4$ km²) and numerous to ensure their long-term viability. Larger
1124 reserves will also be more resilient to future climatic change and extreme weather events.

1125

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1134

1135 **XVI. REFERENCES**

- 1136 ANDRESEN, E. (2003) Effect of forest fragmentation on dung beetle communities and
1137 functional consequences for plant regeneration. *Ecography* **26**, 87-97.
- 1138 ANTONGIOVANNI, M. & METZGER, J. P. (2005) Influence of matrix habitats on the occurrence
1139 of insectivorous bird species in Amazonian forest fragments. *Biological Conservation*
1140 **122**, 441-451.
- 1141 ARROYO-RODRÍGUEZ, V., PINEDA, E., ESCOBAR, F. & BENÍTEZ-MALVIDO, J. (2009)
1142 Conservation value of small patches to plant species diversity in highly fragmented
1143 landscapes. *Conservation Biology* **23**, 729-739.
- 1144 ASNER, G. P., KNAPP, D., BROADBENT, E., OLIVEIRA, P., KELLER, M. & SILVA, J. (2005)
1145 Selective logging in the Brazilian Amazon. *Science* **310**, 480-482.
- 1146 AVISSAR, R. & LIU, Y. (1996) A three-dimensional numerical study of shallow convective
1147 clouds and precipitation induced by land-surface forcing. *Journal of Geophysical*

- 1148 *Research* **101**, 7499-7518.
- 1149 AVISSAR, R. & SCHMIDT, T. (1998) An evaluation of the scale at which ground-surface heat
1150 flux patchiness affects the convective boundary layer using a large-eddy simulation
1151 model. *Journal of Atmospheric Science* **55**, 2666-2689.
- 1152 AVISSAR, R. & WIRTH, D. (2005) Global hydroclimatological teleconnections resulting from
1153 tropical deforestation. *Journal of Hydrometeorology* **6**, 134-145.
- 1154 AVISSAR, R., SILVA DIAS, P., SILVA DIAS, M. & NOBRE, C. (2002) The Large-scale Biosphere-
1155 Atmosphere Experiment in Amazonia (LBA): Insights and future research needs.
1156 *Journal of Geophysical Research* **107**, doi 10.1029/2002JD002704.
- 1157 BAKER, T. R., PHILLIPS, O. L., MALHI, Y., ALMEIDA, S., ARROYO, L., DI FIORE, A., ERWIN, T.,
1158 HIGUCHI, N., KILLEEN, T., LAURANCE, S. G., LAURANCE, W. F., LEWIS, S. L.,
1159 MONTEAGUDO, A., NEILL, D., NÚÑEZ VARGAS, P. *et al.* (2004) Increasing biomass in
1160 Amazonian forest plots. *Philosophical Transactions of the Royal Society B* **359**, 353-
1161 365.
- 1162 BALA, G., CALDEIRA, K., WICKETT, M, PHILLIPS, T., LOBELL, D. DELIRE, C. & MIRIN, A.
1163 (2007) Combined climate and carbon-cycle effects of large-scale deforestation.
1164 *Proceedings of the National Academy of Sciences USA* **104**, 6550-6555.
- 1165 BALLANTYNE, A. P., ALDEN, C., MILLER, J., TANS, P. & WHITE, J. (2013) Increase in observed
1166 net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* **488**,
1167 70-72.
- 1168 BARLOW, J., PERES, C. A., HENRIQUES, L., STOUFFER, P. C. & WUNDERLE, J. (2006) The
1169 responses of understory birds to forest fragmentation, logging and wildfires: an
1170 Amazonian synthesis. *Biological Conservation* **128**, 182-192.
- 1171 BARROS, H. S. & FEARNSIDE, P. M. (2016) Soil carbon stock changes due to edge effects in
1172 central Amazon forest fragments. *Forest Ecology and Management* **379**, 30-36.

- 1173 BARNI, P. E., FEARNSIDE P. M. & GRAÇA, P. (2015) Simulating deforestation and carbon loss
1174 in Amazonia: impacts in Brazil's Roraima state from reconstructing Highway BR-319
1175 (Manaus-Porto Velho). *Environmental Management* **55**, 259-278.
- 1176 BASSINI, F. & BECKER, P. (1990) Charcoal's occurrence in soil depends on topography in terra
1177 firme forest near Manaus, Brazil. *Biotropica* **22**:420-422.
- 1178 BECKER, P., MOURE, J. B. & PERALTA, F. (1991) More about euglossine bees in Amazonian
1179 forest fragments. *Biotropica* **23**, 586-591.
- 1180 BENÍTEZ-MALVIDO, J. (1998) Impact of forest fragmentation on seedling abundance in a
1181 tropical rain forest. *Conservation Biology* **12**, 380-389.
- 1182 BENÍTEZ-MALVIDO, J. & MARTINEZ-RAMOS, M. (2003a) Influence of edge exposure on tree
1183 seedling species recruitment in tropical rain forest fragments. *Biotropica* **35**, 530-541.
- 1184 BENÍTEZ-MALVIDO, J. & MARTINEZ-RAMOS, M. (2003b) Impact of forest fragmentation on
1185 understory plant species richness in Amazonia. *Conservation Biology* **17**, 389-400.
- 1186 BENITEZ-MALVIDO, J., GARCIA-GUZMAN, G. & KOSSMAN-FERRAZ, I. (1999) Leaf-fungal
1187 incidence and herbivory on tree seedlings in tropical rainforest fragments: an
1188 experimental study. *Biological Conservation* **91**, 143–150.
- 1189 BENTOS, T. V., NASCIMENTO, H. E. M. & WILLIAMSON, G. B. (2013) Tree seedling recruitment
1190 in Amazon secondary forest: Importance of topography and gap micro-site conditions.
1191 *Forest Ecology and Management* **287**, 140-146.
- 1192 BIERREGAARD, R. O., LOVEJOY, T. E., KAPOV, V., DOS SANTOS, A. & HUTCHINGS, R. (1992)
1193 The biological dynamics of tropical rainforest fragments. *BioScience* **42**, 859-866.
- 1194 BIERREGAARD, R. O., GASCON, C., LOVEJOY, T. E. & MESQUITA, R., eds (2001). *Lessons from*
1195 *Amazonia: Ecology and Conservation of a Fragmented Forest*. Yale University Press,
1196 New Haven, Connecticut.
- 1197 BOBROWIEC, P. & GRIBEL, R. (2010) Effects of different secondary vegetation types on bat

- 1198 community composition in Central Amazonia, Brazil. *Animal Conservation* **13**, 204-
1199 216.
- 1200 BOHLMAN, S., LAURANCE, W. F., LAURANCE, S. G., NASCIMENTO, H., FEARNside, P. M. &
1201 ANDRADE, A. (2008) Effects of soils, topography, and geographic distance in
1202 structuring central Amazonian tree communities. *Journal of Vegetation Science* **19**,
1203 863-874.
- 1204 BOYLE, S. A. & SMITH, A. T. (2010a) Can landscape and species characteristics predict
1205 primate presence in forest fragments in the Brazilian Amazon? *Biological*
1206 *Conservation* **143**, 1134-1143.
- 1207 BOYLE, S. A. & SMITH, A. T. (2010b) Behavioral modifications in northern bearded saki
1208 monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia.
1209 *Primates* **51**, 43-51.
- 1210 BRIANT, G., GOND, V. & LAURANCE, S. G. (2010) Habitat fragmentation and the desiccation
1211 of forest canopies: a case study from eastern Amazonia. *Biological Conservation* **143**,
1212 2763-2769.
- 1213 BROADBENT, E., ASNER, G. P., KELLER, M., KNAPP, D., OLIVEIRA, P. & SILVA, J. (2008) Forest
1214 fragmentation and edge effects from deforestation and selective logging in the
1215 Brazilian Amazon. *Biological Conservation* **140**, 142-155.
- 1216 BROOK, B. W., SODHI, N. S. & BRADSHAW, C. J. A. (2008) Synergisms among extinction
1217 drivers under global change. *Trends in Ecology and Evolution* **23**, 453-460.
- 1218 BROWN, K. S. & HUTCHINGS, R. W. (1997) Disturbance, fragmentation, and the dynamics of
1219 diversity in Amazonian forest butterflies. In *Tropical Forest Remnants: Ecology,*
1220 *Management, and Conservation of Fragmented Communities* (eds W. F. Laurance &
1221 R. O. Bierregaard), pp. 91-110. University of Chicago Press, Chicago.
- 1222 BRUM, H. D., NASCIMENTO, H., LAURANCE, W. F., ANDRADE, A., LAURANCE, S. G. & LUIZÃO,

- 1223 R. (2008) Rainforest fragmentation and the demography of the economically
1224 important palm *Oenocarpus bacaba* in central Amazonia. *Plant Ecology* **199**, 209-
1225 215.
- 1226 BRUNA, E. M. (1999) Seed germination in rainforest fragments. *Nature* **402**, 139.
- 1227 BRUNA, E. M., VASCONCELOS, H. L. & HEREDIA, S. (2005) The effect of habitat fragmentation
1228 on communities of mutualists: a test with Amazonian ants and their host plants.
1229 *Biological Conservation* **124**, 209-216.
- 1230 BÜHRNHEIM, C. M. & FERNANDES, C. C. (2003) Structure of fish assemblages in Amazonian
1231 rainforest streams: effects of habitats and locality. *Copeia* **2003**, 255-262.
- 1232 BUTLER, R. A. & LAURANCE, W. F. (2009) Is oil palm the next emerging threat to the
1233 Amazon? *Tropical Conservation Science* **2**, 1-10.
- 1234 CAMARGO, J. L. C. & KAPOS, V. (1995) Complex edge effects on soil moisture and
1235 microclimate in central Amazonian forests. *Journal of Tropical Ecology* **11**, 205-211.
- 1236 CARVALHO, K. S. & VASCONCELOS, H. L. (1999) Forest fragmentation in central Amazonia
1237 and its effects on litter-dwelling ants. *Biological Conservation* **91**, 151-158.
- 1238 CHAMBERS, J. Q., HIGUCHI, N. & SCHIMEL, J. P. (1998) Ancient trees in Amazonia. *Nature*
1239 **391**, 135-136.
- 1240 CHAVE, J., MULLER-LANDAU, H. C., BAKER, T. R., EASDALE, T. A., TER STEEGE, H. & WEBB,
1241 C. O. (2006) Regional and phylogenetic variation of wood density across 2,456
1242 neotropical tree species. *Ecological Applications* **16**, 2356-2367.
- 1243 CHAZDON, R. L., HARVEY, C. A., KOMAR, O., GRIFFITH, D., FERGUSON, B., MARTINEZ-
1244 RAMOS, M., MORALES, H., NIGH, R., SOTO-PINTO, L., VAN BREUGEL, M. & PHILPOTT,
1245 S. M. (2008) Beyond reserves: a research agenda for conserving biodiversity in
1246 human-modified tropical landscapes. *Biotropica* **41**, 142-153.
- 1247 CHOU, C., CHIANG, J., LAN, C.-W., CHUNG, C.-H., LIAO, Y.-C. & LEE, C.-J. (2013) Increase in

- 1248 the range between wet and dry season precipitation. *Nature Geoscience* **6**, 263-267.
- 1249 CLARK, D. A. (2004) Tropical forests and global warming: slowing it down or speeding it up?
1250 *Frontiers in Ecology and the Environment* **2**, 73-80.
- 1251 COCHRANE, M. A. & LAURANCE, W. F. (2002) Fire as a large-scale edge effect in Amazonian
1252 forests. *Journal of Tropical Ecology* **18**, 311-325.
- 1253 COCHRANE, M. A. & LAURANCE, W. F. (2008) Synergisms among fire, land use, and climate
1254 change in the Amazon. *Ambio* **37**, 522-527.
- 1255 CONDON, M. A., SASEK, T. W. & STRAIN, B. R. (1992) Allocation patterns in two tropical
1256 vines in response to increased atmospheric CO₂. *Functional Ecology* **6**, 680-685.
- 1257 COX, P. M., BETTS, R. A., COLLINS, M., HARRIS, P. P., HUNTINGFORD, C. & JONES, C. D.
1258 (2004) Amazonian forest dieback under climate-carbon cycle projections for the 21st
1259 century. *Theoretical Applied Climatology* **78**, 137-156.
- 1260 COX, P. M., BETTS, R. A., JONES, C. D., SPALL, S. A. & TOTTERDELL, I. J. (2000) Acceleration
1261 of global warming due to carbon cycle feedbacks in a coupled climate model. *Nature*
1262 **408**, 184-187
- 1263 COX, P. M., PEARSON, D., BOOTH, B., FRIEDLINGSTEIN, P., HUNTINGFORD, C., JONES, C. D. &
1264 LUKE, C. (2013) Sensitivity of tropical carbon to climate change constrained by
1265 carbon dioxide variability. *Nature* **494**, 341-344.
- 1266 CRAMER, J. M., MESQUITA, R., BENTOS, T., MOSER, B. & WILLIAMSON, G. B. (2007a) Forest
1267 fragmentation reduces seed dispersal of *Duckeodendron cestroides*, a Central Amazon
1268 endemic. *Biotropica* **39**, 709-718.
- 1269 CRAMER, J. M., MESQUITA, R. & WILLIAMSON, G. B. (2007b) Forest fragmentation
1270 differentially affects seed dispersal of large and small-seeded tropical trees. *Biological*
1271 *Conservation* **137**, 415-423.

- 1272 DAI, A. (2012) Increasing drought under global warming in observations and models. *Nature*
1273 *Climate Change* **3**, 52-58.
- 1274 D'ANGELO, S., ANDRADE, A., LAURANCE, S. G., LAURANCE, W. F. & MESQUITA, R. (2004)
1275 Inferred causes of tree mortality in fragmented and intact Amazonian forests. *Journal*
1276 *of Tropical Ecology* **20**, 243-246.
- 1277 DA SILVA, J. M. C. & TABARELLI, M. (2000) Tree species impoverishment and the future flora
1278 of the Atlantic forest of northeast Brazil. *Nature* **404**, 72-74.
- 1279 DEVELEY, P. & STOUFFER, P. C. (2001) Roads affect movements by understory mixed-species
1280 flocks in central Amazonian Brazil. *Conservation Biology* **15**, 1416-1422.
- 1281 DEICHMANN, J. L., LIMA, A. & WILLIAMSON, G. B. (2011) Effects of geomorphology and
1282 primary productivity on Amazonian leaf litter herpetofauna. *Biotropica* **43**, 149-156.
- 1283 DEICHMANN, J. L., TOFT, C. A., DEICHMANN, P. M., LIMA, A. & WILLIAMSON, G. B. (2013)
1284 Neotropical primary productivity affects biomass of leaf-litter herpetofaunal
1285 assemblage. *Journal of Tropical Ecology* **28**, 427-435.
- 1286 DIAMOND, J. M., BISHOP, K. D. & BALEN, S. V. (1987) Bird survival in an isolated Javan
1287 woodland: island or mirror? *Conservation Biology* **1**, 132-142.
- 1288 DICK, C. W. (2001) Genetic rescue of remnant tropical trees by an alien pollinator.
1289 *Proceedings of the Royal Society B* **268**, 2391-2396.
- 1290 DICK, C. W., ETCHOLECU, G. & AUSTERLITZ, F. (2003) Pollen dispersal of tropical trees
1291 (*Dinizia excelsa*, Fabaceae) by native insects and African honeybees in pristine and
1292 fragmented Amazonian rainforest. *Molecular Ecology* **12**, 753-764.
- 1293 DICKINSON, R. & KENNEDY, P. (1992) Impacts on regional climate of Amazon deforestation.
1294 *Geophysical Research Letters* **19**, 1947-1950.
- 1295 DIDHAM, R. K. & LAWTON, J. H. (1999) Edge structure determines the magnitude of changes
1296 in microclimate and vegetation structure in tropical forest fragments. *Biotropica* **31**,

- 1297 17-30.
- 1298 DIDHAM, R. K., HAMMOND, P. M., LAWTON, J. H., EGGLETON, P. & STORK, N. E. (1998a)
- 1299 Beetle species responses to tropical forest fragmentation. *Ecological Monographs* **68**,
- 1300 295-303.
- 1301 DIDHAM, R. K., LAWTON, J. H., HAMMOND, P. M. & EGGLETON, P. (1998b) Trophic structure
- 1302 stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments.
- 1303 *Proceedings of the Royal Society B* **353**, 437-451.
- 1304 ELTAHIR, E. A. B. & BRAS, R. L. (1994) Precipitation recycling in the Amazon basin.
- 1305 *Quarterly Journal of the Royal Meteorological Society* **120**, 861-880.
- 1306 EWERS, R. M. & DIDHAM, R. K. (2006) Confounding factors in the detection of species
- 1307 responses to habitat fragmentation. *Biological Reviews* **81**, 117-142.
- 1308 Ewers, R. M., Andrade, A., Laurance, S. G., Camargo, J. L. C., Lovejoy, T. E. & Laurance,
- 1309 W. F. (2017) Predicted trajectories of tree community change in Amazonian rainforest
- 1310 fragments. *Ecography* **40**, 26-35.
- 1311 FARNEDA, F. Z., ROCHA, R., LOPEZ-BAUCCELLS, A., GROENENBERG, M., SILVA, I., PALMEIRIM,
- 1312 J. M., BOBROWIEC, P. & MEYER, C. F. J. (2015) Trait-related responses to habitat
- 1313 fragmentation in Amazonian bats. *Journal of Applied Ecology* **52**, 1381-1391.
- 1314 FÁVERI, S. B., VASCONCELOS, H. L. & DIRZO R. (2008) Effects of Amazonian forest
- 1315 fragmentation on the interaction between plants, insect herbivores, and their natural
- 1316 enemies. *Journal of Tropical Ecology* **24**, 57-64.
- 1317 FEARNSIDE, P. M. (1997) Wood density for estimating forest biomass in Brazilian Amazonia.
- 1318 *Forest Ecology and Management* **90**, 59-89. |
- 1319 FEARNSIDE, P. M. (2000) Global warming and tropical land-use change: Greenhouse gas
- 1320 emissions from biomass burning, decomposition and soils in forest conversion,
- 1321 shifting cultivation and secondary vegetation. *Climatic Change* **46**, 115-158.

- 1322 FEARNSSIDE, P. M. (2001a) Soybean cultivation as a threat to the environment in Brazil.
1323 *Environmental Conservation* **28**, 23-38.
- 1324 FEARNSSIDE, P. M. (2002) Avanço Brasil: Environmental and social consequences of Brazil's
1325 planned infrastructure in Amazonia. *Environmental Management* **30**, 748-763.
- 1326 FEARNSSIDE, P. M. (2004) Are climate change impacts already affecting tropical forest
1327 biomass? *Global Environmental Change* **14**, 299-302.
- 1328 FEARNSSIDE, P. M. (2007) Brazil's Cuiabá-Santarém (BR-163) Highway: The environmental
1329 cost of paving a soybean corridor through the Amazon. *Environmental Management*
1330 **39**, 601-614.
- 1331 Fearnside, P. M. (2015) Highway construction as a force in destruction of the Amazon forest.
1332 In *Handbook of Road Ecology* (eds. R. van der Ree, D.J. Smith & C. Grilo), pp. 414-
1333 424. John Wiley & Sons Publishers, Oxford, UK.
- 1334 FEARNSSIDE, P. M. (2016a) Tropical dams: To build or not to build? *Science* **351**, 456-457.
- 1335 FEARNSSIDE, P. M. (2016b) The impact of land use on carbon stocks and fluxes. In *Interactions*
1336 *Between Biosphere, Atmosphere and Human Land Use in the Amazon Basin* (eds. L.
1337 Nagy, B. Forsberg, P. Artaxo), pp. 385-405. Springer, Heidelberg, Germany.
- 1338 FEARNSSIDE, P. M. & GRAÇA, P. (2006) BR-319: Brazil's Manaus-Porto Velho highway and
1339 the potential impact of linking the arc of deforestation to central Amazonia.
1340 *Environmental Management* **38**, 705-716.
- 1341 FEARNSSIDE, P. M. & LEAL FILHO, N. (2001) Soil and development in Amazonia: Lessons from
1342 the Biological Dynamics of Forest Fragments Project. In *Lessons from Amazonia: The*
1343 *Ecology and Conservation of a Fragmented Forest* (eds R. O. Bierregaard, C. Gascon,
1344 T. E. Lovejoy, R. Mesquita), pp. 291-312. Yale University Press, New Haven.
- 1345 FELDPAUSCH, T. R., LLOYD, J., BRIENEN, R., LEWIS, S., GLOOR, E., MONTEAGUDO MENDOZA,
1346 A., LOPEZ-GONZALEZ, G., BANIN, L., ABU SALIM, K., AFFUM-BAFFOE, K., ALEXIADES,

- 1347 M., ALMEIDA, S., AMARAL, I., ANDRADE, A., ARAGÃO, L. *et al.* (2012) Tree height
1348 integrated into global tropical biomass estimates. *Biogeosciences* **9**, 3381-3403.
- 1349 FELDPAUSCH, T., PHILLIPS, O., BRIENEN, R., GLOOR, E., LLOYD, J., LOPEZ, G., GONZALEZ, A.,
1350 MONTEAGUDO, A., MALHI, Y., ALARCÓN, A., ÁLVAREZ DÁVILA, E., ALVAREZ, P.,
1351 ANDRADE, A., ARAGAO, L., ARROYO, L. *et al.* (2016) Amazon forest response to
1352 repeated droughts. *Global Biogeochemical Cycles* **7**, 964-982.
- 1353 FERRAZ, G., NICHOLS, J. D., HINES, J., STOUFFER, P. C., BIERREGAARD, R. O. & LOVEJOY, T. E.
1354 (2007) A large-scale deforestation experiment: effects of patch area and isolation on
1355 Amazon birds. *Science* **315**, 238-241.
- 1356 FERRAZ, G., RUSSELL, G. J., STOUFFER, P. C., BIERREGAARD, R. O., PIMM, S. L. & LOVEJOY, T.
1357 E. (2003) Rates of species loss from Amazonian forest fragments. *Proceedings of the*
1358 *National Academy of Sciences USA* **100**, 14069-14073.
- 1359 FINER, M., JENKINS, C., PIMM, S. L., KEANE, B. & ROSS, C. (2008) Oil and gas projects in the
1360 western Amazon: threats to wilderness, biodiversity, and indigenous peoples. *PLoS*
1361 *ONE* **3**, e2932.
- 1362 FOWLER, H. G., SILVA, C. A. & VENTICINQUE, E. (1993) Size, taxonomic and biomass
1363 distributions of flying insects in central Amazonia: forest edge vs. understory. *Revista*
1364 *Biologia Tropical* **41**, 755-760.
- 1365 FREITAS, S., SILVA DIAS, M. & SILVA DIAS, P. (2000) Modeling the convective transport of
1366 trace gases by deep and moist convection. *Hybrid Methods in Engineering* **3**, 317-330.
- 1367 FU, R., LI, W., ARIAS, P., DICKINSON, R., HUANG, L., CHADRABORTY, S., FERNANDES, K.,
1368 LIEBMANN, B., FISHER, R. & MYNENI, R. (2013) Increased dry-season length over
1369 southern Amazonia in recent decades and its implication for future climate projection.
1370 *Proceedings of the National Academy of Sciences USA*,
1371 doi:10.1073/pnas.1302584110.

- 1372 GARDNER, T. A., BARLOW, J., CHAZDON, R., EWERS, R., HARVEY, C., PERES, C. A. & SODHI,
1373 N. S. (2009) Prospects for tropical forest biodiversity in a human-modified world.
1374 *Ecology Letters* **12**, 561-582.
- 1375 GASCON, C. (1993) Breeding habitat use by Amazonian primary-forest frog species at the
1376 forest edge. *Biodiversity and Conservation* **2**, 438-444.
- 1377 GASCON, C., LOVEJOY, T. E., BIERREGAARD, R. O., MALCOLM, J. R., STOUFFER, P. C.,
1378 VASCONCELOS, H., LAURANCE, W. F., ZIMMERMAN, B., TOCHER, M. & BORGES, S.
1379 (1999) Matrix habitat and species persistence in tropical forest remnants. *Biological*
1380 *Conservation* **91**, 223-229.
- 1381 GIBBS, H. K., REUSCH, A. S., ACHARD, F., CLAYTON, M. K., HOLMGREN, P., RAMANKUTTY, N.
1382 & FOLEY, J. A. (2010) Tropical forests were the primary sources of new agricultural
1383 lands in the 1980s and 1990s. *Proceedings of the National Academy of Sciences USA*
1384 **107**, 16732-16737.
- 1385 GIBSON, L., LEE, T. M., KOH, L. P., BROOK, B. W., GARDNER, T. A., BARLOW, J., PERES, C. A.,
1386 BRADSHAW, C. J. A., LAURANCE, W. F., LOVEJOY, T. E. & SODHI, N. S. (2011) Primary
1387 forests are irreplaceable for sustaining tropical biodiversity. *Nature* **478**, 378-381.
- 1388 GIBSON, L., LYNAM, A.J., BRADSHAW, C. J. A., HE, F., BICKFORD, D., WOODRUFF, D. S.,
1389 BUMRUNGSRI, S. & LAURANCE, W. F. (2013) Near-complete extinction of a native
1390 small mammal fauna 25 years following forest fragmentation. *Science* **341**, 1508-
1391 1510.
- 1392 GILBERT, B., LAURANCE, W. F., LEIGH, E. G. & NASCIMENTO, H. (2006) Can neutral theory
1393 predict the responses of Amazonian tree communities to forest fragmentation?
1394 *American Naturalist* **168**, 304-317.
- 1395 GILBERT, K. A. & SETZ, E. (2001) Primates in a fragmented landscape: six species in central
1396 Amazonia. In *Tropical Forest Remnants: Ecology, Management, and Conservation of*

- 1397 *Fragmented Communities* (eds W. F. Laurance & R. O. Bierregaard), pp. 262-270.
1398 University of Chicago Press, Chicago.
- 1399 GIRÃO, L. C., LOPES, A. V., TABARELLI, M. & BRUNA, E. M. (2007) Changes in tree
1400 reproductive traits reduce functional diversity in a fragmented Atlantic forest
1401 landscape. *PLoS ONE* **2**, e908.
- 1402 GOOD, P., JONES, C. D., LOWE, J. A., BETTS, R. A. & GEDNEY, N. (2013) Comparing tropical
1403 forest projections from two generations of Hadley Centre Earth System models,
1404 HadGEM2-ES and HadCM3LC. *Journal of Climate* **26**, 495-511.
- 1405 GRANADOS, J. & KÖRNER, C. (2002) In deep shade, elevated CO₂ increases the vigor of
1406 tropical climbing plants. *Global Change Biology* **8**, 1109-1117
- 1407 GROENEVELD, J., ALVES, L., BERNACCI, L., CATHARINO, E., KNOGGE, C., METZGER, J., PÜTZ,
1408 S. & HUTH, A. (2009) The impact of fragmentation and density regulation on forest
1409 succession in the Atlantic rain forest. *Ecological Modeling* **220**, 2450-2459.
- 1410 HARPER, L. H. (1989) The persistence of ant-following birds in small Amazonian forest
1411 fragments. *Acta Amazonica* **19**, 249-263.
- 1412 HERRING, S. C., HOERLING, M., KOSSIN, J., PETERSON, T. & STOTT, P., eds (2015) Explaining
1413 extreme events of 2014 from a climate perspective. *Bulletin of the American*
1414 *Meteorological Society* **96**, S1-S172
- 1415 HOUGHTON, R. A., BYERS, B. & NASSIKAS, A. A. (2015) A role for tropical forests in
1416 stabilizing atmospheric CO₂. *Nature Climate Change* **5**, 1022-1023.
- 1417 HUBBELL, S. P. (2001) *The Neutral Theory of Biodiversity and Biogeography*. Princeton
1418 University Press, Princeton.
- 1419 HUNTINGFORD, C., ZELAZOWSKI, P., GALBRAITH, D., MERCADO, L., SITCH, S., FISHER, R.,
1420 LOMAS, M., WALKER, A., JONES, C., BOOTH, B., MALHI, Y., HEMMING, D., KAY, G.,
1421 GOOD, P., LEWIS, S. L. *et al.* (2013) Simulated resilience of tropical rainforests to CO₂-

- 1422 induced climate change. *Nature Geoscience* **6**, 268-273.
- 1423 INGWELL, L. L., WRIGHT, S. J., BECKLUND, K., HUBBELL, S. P. & SCHNITZER, S. A. (2010) The
1424 impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island,
1425 Panama. *Journal of Ecology* **98**, 879-887.
- 1426 IPCC (2013) *Climate Change 2013: The Physical Science Basis*. Intergovernmental Panel on
1427 Climate Change, Cambridge University Press, Cambridge.
- 1428 JAKOVAC, C. C., PEÑA-CLAROS, M., KUYPER, T. W. & BONGERS, F. (2015) Loss of secondary
1429 forest resilience by land-use intensification in the Amazon. *Journal of Ecology* **103**,
1430 67-77.
- 1431 JANZEN, D. H. (1983) No park is an island: Increase in interference from outside as park size
1432 increases. *Oikos* **41**, 402-410.
- 1433 JIMÉNEZ-MUÑOZ, J. C., MATTAR, C., BARICHIVICH, J., SANTAMARÍA-ARTIGAS, A.,
1434 TAKAHASHI, K., MALHI, Y., SOBRINO, J. & VAN DER SCHRIER, G. (2016) Record-
1435 breaking warming and extreme drought in the Amazon rainforest during the course of
1436 El Niño 2015-2016. *Scientific Reports* **6**, 33130.
- 1437 JIPP, P., NEPSTAD, D., CASSEL, K. & DE CARVALHO, C. (1998) Deep soil moisture storage and
1438 transpiration in forests and pastures of seasonally dry Amazonia. *Climatic Change* **39**,
1439 395-412.
- 1440 JORGE, M. L. (2008) Effects of forest fragmentation on two sister genera of Amazonian
1441 rodents (*Myoprocta acouchy* and *Dasyprocta leporina*). *Biological Conservation* **141**,
1442 617- 623.
- 1443 KAPOS, V. (1989) Effects of isolation on the water status of forest patches in the Brazilian
1444 Amazon. *Journal of Tropical Ecology* **5**, 173-185.
- 1445 KAPOS, V., GANADE, G., MATUSI, E. & VICTORIA, R. L. (1993) Delta 13C as an indicator of
1446 edge effects in tropical rainforest reserves. *Journal of Ecology* **81**, 425-432.

- 1447 KILLEEN, T. J. (2007) *A Perfect Storm in the Amazon Wilderness: Development and*
1448 *Conservation in the Context of the Initiative for the Integration of the Regional*
1449 *Infrastructure of South America (IIRSA)*. Conservation International, Washington,
1450 D.C.
- 1451 KIMBALL, B. A., MAUNEY, J. R., NAKAYAMA, F. S. & IDSO, S. B. (1993) Effects of increasing
1452 atmospheric CO₂ on vegetation. *Vegetatio* **104/105**, 65-75
- 1453 KLEIN, B. C. (1989) Effects of forest fragmentation on dung and carrion beetle communities
1454 in central Amazonia. *Ecology* **70**, 1715-1725.
- 1455 KÖRNER, C. (2004) Through enhanced tree dynamics carbon enrichment may cause tropical
1456 forests to lose carbon. *Philosophical Transactions of the Royal Society of London B*
1457 **359**, 493-498.
- 1458 KÖRNER, C. (2017) A matter of tree longevity. *Science* **355**, 130-131.
- 1459 LAURANCE, S. G. (2004) Responses of understory rain forest birds to road edges in central
1460 Amazonia. *Ecological Applications* **14**, 1344-1357.
- 1461 LAURANCE, S. G. & GOMEZ, M. S. (2005) Clearing width and movements of understory
1462 rainforest birds. *Biotropica* **37**, 149-152.
- 1463 LAURANCE, S. G., STOUFFER, P. C. & LAURANCE, W. F. (2004) Effects of road clearings on
1464 movement patterns of understory rainforest birds in central Amazonia. *Conservation*
1465 *Biology* **18**, 1099-1109.
- 1466 LAURANCE, S. G., LAURANCE, W. F., NASCIMENTO, H., ANDRADE, A., FEARNSIDE, P. M.,
1467 REBELLO, E. & CONDIT, R. (2009) Long-term variation in Amazon forest dynamics.
1468 *Journal of Vegetation Science* **20**, 323-333.
- 1469 LAURANCE, S. G., ANDRADE, A. & LAURANCE, W. F. (2010a) Unanticipated effects of stand
1470 dynamism on Amazonian tree diversity. *Biotropica* **42**, 429-434.
- 1471 LAURANCE, S. G., LAURANCE, W. F., ANDRADE, A., FEARNSIDE, P. M., HARMS, K. & LUIZÃO,

- 1472 R. (2010b) Influence of soils and topography on Amazonian tree diversity: a
1473 landscape-scale study. *Journal of Vegetation Science* **21**, 96-106.
- 1474 LAURANCE, W. F. (1991) Ecological correlates of extinction proneness in Australian tropical
1475 rainforest mammals. *Conservation Biology* **5**, 79-89.
- 1476 LAURANCE, W. F. (2001) The hyper-diverse flora of the central Amazon: an overview. In
1477 *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest* (eds
1478 R. O. Bierregaard, C. Gascon, T. E. Lovejoy, R. Mesquita), pp. 47-53. Yale University
1479 Press, New Haven.
- 1480 LAURANCE, W. F. (2002) Hyperdynamism in fragmented habitats. *Journal of Vegetation*
1481 *Science* **13**, 595-602.
- 1482 LAURANCE, W. F. (2004) Forest-climate interactions in fragmented tropical landscapes.
1483 *Philosophical Transactions of the Royal Society B* **359**, 345-352.
- 1484 LAURANCE, W. F. (2005) When bigger is better: the need for Amazonian megareserves.
1485 *Trends in Ecology and Evolution* **20**, 645-648.
- 1486 LAURANCE, W. F. (2007) Have we overstated the tropical biodiversity crisis? *Trends in*
1487 *Ecology and Evolution* **22**, 65-70.
- 1488 LAURANCE, W. F. (2008) Theory meets reality: How habitat fragmentation research has
1489 transcended island biogeographic theory. *Biological Conservation* **141**, 1731-1744.
- 1490 LAURANCE, W. F. (2016) Lessons from research for sustainable development and
1491 conservation in Borneo. *Forests* **7**, 314; doi:10.3390/f7120314.
- 1492 LAURANCE, W. F. & BIERREGAARD, R. O., eds (1997) *Tropical Forest Remnants: Ecology,*
1493 *Management, and Conservation of Fragmented Communities*. University of Chicago
1494 Press, Chicago.
- 1495 LAURANCE, W. F. & COCHRANE, M. A. (2001) Synergistic effects in fragmented landscapes.
1496 *Conservation Biology* **15**, 1488-1489.

- 1497 LAURANCE, W. F. & LUIZÃO, R. C. C. (2007) Driving a wedge into the Amazon. *Nature* **448**,
1498 409-410.
- 1499 LAURANCE, W. F. & PERES, C. A., eds (2006) *Emerging Threats to Tropical Forests*.
1500 University of Chicago Press, Chicago.
- 1501 LAURANCE, W. F. & USECHE, D. C. (2009) Environmental synergisms and extinctions of
1502 tropical species. *Conservation Biology* **23**, 1427-1437.
- 1503 LAURANCE, W. F. & WILLIAMSON, G. B. (2001) Positive feedbacks among forest
1504 fragmentation, drought, and climate change in the Amazon. *Conservation Biology* **15**,
1505 1529-1535.
- 1506 LAURANCE, W. F., LAURANCE, S. G., FERREIRA, L. V., RANKIN-DE MERONA, J., GASCON, C. &
1507 LOVEJOY, T. E. (1997) Biomass collapse in Amazonian forest fragments. *Science* **278**,
1508 1117-1118.
- 1509 LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M. & LAURANCE, S. G. (1998a)
1510 Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*
1511 **79**, 2032-2040.
- 1512 LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M., LAURANCE, S. G.,
1513 HUTCHINGS, R. & LOVEJOY, T. E. (1998b) Effects of forest fragmentation on
1514 recruitment patterns in Amazonian tree communities. *Conservation Biology* **12**, 460-
1515 464.
- 1516 LAURANCE, W. F., LAURANCE, S. G. & DELAMONICA, P. (1998c) Tropical forest fragmentation
1517 and greenhouse gas emissions. *Forest Ecology and Management* **110**, 173-180.
- 1518 LAURANCE, W. F., FEARNSIDE, P. M., LAURANCE, S. G., DELAMONICA, P., LOVEJOY, T. E.,
1519 RANKIN-DE MERONA, J. M., CHAMBERS, J. Q. & GASCON, C. (1999) Relationship
1520 between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology*
1521 *and Management* **118**, 127-138.

- 1522 LAURANCE, W. F., DELAMONICA, P., LAURANCE, S. G., VASCONCELOS, H. L. & LOVEJOY, T. E.
1523 (2000) Rainforest fragmentation kills big trees. *Nature* **404**, 836.
- 1524 LAURANCE, W. F., COCHRANE, M., BERGEN, S., FEARNSIDE, P. M., DELAMONICA, P., BARBER,
1525 C., D'ANGELO, S. & FERNANDES, T. (2001a) The future of the Brazilian Amazon.
1526 *Science* **291**, 438-439.
- 1527 LAURANCE, W. F., PEREZ-SALICRUP, D., DELAMONICA, P., FEARNSIDE, P. M., D'ANGELO, S.,
1528 JEROZOLINSKI, A., POHL, L. & LOVEJOY, T. E. (2001b) Rain forest fragmentation and
1529 the structure of Amazonian liana communities. *Ecology* **82**, 105-116.
- 1530 LAURANCE, W. F., WILLIAMSON, G. B., DELAMONICA, P., OLIVERA, A., GASCON, C., LOVEJOY,
1531 T. E. & POHL, L. (2001c) Effects of a strong drought on Amazonian forest fragments
1532 and edges. *Journal of Tropical Ecology* **17**, 771-785.
- 1533 LAURANCE, W. F., LOVEJOY, T. E., VASCONCELOS, H., BRUNA, E., DIDHAM, R., STOUFFER, P.
1534 C., GASCON, C., BIERREGAARD, R., LAURANCE, S. G. & SAMPAIO, E. (2002) Ecosystem
1535 decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*
1536 **16**, 605-618.
- 1537 LAURANCE, W. F., OLIVEIRA, A. A., LAURANCE, S. G., CONDIT, R., NASCIMENTO, H.,
1538 SANCHEZ-THORIN, A., LOVEJOY, T. E., ANDRADE, A., D'ANGELO, S. & DICK, C.
1539 (2004a) Pervasive alteration of tree communities in undisturbed Amazonian forests.
1540 *Nature* **428**, 171-175.
- 1541 LAURANCE, W. F., NASCIMENTO, H., LAURANCE, S. G., CONDIT, R., D'ANGELO, S. & ANDRADE,
1542 A. (2004b) Inferred longevity of Amazonian rainforest trees based on a long-term
1543 demographic study. *Forest Ecology and Management* **190**, 131-143.
- 1544 LAURANCE, W. F., OLIVEIRA, A. A., LAURANCE, S. G., CONDIT, R., DICK, C., ANDRADE, A.,
1545 NASCIMENTO, H., LOVEJOY, T. E. & RIBEIRO, J. (2005). Altered tree communities in
1546 undisturbed Amazonian forests: A consequence of global change? *Biotropica* **37**, 160-

- 1547 162.
- 1548 LAURANCE, W. F., NASCIMENTO, H., LAURANCE, S. G., ANDRADE, A., FEARNSIDE, P. M. &
1549 RIBEIRO, J. (2006a) Rain forest fragmentation and the proliferation of successional
1550 trees. *Ecology* **87**, 469-482.
- 1551 LAURANCE, W. F., NASCIMENTO, H., LAURANCE, S. G., ANDRADE, A., RIBEIRO, J., GIRALDO
1552 JP, LOVEJOY, T. E., CONDIT, R., CHAVE, J. & D'ANGELO, S. (2006b) Rapid decay of
1553 tree community composition in Amazonian forest fragments. *Proceedings of the*
1554 *National Academy of Sciences USA* **103**, 19010-19014.
- 1555 LAURANCE, W. F., NASCIMENTO, H., LAURANCE, S. G., ANDRADE, A., EWERS, R., HARMS, K.,
1556 LUIZÃO, R. & RIBEIRO, J. (2007) Habitat fragmentation, variable edge effects, and the
1557 landscape-divergence hypothesis. *PLoS ONE* **2**, e1017.
- 1558 LAURANCE, W. F., GOOSEM, M. & LAURANCE, S. G. (2009b) Impacts of roads and linear
1559 clearings on tropical forests. *Trends in Ecology and Evolution* **24**, 659-669.
- 1560 LAURANCE, W. F., ANDRADE, A., MAGRACH, A., CAMARGO, J. L. C., VALSKO, J., CAMPBELL,
1561 M., FEARNSIDE, P. M., EDWARDS, W., LOVEJOY, T. E. & LAURANCE, S. G. (2014a)
1562 Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian
1563 forests. *Ecology* **95**, 1604-1611.
- 1564 LAURANCE, W. F., ANDRADE, A., MAGRACH, A., CAMARGO, J. L. C., CAMPBELL, M.,
1565 FEARNSIDE, P. M., EDWARDS, W., VALSKO, J., LOVEJOY, T. E. & LAURANCE, S. G.
1566 (2014b) Apparent environmental synergism drives the dynamics of Amazonian forest
1567 fragments. *Ecology* **95**, 3018-3026.
- 1568 LAURANCE, W. F., CAMARGO, J., LUIZÃO, R., LAURANCE, S. G., PIMM, S. L., BRUNA, E.,
1569 STOUFFER, P. C., WILLIAMSON, G. B., BENITEZ-MALVIDO, J., VASCONCELOS, H., VAN
1570 HOUTAN, K., ZARTMAN, C. E., BOYLE, S., DIDHAM, R. K., ANDRADE, A. & LOVEJOY, T.
1571 E. (2011) The fate of Amazonian forest fragments: A 32-year investigation. *Biological*

- 1572 *Conservation* **144**, 56-67.
- 1573 LEAN, J. & ROWNTREE, P. 1993. A GCM simulation of the impact of Amazonian deforestation
1574 on climate using an improved canopy representation. *Quarterly Journal of the Royal*
1575 *Meteorological Society* **119**, 509-530.
- 1576 LEIDNER, A. K., HADDAD, N. M. & LOVEJOY, T. E. (2010) Does tropical forest fragmentation
1577 increase long-term variability of butterfly communities? *PLoS ONE* **5**, e9534.
- 1578 LEWIS, S. L., MALHI, Y. & PHILLIPS, O. L. (2004a) Fingerprinting the impacts of global
1579 change on tropical forests. *Philosophical Transactions of the Royal Society B* **359**,
1580 437-462.
- 1581 LEWIS, S. L., PHILLIPS, O., BAKER, T., LLOYD, J., MALHI, Y., ALMEIDA, S., HIGUCHI, N.,
1582 LAURANCE, W. F., NEILL, D., SILVA, N., TERBORGH, J., LEZAMA, A., BROWN, S.,
1583 VASQUEZ, R., CHAVE, J. *et al.* (2004b) Concerted changes in tropical forest structure
1584 and dynamics: evidence from 50 South American long-term plots. *Philosophical*
1585 *Transactions of the Royal Society B* **359**, 421-436.
- 1586 LEWIS, S. L., LOPEZ-GONZALEZ, G., SONKE, B., AFFUM-BAFFOE, K., BAKER, T., OJO, L.,
1587 PHILLIPS, O., REITSMA, J., WHITE, W., COMISKEY, J., DJUIKOUO, M., EWANGO, C.,
1588 FELDPAUSCH, T., HAMILTON, A., GLOOR, M. *et al.* (2009a) Increasing carbon storage
1589 in intact African tropical forests. *Nature* **457**, 1003-1007.
- 1590 LEWIS, S. L., LLOYD, J., SITCH, S., MITCHARD, E. & LAURANCE, W. F. (2009b) Changing
1591 ecology of tropical forests: Evidence and drivers. *Annual Review of Ecology,*
1592 *Evolution, and Systematics* **40**, 529-549.
- 1593 LEWIS, S. L., BRANDO, P. M., PHILLIPS, O. L., VAN DER HEIJDEN, G. M. F. & NEPSTAD, D.
1594 (2011). The 2010 Amazon drought. *Science* **331**, 554.
- 1595 LIMA, M. & GASCON, C. (1999) The conservation value of linear forest remnants in central
1596 Amazonia. *Biological Conservation* **91**, 241-247.

- 1597 LINDENMAYER, D. B. & LAURANCE, W. F. (2016) The ecology, distribution, conservation and
1598 management of large old trees. *Biological Reviews*, DOI:10.1111/brv.12290.
- 1599 LONGWORTH, J. B., MESQUITA, R., BENTOS, T. V., MOREIRA, M., MASSOCA, P. &
1600 WILLIAMSON, G. B. (2014) Shifts in dominance and species assemblages over two
1601 decades in alternative successions in Central Amazonia. *Biotropica* **46**, 529-537.
- 1602 LOVEJOY, T. E., BIERREGAARD, R. O., RYLANDS, A. B., MALCOLM, J. R., QUINTELA, C.,
1603 HARPER, L., BROWN, K., POWELL, A., POWELL, G., SCHUBART, H. & HAYS, M. (1986)
1604 Edge and other effects of isolation on Amazon forest fragments. In *Conservation*
1605 *Biology: The Science of Scarcity and Diversity* (ed M. E. Soulé), pp. 257-285. Sinauer,
1606 Sunderland, Massachusetts.
- 1607 LOVEJOY, T. E. & OREN, D. C. (1981) Minimum critical size of ecosystems. In *Forest-Island*
1608 *Dynamics in Man-dominated Landscapes* (eds R. L. Burgess, D. M. Sharp), pp. 7-12.
1609 Springer-Verlag, New York.
- 1610 LOVEJOY, T. E., RANKIN, J. M., BIERREGAARD, R. O., BROWN, K., EMMONS, L. H. & VAN DER
1611 VOORT, M. E. (1984) Ecosystem decay of Amazon forest fragments. In *Extinctions* (ed
1612 M. H. Nitecki, pp. 295-325. University of Chicago Press, Chicago.
- 1613 MALCOLM, J. R. (1994) Edge effects in central Amazonian forest fragments. *Ecology* **75**,
1614 2438-2445.
- 1615 MALCOLM, J. R. (1997) Biomass and diversity of small mammals in Amazonian forest
1616 fragments. In *Tropical Forest Remnants: Ecology, Management, and Conservation of*
1617 *Fragmented Communities* (eds W. F. Laurance & R. O. Bierregaard), pp. 207-221.
1618 University of Chicago Press, Chicago.
- 1619 MALCOLM, J. R. (1998) A model of conductive heat flow in forest edges and fragmented
1620 landscapes. *Climatic Change* **39**, 487-502.
- 1621 MALHI, Y., WOOD, D., BAKER, T., WRIGHT, J., PHILLIPS, O., COCHRANE, T., MEIR, P., CHAVE,

- 1622 J., ALMEIDA, S., ARROYO, L., HIGUCHI, N., KILLEEN, T., LAURANCE, S. G., LAURANCE,
1623 W. F., LEWIS, S. *et al.* (2006) The regional variation of aboveground biomass in old-
1624 growth Amazonian forests. *Global Change Biology* **12**, 1-32.
- 1625 MALHI, Y., ROBERTS, J., BETTS, R., KILLEEN, T., WENHONG, L. & NOBRE, C. A. (2008)
1626 Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169-172.
- 1627 MARENGO, J. A., TOMASELLA, J., ALVES, L. M., SOARES, W. R. & RODRIGUEZ, D. A. (2011)
1628 The drought of 2010 in the context of historical droughts in the Amazon region,
1629 *Geophysical Research Letters* **38**, L12703.
- 1630 MARENGO J. A., TOMASELLA, J., SOARES, W., ALVES, L. & NOBRE, C. A. (2012) Extreme
1631 climatic events in the Amazon basin climatological and hydrological context of recent
1632 floods. *Theoretical Applied Climatology* **107**, 73-85.
- 1633 MARVIN, D. C., WINTER, K., BURNHAM, R. J. & AND SCHNITZER, S. A. (2015) No evidence
1634 that elevated CO₂ gives tropical lianas an advantage over tropical trees. *Global*
1635 *Change Biology* **21**, 2055-2069.
- 1636 MASSOCA, P, JAKOVAC, A., VIZCARRA, T., WILLIAMSON, G. B. & MESQUITA, R. (2012)
1637 Dinâmica e trajetórias da sucessão secundária na Amazônia central. *Boletim do Museu*
1638 *Paraense Emílio Goeldi Ciências Naturais* **7**, 235-250.
- 1639 MEGGERS, B. J. (1994) Archeological evidence for the impact of mega-Niño events on
1640 Amazonia during the past two millenia. *Climatic Change* **28**, 321-338.
- 1641 MESQUITA, R. C. G., DELAMÔNICA, P. & LAURANCE, W. F. (1999) Effects of surrounding
1642 vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological*
1643 *Conservation* **91**, 129-134.
- 1644 MESQUITA, R. C. G., ICKES, K., GANADE, G. & WILLIAMSON, G. B. (2001) Alternative
1645 successional pathways in the Amazon basin. *Journal of Ecology* **89**, 528-537.
- 1646 MESQUITA, R. C. G., MASSOCA, P., JAKOVAC, C., BENTOS, T. & WILLIAMSON, G. B. (2015)

- 1647 Amazon rain forest succession: Stochasticity or land-use legacy? *BioScience* **65**, 849-
1648 861.
- 1649 MESTRE, L. & GASNIER, T. R. (2008) Populações de aranhas errantes do gênero *Ctenus* em
1650 fragmentos florestais na Amazônia Central. *Acta Amazonica* **38**, 159-164.
- 1651 MEYER, C. F. J., AGUIAR, L., AGUIRRE, L., BAUMGARTEN, J., CLARKE, F., COSSON, J.-F.,
1652 ESTRADA VILLEGAS, S., FAHR, J., FARIA, D., FUREY, N., HENRY, M., JENKINS, R.,
1653 KUNZ, T., MACSWINEY GONZALEZ, M. *et al.* (2015) Species undersampling in tropical
1654 bat surveys: Effects on emerging biodiversity patterns. *Journal of Animal Ecology*
1655 **84**, 113-123.
- 1656 MEYER, C. F. J., STRUEBIG, M. J. & WILLIG, M. R. (2016) Responses of tropical bats to habitat
1657 fragmentation, logging, and deforestation. In *Bats in the Anthropocene: Conservation*
1658 *of Bats in a Changing World* (eds C. C. Voigt, T. Kingston), pp.63-103. Springer,
1659 New York.
- 1660 MICHALSKI, F. & PERES, C. A. (2005) Anthropogenic determinants of primate and carnivore
1661 local extinctions in a fragmented forest landscape of Southern Amazonia. *Biological*
1662 *Conservation* **124**, 383-396.
- 1663 MIRALDO, A., LI, S., BORREGAARD, A., GOPALAKRISHNAN, S., RIZVANOVIC, M., WANG, Z.,
1664 RAHBEK, C., MARSKE, K. & NOGUÉS-BRAVO, D. (2016) An Anthropocene map of
1665 genetic diversity. *Science* **353**, 1532-1535.
- 1666 MOKROSS, K., RYDER, T., CÔRTEZ, M., WOLFE, J. & STOUFFER, P. C. (2014) Decay of
1667 interspecific avian flock networks along a disturbance gradient in Amazonia.
1668 *Proceedings of the Royal Society B* **281**, 20132599.
- 1669 MORI, S. A. & BECKER, P. (1991) Flooding affects survival of *Leythidaceae* in terra firme
1670 forest near Manaus, Brazil. *Biotropica* **23**, 87-90.
- 1671 MOURA, N. G., LEES, A. C., ANDRETTI, C., DAVIS, B., SOLAR, R., ALEIXO, A., BARLOW, J.,

- 1672 FERREIRA J. & GARDNER, T. A. (2014) Avian biodiversity in multiple-use landscapes
1673 of the Brazilian Amazon. *Biological Conservation* **167**, 339-348.
- 1674 MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., FONSECA, G. A. B. & KENT, J. (2000)
1675 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858.
- 1676 NAGY, L., FORSBERG, B. & ARTAXO, P., eds. (2016) *Interactions Between Biosphere,*
1677 *Atmosphere and Human Land Use in the Amazon Basin.* Springer, Heidelberg,
1678 Germany.
- 1679 NASCIMENTO, H. E. M., ANDRADE, A., CAMARGO, J., LAURANCE, W. F., LAURANCE, S. G. &
1680 RIBEIRO, J. (2006) Effects of the surrounding matrix on tree recruitment in Amazonian
1681 forest fragments. *Conservation Biology* **20**, 853-860.
- 1682 NASCIMENTO, H. E. M. & LAURANCE, W. F. (2002) Total aboveground biomass in
1683 central Amazonian rainforests: A landscape-scale study. *Forest Ecology and*
1684 *Management* **168**, 311-321.
- 1685 NASCIMENTO, H. E. M. & LAURANCE, W. F. (2004) Biomass dynamics in Amazonian forest
1686 fragments. *Ecological Applications* **14**, S127-S138.
- 1687 NAVARRO, M. M. (2014) *Vertical stratification on insectivorous bats ensembles in Central*
1688 *Amazon.* M.Sc. Thesis, Universidad de Barcelona, Barcelona, Spain.
- 1689 NECKEL-OLIVEIRA, S. & GASCON, C. (2006) Abundance, body size and movement patterns of
1690 a tropical tree frog in continuous and fragmented forests of the Brazilian Amazon.
1691 *Biological Conservation* **128**, 308-315.
- 1692 NESSIMIAN, J. L., VENTICINQUE, E. M., ZUANON, J., DE MARCO, P., GORDO, M., FIDELIS, L.,
1693 BATISTA, J. & JUEN, L. (2008) Land use, habitat integrity, and aquatic insect
1694 assemblages in central Amazonian streams. *Hydrobiologia* **614**, 117-131.
- 1695 NOBRE, C. A., SAMPAIO, G., BORMA, L., CASTILL-RUBIO, J., SILVA, J. & CARDOSO, M. (2016)
1696 Land-use and climate change risks in the Amazon and the need of a novel sustainable

- 1697 development paradigm. *Proceedings of the National Academy of Sciences USA*,
1698 DOI:10.1073/pnas.1605516113.
- 1699 NOBRE, C. A., SELLERS, P., AND SHUKLA, J. (1991) Amazonian deforestation and regional
1700 climate change. *Journal of Climate* **4**, 411-413.
- 1701 NOGUEIRA, E. M., FEARNSIDE, P. M., NELSON, B. W., BARBOSA, R. I. & KEIZER, E. (2008)
1702 Estimates of forest biomass in the Brazilian Amazon: New allometric equations and
1703 adjustments to biomass from wood-volume inventories. *Forest Ecology and*
1704 *Management* **256**, 1853-1857.
- 1705 NOGUEIRA, E. M., FEARNSIDE, P. M., NELSON, B. W. & FRANÇA, M. B. (2007) Wood density
1706 in forests of Brazil's 'arc of deforestation': Implications for biomass and flux of
1707 carbon from land-use change in Amazonia. *Forest Ecology and Management* **248**,
1708 119-135.
- 1709 NOGUEIRA, E. M., NELSON, B. W. & FEARNSIDE, P. M. (2005) Wood density in dense forest in
1710 central Amazonia, Brazil. *Forest Ecology and Management* **208**, 261-286.
- 1711 NOGUEIRA, E. M., YANAI, A. M., FONSECA, F. & FEARNSIDE, P. M. (2015) Carbon stock loss
1712 from deforestation through 2013 in Brazilian Amazonia. *Global Change Biology* **21**,
1713 1271-1292.
- 1714 NORDEN, N., MESQUITA, R., BENTOS, T., CHAZDON, R. & WILLIAMSON, G. B. (2011)
1715 Contrasting community compensatory trends in alternative successional pathways in
1716 central Amazonia. *Oikos* **120**, 143-151.
- 1717 OBERBAUER, S. F., STRAIN, B. & FLETCHER, N. (1985) Effect of CO₂ enrichment on seedling
1718 physiology and growth of two tropical tree species. *Physiologica Plantarum* **65**, 352-
1719 356.
- 1720 OLIVEIRA DE, A. A. & MORI, S. A. (1999) A central Amazonian terra firme forest. I. High tree
1721 species richness on poor soils. *Biodiversity and Conservation* **8**, 1219-1244.

- 1722 OLSON, D. M., DINERSTEIN, E., WIDRAMANAYAKE, E., BURGESS, N., POWELL, G.,
1723 UNDERWOOD, E., D'AMICO, J., ITOUA, I., STRAND, H., MORRISON, J., LOUCKS, C.,
1724 ALLNUTT, T., RICKETTS, T., KURA, Y., LAMOREUX, J. *et al.* (2001) Terrestrial
1725 ecoregions of the world: A new map of life on Earth. *BioScience* **51**, 933-938.
- 1726 PERES, C. A. (2005) Why we need megareserves in Amazonia. *Conservation Biology* **19**, 728-
1727 733.
- 1728 PERES, C. A., GARDNER, T. A., BARLOW, J., ZUANON, J., MICHALSKI, F., LEES, A., VIEIRA, I.,
1729 MOREIRA, F. & FEELEY, K. J. (2010) Biodiversity conservation in human-modified
1730 Amazonian forest landscapes. *Biological Conservation* **143**, 2314-2327.
- 1731 PHILLIPS, O. L. & GENTRY, A. H. (1994) Increasing turnover through time in tropical forests.
1732 *Science* **263**, 954-958.
- 1733 PHILLIPS, O. L., MALHI, Y., HIGUCHI, N., LAURANCE, W. F., NUNEZ, P., VASQUEZ, R.,
1734 LAURANCE, S. G., FERREIRA, L. V., STERN, M., BROWN, S. & GRACE, J. (1998)
1735 Changes in the carbon balance of tropical forests: Evidence from long-term plots.
1736 *Science* **282**, 439-442.
- 1737 PHILLIPS, O. L., MARTINEZ, R., ARROYA, L., BAKER, T., KILLEEN, T., LEWIS, S. L., MALHI, Y.,
1738 MENDOZA, A. NEILL, D., VARGAS, P., ALEXIADES, M., CERON, C. DI FIORE, A., ERWIN,
1739 T., JARDIM, A. *et al.* (2002) Increasing dominance of large lianas in Amazonian
1740 forests. *Nature* **418**, 770-774.
- 1741 PITMAN, N. C. A., WIDMER, J., JENKINS, C. N., STOCKS, G., SEALES, L., PANIAGUA, F. &
1742 BRUNA, E. (2011) Volume and geographical distribution of ecological research in the
1743 Andes and the Amazon, 1995-2008. *Tropical Conservation Science* **4**, 64-81.
- 1744 PIMM, S. L. (1998) The forest fragment classic. *Nature* **393**, 23-24.
- 1745 PIMM, S. L. & JENKINS, C. (2005) Sustaining the variety of life. *Scientific American*,
1746 **September**, 66-73.

- 1747 POWELL, A. H. & POWELL, G. V. N. (1987) Population dynamics of male euglossine bees in
1748 Amazonian forest fragments. *Biotropica* **19**, 176-179.
- 1749 POWELL, L. L., STOUFFER, P. C. & JOHNSON, E. I. (2013) Recovery of understory bird
1750 movement across the interface of primary and secondary Amazon rainforest. *Auk* **130**,
1751 459-468.
- 1752 PUERTA, R. (2002) Regeneração arbórea em pastagens abandonadas na região de Manaus em
1753 função da distância da floresta contínua. *Scientia Forestalis* **62**, 32-39.
- 1754 QUINTELA, C. E. (1985) *Forest fragmentation and differential use of natural and man-made*
1755 *edges by understory birds in central Amazonia*. M.Sc. Thesis, University of Illinois,
1756 Chicago.
- 1757 QUINTERO, I. & ROSLIN, T. (2005) Rapid recovery of dung beetle communities following
1758 habitat fragmentation in Central Amazonia. *Ecology* **86**, 3303-3311.
- 1759 RADTKE, M. G., DA FONSECA, C. & WILLIAMSON, G. B. (2008) Forest fragment size effects on
1760 dung beetle communities. *Biological Conservation* **141**, 613-614.
- 1761 REGO, F., VENTICINQUE, E. M. & BRESCOVIT, A. (2007) Effects of forest fragmentation on
1762 four *Ctenus* spider populations (Araneae, Ctenidae) in central Amazonia, Brazil.
1763 *Studies of Neotropical Fauna and Environment* **42**, 137-144.
- 1764 RIBEIRO, M., BRUNA, E. M. & MANTOVANI, W. (2009) Influence of post-clearing treatment on
1765 the recovery of herbaceous plant communities in Amazonian secondary forests.
1766 *Restoration Ecology* **18**, 50-58.
- 1767 ROCHA, R. (2016) *Tropical forest fragmentation: Effects on the spatio-temporal dynamics of*
1768 *its bat communities*. Ph.D. thesis, University of Lisbon, Portugal.
- 1769 ROCHA, R., LÓPEZ-BAUCCELLS, A., FARNEDA, F. Z., GROENENBERG, M., BOBROWIEC, P.,
1770 CABEZA, M., PALMEIRIM, J. & MEYER, C. F. J. (2016) Consequences of a large-scale
1771 deforestation experiment for Central Amazonian bats: Disentangling the relative

- 1772 importance of local and landscape-scale effects. *Landscape Ecology*,
1773 DOI:10.1007/s10980-016-0425-3.
- 1774 ROSENFELD, D. (1999) TRMM observed first direct evidence of smoke from forest fires
1775 inhibiting rainfall. *Geophysical Research Letters* **26**, 3105-3108.
- 1776 SALATI, E. & VOSE, P. B. (1984) Amazon Basin: A system in equilibrium. *Science* **225**, 129-
1777 138.
- 1778 SALAZAR, L. F., NOBRE, C. A. & OYAMA, M. D. (2007) Climate change consequences on the
1779 biome distribution in South America. *Geophysical Research Letters* **34**, L09708.
- 1780 SAMPAIO, E. M. 2000. *Effects of forest fragmentation on the diversity and abundance patterns*
1781 *of central Amazonian bats*. Ph.D. Thesis, University of Tübingen, Germany.
- 1782 SAMPAIO, E. M., KALKO, E., BERNARD, E., RODRIGUEZ-HERRERA, B. & HANDLEY, C. (2003)
1783 A biodiversity assessment of bats (Chiroptera) in a tropical lowland forest of central
1784 Amazonia, including methodological and conservation considerations. *Studies of*
1785 *Neotropical Fauna and Environment* **28**, 17-31.
- 1786 SANTOS, B. A., ARROYO-RODRÍGUEZ, V., MORENO, C. & TABARELLI, M. (2010) Edge-related
1787 loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest.
1788 *PLoS ONE* **5**, e12625.
- 1789 SANTOS, B. A., TABARELLI, M., MELO, F. P. L., CAMARGO, J. L. C., ANDRADE, A., LAURANCE,
1790 S. G., LAURANCE, W. F. (2014) Phylogenetic impoverishment of Amazonian tree
1791 communities in an experimentally fragmented forest landscape. *PLoS ONE* **9**,
1792 e113109.
- 1793 SARMIENTO, J. L., GLOOR, M., GRUBER, N., BEAULIEU, C., JACOBSON, A., MIKALOFF F. S.,
1794 PACALA, S. & RODGERS, K. (2010) Trends and regional distributions of land and ocean
1795 carbon sinks. *Biogeosciences* **7**, 2351-2367.
- 1796 SCARIOT, A. (1999) Forest fragmentation effects on diversity of the palm community in

- 1797 central Amazonia. *Journal of Ecology* **87**, 66-76.
- 1798 SCARIOT, A. (2001) Weedy and secondary palm species in central Amazonian forest
1799 fragments. *Revista Brasileira do Botanica* **15**, 271-280.
- 1800 SCHNITZER, S. A. & BONGERS, F. (2011) Increasing liana abundance and biomass in tropical
1801 forests: Emerging patterns and putative mechanisms. *Ecology Letters* **14**, 397-406.
- 1802 SIZER, N. & TANNER, E. V. J. (1999) Responses of woody plant seedlings to edge formation in
1803 a lowland tropical rainforest. Amazonia. *Biological Conservation* **91**, 135-142.
- 1804 SIZER, N. TANNER, E. V. J. & KOSSMAN-FERRAZ, I. (2000) Edge effects on litterfall mass and
1805 nutrient concentrations in forest fragments in central Amazonia. *Journal of Tropical
1806 Ecology* **16**, 853-863.
- 1807 SKOLE, D. S. & TUCKER, C. J. (1993) Tropical deforestation and habitat fragmentation in the
1808 Amazon: Satellite data from 1978 to 1988. *Science* **260**, 1905-1910.
- 1809 SLOAN, S. P., JENKINS, C., JOPPA, L., GAVEAU, D. & LAURANCE, W. F. (2014) Remaining
1810 natural vegetation in the global biodiversity hotspots. *Biological Conservation* **177**,
1811 12-24.
- 1812 SOUZA, F. C., DEXTER, K., PHILLIPS, O., BRIENEN, R., CHAVE, J., GALBRAITH, D., GONZALEZ,
1813 G., MENDOZA, A., PENNINGTON, T., POORTER, L., ALEXIADES, M., DAVILA, E.,
1814 ANDRADE, A., ARAGAO, L., ARAUJO-MURAKAMI, A., *et al.* (2016) Evolutionary
1815 heritage influences Amazon tree ecology. *Proceedings of the Royal Society B* **283**,
1816 20161587; <http://dx.doi.org/10.1098/rspb.2016.1587>.
- 1817 STICKLER, C. M., NEPSTAD, D., COE, M., MCGRATH, D., RODRIGUES, H., WALKER, W.,
1818 SOARES-FILHO, B. & DAVIDSON, E. A. (2009) The potential ecological costs and co-
1819 benefits of REDD: A critical review and case study from the Amazon region. *Global
1820 Change Biology* **15**, 2803-2824.
- 1821 STOUFFER, P. C. & BIERREGAARD, R. O. (1995a) Effects of forest fragmentation on understory

- 1822 hummingbirds in Amazonian Brazil. *Conservation Biology* **9**, 1085-1094.
- 1823 STOUFFER, P. C. & BIERREGAARD, R. O. (1995b) Use of Amazonian forest fragments by
1824 understory insectivorous birds. *Ecology* **76**, 2429-2445.
- 1825 STOUFFER, P. C., BIERREGAARD, R. O., STRONG, C. & LOVEJOY, T. E. (2006) Long-term
1826 landscape change and bird abundance in Amazonian rainforest fragments.
1827 *Conservation Biology* **20**, 1212-1223.
- 1828 STOUFFER, P. C., STRONG, C. & NAKA, L. N. (2008) Twenty years of understory bird
1829 extinctions from Amazonian rain forest fragments: Consistent trends and landscape-
1830 mediated dynamics. *Diversity and Distributions* **15**, 88-97.
- 1831 STOUFFER, P. C., JOHNSON, E. I., BIERREGAARD, R. O. & LOVEJOY, T. E. (2011) Understory
1832 bird communities in Amazonian rainforest fragments: Species turnover through 25
1833 years post-isolation in recovering landscapes. *PLoS ONE* **6**, e20543.
- 1834 STRATFORD, J. A. & STOUFFER, P. C. (1999) Local extinctions of terrestrial insectivorous birds
1835 in Amazonian forest fragments. *Conservation Biology* **13**, 1416-1423.
- 1836 SUD, Y., YANG, R. & WALKER, G. (1996) Impact of in situ deforestation in Amazonia on the
1837 regional climate: general circulation model simulation study. *Journal of Geophysical*
1838 *Research* **101**, 7095-7109.
- 1839 TERBORGH, J., LOPEZ, L., NUÑEZ, P., RAO, M., SHAHABUDDIN, G., ORIHUELA, G., RIVEROS,
1840 M., ASCANIO, R., ADLER, G., LAMBERT, T. & BALBAS, L. (2001) Ecological meltdown
1841 in predator-free forest fragments. *Science* **294**, 1923-1926.
- 1842 TER STEEGE, H., PITMAN, N. C. A., SABATIER, D., BARALOTO, C., SALOMAO, R., GUEVARA, J.,
1843 PHILLIPS, O. L., VOLKMER, C., MAGNUSSON, W., MOLINO, J.-F., BANKI, O., MENDOZA,
1844 M., NUNEZ, P., MONTERO, J. FELDPAUSCH, T. *et al.* (2013) Hyperdominance in the
1845 Amazonia flora. *Science* **342**, 326-334.
- 1846 TIMO, T. P. C. (2003) *Influência de fragmentação e matriz sobre a comunidade de mamíferos*

- 1847 *de médio e grande porte em uma floresta de terra firme na Amazônia central*. M.Sc.
- 1848 Thesis, National Institute for Amazonian Research (INPA), Manaus, Brazil.
- 1849 TOCHER, M., GASCON, C. & ZIMMERMAN, B. L. (1997) Fragmentation effects on a central
- 1850 Amazonian frog community: A ten-year study. In *Tropical Forest Remnants: Ecology,*
- 1851 *Management, and Conservation of Fragmented Communities* (eds W. F. Laurance &
- 1852 R. O. Bierregaard), pp. 124-137. University of Chicago Press, Chicago.
- 1853 TRANCOSO, R. (2008) *Hydrological impacts of deforestation in small catchments in Brazilian*
- 1854 *Amazonia*. M.Sc. Thesis, National Institute for Amazonian Research (INPA), Manaus,
- 1855 Brazil.
- 1856 Tschardtke, T., Tylianakis, J., Rand, T., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J.,
- 1857 Clough, Y. Crist, T., Dormann, C., Ewers, R., Frund, J., Holt, R., Holzschuh, A.,
- 1858 Klein, A. *et al.* (2012) Landscape moderation of biodiversity patterns and processes—
- 1859 eight hypotheses. *Biological Reviews* **87**, 661-685.
- 1860 URIARTE, M., BRUNA, E. M., RUBIM, P., ANCIÃES, M. & JONCKHEERE, I. (2010) Effects of
- 1861 forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs.
- 1862 safe-site limitation. *Ecology* **91**, 1317-1328.
- 1863 VAN BREUGEL, M., HALL, J. S., CRAVEN, D., BAILON, M., HERNANDEZ, A., ABBENE, M. &
- 1864 VAN BREUGEL, P. (2013) Succession of ephemeral secondary forests and their limited
- 1865 role for the conservation of floristic diversity in a human-modified tropical landscape.
- 1866 *PLoS ONE* **8**, e82433.
- 1867 VAN HOUTAN, K. S., PIMM, S. L., BIERREGAARD, R. O., LOVEJOY, T. E. & STOUFFER, P. C.
- 1868 (2006) Local extinctions in Amazonian forest fragments. *Evolutionary Ecology*
- 1869 *Research* **8**, 129- 148.
- 1870 VAN HOUTAN, K. S., PIMM, S. L., HALLEY, J., BIERREGAARD, R. O. & LOVEJOY, T. E. (2007)
- 1871 Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters*

- 1872 **10**, 219-229.
- 1873 VASCONCELOS, H. L. & LUIZÃO, F. J. (2004) Litter production and litter nutrient concentrations
1874 in a fragmented Amazonian landscape: Edge and soil effects. *Ecological Applications*
1875 **14**, 884-892.
- 1876 VERA, C., SILVESTRI, G., LIEBMANN B. & GONZÁLEZ, P. (2006) Climate change scenarios for
1877 seasonal precipitation in South America from IPCC-AR4 models. *Geophysical*
1878 *Research Letters* **33**, DOI:10.1029/2006GL025759.
- 1879 WALKER, G., SUD, Y. & ATLAS, R. (1995) Impact of ongoing Amazonian deforestation on
1880 local precipitation: a GCM simulation study. *Bulletin of the American Meteorological*
1881 *Society* **76**, 346-361.
- 1882 WANDELLI, E. V. & FEARNSIDE, P. M. (2015) Secondary vegetation in central Amazonia:
1883 Land-use history effects on aboveground biomass. *Forest Ecology and Management*
1884 **347**, 140-148.
- 1885 WILCOX, B. A. & MURPHY, D. D. (1985) Conservation strategy: the effects of fragmentation
1886 on extinction. *American Naturalist* **125**, 879-887.
- 1887 WIELAND, L. M., MESQUITA, R., BOBROWIEC, P., BENTOS, T. & WILLIAMSON, G. B. (2011)
1888 Seed rain and advance regeneration in secondary succession in the Brazilian Amazon.
1889 *Tropical Conservation Science* **4**, 300-316.
- 1890 WILLIAMSON, G. B., LAURANCE, W. F., OLIVEIRA, A., DELAMONICA, P., GASCON, C.,
1891 LOVEJOY, T. E. & POHL, L. (2000) Amazonian wet forest resistance to the 1997-98 El
1892 Niño drought. *Conservation Biology* **14**, 1538-1542.
- 1893 WILLIAMSON, G. B., LONGWORTH, J., BENTOS, T. & MESQUITA, R. (2014) Convergence and
1894 divergence in alternative successional pathways in Central Amazonia. *Plant Ecology*
1895 *and Diversity* **7**, 341-348.
- 1896 WILLIAMSON, G. B. & MESQUITA, R. (2001) Effects of fire on rain forest regeneration in the

- 1897 Amazon Basin. In *Tropical Forest Remnants: Ecology, Management, and*
1898 *Conservation of Fragmented Communities* (eds W. F. Laurance & R. O. Bierregaard),
1899 pp. 325-334. University of Chicago Press, Chicago.
- 1900 WOLFE, J. D., STOUFFER, P. C., MOKROSS, K., POWELL, L. L. & ANCIÃES, M. (2015) Island vs.
1901 countryside biogeography: an examination of how Amazonian birds respond to forest
1902 clearing and fragmentation. *Ecosphere* **6**, 1-14.
- 1903 ZARTMAN, C. E. (2003) Forest fragmentation effects on epiphyllous bryophyte communities
1904 in central Amazonia. *Ecology* **84**, 948-954.
- 1905 ZARTMAN, C. E. & NASCIMENTO, H. E. M. (2006) Are patch-tracking metacommunities
1906 dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in
1907 Amazonian forest fragments. *Biological Conservation* **127**, 46-54.
- 1908 ZARTMAN, C. E. & SHAW, A. J. (2006) Metapopulation extinction thresholds in rainforest
1909 remnants. *American Naturalist* **167**, 177-189.
- 1910

FIGURE CAPTIONS

1911

1912

1913 **Fig. 1.** Map of the Biological Dynamics of Forest Fragments Project in central Amazonia.

1914

1915 **Fig. 2.** Habitat fragmentation in eastern Amazonia caused by a forest-colonization project
1916 (Tailândia) and cattle ranching (Paragominas). Forests are black and cleared areas are grey.

1917 Each scene shows an area of about 600 km² (adapted from Cochrane & Laurance, 2002).

1918

1919 **Fig. 3.** The vegetation-breeze phenomenon, which can promote forest desiccation in the
1920 general vicinity of pastures and clearings (from Cochrane & Laurance, 2008).

1921

1922 **Fig. 4.** Rates of tree growth in intact forests of the BDFFP accelerated over time for the large
1923 majority (84%) of tree genera (from Laurance *et al.*, 2004a). Data shown are mean rates of
1924 trunk-diameter growth for genera that increased or decreased significantly in abundance over
1925 time in the plots, as well as those that showed no significant trend. Interval 1 was 1984-1991,
1926 and interval 2 was 1992-1999.

1927

1928 **Fig. 5.** Increase in the abundance of lianas in intact-forest plots of the BDFFP (from Laurance
1929 *et al.*, 2014a). The solid line shows $y=x$ whereas the dotted line is a linear regression fitted to
1930 the data.

1931

1932 **Fig. 6.** Negative association between liana abundance and the aboveground biomass of live
1933 trees in BDFFP forest-dynamics plots (from Laurance *et al.*, 2001b).

1934

1935 **Fig. 7.** The diversity of edge-effect phenomena studied at the BDFFP and the distance to

1936 which each was found to penetrate into fragment interiors (adapted from Laurance *et al.*,
1937 2002).

1938

1939 **Fig. 8.** The effects of single versus multiple nearby forest edges on (a) stand-level tree
1940 mortality and the (b) density and (c) species richness of disturbance-loving pioneer tree
1941 species. Values shown are the mean \pm SD (from Laurance *et al.*, 2006a).

1942

1943 **Fig. 9.** Elevated temporal variation in butterfly species richness in fragmented forests. Shown
1944 is an index of variability in species richness for fragmented and intact sites sampled in
1945 consecutive years (adapted from Leidner *et al.*, 2010).

1946

1947 **Fig. 10.** Elevated temporal variation (coefficient of variation) in the number of tree stems per
1948 plot, shown as a function of distance from the nearest forest edge.

1949

1950 **Fig. 11.** Increasing divergence over time of tree-community composition in three fragmented
1951 landscapes at the BDFFP. Tree communities in forest-edge plots (<100 m from the nearest
1952 edge) are shown before forest fragmentation and 13-18 years after fragmentation, based on an
1953 ordination analysis. The ordination used importance values for all 267 tree genera found in the
1954 study plots (from Laurance *et al.*, 2007).

1955

1956 **Fig. 12.** Plots near forest edges (<100 m from edge) generally have higher tree mortality,
1957 more small trees, and more woody debris, relative to plots in forest interiors. Data shown are
1958 from an ordination analysis of 14 forest-biomass and necromass variables from 50 BDFFP
1959 plots (from Nascimento and Laurance, 2004).

1960

1961 **Fig. 13.** Striking increases over time in the density of 52 species of early successional trees in
1962 forest fragments in the BDFFP study area. Note that vertical axes are \log_{10} -transformed (after
1963 Laurance *et al.*, 2006a).

1964

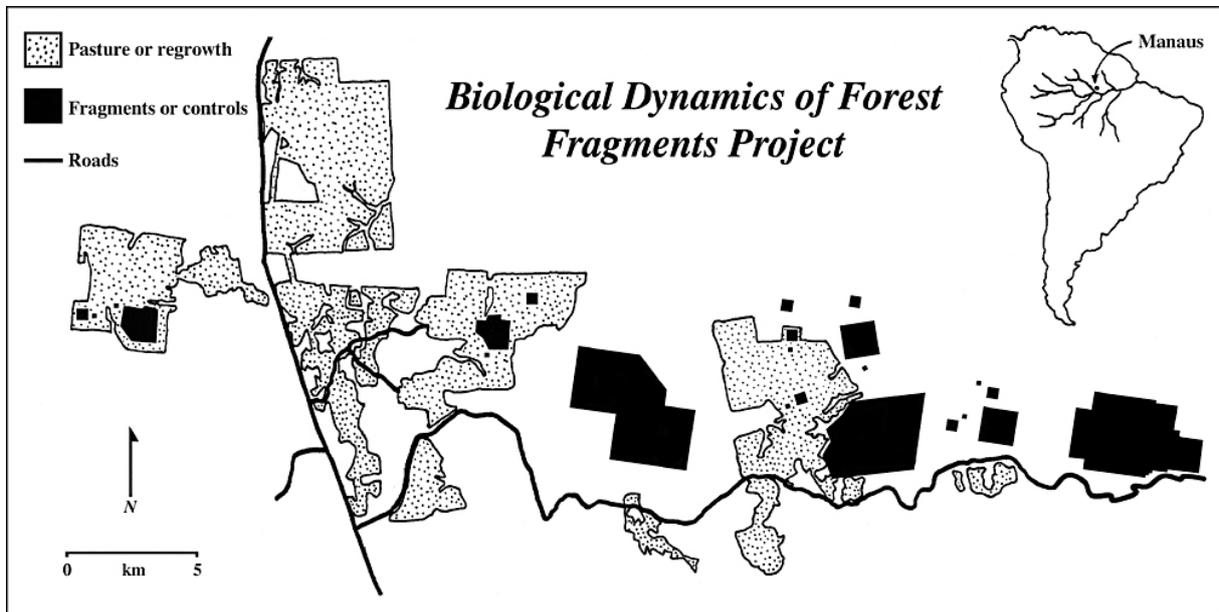
1965 **Fig. 14.** Changes over time in the phylogenetic diversity of tree communities in 1-ha plots in
1966 the BDFFP study area (adapted from Santos *et al.*, 2014). Points with positive values (above
1967 the horizontal line) exhibited declining phylogenetic diversity over time, whereas those with
1968 negative values had opposite trends.

1969

1970

1971 Fig. 1

1972

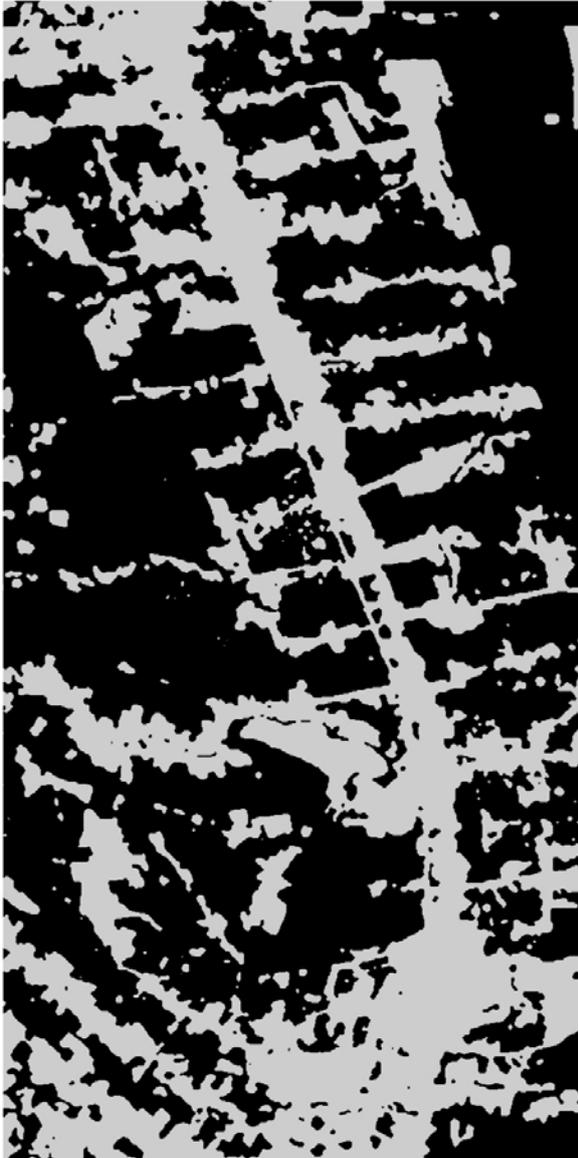


1973
1974

1975 Fig. 2

1976

Tailândia



Paragominas

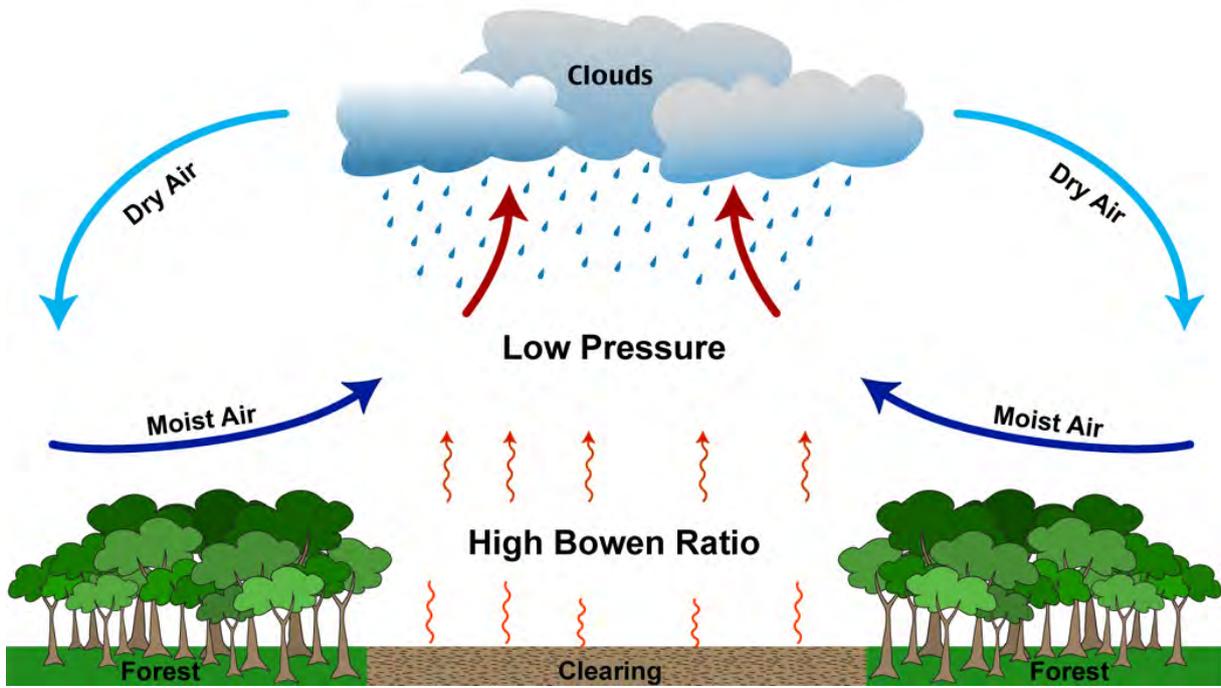


1977
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1979 Fig. 3

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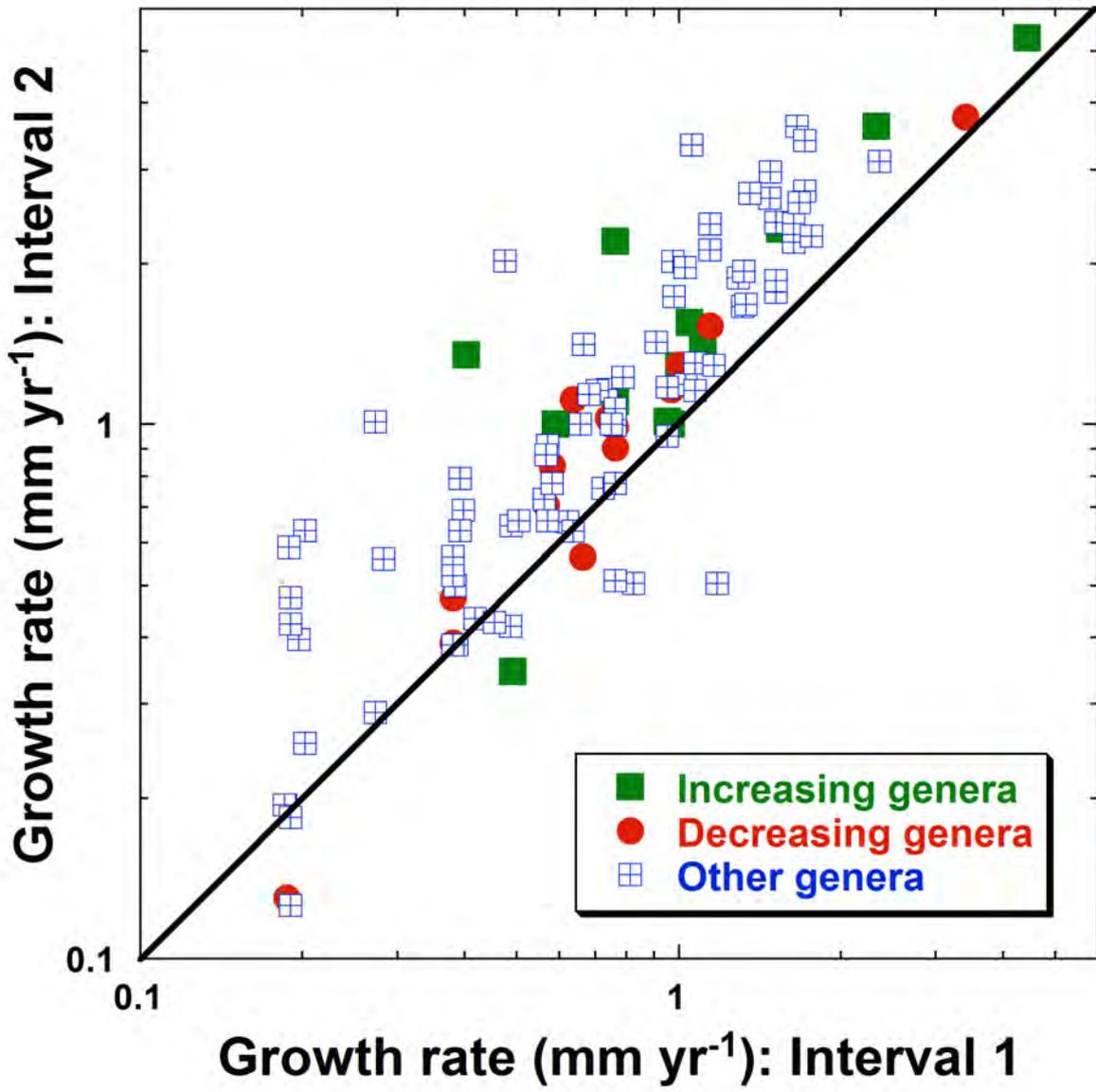
The Vegetation Breeze



1981
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1983 Fig. 4

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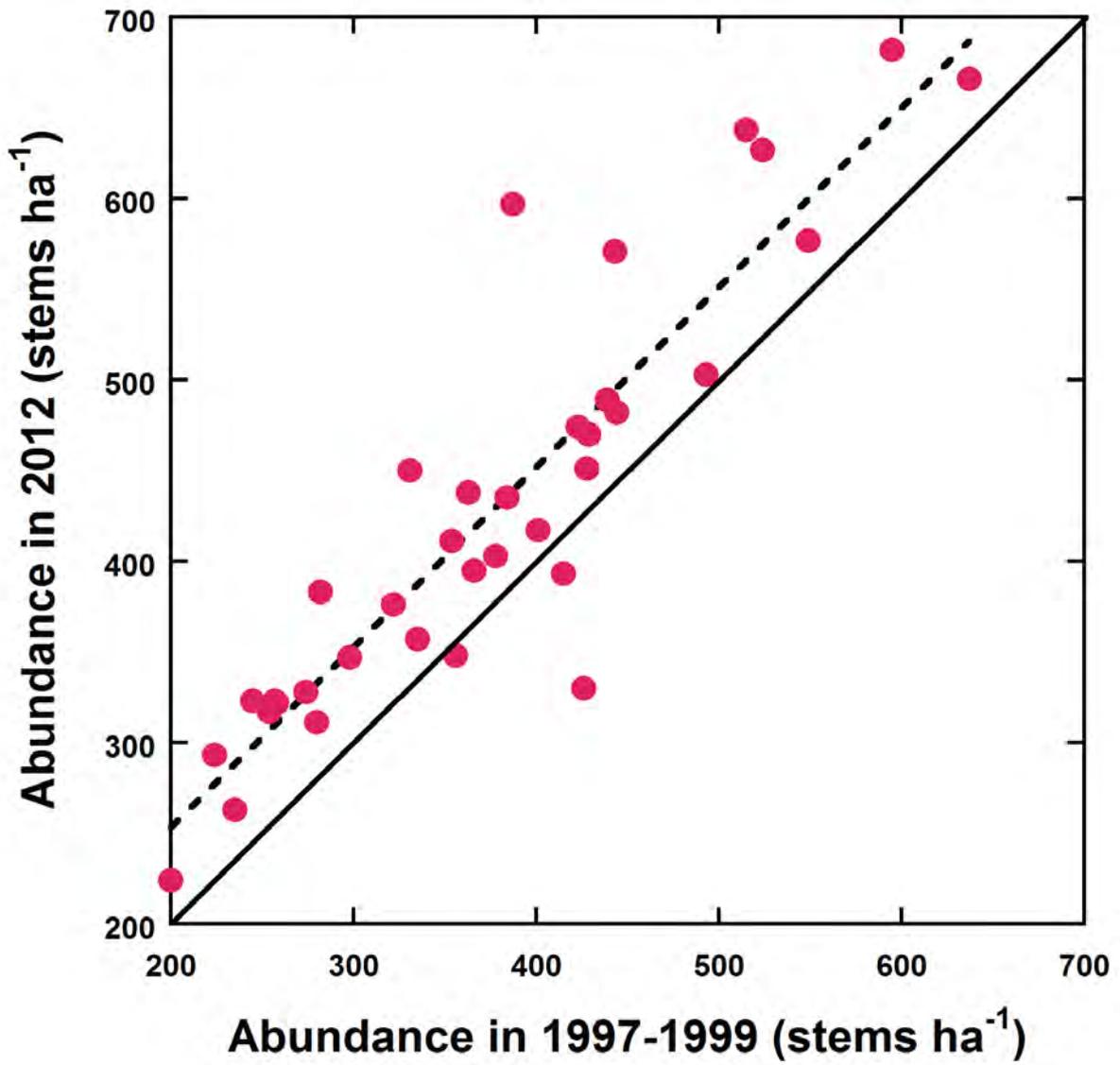
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1988 Fig. 5

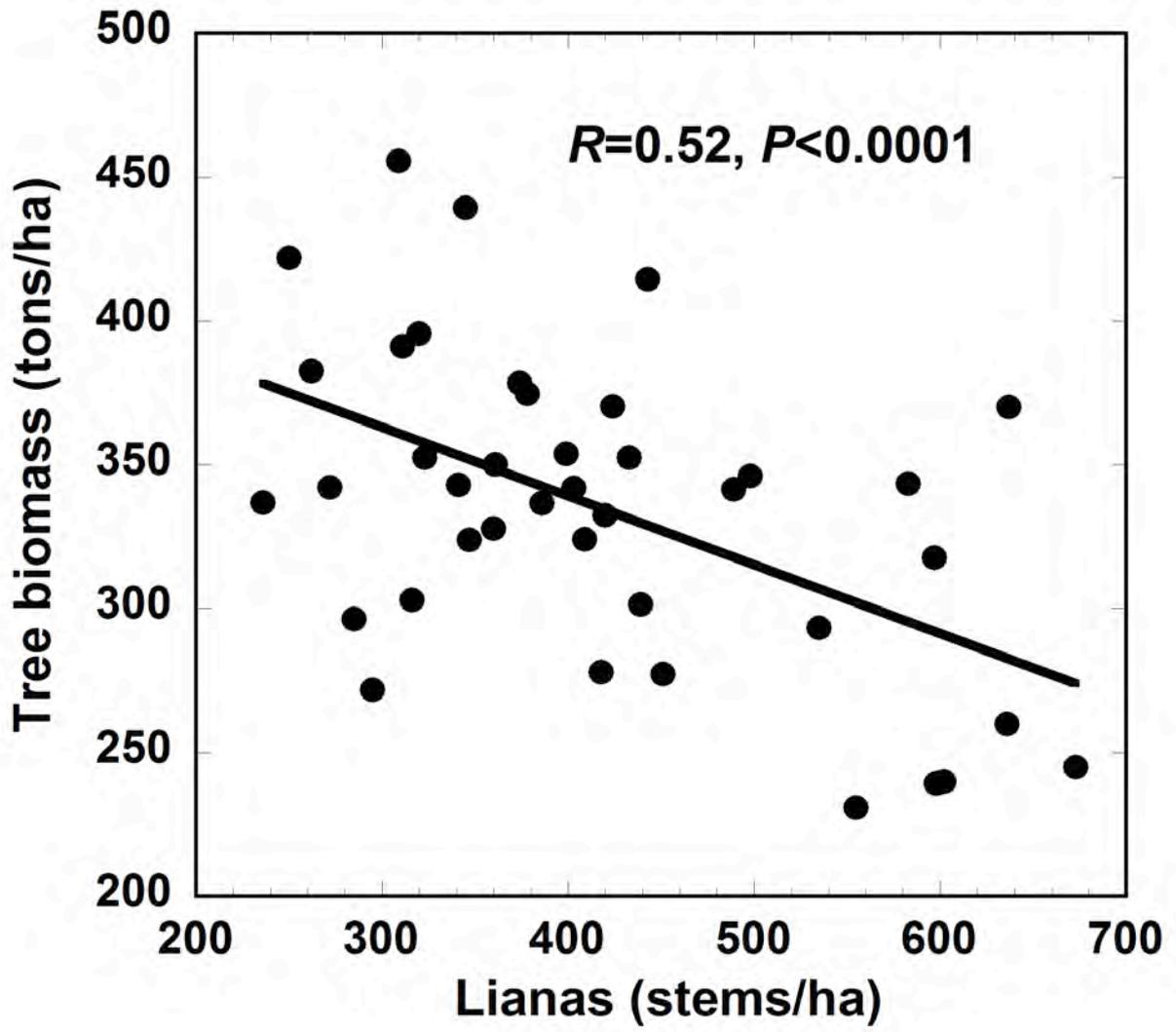
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1992 Fig. 6

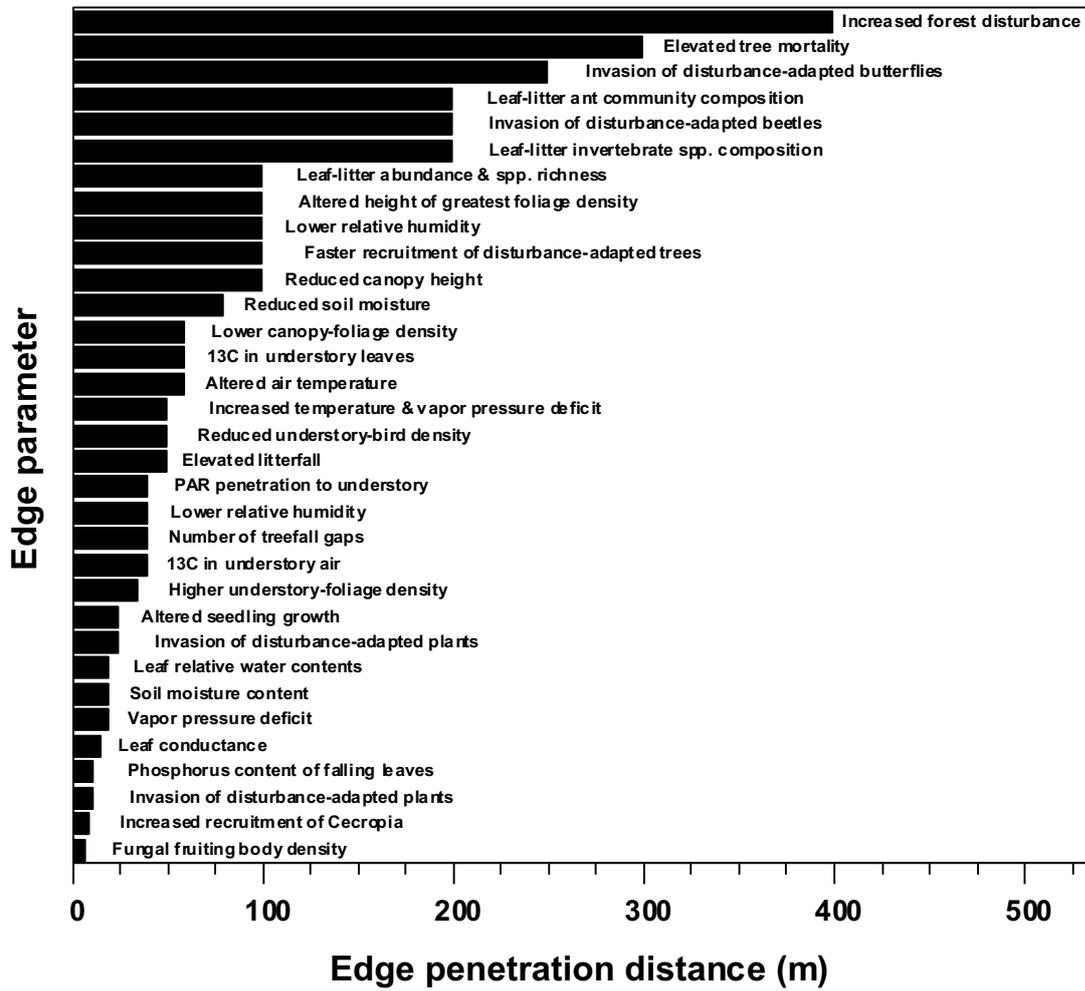
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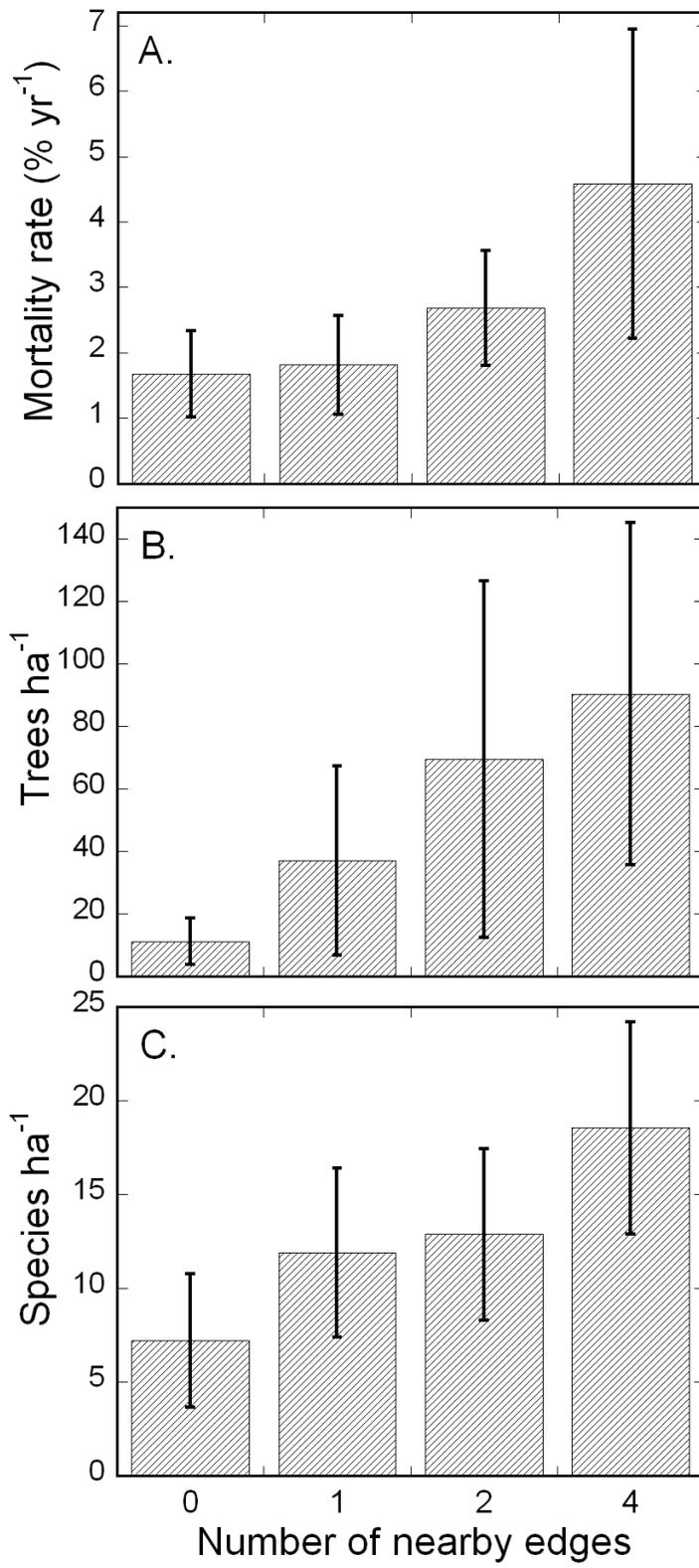
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2002 Fig. 8

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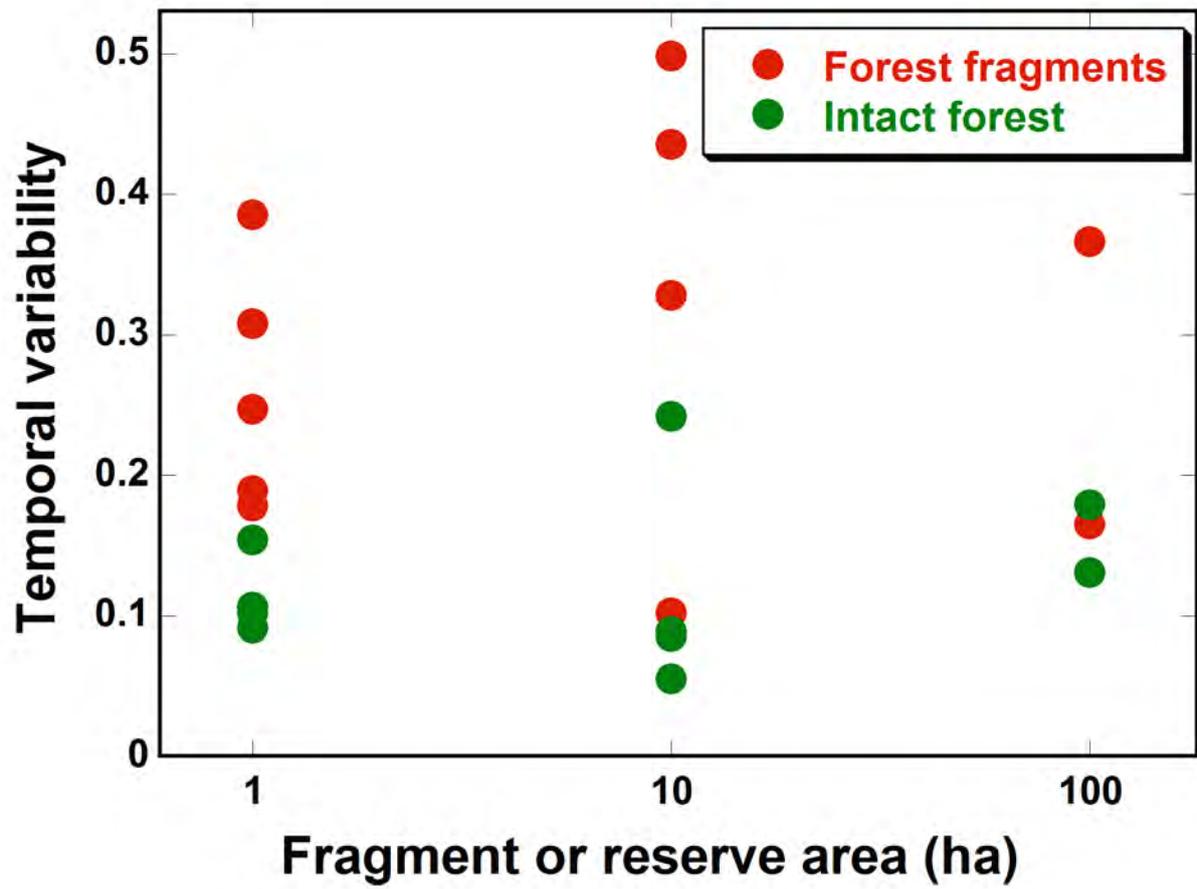


2004

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2006 Fig. 9

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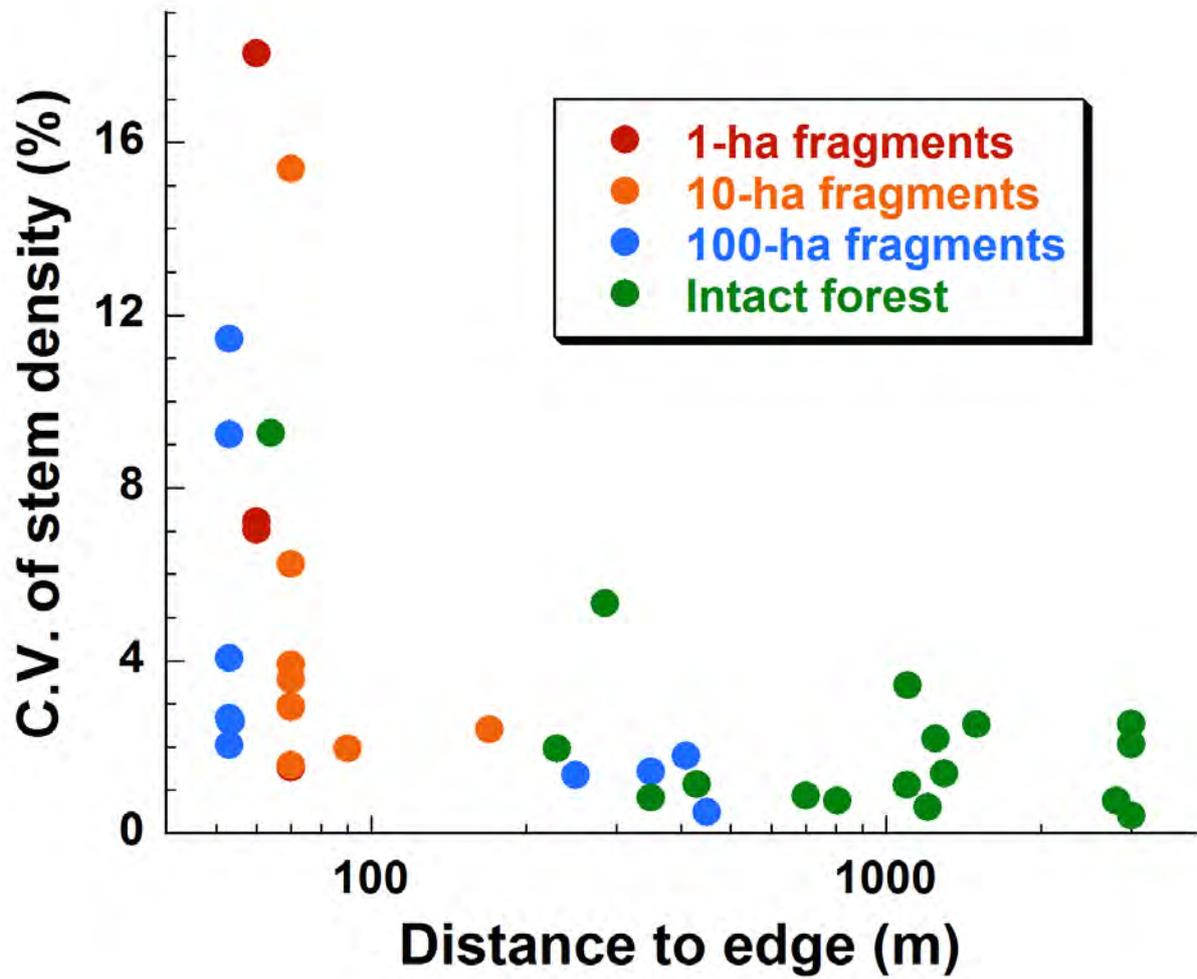


2008

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2010 Fig. 10

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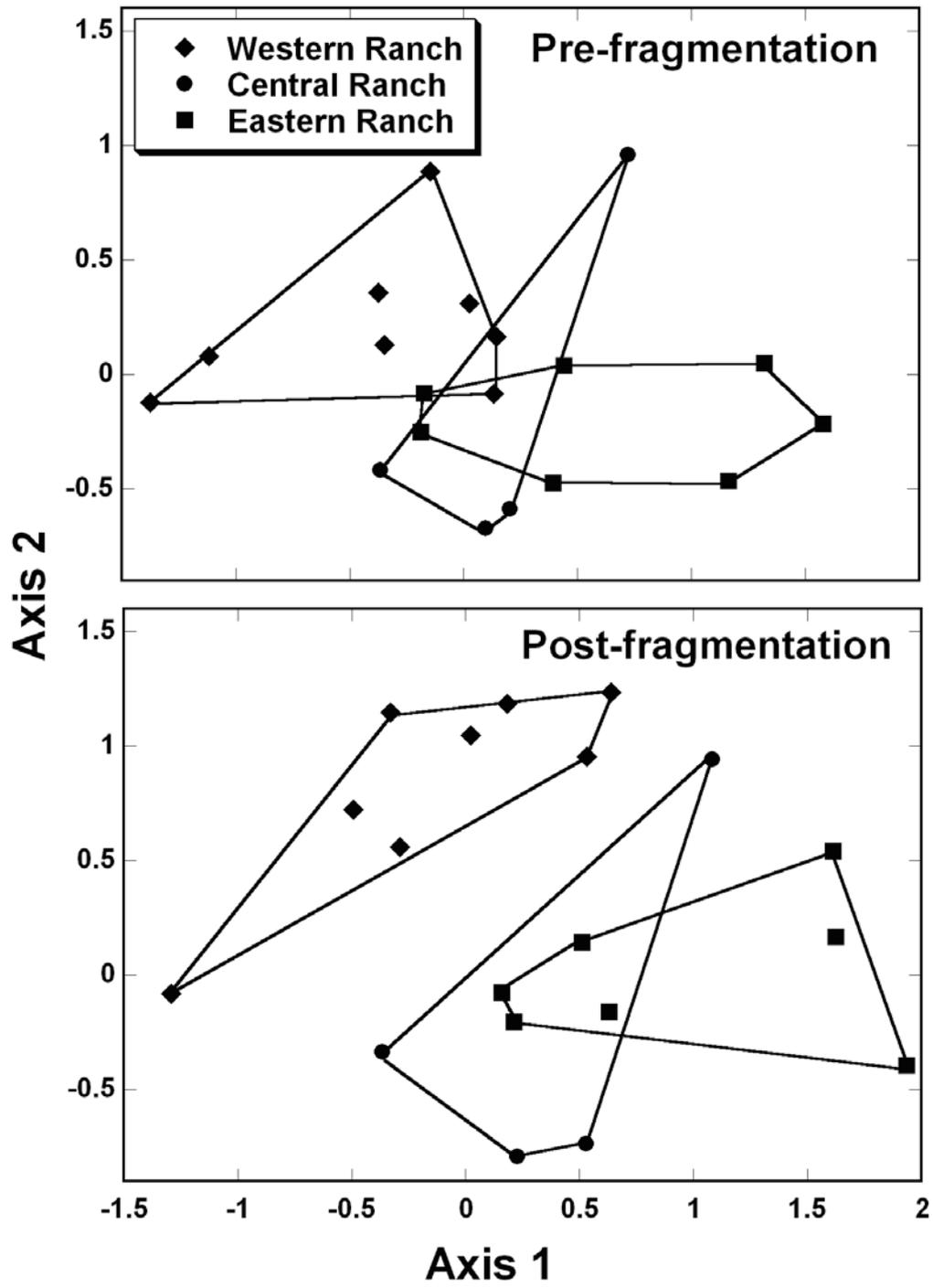


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2013

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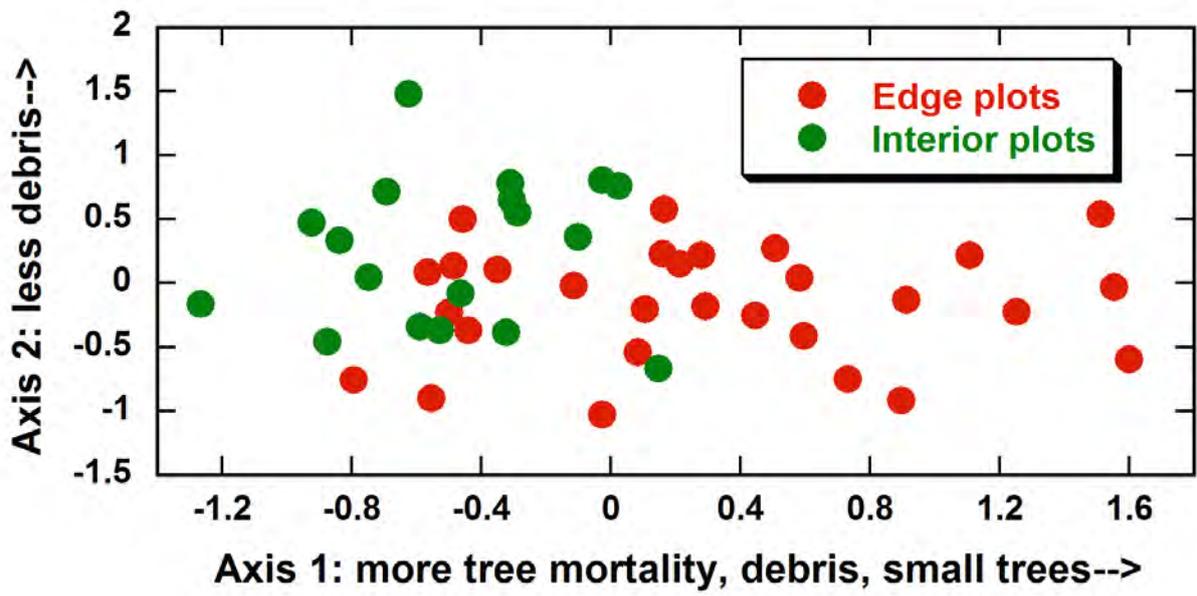
2015 Fig. 11



2016
2017

2018 Fig. 12

2019



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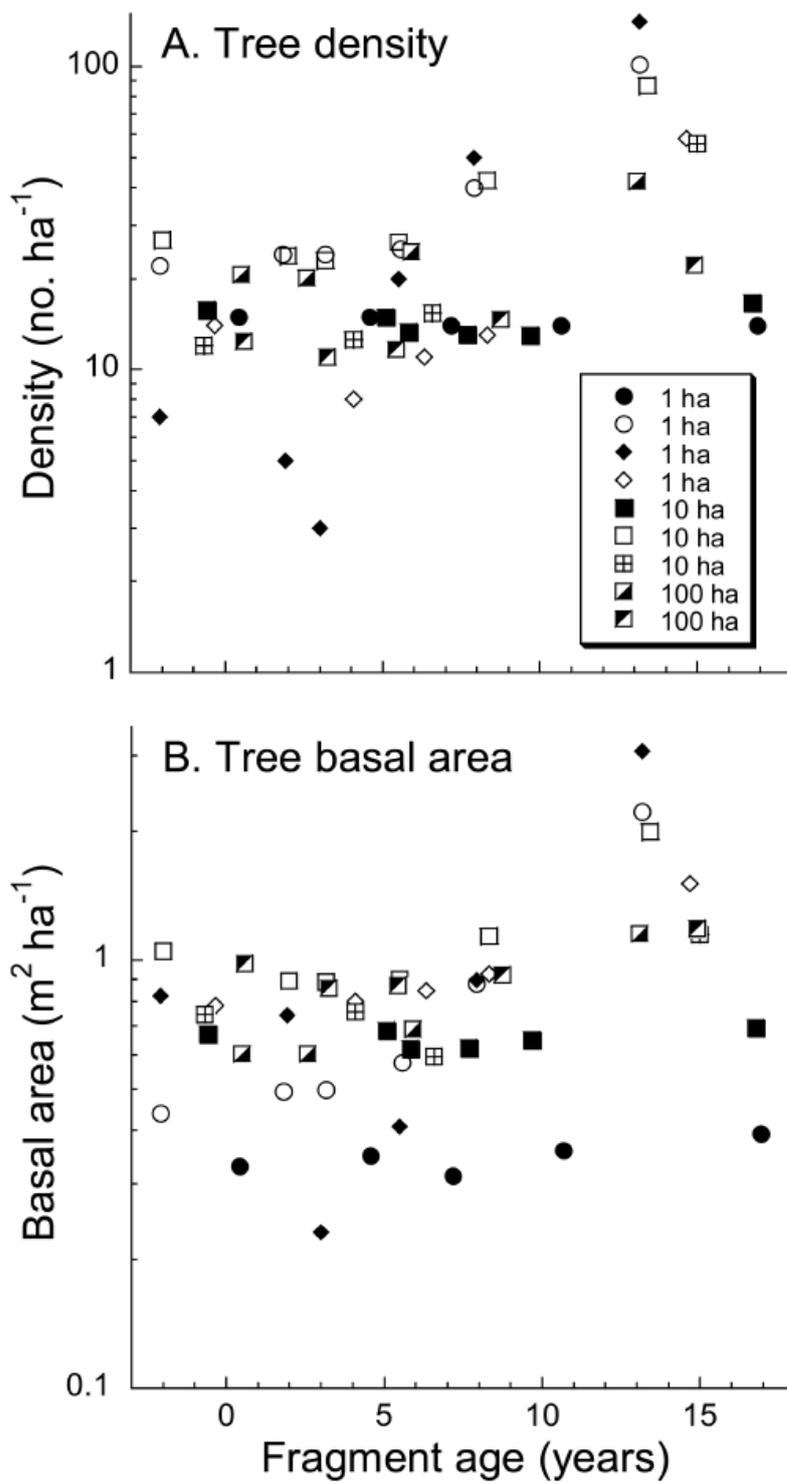
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2025 Fig. 13

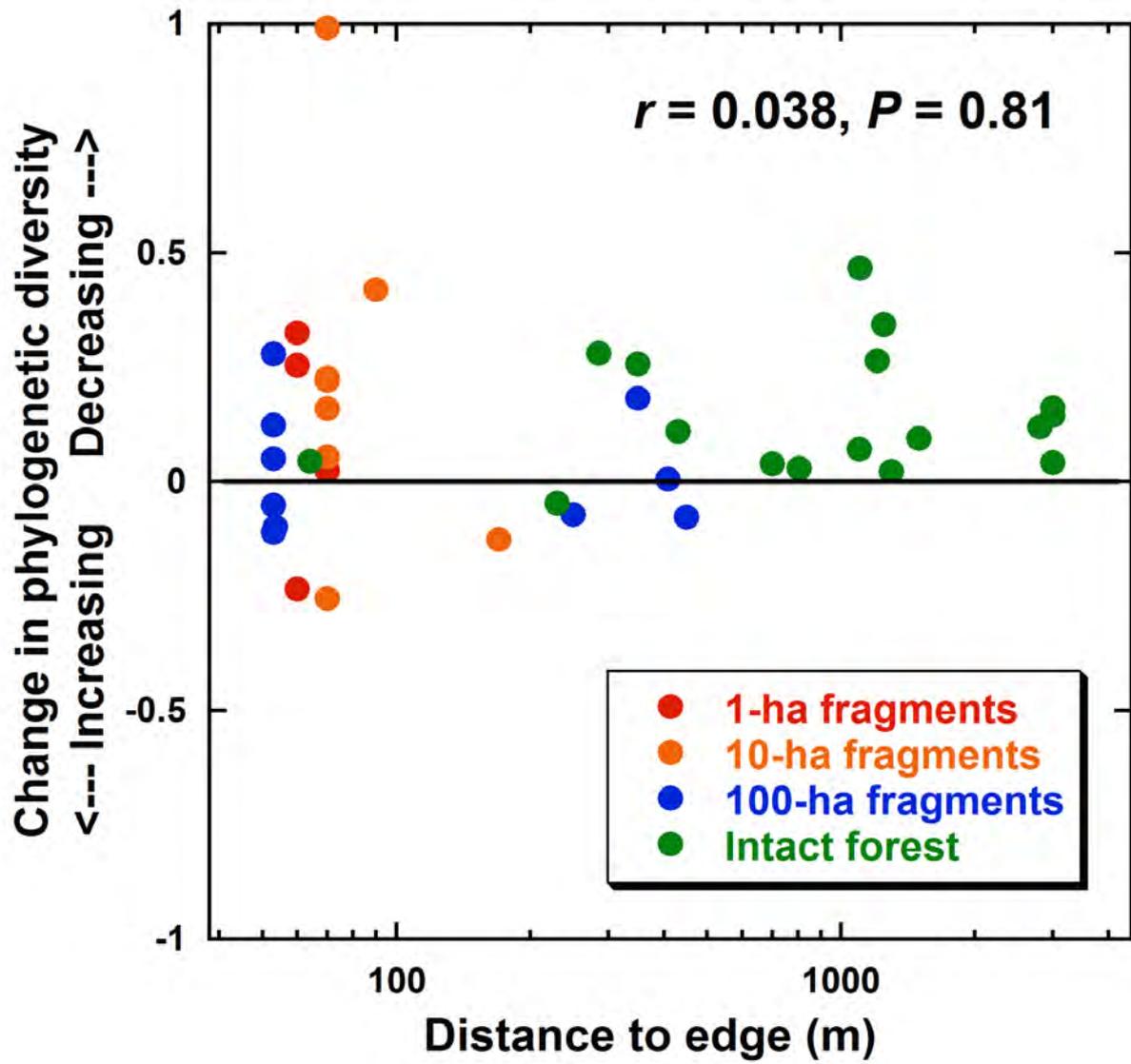


2026

2027

2028 Fig. 14

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