

Socolar, Valderrama Sandoval & Wilcove: Biodiversity in Amazonian slash-and-burn

1 **Overlooked biodiversity loss in Amazonian smallholder agriculture**

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## 16 **ABSTRACT**

17 Diversified smallholder agriculture is the main human land-use affecting the western Amazon, home  
18 to the world's richest terrestrial biota, but the scant available data to date have suggested that the  
19 biodiversity impacts of this land-use are small. Here, we present comprehensive surveys of birds and  
20 trees in primary forest and smallholder agricultural mosaics in northern Peru. These surveys reveal  
21 substantial biodiversity losses that have been overlooked by other studies. Avian biodiversity losses  
22 arise primarily from biotic homogenization across infrequently surveyed forest habitats (a loss of  
23 beta-diversity). Furthermore, tree species richness declines much more steeply than bird richness.  
24 Statistical modeling of local habitat features that allow forest-associated species to persist in the  
25 smallholder mosaic strongly suggests that our results represent a best-case scenario for Amazonian  
26 agricultural biodiversity. We conclude that previous assessments of the biodiversity value of  
27 Amazonian smallholder agriculture have been overly optimistic because they are restricted to upland  
28 habitat, thereby missing losses in beta diversity; do not evaluate trees; and/or rely on generalizations  
29 from less speciose areas of the Neotropics, where habitat specialization amongst species is less  
30 prevalent. Smallholder agriculture will likely expand in western Amazonia due to infrastructure  
31 development, and it must be seen as a serious threat to the region's biodiversity.

32 **Key words:** Amazon, beta diversity, birds, Peru, trees

33

## 34 **INTRODUCTION**

35 The western Amazon is the global epicenter of terrestrial biodiversity (Jenkins et al. 2013)  
36 and the largest remaining tropical forest wilderness (Tyukavina et al. 2015), but it is nevertheless  
37 threatened by human activities. In contrast to the mechanized agriculture and ranching in  
38 southeastern Amazonia, the principal driver of forest loss in the western Amazon is smallholder  
39 slash-and-burn agriculture (Finer & Novoa 2016; Ravikumar et al. 2017). This practice creates

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40 mosaics of cultivations and secondary forest surrounding human settlements. The prospect of  
41 increased smallholder settlement in western Amazonia in the wake of roadbuilding and  
42 hydrocarbons development has raised alarm for this bastion of tropical biodiversity. For example,  
43 most of western Amazonia is covered in hydrocarbons concessions, the development of which  
44 would provide road access for settlers (Finer & Orta-Martínez 2010; Laurance et al. 2014).

45 Existing data on biodiversity in western Amazonian agriculture are extremely scant,  
46 consisting of two small-scale studies of birds and dung beetles, respectively (Andrade & Torgler  
47 1994; Korasaki et al. 2013). These studies document comparable avian richness in slash-and-burn  
48 mosaic and primary forest (Andrade & Torgler 1994), and comparable dung beetle richness in young  
49 secondary forest and primary forest (Korasaki et al. 2013). These isolated results contrast with  
50 results obtained from more intensive land-use change in the eastern Amazon (e.g. large-scale  
51 agriculture, fragmentation, silviculture, or fire; Ferraz et al. 2007; Barlow et al. 2007; Berry et al.  
52 2008; Mahood et al. 2011; Gardner et al. 2013; Lees et al. 2015; Moura et al. 2016). However, they  
53 agree with numerous Mesoamerican studies that have documented high levels of biodiversity in  
54 smallholder mosaics (Daily et al. 2001; Sekercioglu et al. 2007; Ranganathan et al. 2008; Karp et al.  
55 2011; Mendenhall et al. 2011) and have generated sustained debates over the relative conservation  
56 benefits of protecting primary-forest versus preventing agricultural intensification/industrialization  
57 of smallholder mosaics, especially given limited funding for conservation (Phalan et al. 2011; Gibson  
58 et al. 2011). This debate has a special urgency in the western Amazon, where forests remain largely  
59 intact but under increasing threat from smallholder agriculture, including inside protected areas  
60 (Finer & Novoa 2016).

61 Despite concordant results from Andrade and Torgler (1994) and Korasaki et al.  
62 (2013) that would downplay the significance of smallholder agriculture and conversion of primary  
63 forest to secondary forest, there are strong reasons to think that the impacts of smallholder activities

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64 on Amazonian biodiversity might be more severe than previously recognized. Thus, the biodiversity  
65 impacts of the main land-use affecting the world's richest terrestrial biota remain unknown. First,  
66 the few Amazonian studies that have examined smallholder agriculture either have included  
67 relatively few smallholder sites (e.g. 7 out of 361 sites in smallholder habitats in Moura et al. 2013) or  
68 are limited in their total sampling (Andrade & Torgler 1994; Korasaki et al. 2013). For example,  
69 Andrade and Torgler (1994) found bird diversity comparable to primary forest in Colombian slash-  
70 and-burn mosaics, but this conclusion rests on only understory birds sampled over a relatively small  
71 area.

72 Second, Amazonia is more species-rich than other areas of the Neotropics, so data from  
73 Mesoamerica might not generalize to the Amazon. Ecological theory predicts that habitat  
74 specialization among species should be more frequent in hyperdiverse communities (MacArthur &  
75 Levins 1967), and this might predispose Amazonian communities to be more sensitive to habitat  
76 alteration. Consistent with this idea, modelling work suggests that a given deforestation scenario  
77 would impact Amazonian bird communities more heavily than their Mesoamerican counterparts  
78 (Newbold et al. 2014).

79 Third, previous studies focused on the upland (*terra firme*) forest of uplifted clay terraces. Yet  
80 Amazonia contains additional forest types that are critical for biodiversity and are also impacted by  
81 slash-and-burn. These include floodplain habitats, bamboo forests, and forests on white-sand soils,  
82 all of which harbor specialist species that do not occur in terra firme forests (Remsen & Parker 1983;  
83 Wittmann et al. 2006; Fine et al. 2010; Alvarez Alonso et al. 2013; Socolar et al. 2013). Because biotic  
84 homogenization can drive landscape-scale biodiversity loss in tropical forests (Karp et al. 2012; Solar  
85 et al. 2015; Alroy 2017; Giam 2017), effective conservation planning requires an extensive  
86 comparison of biodiversity in intact and degraded landscapes across multiple forest types (Socolar et

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87 al. 2016). However, we are unaware of any data from the western Amazon that evaluate the  
88 biodiversity consequences of land-use change across multiple forest-types simultaneously.

89 Here, we quantify the biodiversity consequences of Amazonian slash-and-burn agriculture  
90 based on extensive field surveys of bird and tree diversity in Loreto department, Peru. In Loreto,  
91 upland, floodplain, and white-sand forests collectively harbor the richest avifauna and tree flora on  
92 Earth (ter Steege et al. 2013). Although the area remains largely roadless, the city of Iquitos is the  
93 world's largest city without an outside road link (circa 0.5 million inhabitants), and slash-and-burn  
94 mosaics are ubiquitous along rivers and local roads (Mäki et al. 2001). Furthermore, slash-and-burn  
95 is practiced to varying degrees, often legally, inside the region's protected areas (Pulgar Vidal &  
96 Gamboa Moquillaza 2013). Therefore, our results stand to inform conservation practices and  
97 priorities across this hyperdiverse yet understudied region in the face of ongoing smallholder  
98 expansion.

99 Despite previous work suggesting that the biodiversity value of tropical smallholder  
100 landscapes is very high (Sekercioglu et al. 2007; Karp et al. 2011; Mendenhall et al. 2011), we  
101 hypothesized that habitat specialists would fare poorly at disturbed sites, driving landscape-scale  
102 biodiversity declines via a reduction in beta-diversity (Karp et al. 2012; Socolar et al. 2016).

103

## 104 **METHODS**

### 105 **STUDY SITES**

106 We conducted fieldwork in the Amazonian lowlands of Loreto Department, Peru within 230  
107 km of the city of Iquitos. Natural habitats in the region are varied and interdigitate at fine spatial  
108 scales. We focused on four terrestrial habitats that harbor distinctive biological communities.  
109 Quintessential *upland forest* grows on uplifted clay-soil terraces of (Higgins et al. 2011). These uplands  
110 are the most spatially extensive habitat in the region and the richest in bird and tree species.

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111 *Floodplain forest* along major rivers, subject to protracted flooding during January-June (Espinoza et al.  
112 2013), differs from the uplands in tree and bird species composition (Remsen & Parker 1983;  
113 Wittmann et al. 2004). *White-sand forest* occurs on deposits of pure white-sand soil (arenosols) and  
114 supports a characteristic avifauna and flora that is absent from other habitats (Fine et al. 2010;  
115 Alvarez Alonso et al. 2013). Lastly, *river islands* harbor *Cecropia* (Urticaceae)-dominated woodland  
116 with a characteristic suite of specialist birds (Rosenberg 1990). Slash-and-burn agriculture affects all  
117 of these habitats, removing primary forest vegetation and replacing it with a heterogeneous mosaic  
118 of clearings, hedgerows, and secondary forests (Figure 1). Typical crops include manioc, corn, camu-  
119 camu, and watermelon on floodplains; manioc, plantain, rice, small buffalo pastures, and small  
120 aquaculture ponds in uplands; manioc and pineapple on white sands; and rice, watermelon, and  
121 manioc on islands.

122 We sampled bird and tree communities at intact sites (primary forest) and disturbed sites  
123 (slash-and-burn mosaics of active cultivation and fallow secondary forest). We selected twenty intact  
124 sites within 230 km of Iquitos harboring accessible habitat that is largely undisturbed by humans for  
125 as long as records are available, except for light selective logging at floodplain sites and widespread  
126 hunting of game animals (see supplementary material). These sites spanned the major forest habitats  
127 of the region: ten in uplands spanning both banks of the Amazon River, six on floodplains, and four  
128 in white-sand forest. We were unable to find intact examples of river islands large enough to  
129 accommodate our sampling scheme. We then selected twenty disturbed sites in slash-and-burn  
130 mosaic, each paired with an intact site for forest type, soil texture, and geographic proximity. At each  
131 study site, we established six sampling points spaced by at least 210 meters to avoid double-counting  
132 during avian point counts.

133 During subsequent vegetation assessment, we determined that six sampling points on  
134 different transects were unsuitable for analysis due to their inadvertent location in transitional

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135 habitat at the edge of the forest-type of interest. Flooding and time constraints prevented us from  
136 sampling trees at two study sites (one in intact floodplain and another in intact uplands), and we  
137 removed their paired disturbed sites from the tree dataset. Thus, the final dataset contained 234 bird  
138 sampling points and 209 tree sampling points. See supplementary material for details of site  
139 selection, site spacing, and site characteristics.

140

141 BIODIVERSITY DATA

142 We surveyed birds and trees at each sampling point. For birds, a single observer  
143 (REDACTED) conducted four ten-minute 100-meter-radius point-counts at each sampling point  
144 during July-December 2013-2014. Surveys ran from first light until mid-morning, and were not  
145 conducted in rain or windy conditions. We visited most points in both years and rotated the visit  
146 order to ensure that each point received early-morning coverage. To assemble our final dataset for  
147 analysis, we aggregated data across the four visits to each point by taking the maximum count for  
148 each species from any visit.

149 We made two modifications to standard point-count protocols, tailored to the challenges of  
150 detecting skittish species and birds in mixed-species flocks (see supplementary material). First, we  
151 included detections of species that flushed during our approach to and departure from each point  
152 (within 100 m). Second, when mixed flocks detected during the point count lingered within 100  
153 meters after the count period, we proceeded to follow the flock until we identified all of its  
154 participants or until it moved >100 m from the point. We separately recorded individuals detected  
155 via these modifications, permitting us to include them or exclude them from analysis (see  
156 SENSITIVITY ANALYSIS, below).

157 To survey trees, we established a 50x2 m<sup>2</sup> tree plot at a fully randomized location within 100  
158 m of each sampling point (equivalent to 0.6 Gentry transects per site; (Gentry 1988). Within these

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159 plots, we identified every tree greater than 2.5 cm diameter at breast height. We collected a voucher  
160 for each species (except for palms with very large leaves), deposited in the herbarium at the  
161 Universidad Nacional de la Amazonía Peruana (UNAP). One botanist (REDACTED) conducted all  
162 sampling and made all species determinations with reference to the UNAP herbarium collections.  
163 See supplementary information for detailed bird and tree survey protocols.

164

165 BIODIVERSITY COMPARISONS

166 We used sample-based rarefaction to compare bird and tree richness in intact and disturbed  
167 landscapes on a per-area basis (Chao et al. 2014). For trees, this revealed dramatic diversity loss due  
168 to massively reduced densities of individuals at disturbed sites (i.e., cleared areas have fewer trees).  
169 Therefore, we used individual-based rarefaction to test for a second-order effect of slash-and-burn  
170 on tree diversity, controlling for the number of individuals sampled. For both birds and trees, we  
171 performed rarefaction analysis on each forest type separately (upland, floodplain, white-sand) and  
172 for all forest types combined. We also visualized patterns of community change using non-metric  
173 multidimensional scaling.

174 Some bird species that we did not record at intact sites are well known to be common on  
175 intact river-islands (Rosenberg 1990). As noted above, we were unable to sample intact river island  
176 habitat because in our study area all accessible river islands large enough to accommodate our  
177 sampling scheme have been settled, cleared, or otherwise disturbed by people. Therefore, we  
178 conducted a follow-up analysis to account for bias related to the intact river-island avifauna. We  
179 obtained a comprehensive list of bird species that were common on intact river-islands within the  
180 study area thirty years ago (Rosenberg 1990). We then repeated our analysis while excluding these  
181 species from all datasets, thereby removing their influence on our conclusions. We stress that we  
182 selected these species not because they are prevalent in disturbed samples, but because they are



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183 known to be prevalent in an intact river-island habitat that we were unable to sample. By removing  
184 only common river-island species, we are confident that we removed very few species that would  
185 not have appeared in the dataset for intact forest types, had we been able to sample river islands.  
186 Therefore, this analysis mitigates bias in the comparison between intact and disturbed habitats.

187

188 POPULATION COMPARISONS

189 For every species of bird and tree in the dataset, we calculated Bayesian point-estimates and  
190 95% credible intervals for the multiplicative change (fold-change) in abundance between intact and  
191 disturbed sites. To do so, we assumed that the number of individuals detected at intact and  
192 disturbed sites were realizations of Poisson processes. This implies that the total count at disturbed  
193 sites is a binomial draw from the summed count at intact and disturbed sites, and furthermore that  
194 the logarithm of the fold-change between the Poisson means is equal to the logit of the binomial  
195 proportion  $p$  (Przyborowski & Wilenski 1940). We computed the posterior density of  $p$  using the  
196 Jeffreys prior, and we used the posterior density of  $p/(1-p)$  for inference on the fold-change (Brown  
197 et al. 2001).

198

199 DISTRIBUTION OF DISTURBANCE-SENSITIVE SPECIES

200 To understand what features of disturbed points allow them to support species characteristic  
201 of intact forests, we defined *disturbance-sensitive species* as those that are more abundant in intact forest  
202 than disturbed forest, and *disturbance-sensitive counts* as the total number of individuals belonging to  
203 disturbance-sensitive species detected at each point. We then fit generalized linear mixed models for  
204 birds and trees to assess the relationship between disturbance-sensitive counts and local habitat data  
205 (see below) across the disturbed points.

206 *Local habitat data*

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207           At every sampling point, we recorded the number and size of streams and estimates of  
208 percent cover of 10 vegetation formations within 100 m of the point (see supplementary material).  
209 Using Landsat 8 imagery downloaded from the Global Forest Change Data website (Hansen et al  
210 2013), we built a random-forest classifier of the study landscape as intact, disturbed, or open water at  
211 30 m resolution. We validated our classification against the central coordinates of our 240 sampling  
212 points, and then we extracted the area classified as intact within 200, 500, and 5000 m of each  
213 disturbed sampling point. We also measured the distance from each disturbed point to the nearest  
214 primary forest (continuously forested since 1985, before the acceleration of forest clearance in the  
215 region; (Mäki et al. 2001) and to the nearest river (channel width > 30 m) based on visual  
216 examination of Landsat imagery in the USGS Landsat Look viewer, supplemented with aerial  
217 imagery in Google Earth.

218 *Mixed models*

219           Initially, we assumed that any species recorded in higher numbers in intact than disturbed  
220 habitat is disturbance-sensitive. For birds and trees, we fit ordinary and zero-inflated Poisson and  
221 negative binomial mixed models (treating study-site as a random effect) for the disturbance-sensitive  
222 counts using a variety of predictors describing local vegetation cover at the 100 m scale, forest cover  
223 at 0.2 – 5 km spatial scales, and proximity to major rivers (see supplementary material). We used the  
224 small-sample corrected Akaike information criterion (AICc) to select covariates and error structure  
225 that yielded parsimonious models, and we base inference on broad agreement across all top-  
226 performing models.

227           To verify that our conclusions were robust to uncertainty in which species are disturbance-  
228 sensitive, we re-analyzed the model with the lowest AICc score as follows. Using the binomial  
229 likelihood described above, we computed the probability that each species in the dataset is  
230 disturbance-sensitive by integrating the posterior distribution for the binomial proportion (based on

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231 a uniform prior) from 0 to 0.5. We then randomly assigned each species to be disturbance-sensitive  
232 or not based on these probabilities, re-computed the disturbance-sensitive counts, and fit the  
233 regression model to these counts under a Bayesian mode of inference using Markov-chain Monte  
234 Carlo sampling implemented in JAGS (Plummer 2003). We repeated this process 500 times,  
235 combined the posterior chains for inference, and compared the resulting parameter estimates to the  
236 corresponding frequentist estimates.

237

238 SENSITIVITY AND DETECTABILITY ANALYSIS FOR BIRDS

239 To ensure that our non-standard point-count methodology did not bias avian sampling, we  
240 repeated our analyses using only detections obtained via standard protocols. We used an N-mixture  
241 model to determine that avian detectability is likely to be at least as high in disturbed habitats as  
242 intact habitats (see supplementary material). Therefore, if anything, our results overestimate the  
243 biodiversity value of smallholder landscapes.

244

## 245 **RESULTS**

246 Across pristine and disturbed habitats combined we recorded 455 bird species and 751 tree  
247 species; the bird dataset is among the richest single-observer point-count datasets ever assembled.  
248 We found very high avian richness in slash-and-burn mosaics. In fact, in each habitat studied  
249 (uplands, floodplain, white-sands), sample-based rarefaction revealed that bird richness at disturbed  
250 sites was comparable to intact sites (Figure 2). However, tree richness declined severely. This decline  
251 partly resulted from dramatic reductions in the number of individuals at disturbed sites (i.e. cleared  
252 areas have fewer trees) but was exacerbated by changes in the species-abundance distribution (Figure  
253 2).

254           Importantly, considering each habitat in isolation substantially underestimated the difference  
255 in bird richness between intact and disturbed landscapes. Across habitats, reductions in beta-  
256 diversity caused modest but significant declines in bird richness. Moreover, the apparent biodiversity  
257 value of smallholder landscapes was substantially inflated by the spurious absence of river-island  
258 species from our intact sites (an artifact of our inability to sample intact river islands). When the  
259 influence of these poorly sampled river-island species is removed from both the intact and disturbed  
260 points, it becomes apparent that intact landscapes have dramatically higher avian richness than  
261 disturbed landscapes in our study region (Figure 2). This occurs because the river-island avifauna  
262 overlaps more with disturbed habitats than with other intact habitats in the study area. We did not  
263 observe a similar pattern in trees, though non-metric multidimensional scaling suggests that some  
264 homogenization might have occurred (Figure 3). Instead, uplands dominated the tree species  
265 richness of all intact sites combined, minimizing the opportunity for specialists in other habitats to  
266 contribute to richness patterns (Figure 2).

267           Disturbed sites consistently clustered separately from intact sites in terms of their species  
268 composition, and non-metric multidimensional scaling of community composition revealed that the  
269 difference between intact and disturbed sites corresponded to the first axis of variation (Figure 3).  
270 The second axis of variation, corresponding to an edaphic gradient from floodplains through  
271 uplands to white sands, was collapsed at disturbed sites, reflecting the loss of beta-diversity among  
272 forest types. These patterns are consistent for birds and trees and for a variety of incidence- and  
273 abundance-based dissimilarity metrics (Figure S5). Thus, disturbance in addition to driving species  
274 loss, smallholder agriculture drives the disassembly and re-arrangement of primary forest bird  
275 communities.

276           Furthermore, large numbers of disturbance-sensitive species showed dramatically reduced  
277 abundance at disturbed sites (Figure 4). For example, we detected the Screaming Piha (*Lipangus*

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278 *vociferans*) 137 times at intact sites, and only once at disturbed sites. Similarly, we detected the tree  
279 *Eschweilera coriacea* (Lecythidaceae) thirty-one times at intact sites and only once at disturbed sites. In  
280 the rarefaction analysis, such species contribute to the disturbed-site total, but in fact they are  
281 severely harmed by slash-and-burn practices. Among the 249 bird and 221 tree species for which we  
282 detected a significant change in abundance, 57% and 86% declined, respectively. Of the birds that  
283 significantly increased in abundance in our dataset, fully 39% are common on intact river islands  
284 (Rosenberg 1990). Failure to detect significant abundance changes was generally a consequence of  
285 low sample size (and probably not a consequence of small effect size). The median sample size  
286 among species without a significant effect was two for birds and one for trees.

287 Mixed models revealed a major positive influence of local forest cover and nearby primary  
288 forest on the abundance of disturbance-sensitive birds and trees that was consistent across all well-  
289 performing models (Table 1). For birds, the most important components of this effect were primary  
290 forest cover at a radius of 5 km and secondary forest cover at a radius of 100 m. For trees, the key  
291 components were secondary forest cover at a radius of 100 m and primary forest cover at a radius of  
292 200 m. These effects were robust despite uncertainty in which species are disturbance-sensitive.

293

## 294 **DISCUSSION**

295 Our results constitute the first large-scale biodiversity assessment of slash-and-burn  
296 agriculture in western Amazonia, and one of the first biodiversity assessments in degraded  
297 Amazonian landscapes to explicitly consider multiple natural habitat types. These features define a  
298 key knowledge gap for conservation science, because western Amazonia is the epicenter of terrestrial  
299 biodiversity on Earth (Jenkins et al. 2013), harbors multiple types of forest, is heavily affected by  
300 slash-and-burn agriculture (Finer & Novoa 2016), and features extensive species turnover (beta-  
301 diversity) between natural habitats (Tuomisto et al. 1995; Pomara et al. 2012).

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302 Our results are sobering. Diversity loss, community turnover, and large numbers of  
303 declining, disturbance-sensitive species characterize the transition from intact forest to slash-and-  
304 burn mosaic. Slash-and-burn agriculture collapses avian beta-diversity across forest-types, and this  
305 process drives substantial reductions in gamma-diversity for birds. Because slash-and-burn mosaics  
306 are as diverse as primary forest within any single forest type (e.g. within upland forest), previous  
307 work was unable to detect this decline (Andrade & Torgler 1994; Korasaki et al. 2013). Previous  
308 studies have treated an environmental domain equivalent to the first panel of our Figure 2.

309 Moreover, within the slash-and-burn mosaic, secondary forest cover and proximity to  
310 primary forest were consistent, strong predictors of the occurrence of disturbance-sensitive species.  
311 According to our vegetation classifier, the median disturbed point in our dataset was surrounded by  
312 over 19% primary forest at a radius of 0.2 km, 28% at 0.5 km, and 57 % at 5 km. The proximity of  
313 intact habitat, coupled with the high heterogeneity and low land-use intensity of the slash-and-burn  
314 mosaic (the median disturbed point contained 30% closed-canopy secondary-forest cover within a  
315 100 m radius), strongly suggests that our results are a best-case scenario for biodiversity in  
316 Amazonian smallholder agriculture. The conservation value of slash-and-burn mosaics in our study  
317 area depends on extensive fallow areas (i.e. secondary forests) and spillover from primary forest.

318 Recent work from elsewhere in Amazonia suggests that the biodiversity impacts of  
319 smallholder agriculture might be even more severe than our methods can detect. Space-for-time  
320 substitutions might underestimate the severity of impacts in Amazonia (França et al. 2016), perhaps  
321 due to inadequate primary-forest baseline data. Furthermore, the negative impacts of agricultural  
322 disturbance can spill across into adjacent primary forest, leading to substantial additional losses of  
323 conservation value (Barlow et al. 2016). In our study area, a few species (e.g. curassows in the genus  
324 *Mitu*) are so heavily hunted that they are absent even at intact sites, and our analyses cannot shed  
325 light on their disturbance-sensitivity.

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326           Some implications of our results extend beyond the western Amazon. In particular, we note  
327 that many previous comparisons of biodiversity value at intact and degraded tropical sites have been  
328 restricted to a single natural habitat (or have analyzed multiple habitats separately), with variable  
329 results (e.g Daily et al. 2003; Peh et al. 2006; Ranganathan et al. 2008; Phalan et al. 2011; Kurz et al.  
330 2014). Our results show that the large-scale pattern across multiple habitats is gloomier than single-  
331 habitat results suggest, at least for birds. This conclusion is consistent with the observation that  
332 smallholder agriculture reduces pairwise avian compositional dissimilarities across biogeographic  
333 regions of Costa Rica (Karp *et al.* 2012). We expand on this result by showing that the  
334 homogenization produced by smallholder agriculture drives substantial losses of regional gamma-  
335 diversity (this is not a forgone conclusion; see Socolar *et al.* 2016). Moreover, we show that  
336 homogenizing effects are important not only across widely spaced biogeographic regions, but also  
337 across fine-scale habitat formations that structure Amazonian communities. The vast majority of  
338 biodiversity assessments of Neotropical agriculture have focused on uplands and therefore missed  
339 the additional biodiversity losses driven by homogenization across forest-types. Habitat differences  
340 within biogeographic regions are globally ubiquitous (e.g. due to variation in elevation, soils,  
341 hydrology, climate, etc), and revealing the full impacts of disturbance requires sampling that is both  
342 spatially extensive and locally comprehensive with respect to habitat variation (Gardner et al. 2013;  
343 Solar et al. 2015). Habitat specialization and spatial turnover are characteristic of hyperdiverse  
344 species communities, suggesting that habitat degradation might have its worst effects precisely where  
345 biodiversity is highest.

346           We also note that previous studies of biodiversity in Neotropical agricultural landscapes have  
347 broadly neglected trees. A recent meta-analysis of the biodiversity value of degraded tropical  
348 landscapes was unable to include a single study of tree diversity in Neotropical agriculture (Gibson  
349 et al. 2011). This situation might arise because lower tree diversity in cleared areas is perceived as a

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350 forgone conclusion (more attention has been paid to shrubs and forbs, e.g. (Mayfield & Daily 2005).  
351 Nevertheless, trees make up a critical component of tropical biodiversity, and maintaining tropical  
352 tree diversity is likely essential for the long-term conservation a variety of coevolved species (Koh et  
353 al. 2004). Moreover, the impacts of agriculture on tree diversity are even more severe than could be  
354 predicted by declines in abundance alone; agricultural landscapes are species-poor even after  
355 controlling for the number of individual trees sampled. Thus, field inventories of tree communities  
356 are crucial for accurately assessing the biodiversity consequences of slash-and-burn agriculture, and  
357 our results paint a bleak picture.

358         We do not mean to dismiss innovative efforts, including efforts inside protected areas, to  
359 harmonize conservation objectives with the livelihoods of local people (Pulgar Vidal & Gamboa  
360 Moquillaza 2013). There is a clear humanitarian mandate for such efforts, and they can prevent the  
361 even greater losses of biodiversity that result from the conversion of disturbed forests and  
362 agricultural mosaics to soy monocultures or tree plantations. However, we do mean to sound the  
363 alarm over the potential consequences of ongoing smallholder expansion. There will be severe  
364 biodiversity losses if settlers gain access to the last remaining tropical wildernesses in western  
365 Amazonia, no matter how lightly they tread.

366

## 367 **ACKNOWLEDGMENTS**

368 REDACTED FOR REVIEW.

369

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505 **FIGURE AND TABLE CAPTIONS**  
506

507 **Figure 1:** In western Amazonia, slash-and-burn agriculture converts primary forest (**a**) to various  
508 disturbed habitats across uplands, floodplains, and white-sands, resulting in a heterogeneous mosaic  
509 of secondary habitats. Shown here are tangles following abandonment of a floodplain agricultural  
510 plot (**b**), barren ground and scrub following agricultural abandonment on white-sands (**c**), and a  
511 mosaic of upland secondary forest and active agricultural plots (**d**). (**b-d**) represent the range of  
512 slash-and-burn habitats in a highly diversified mosaic, not typical differences between soil types.  
513

514 **Figure 2:** Sample-based rarefaction (mean and 95% confidence interval) for birds (top row) shows  
515 that within each forest type, disturbed sites are as species-rich as their intact counterparts. However,  
516 when forest-types are aggregated, intact forest is more diverse, especially after accounting for the  
517 distribution of river-island species. For trees (bottom row), individual-based rarefaction shows that  
518 richness plummets in disturbed forests, due to low individual abundance and a second-order effect  
519 of altered species-abundance distributions after controlling for the number of individuals sampled.  
520 Aggregated forest-types do not show greater tree-richness differences than individual forest-types;  
521 instead, the uplands dominate the species pool and are effectively as diverse as all habitats combined.  
522

523 **Figure 3:** Non-metric multidimensional scaling (NMDS) based on Raup-Crick dissimilarities for  
524 point-scale bird data (top; stress = 0.21) and site-scale tree data (bottom; stress = 0.22; point-scale  
525 tree data were too sparse for NMDS). In both cases, the first NMDS axis captures the difference  
526 between intact and disturbed sites, while the second axis captures the gradient from nutrient-rich  
527 floodplains to nutrient-poor white-sands. Intact and disturbed sites segregate almost completely.  
528 Heterogeneity between forest types at intact sites is collapsed at disturbed sites.  
529

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530 **Figure 4:** Multiplicative changes in abundance for birds (top) and trees (bottom). Species  
531 significantly different from one (i.e. abundance differs by land-use class) are given by dark points  
532 with 95% credible intervals. Most tree species plummet in abundance. Bird communities include  
533 species that fare well following disturbance, but 57% of species with significant abundance-changes  
534 declined, often dramatically (note the logarithmic y-axis).

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543 **Table 1:** Results of models for counts of disturbance-sensitive birds and trees, summarizing results  
 544 for the top performing model (credible intervals for the effect size) and for all models within 2 AICc  
 545 units of the top performing model (frequency of inclusion and sign of effect). Forest type was  
 546 included in all models as a control. All of the best-performing bird models used a NB1 negative  
 547 binomial error structure without zero-inflation. Five of the best-performing tree models (including  
 548 the top model) used a zero-inflated NB2 negative binomial error structure, one used NB2 error  
 549 without zero-inflation.  
 550

Predictor/Interpretation	Birds			Trees		
	freq <sup>†</sup>	sign <sup>‡</sup>	95% CI*	freq <sup>†</sup>	sign <sup>‡</sup>	95% CI*
ForestType: Upland		-	-0.706 – -0.695		-	-3.285 – -0.002
ForestType: Floodplain		-	-1.268 – 0.366		-	-3.939 – -0.026
Secondary forest (% cover within 100 m)	11/11	+	0.002 – 0.015	6/6	+	0.004 – 0.032
Tall secondary forest: canopy > 20 m (% cover within 100 m)	11/11	+	0.010 – 0.022	1/6	+	
Scrub/gap lacking closed canopy > 5 m tall (% cover within 100 m)	5/11	-		0/6		
Non-habitat: water, grass, dirt, buildings (% cover within 100 m)	6/11	-	-0.020 – -0.001	0/6		
Streams: width (m) of incised channel within 100 m	4/11	+		1/6	+	
intact200: % cover of primary forest within 200 m	3/11	+		6/6	+	1.491 – 7.464
intact500: % cover of primary forest within 500 m	0/11			0/6		
intact5000: % cover of primary forest within 5000 m	11/11	+	0.417 – 2.529	0/6		
PrimaryDist: distance (km) to nearest primary forest	0/11			1/6	-	
RiverDist: distance (km) to nearest river > 30 m wide	11/11	-	-0.222 – -0.022	1/6	+	

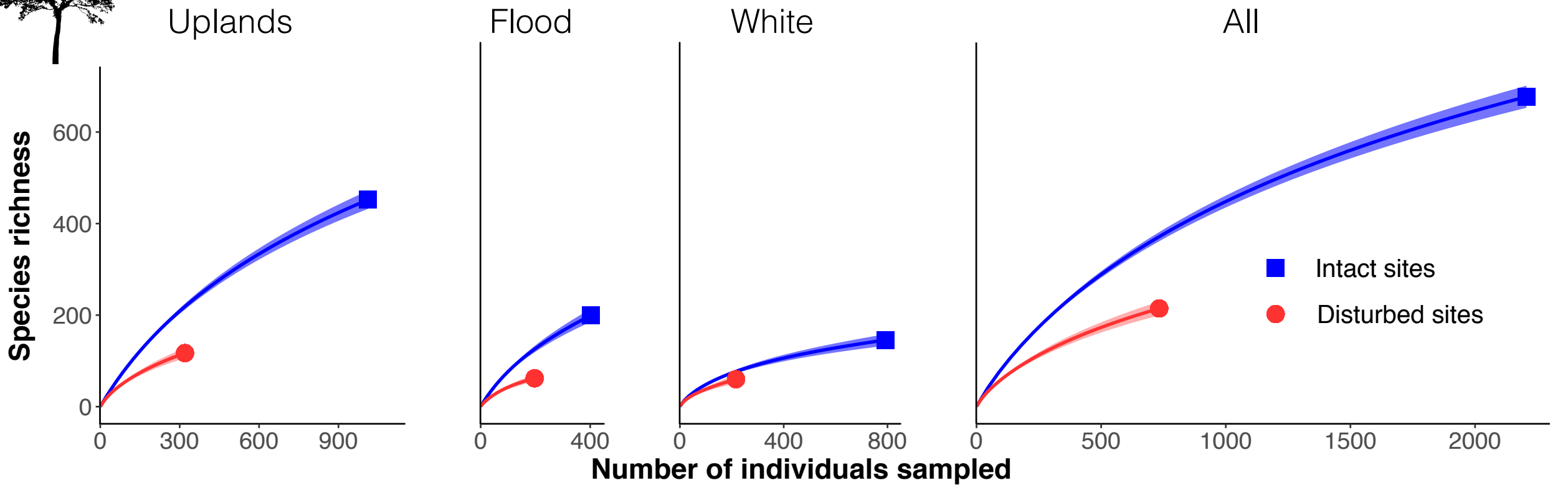
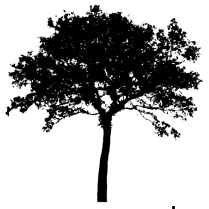
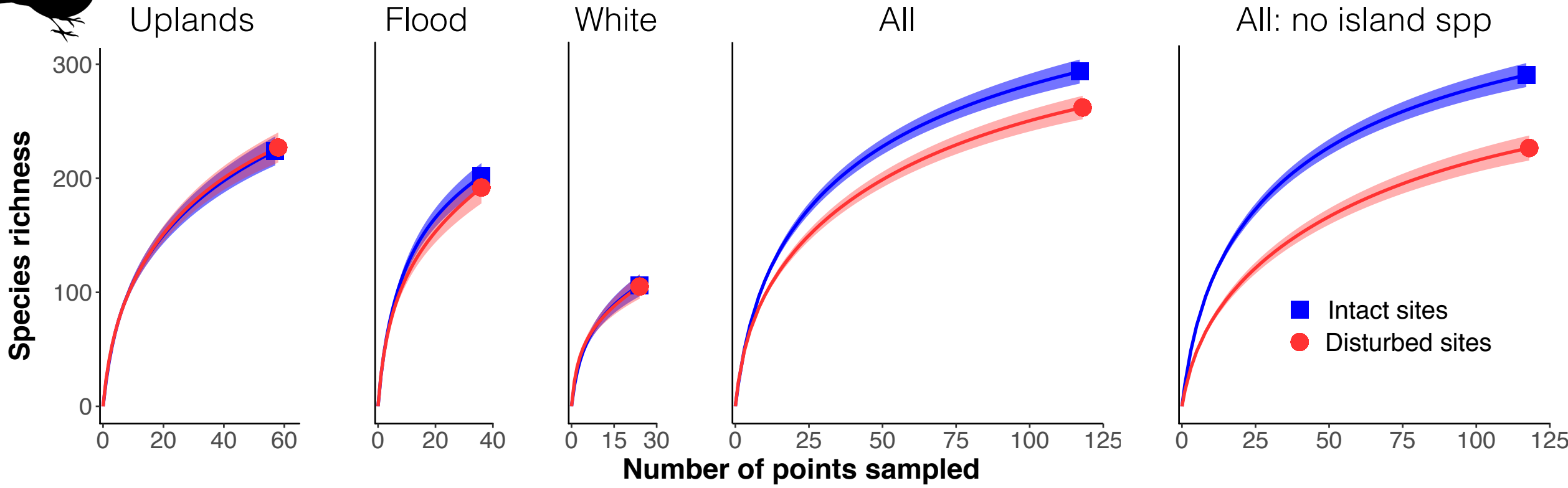
551 <sup>†</sup> Frequency of predictor's inclusion among models within two AICc units of the top-performing model.

552 <sup>‡</sup> No predictor for either birds or trees entered multiple models within two AICc units of the top-performing model with opposite signs.

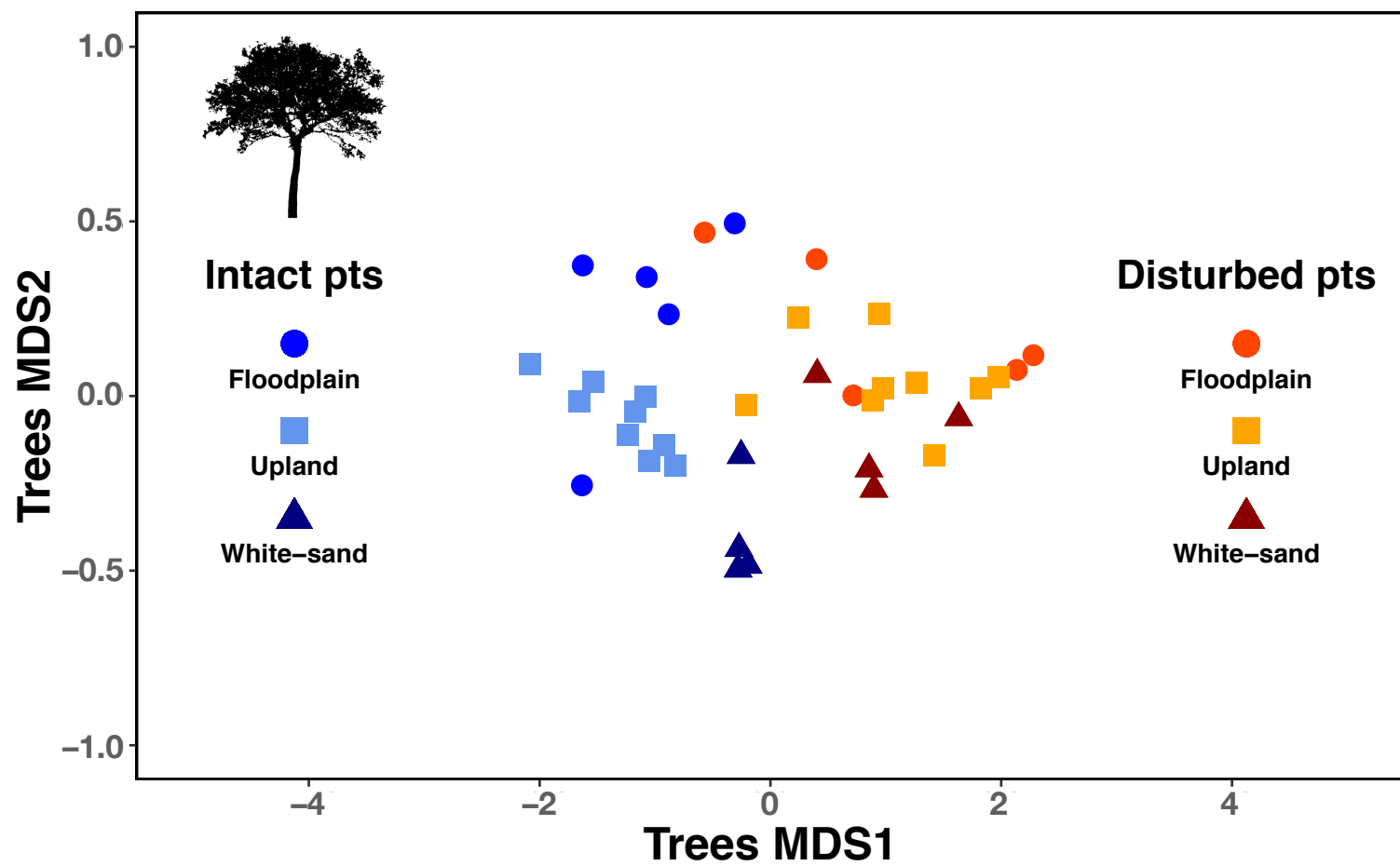
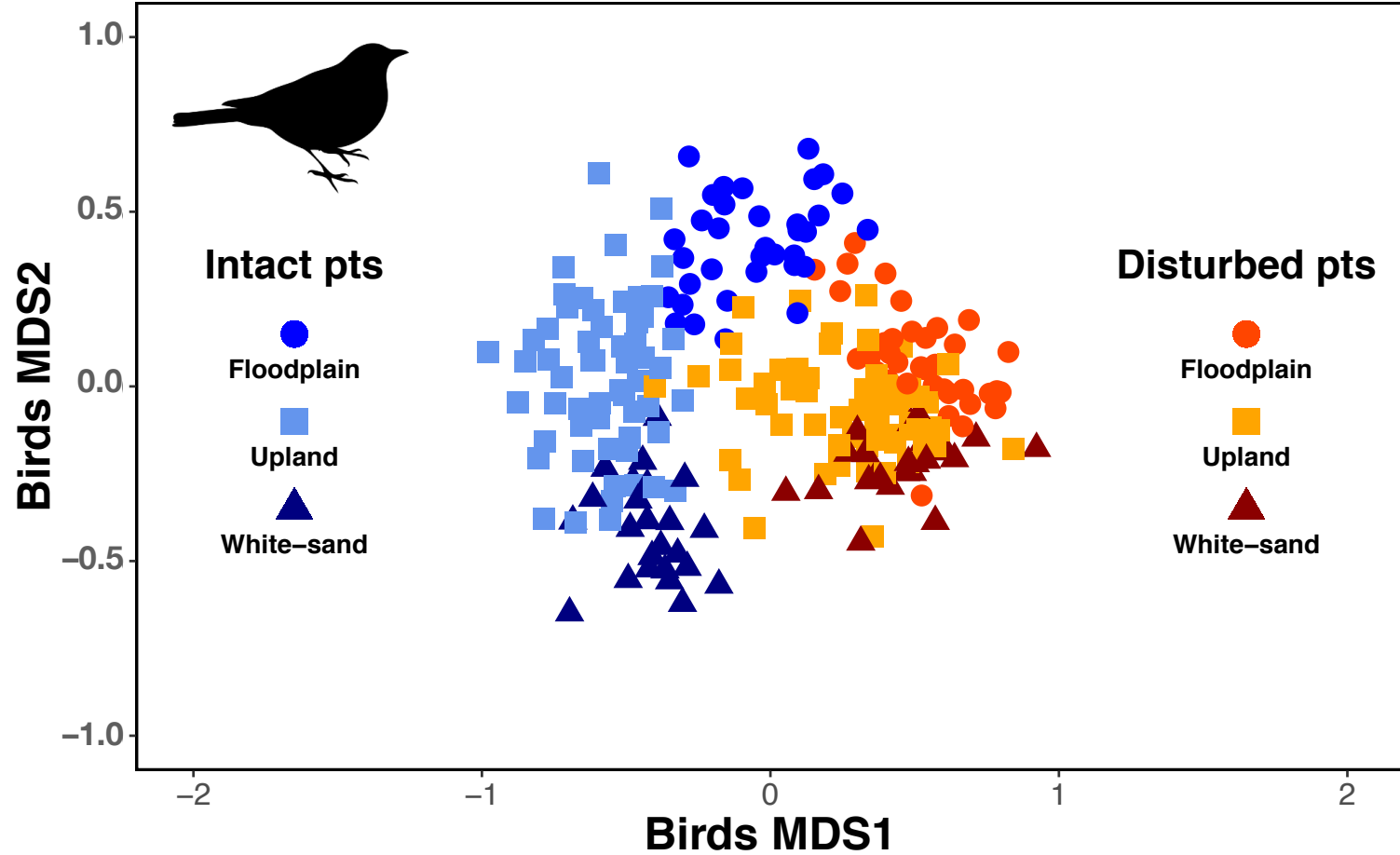
553 \* 95% Bayesian credible interval from top-performing model, accounting uncertainty in which species are disturbance-sensitive.

554









**Abundance ratio (Disturbed / Intact)**

