Smallholder agriculture and the fate of a hyperdiverse tropical biota

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ABSTRACT
Diversified smallholder agriculture is the main land-use affecting the western Amazon, home to the world's richest terrestrial biota, yet the decades-long debate over the conservation value of smallholder agriculture relies almost entirely on data collected in less biodiverse settings. Habitat specialization in hyperdiverse Amazonian assemblages might predispose species towards sensitivity to habitat degradation, and degradation might homogenize distinctive communities in different forest-types. We comprehensively surveyed birds and trees in primary forest and smallholder mosaics spanning major edaphic and hydrological gradients in northern Peru to quantify how Amazonian biodiversity responds to smallholder agriculture. We found that smallholder agriculture devastates tree richness and reduces bird richness via beta-diversity losses across distinct forest-types. Many of the tree and bird species that persist in disturbed sites do so at greatly reduced densities. Their persistence is associated with extensive forest cover at disturbed sites, including local secondary forest and nearby primary forest, suggesting that our results represent a best-case scenario for Amazonian agricultural biodiversity. Thus, regional conservation efforts should focus on preserving primary forest. For birds, this conclusion emerges only after extensive sampling across multiple forest types, suggesting that existing literature's focus on upland (*terra firme*) forest masks the true biodiversity cost of slash-and-burn agriculture.

Key words: Amazon, biodiversity, conservation, birds, trees

INTRODUCTION

The western Amazon is the global epicenter of terrestrial biodiversity [1] and the largest remaining tropical forest wilderness [2], but it is nevertheless threatened by human activities. In contrast to the mechanized agriculture and ranching in southeastern Amazonia, the principal driver of forest loss in the western Amazon is smallholder slash-and-burn agriculture [3,4]. This practice creates mosaics of cultivations and secondary forest surrounding human settlements. The prospect of increased smallholder settlement in western Amazonia in the wake of roadbuilding and hydrocarbons development has raised alarm for the future of this bastion of tropical biodiversity [5,6].

However, numerous studies have documented high levels of biodiversity in smallholder mosaics elsewhere in the Neotropics [7-11]. These studies have generated sustained debates over the relative conservation benefits of protecting primary-forest versus a focus on preventing agricultural intensification/industrialization of smallholder mosaics, especially given limited funding for conservation [12,13]. The resolution to these debates depends largely on assessing the biodiversity value of smallholder mosaics relative to primary forest [14].

There are several reasons to suspect that existing biodiversity data from elsewhere in the Neotropics may not generalize to smallholder mosaics of the western Amazon, so the biodiversity impacts of the main land-use affecting the world's richest terrestrial biota and largest tropical forest wilderness remain unknown. First, Amazonia is more species-rich than other areas of the Neotropics. Ecological theory predicts that habitat specialization among species should be more frequent in hyperdiverse communities [15], and this might predispose Amazonian communities to be more sensitive to habitat alteration. Consistent with this idea, modelling work suggests that a given deforestation scenario would impact Amazonian bird communities more heavily than their Mesoamerican counterparts [16].

Second, comparisons of biodiversity in intact and human-modified Amazonian landscapes have generally focused on more acute disturbances (e.g. large-scale agriculture, fragmentation, silviculture, or fire) in eastern and central Amazonia [17-23]. Many of these studies report low levels of biodiversity in intensive agriculture (e.g. less than 30% of the regional avifauna), but these results likely do not apply to smallholder landscapes in western Amazonia. The few Amazonian studies that have examined smallholder agriculture either have included relatively few smallholder sites (e.g. 7 out of 361 sites in smallholder habitats [24]) or are limited in their total sampling [25,26]. For example, Andrade and Torgler [25] found bird diversity comparable to primary forest in Colombian slash-and-burn mosaics, but this conclusion rests on only understory birds sampled over a relatively small area.

Third, most of these studies focused on the upland (*terra firme*) forest of uplifted clay terraces. Yet Amazonia contains additional forest types that are critical for biodiversity and are also impacted by slash-and-burn. These include floodplain habitats, bamboo forests, and forests on white-sand soils, all of which harbor specialist species that do not occur in terra firme forests [27-31]. Because biotic homogenization can drive landscape-scale biodiversity loss in tropical forests [32-35], effective conservation planning requires an extensive comparison of biodiversity in intact and degraded landscapes across multiple forest types [36].

Here, we quantify the biodiversity consequences of Amazonian slash-and-burn agriculture based on extensive field surveys of bird and tree diversity in Loreto department, Peru. In Loreto, upland, floodplain, and white-sand forests collectively harbor the richest avifauna and tree flora on Earth [37]. Although the area remains largely roadless, the city of Iquitos is the world's largest city without an outside road link (circa 0.5 million inhabitants), and slash-and-burn mosaics are ubiquitous along rivers and local roads [38]. Furthermore, slash-and-burn is practiced to varying degrees, often legally, inside the region's protected areas [39]. Therefore, our results stand to inform conservation practices and priorities across this hyperdiverse yet understudied region in the face of ongoing smallholder expansion.

Despite previous work suggesting that the biodiversity value of tropical smallholder landscapes is very high [7,8,11], we hypothesized that habitat specialists would fare poorly at disturbed sites, driving landscape-scale biodiversity declines via a reduction in beta-diversity [32,36]. We also hypothesized that, regardless of overall biodiversity patterns, a diverse suite of disturbance-sensitive species would decline severely following slash-and-burn agriculture. Finally, we hypothesized that the extent of local forest cover, including secondary forest at the survey sites and primary forest in the surrounding landscape, would determine the ability of slash-and-burn sites to support disturbance-sensitive species.

METHODS

STUDY SITES

We conducted all fieldwork in the Amazonian lowlands of Loreto Department, Peru within 230 km of the city of Iquitos. The climate is hot and wet, with a mean annual temperature of 26.5 °C

and annual rainfall of 2400-3100 mm [40]. Natural habitats in the region are varied and interdigitate at fine spatial scales. We focused on four terrestrial habitats that harbor distinctive biological communities. Quintessential *upland forest* grows on uplifted clay-soil terraces of predominantly alluvial origin [41]. These uplands are the most spatially extensive habitat in the region and the richest in bird and tree species. The Amazon River bisects the uplands and forms a range limit for numerous bird species [42]. *Floodplain forest* along major rivers is subject to regular protracted flooding during January-June [43]. The floodplains differ from the uplands both in terms of vegetation structure (e.g., abundant light gaps) and tree and bird species composition [27,44]. *White-sand forest* occurs on patchy deposits of pure white-sand soil (arenosols) and supports a characteristic avifauna and flora that is absent from other habitats [29,31]. Lastly, *river islands* harbor *Cecropia* (Urticaceae)-dominated woodland with a characteristic suite of specialist birds [45]. Slash-and-burn agriculture affects all of these habitats, removing primary forest vegetation and replacing it with a heterogeneous mosaic of clearings, hedgerows, and secondary forests in varying stages of regeneration (Figure 1). Typical crops include manioc, corn, camu-camu, and watermelon on floodplains; manioc, plantain, rice, small buffalo pastures, and small aquaculture ponds in uplands; manioc and pineapple on white sands; and rice, watermelon, and manioc on islands.

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

During subsequent vegetation assessment, we determined that six sampling points on different transects were unsuitable for analysis due to their inadvertent location in transitional habitat at the edge of the forest-type of interest. Water levels and time constraints prevented us from sampling trees at two study sites (one in intact floodplain and another in intact uplands), and we removed their paired disturbed sites from the tree dataset. Thus, the final dataset contained 234 bird sampling points and 209 tree sampling points. See supplementary material for details of site selection, site spacing, and site characteristics.

BIODIVERSITY DATA

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

We made two modifications to standard point-count protocols, tailored to the challenges of detecting skittish species and birds in mixed-species flocks (see supplementary material). First, we included detections of species that flushed during our approach to and departure from each point (within 100 m). Second, when we detected mixed flocks during the point count that lingered within 100 meters of the point after the ten-minute count period, we proceeded to follow the flock until we

identified all of its participants or until it moved >100 m from the point. We separately recorded individual birds detected via these modifications, permitting us to include them or exclude them from analysis (see SENSITIVITY ANALYSIS, below).

To survey trees, we established a 50x2 m^2 tree plot at a fully randomized location within 100 m of each sampling point (equivalent to 0.6 Gentry transects per site; [46]. Within these plots, we identified every tree greater than 2.5 cm diameter at breast height. A voucher was collected for each species detected in the dataset (except for palms with very large leaves) and deposited in the herbarium at the Universidad Nacional de la Amazonía Peruana (UNAP). One botanist (EVS) conducted all of the field sampling and made all species determinations with reference to the herbarium collections at the UNAP. See supporting information for detailed bird and tree survey protocols.

BIODIVERSITY COMPARISONS

We used a space-for-time substitution and sample-based rarefaction to compare bird and tree richness in intact and disturbed landscapes on a per-area basis [47]. For trees, sample-based rarefaction revealed dramatic diversity loss due to a massive reduction in the number of individuals at disturbed sites (i.e., cleared areas have fewer trees). Therefore, we used individual-based rarefaction to test for a second-order effect of slash-and-burn on tree diversity, controlling for the number of individuals sampled. For both birds and trees, we performed rarefaction analysis on each forest type separately (upland, floodplain, white-sand) and for all forest types combined. We also visualized overall patterns of community change using non-metric multidimensional scaling.

Some species that we recorded only at disturbed sites are known to occur on intact river-islands [45]. We were unable to sample intact river island habitat because in our study area virtually all river islands large enough to accommodate our sampling scheme have been settled, cleared, or otherwise disturbed by people. Therefore, we conducted a follow-up analysis to account for patterns of species diversity on intact river islands. We obtained a comprehensive list of bird species that were common on intact river-islands within the study area thirty years ago [45]. We then repeated our analysis while excluding these species from all datasets, thereby removing their influence on our conclusions. We stress that we selected these species not because they are prevalent in disturbed samples, but because they are known to be prevalent in an intact habitat that we were unable to sample. By removing only common river-island species, we are confident that we removed very few species that would not have appeared in the dataset for intact forest types, had we been able to sample river islands. Therefore, this analysis mitigates bias in the comparison between intact and disturbed habitats.

POPULATION COMPARISONS

For every species of bird and tree in the dataset, we calculated Bayesian point-estimates and 95% credible intervals for the multiplicative change (fold-change) in abundance between intact and disturbed sites. To do so, we assumed that the number of individuals detected at intact and disturbed sites were realizations of Poisson processes. This implies that the total count at disturbed sites is a binomial draw from the summed count at intact and disturbed sites, and furthermore that the logarithm of the fold-change between the Poisson means is equal to the logit of the binomial proportion p [48]. We computed the posterior density of p using the Jeffreys prior, and we used the posterior density of $p/(1-p)$ for inference on the fold-change [49].

DISTRIBUTION OF DISTURBANCE-SENSITIVE SPECIES

To understand what features of disturbed points allow them to support species characteristic of intact forests, we defined *disturbance-sensitive species* as those that are more abundant in intact forest

types than disturbed forest types, and *disturbance-sensitive counts* as the total number of individuals belonging to disturbance-sensitive species detected at each point. We then fit generalized linear mixed models for birds and trees to assess the relationship between disturbance-sensitive counts and local habitat data (see below) across our disturbed points.

Local habitat data

At every sampling point we recorded the number and size of streams and estimates of percent cover of 10 vegetation formations within 100 m of the point (see supplementary material). Using Landsat 8 imagery downloaded from the Global Forest Change Data website (Hansen et al 2013), we built a random-forest classification of the study landscape as intact, disturbed, or open water at 30 m resolution. We validated our classification against the central coordinates of our 240 sampling points, and then we extracted the area classified as intact within 200, 500, and 5000 m of each disturbed sampling point. We also measured the distance from each disturbed point to the nearest primary forest (continuously forested since 1985, before the acceleration of forest clearance in the region [38]) and to the nearest river (channel width > 30 m) based on visual examination of Landsat imagery in the USGS Landsat Look viewer, supplemented with aerial imagery in Google Earth.

Mixed models

Initially, we assumed that any species with a higher count in intact than disturbed habitat is disturbance-sensitive. For birds and trees, we fit ordinary and zero-inflated Poisson and negative binomial mixed models for the disturbance-sensitive counts using a variety of predictors describing local vegetation cover at the 100 m scale, forest cover at 0.2 – 5 km spatial scales, and proximity to geographic features such as forest streams and major rivers (see supplementary material). We used the small-sample corrected Akaike information criterion (AICc) to select covariates and error structure that yielded parsimonious models. We base our inference about the impacts of various covariates on broad agreement across all top-performing models.

To verify that our conclusions were robust to uncertainty as to which species are disturbance-sensitive, we re-analyzed the model with the lowest AICc score as follows: We used the binomial likelihood described above to compute the probability that each species in the dataset is disturbance-sensitive by integrating the posterior distribution for the binomial proportion (based on a uniform prior) from 0 to 0.5. We then randomly assigned each species to be disturbance-sensitive or not based on these probabilities, re-computed the disturbance-sensitive counts, and fit the regression model to these counts under a Bayesian mode of inference using Markov-chain Monte Carlo sampling implemented in JAGS [50]. We repeated this process 500 times, combined the posterior chains for inference, and compared the resulting parameter estimates to the corresponding frequentist estimates.

SENSITIVITY AND DETECTABILITY ANALYSIS FOR BIRDS

To ensure that our avian sampling was not biased by our non-standard point-count methodology, we repeated our analyses using only detections obtained via standard point-count protocols. To address the possibility of systematic differences in intact versus disturbed habitats, we used an N-mixture model to estimate detection probabilities in both habitats. We determined that avian detectability is likely to be at least as high in disturbed habitats as intact habitats (see supplementary material). Therefore, if anything, our results overestimate the biodiversity value of smallholder landscapes.

RESULTS

Across pristine and disturbed habitats combined we recorded 455 bird species and 751 tree species; the bird dataset is among the richest single-observer point-count datasets ever assembled.

We found very high avian richness in slash-and-burn mosaics. In fact, in each habitat studied (uplands, floodplain, white-sands) sample-based rarefaction revealed that bird richness at disturbed sites was comparable to intact sites (Figure 2). However, tree richness declined severely. This decline partly resulted from dramatic reductions in the number of individuals at disturbed sites (i.e. cleared areas have fewer trees) but was exacerbated by changes in the species-abundance distribution (Figure 2).

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

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

Furthermore, large numbers of disturbance-sensitive species showed dramatically reduced abundance at disturbed sites (Figure 4). For example, we detected the Screaming Piha (*Lipaugus vociferans*) 137 times at intact sites, and only once at disturbed sites. Similarly, we detected the tree *Eschweilera coriacea* (Lecythidaceae) thirty-one times at intact sites and only once at disturbed sites. In the rarefaction analysis, such species appear in the total for disturbed sites, but in fact they are severely harmed by slash-and-burn practices. Among the 249 bird and 221 tree species for which we detected a significant change in abundance, 57% and 86% declined, respectively. Of the birds that significantly increased in abundance, fully 39% are common on intact river islands [45]. Failure to detect significant abundance changes was generally a consequence of low sample size (and probably not a consequence of small effect size). The median sample size among species without a significant effect was two for birds and one for trees.

Mixed models revealed a major positive influence of local forest cover and nearby primary forest on the abundance of disturbance-sensitive birds and trees that was consistent across all well-performing models (Table 1). For birds, the most important components of this effect were primary forest cover at a radius of 5 km and secondary forest cover at a radius of 100 m. For trees, the key components were secondary forest cover at a radius of 100 m and primary forest cover at a radius of 200 m. Additionally, disturbance-sensitive birds were negatively affected by non-habitat (water, grass, bare dirt, or buildings) at a radius of 100 m, and disturbance-sensitive trees were less common on disturbed floodplains than disturbed white-sands after controlling for other factors. However, disturbed white-sands had very low secondary forest cover, so nonlinearities in cover-abundance

relationships could drive spurious differences between floodplains and white-sands. All of these effects were robust despite uncertainty in which species are disturbance-sensitive.

DISCUSSION

Our results constitute the first large-scale biodiversity assessment of slash-and-burn agriculture in western Amazonia, and one of the first biodiversity assessments in degraded Amazonian landscapes to explicitly consider multiple natural habitat types. These features define a key knowledge gap for conservation science, because western Amazonia is the epicenter of terrestrial biodiversity on Earth [1], harbors multiple types of forest, is heavily affected by slash-and-burn agriculture [3], and features extensive species turnover (beta-diversity) between natural habitats [51,52].

Our results are sobering. Diversity loss, community turnover, and large numbers of declining, disturbance-sensitive species characterize the transition from intact forest to slash-and-burn mosaic. Slash-and-burn agriculture collapses beta-diversity across forest-types, and this process drives substantial reductions in gamma diversity for birds. A moderately diverse bird assemblage occupies the slash-and-burn mosaic, and 43% of birds with significant changes in abundance were commoner at disturbed sites; however, these increasing species generally widespread. They form an assemblage that is replicated across disturbed forest-types, and all of them are evaluated as Least Concern by BirdLife International.

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

Recent work from elsewhere in Amazonia suggests that the biodiversity impacts of smallholder agriculture might be even more severe than our methods can detect. Space-for-time substitutions might underestimate the severity of impacts in Amazonia [53], perhaps due to inadequate primary-forest baseline data. Furthermore, the negative impacts of agricultural disturbance can spill across into adjacent primary forest, leading to substantial additional losses of conservation value [54]. In our study area, a few species have been so heavily impacted by logging and hunting that they are absent even at intact sites, and our analyses cannot shed light on their disturbance-sensitivity.

The implications of our results extend beyond the western Amazon. In particular, we note that many previous comparisons of biodiversity value at intact and degraded tropical sites have been restricted to a single natural habitat (or have analyzed multiple habitats separately), with variable results (e.g [10,13,55-57]). Our results show that the large-scale pattern across multiple habitats is gloomier than single-habitat results suggest, at least for birds. This conclusion is consistent with the observation that smallholder agriculture reduces pairwise avian compositional dissimilarities across biogeographic regions of Costa Rica [32]. We expand on this result by showing that the homogenization produced by smallholder agriculture drives substantial losses of regional gamma-diversity (this is not a forgone conclusion; see [36]). Moreover, we show that homogenizing effects are important not only across widely spaced biogeographic regions, but also across fine-scale habitat formations that structure Amazonian communities. The vast majority of biodiversity assessments of Neotropical agriculture have focused on uplands and therefore missed the additional biodiversity

losses driven by homogenization across forest-types. Habitat differences within biogeographic regions are globally ubiquitous (e.g. due to variation in elevation, soils, hydrology, climate, etc), and revealing the full impacts of disturbance requires sampling that is both spatially extensive and locally comprehensive with respect to habitat variation [22,33]. Habitat specialization and spatial turnover are characteristic of hyperdiverse species communities, suggesting that habitat degradation might have its worst effects precisely where biodiversity is highest.

We also note that previous studies of biodiversity in Neotropical agricultural landscapes have broadly neglected trees. A recent meta-analysis of the biodiversity value of degraded tropical landscapes was unable to include a single study of tree diversity in Neotropical agriculture [12]. This situation might arise because lower tree diversity in cleared areas is perceived as a forgone conclusion (more attention has been paid to shrubs and forbs [58]). Nevertheless, trees make up a critical component of tropical biodiversity, and maintaining tropical tree diversity is likely essential for the long-term conservation a variety of coevolved species [59]. Moreover, the impacts of agriculture on tree diversity are even more severe than could be predicted by declines in abundance alone; agricultural landscapes are species-poor even after controlling for the number of individual trees sampled. Thus, field inventories of tree communities are crucial for accurately assessing the biodiversity consequences of slash-and-burn agriculture, and our results paint a bleak picture.

We do not mean to dismiss innovative efforts, including efforts inside protected areas, to harmonize conservation objectives with the livelihoods of local people [39]. There is a clear humanitarian mandate for such efforts, and they can prevent the even greater losses of biodiversity that result from the conversion of disturbed forests and agricultural mosaics to soy monocultures or tree plantations. However, we do mean to sound the alarm over the potential consequences of ongoing smallholder expansion. There will be severe biodiversity losses if settlers gain access to the last remaining tropical wildernesses in Amazonia, no matter how lightly they tread.

COMPETING INTERESTS

We have no competing interests.

AUTHORS' CONTRIBUTIONS

JBS and DSW conceived of the study. JBS collected the bird data, performed the analysis, and drafted the manuscript. EVS collected the tree data. DSW provided input at every stage of study design and data analysis. All authors helped to draft the manuscript and gave final approval for publication.

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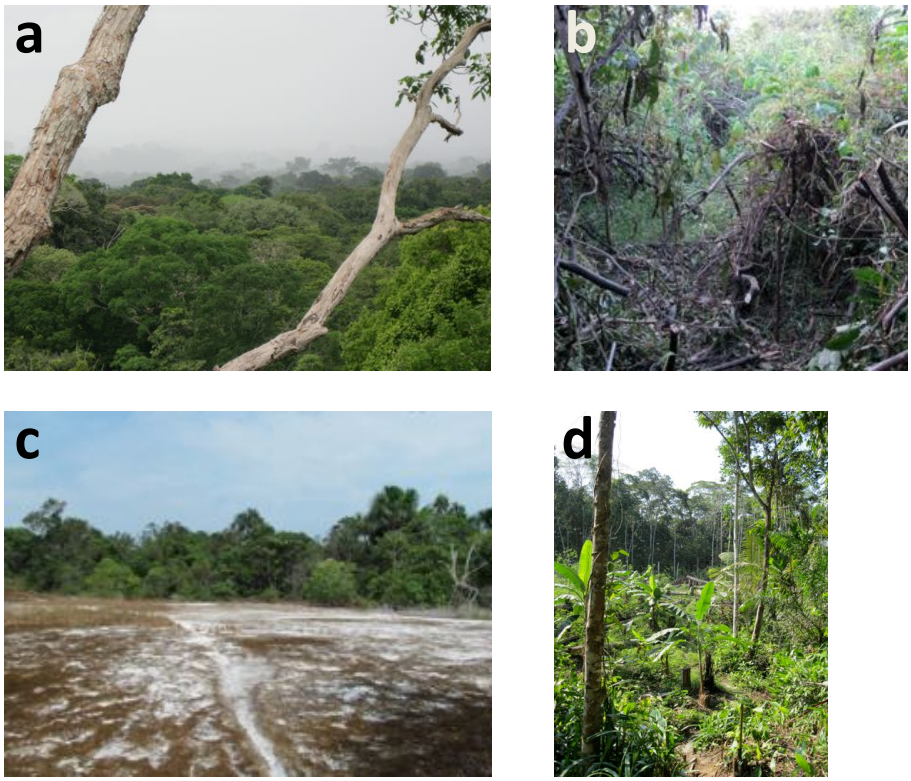

Figure 1: In Western Amazonia, slash-and-burn agriculture converts primary forest (**a**) to a variety of disturbed habitats across uplands, floodplains, and white-sands, resulting in a heterogeneous mosaic of secondary habitats. Shown here are dense tangles following abandonment of a floodplain agricultural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

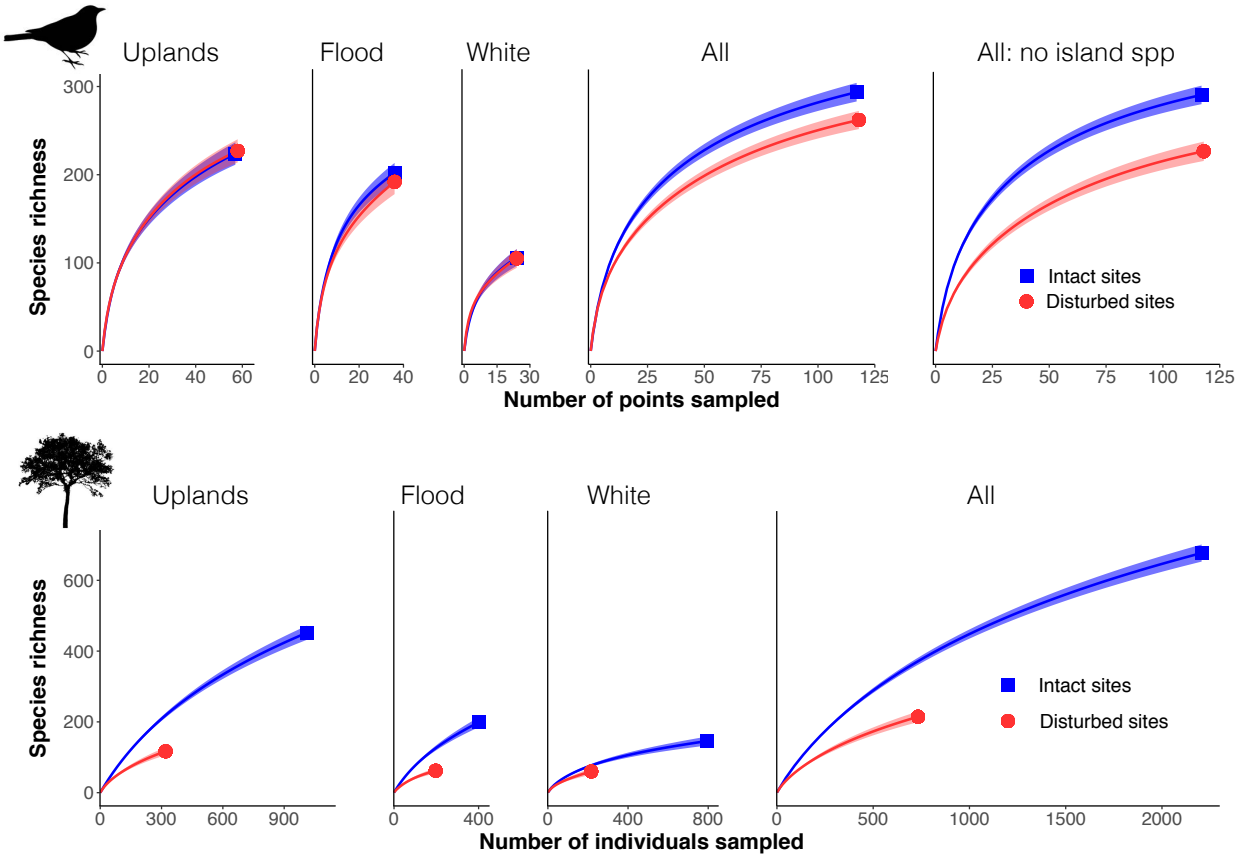

Figure 2: Sample-based rarefaction (mean and 95% confidence interval) for birds (top row) shows that within each forest type, disturbed sites are as species-rich as their intact counterparts. However, when forest-types are aggregated, intact forest is more diverse, especially after accounting for the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

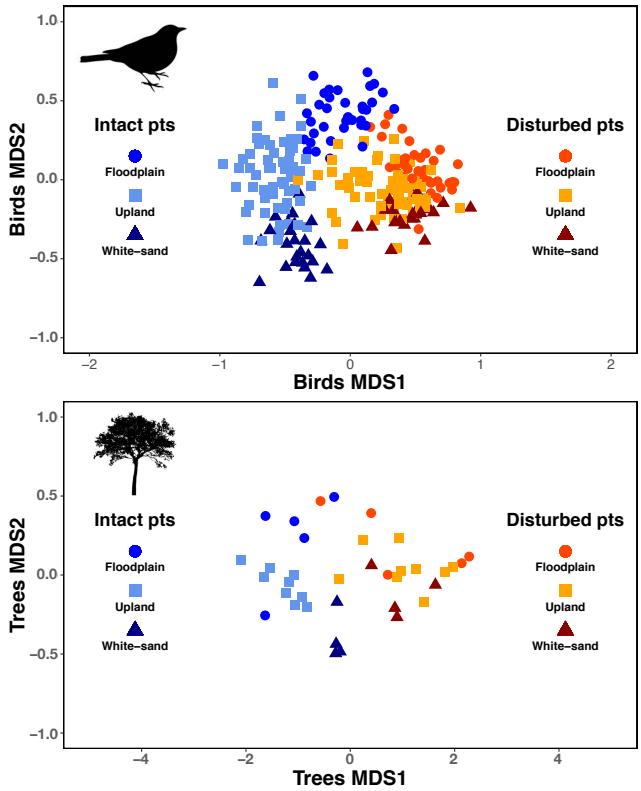

Figure 3: Non-metric multidimensional scaling (NMDS) based on Raup-Crick dissimilarities for point-scale bird data (top; stress = 0.21) and site-scale tree data (bottom; stress = 0.22; point-scale tree data were too sparse for NMDS). In both cases, the first NMDS axis captures the difference between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

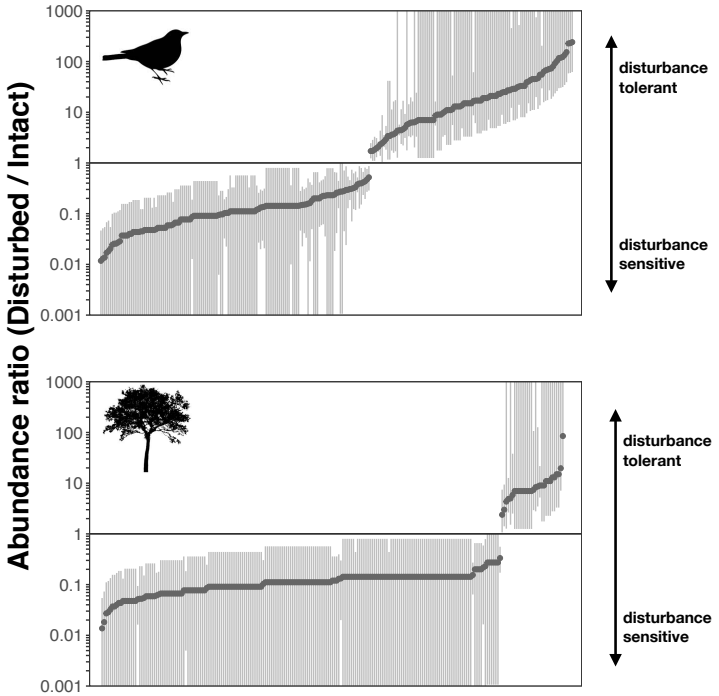

Figure 4: Multiplicative changes in abundance for birds (top) and trees (bottom). Species significantly different from one (where abundance in disturbed forests equals abundance in undisturbed forests) are given by dark points with 95% credible intervals. Most species of trees plummet in abundance. Bird communities include species that fare well following disturbance, but 57% of species with statistically significant changes in abundance declined, often dramatically (note the logarithmic y-axis).

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

	Birds			Trees		
Predictor/Interpretation	**freq**†	**sign**‡	**95% CI***	**freq**†	**sign**‡	**95% CI***
Upland forest type		-	-0.706 – 0.695		-	-3.285 – 0.002
Floodplain forest type		-	-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 of streams 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	+	

† Frequency of predictor's inclusion among models within two AICc units of the top-performing model.
‡ No predictor for either birds or trees entered multiple models within two AICc units of the top-performing model with opposite signs.
* 95% Bayesian credible interval from top-performing model, accounting uncertainty in which species are disturbance-sensitive.