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# Overlooked biodiversity loss in tropical smallholder agriculture

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**Abstract:** *Smallholder agriculture is the main driver of deforestation in the western Amazon, where terrestrial biodiversity reaches its global maximum. Understanding the biodiversity value of the resulting mosaics of cultivated and secondary forest is therefore crucial for conservation planning. However, Amazonian communities are organized across multiple forest types that support distinct species assemblages, and little is known about smallholder impacts across the range of forest types that are essential for sustaining biodiversity. We addressed this issue with a large-scale field inventory of birds (point counts) and trees (transects) in primary forest and smallholder agriculture in northern Peru across 3 forest types that are key for Amazonian biodiversity. For birds smallholder agriculture supported species richness comparable to primary forest within each forest type, but biotic homogenization across forest types resulted in substantial losses of biodiversity overall. These overall losses are invisible to studies that focus solely on upland (terra firma) forest. For trees biodiversity losses in upland forests dominated the signal across all habitats combined and homogenization across habitats did not exacerbate biodiversity loss. Proximity to forest strongly predicted the persistence of forest-associated bird and tree species in the smallholder mosaic, and because intact forest is ubiquitous in our study area, our results probably represent a best-case scenario for biodiversity in Amazonian agriculture. Land-use planning inside and outside protected areas should recognize that tropical smallholder agriculture has pervasive biodiversity impacts that are not apparent in typical studies that cover a single forest type. The full range of forest types must be surveyed to accurately assess biodiversity losses, and primary forests must be protected to prevent landscape-scale biodiversity loss.*

**Keywords:** Amazon, beta diversity, biotic homogenization, birds, Peru, trees

Pérdida de Biodiversidad Pasada por Alto en la Agricultura de Pequeños Propietarios

**Resumen:** *La agricultura de pequeños propietarios es la principal causa de la deforestación en la Amazonía occidental, donde la biodiversidad terrestre alcanza su máximo global. Por lo tanto, comprender el valor de la biodiversidad de los mosaicos resultantes de bosques cultivados y secundarios es crucial para la planificación de la conservación. Sin embargo, las comunidades amazónicas están organizadas a través de múltiples tipos de bosques que soportan ensambles de especies distintas, y poco se sabe sobre los impactos de los pequeños agricultores en toda la gama de tipos de bosques que son esenciales para mantener la biodiversidad. Abordamos este problema con un inventario de campo a gran escala de aves (puntos de conteo) y árboles (transectos) en bosques primarios y agricultura de pequeños productores en el norte de Perú en 3 tipos de bosques que son clave para la biodiversidad amazónica. Para aves, la agricultura de pequeños productores soportó una riqueza de especies comparable a la de los bosques primarios dentro de cada tipo de bosque, pero la homogeneización biótica entre los tipos de bosques dio lugar a pérdidas sustanciales de biodiversidad en general. Estas pérdidas globales son invisibles para los estudios que se centran únicamente en los bosques de tierra firme. En el caso de árboles, las pérdidas de biodiversidad en bosques de tierra firme*

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**Article impact statement:** As smallholder agriculture follows infrastructure expansion in western Amazonia, it poses a serious threat to the region's biodiversity.

Paper submitted June 23, 2018; revised manuscript accepted May 6, 2019.

*fueron dominantes en todos los hábitats combinados y la homogeneización en todos los hábitats no agravó la pérdida de biodiversidad. La proximidad a los bosques predijo robustamente la persistencia de especies de aves y árboles asociadas a bosques en el mosaico de pequeños productores, y debido a la omnipresencia de bosque intacto en el área de estudio, nuestros resultados probablemente representan el mejor escenario para la biodiversidad en la agricultura amazónica. La planificación del uso de suelo dentro y fuera de las áreas protegidas debe reconocer que la agricultura tiene impactos generalizados sobre la biodiversidad que no son evidentes en estudios que solo abarcan un solo tipo de bosque. Se debe examinar toda la gama de tipos de bosque para evaluar con precisión las pérdidas de biodiversidad, y los bosques primarios deben ser protegidos para prevenir la pérdida de biodiversidad a escala de paisaje.*

**Palabras Clave:** Amazonía, árboles, aves, diversidad beta, homogeneización biótica, Perú

**摘要:** 在全球陆地生物多样性最高的亚马逊西部地区, 小型农业生产是森林砍伐的主要驱动因素。因此, 了解小型农业中人工林和次生林镶嵌斑块的生物多样性价值, 对保护规划至关重要。然而, 亚马逊社区跨越了支持不同物种集合的多种森林类型, 而目前关于小型农业对维持生物多样性所必需的各种森林类型的影响研究甚少。为解决这个问题, 我们对秘鲁北部的原始林和小型农业用地中鸟类 (位点计数) 和树木 (样带) 进行了大规模的野外调查, 其中包含了对亚马逊生物多样性至关重要的三种类型的森林。对于鸟类来说, 小型农业用地维持的物种丰富度与各类型原始林相近, 但森林类型之间的生物同质化导致了总体生物多样性严重下降。然而, 只关注山地森林的研究发现不了这样的生物多样性总体丧失。对于树木来说, 山地森林的生物多样性丧失在所有生境中占主导地位, 而生境之间的生物同质化并不会加剧生物多样性丧失。与森林的距离显著地预测了小型农业镶嵌斑块中林鸟和树种的续存情况, 但由于本研究地点有广泛分布的原始林, 以上结果可能代表的是亚马逊农业生物多样性的最佳情况。进行保护地内外的土地利用规划时应认识到, 热带小型农业对生物多样性有普遍影响, 即使这一点在覆盖单一森林类型的典型研究中并不明显。因此, 未来的保护规划应全面调查各种类型的森林、准确评估生物多样性丧失, 并保护原始林以防止景观水平的生物多样性丧失。【翻译: 胡怡思, 审校: 聂永刚】

**关键词:** 亚马逊,  $\beta$ 多样性, 生物同质化, 鸟类, 秘鲁, 树木

## Introduction

The western Amazon is the largest remaining tropical forest wilderness (Tyukavina et al. 2015) but is nevertheless threatened by human activities. In contrast to the large-scale mechanized agriculture and ranching occurring in southeastern Amazonia, the principal driver of forest loss in the western Amazon is smallholder slash-and-burn agriculture (Finer & Novoa 2016; Ravikumar et al. 2017). Accurate estimates of regional slash-and-burn expansion are unavailable due to the difficulty of distinguishing expansion into primary forests from reclearing of secondary-forest fallows (Ravikumar et al. 2017), but the prospect of increased smallholder settlement in the wake of roadbuilding and hydrocarbons development has raised concerns for this bastion of tropical biodiversity. For example, the Inter-oceanic and trans-Amazonian highways of Peru and Brazil have promoted rapid smallholder expansion along their routes (Oliveira et al. 2007), and development plans exist that would dramatically alter the roadless character of much of the Peruvian Amazon (Perú Ministerio de Transportes y Comunicaciones 2017). Furthermore, most of western Amazonia is zoned for hydrocarbon concessions, the development of which would provide additional road access for settlers (Finer & Orta-Martínez 2010; Laurance et al. 2014).

Smallholder systems can form a bulwark against severe biodiversity losses associated with intensive agriculture (Daily et al. 2001). For example, shade-coffee systems in Mesoamerica harbor avian richness that approaches or

equals primary forest (Perfecto et al. 1996; Philpott et al. 2008), and some Amazonian secondary forests quickly accumulate species richness comparable to primary forest (Borges 2007). However, smallholder agriculture may also seriously threaten species that cannot persist even in low-intensity agricultural landscapes (Gibson et al. 2011). The extent to which smallholder landscapes support tropical-forest biodiversity remains a key empirical question, especially because the dynamics of Amazonian smallholder expansion respond to policy instruments such as governmental incentives for colonization (Alvarez & Naughton-Treves 2003; Godar et al. 2014), centrally planned roads (Barber et al. 2014; Laurance et al. 2014), and protected-area management (Terborgh et al. 2002; Barber et al. 2014).

Remarkably few data are available to determine the biodiversity value of smallholder agriculture anywhere in the lowland tropics. In the Neotropics, most assessments of biodiversity in smallholder landscapes have been conducted in highland regions (Hudson et al. 2014), whereas most studies from lowland regions have focused on intensive land-use change in the eastern Amazon (e.g., mechanized agriculture, large-scale ranching, silviculture, or fire) (Barlow et al. 2007; Mahood et al. 2011; Moura et al. 2016). We are aware of only 2 studies reporting on targeted comparisons of biodiversity in primary forest and smallholder mosaics of the western Amazon (Andrade & Torgler 1994; Korasaki et al. 2013). Andrade and Torgler (1994) documented comparable avian richness in slash-and-burn mosaic and primary forest. Korasaki

et al. (2013) documented reduced dung beetle richness in active cultivations and richness comparable to primary forest in secondary-forest fallows. These studies suggest the biodiversity value of slash-and-burn mosaics of the western Amazon may be high; however, Moura et al. (2016) included a limited amount of smallholder agriculture from the eastern Amazon and reached the opposite conclusion.

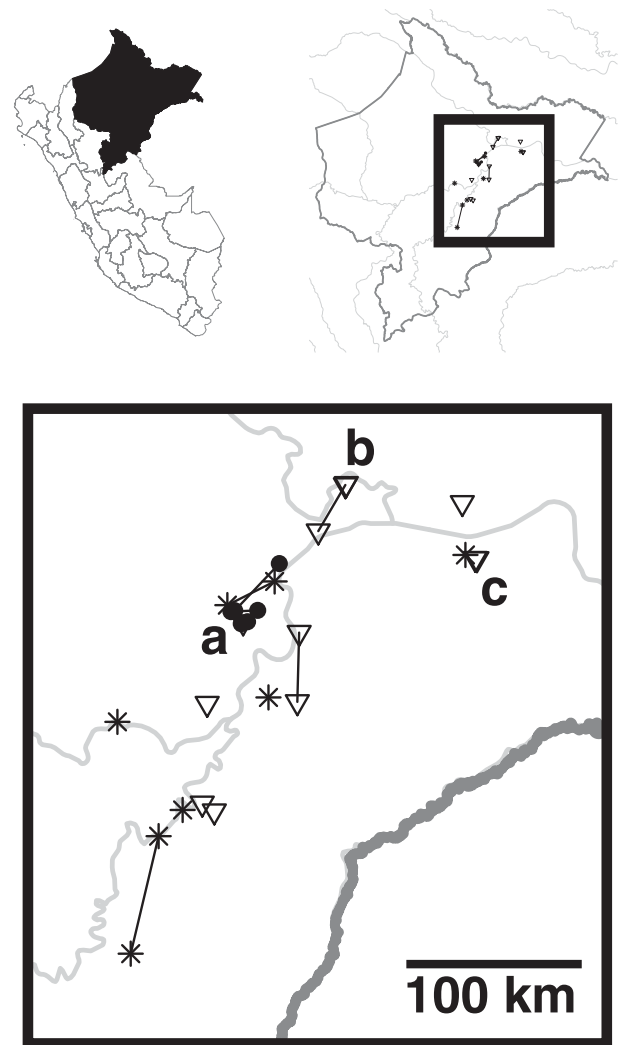
A further impediment to understanding slash-and-burn impacts in the western Amazon is the multiple, distinct forest types that structure regional species assemblages. Nearly all Amazonian studies comparing primary forest and agricultural biodiversity, including Andrade and Torgler (1994) and Korasaki et al. (2013), have focused on upland forest of clay-soil terraces (terra firme). However, Amazonia contains multiple forest types that support specialized species assemblages. Among the most important for biodiversity maintenance are floodplain forests (Remsen & Parker 1983; Wittmann et al. 2006), white-sand forests (Alvarez Alonso & Whitney 2003; Fine et al. 2010), and river-island woodlands (Rosenberg 1990). Biotic homogenization across forest types may exacerbate consequences of smallholder agriculture for regional gamma diversity (Socolar et al. 2016). That is, regional-scale (gamma) diversity losses may occur due to loss of variation in species assemblages among sites (loss of beta diversity). Biotic homogenization sometimes drives landscape-scale biodiversity loss in tropical forests (Karp et al. 2012; Solar et al. 2015; Alroy 2017), but homogenization across distinct lowland forest types remains unstudied except along a precipitation gradient in Costa Rica (Karp et al. 2017).

We investigated the consequences of smallholder agriculture for regional gamma diversity across the key forest types of the western Amazon: uplands, floodplains, white sands, and river islands. Comprehensive surveys of birds (455 species) and trees (751 species) produced a data set that captures diversity dynamics across multiple forest types simultaneously.

## Methods

### Study Sites

We conducted fieldwork in the Amazonian lowlands of Loreto Department, Peru (Fig. 1). We focused on 4 terrestrial habitats that are widespread in western Amazonia and harbor distinctive biological communities. Upland forest grows on uplifted clay-soil terraces of alluvial origin. These uplands are the most spatially extensive habitat in the region and the richest in bird and tree species. Floodplain forest along major rivers, subject to protracted flooding during January–June, differs from the upland forest in tree and bird species composition (Remsen & Parker 1983; Wittmann et al. 2006). White-sand forest occurs on deposits of pure white-sand soil (arenosols)



**Figure 1.** Locations of bird and tree sampling sites in Loreto Department, Peru (triangles, upland; stars, floodplain; circles, white sand; light gray, major rivers). Intact and disturbed site pairs separated by <15 km are plotted as a single point. Pairs separated by >15 km are plotted as 2 points connected by a line segment. Four white-sand sites and 1 upland site overlap near a. Two intact and disturbed pairs of upland sites overlap near b and c.

and supports a characteristic avifauna and flora that are absent from other habitats (Alvarez Alonso & Whitney 2003; Fine et al. 2010). And river islands harbor *Cecropia* (Urticaceae)-dominated woodland with a characteristic suite of specialist birds (Rosenberg 1990). Slash-and-burn agriculture is practiced in all of these habitats, resulting in the removal of primary forest vegetation and its replacement with a heterogeneous mosaic of clearings, hedgerows, and secondary forests (Fig. 2). Typical crops include manioc, corn, camu camu, and watermelon on floodplains; manioc, plantain, rice, small buffalo pastures,





*Figure 2. Primary forest and smallholder mosaics of the western Amazon: (a) primary upland forest, (b) successional tangles following abandonment of a floodplain agricultural plot, (c) barren ground and scrub following agricultural abandonment on white sands, and (d) an upland mosaic of active cultivations and regenerating secondary forest. The range of slash-and-burn areas in b–d shows a highly diversified mosaic, not typical differences among soil types.*

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 20 intact sites within 230 km of Iquitos harboring accessible habitats that were largely undisturbed by humans for as long as records were available, except for light selective logging at floodplain sites and widespread hunting of large game animals (see Supporting Information). These sites spanned the major forest habitats of the region: 10 in upland forests, 6 in floodplains, and 4 in white-sand forest (Fig. 2). To ensure that our study sites were representative of western Amazonia as a whole, we selected upland and floodplain sites spanning both banks of the Amazon River, which is an important biogeographic barrier for birds (Pomara et al. 2014). In white-sand forest, we focused our sampling on the Nanay River basin, which supports the richest assemblage of white-sands specialists in Peru, comparable to other white-sand masses in Colombia and Brazil (Alvarez Alonso & Whitney 2003). We could not find intact examples of river islands large enough to accommodate our sampling scheme because all large river islands accessible to us had already been cleared for agriculture (see “Biodiversity Comparisons” below).

We then selected 20 disturbed sites in slash-and-burn mosaic, each paired with an intact site for forest type, soil texture, and geographic proximity (median distance between intact/disturbed pair 8 km). These sites are situated in heterogeneous mosaics of cultivations (generally 0.3–10 ha), pastures (generally 5–50 ha), and secondary forest. At each study site—primary or disturbed—we established 6 sampling points spaced by at least 210 m to avoid double-counting during avian point counts (Gilroy et al. 2014). During subsequent vegetation assessment, we determined that 6 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. Flooding and time constraints prevented us from sampling trees at 2 study sites (1 in intact floodplain and 1 in intact uplands), and we removed their paired disturbed sites from the tree data set. Thus, the final data set contained 234 bird sampling points and 209 tree sampling points. See Supporting Information for details of site selection and site characteristics.

### Biodiversity Data

We surveyed birds and trees at each sampling point. For birds, a single observer (J.B.S.) conducted 4 10-min, 100-m-radius point counts at each sampling point during July–December 2013–2014. Surveys ran from first light until

midmorning, and were not conducted 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 data set for analysis, we aggregated data across the 4 visits to each point by taking the maximum count for each species from any visit.

We made 2 modifications to standard point-count protocols, tailored to the challenges of detecting skittish species and birds in mixed-species flocks (see Supporting Information). First, we included detections of species that flushed during our approach to and departure from each point (within 100 m). Second, when mixed flocks detected during the point count lingered within the 100-m boundary after the count, we followed the flock until we identified all of its participants or until it moved >100 m from the point. We separately recorded individuals detected via these modifications, permitting us to include them or exclude them from analysis (see “Sensitivity Analysis” below).

To survey trees, we established a  $50 \times 2 \text{ m}^2$  tree plot at a fully randomized location within 100 m of each sampling point (equivalent to 0.6 Gentry transects per site [Gentry 1988]). Within these plots, we identified every tree >2.5 cm diameter at breast height. We collected a voucher for each species (except for palms with very large leaves), deposited in the herbarium at the Universidad Nacional de la Amazonía Peruana (UNAP). One botanist (E.H.V.S.) conducted all sampling and made all species determinations with reference to the UNAP herbarium collections. See Supporting Information for details of bird and tree survey protocols.

### Biodiversity Comparisons

We used sample-based rarefaction to compare bird and tree richness in intact and disturbed landscapes on a per-area basis (Chao et al. 2014). For trees this revealed dramatic and predictable diversity loss due to massively reduced densities of individuals at disturbed sites (i.e., cleared areas have fewer trees). Therefore, we used individual-based rarefaction to test for an additional 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, and white sand) and for all forest types combined.

Some bird species that we did not record at intact sites in any habitat are well known to be common on intact river islands (Rosenberg 1990). We could not sample intact river islands because all accessible river islands large enough to accommodate our sampling scheme were disturbed by people. Therefore, we accounted for bias related to our inability to sample the intact river-island avifauna with a follow-up analysis. We obtained a comprehensive list of bird species that were common on

intact river islands within the study area 30 years ago (Rosenberg 1990). We then repeated our analysis while excluding these species from all data sets, thereby removing their influence on our conclusions. We selected these species not because they are prevalent in disturbed samples, but because they are prevalent in intact river-island habitat that we were unable to sample. By removing only common river-island species, we are confident we removed very few species that would not have appeared in the data set for intact forest types, had we been able to sample intact river islands.

### Population Comparisons

For every species of bird and tree in the data set, we calculated Bayesian point estimates and 95% credible intervals for the abundance ratio between disturbed and intact sites. We assumed that the number  $I$  of individuals detected at intact sites and the number  $D$  detected at disturbed sites were Poisson random variables:  $D \sim \text{Poisson}(d)$  and  $I \sim \text{Poisson}(i)$ . We performed inference on the ratio  $F = d/i$ , which gives the multiplicative difference (fold change) in abundance when primary forest is converted to slash-and-burn mosaic. Full details of our estimation procedure for  $F$ , including prior specification, are in Supporting Information.

### Distribution of Disturbance-Sensitive Species

To determine 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 than agricultural mosaics 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 across the disturbed points. Our modeling approach accounts for uncertainty in which species are disturbance sensitive and is not based on the assumption that all species with relatively high sampled abundance in intact (versus disturbed) habitats are disturbance sensitive (see below).

At every sampling point, we recorded the number and size of streams and estimates of percent cover of 10 vegetation-structure classes within 100 m of the point (tall forest, short forest, closed scrub, open scrub [including most active cultivations], orchard, palm swamp, grass, bare soil, open water, and pavement; see Supporting Information for definitions). Small field sizes and interdigitation of individual crops prevented us from including crop type as a variable, and the difficulty of distinguishing cultivations from regenerating scrub on aerial imagery prevented us from including cultivation age, which is generally equivalent to time since last burning. Using

Landsat 8 imagery downloaded from the Global Forest Change Data website (Hansen et al. 2013), we built a random-forest classifier 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 extracted the area classified as intact within 200, 500, and 5000 m of each disturbed sampling point. Finally, we 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 [Mäki et al. 2001]) and to the nearest river (channel width >30 m) based on visual examination of Landsat imagery in the U.S. Geological Survey Landsat Look viewer and aerial imagery in Google Earth.

Initially, we assumed that any species recorded in higher numbers in intact than in disturbed areas is disturbance sensitive. For birds and trees, we fit ordinary and zero-inflated Poisson and negative binomial mixed models (treating study site as a random effect) for the disturbance-sensitive counts using predictors describing percent cover of vegetation-structure classes at the 100 m scale, primary forest cover at 0.2–5 km spatial scales, and proximity to major rivers (see Table 1 for all predictors used and Supporting Information for details). We used the small sample-corrected Akaike information criterion (AICc) to select covariates and error structure that yielded parsimonious models, and we base inference on broad agreement across all top-performing models.

To verify that our conclusions were robust to uncertainty in which species are disturbance sensitive, we re-analyzed the model with the lowest AICc score as follows. We obtained the probability that each species in the data set is disturbance sensitive by computing the integral of the posterior distribution for the abundance ratio  $F$  (see “Population Comparisons” above) from 0 to 1. We then randomly assigned each species to be disturbance sensitive or not based on these probabilities, recomputed 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 (Plummer 2003). 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 nonstandard point-count methods did not bias avian sampling, we repeated our analyses using only detections obtained via standard protocols. We used an N-mixture model to determine that avian detectability is likely to be at least as high in disturbed habitats as intact habitats (see Supporting Information). Therefore, if anything, our results overestimate the biodiversity value of smallholder landscapes.

## Results

Our field effort recorded 455 bird species and 751 tree species. We found very high avian richness in slash-and-burn mosaics. In fact, in each forest type studied (uplands, floodplain, and white sands), sample-based rarefaction revealed that bird richness at disturbed sites was comparable to intact sites (Fig. 3). 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 it was exacerbated by changes in the species-abundance distribution, as revealed by individual-based rarefaction (Fig. 3).

Considering each forest type in isolation substantially underestimated the difference in bird richness between intact and disturbed landscapes. Across forest types, reductions in beta diversity caused 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). After removing the influence of these poorly sampled river-island species, intact landscapes showed dramatically higher avian richness than disturbed landscapes (Fig. 3). This effect results from substantial avifaunal overlap between river islands and the slash-and-burn mosaic. We did not observe an impact of beta diversity loss on regional tree richness, although nonmetric multidimensional scaling suggested homogenization may have occurred (Fig. 4). Instead, upland forests dominated the tree species richness of all intact sites combined, minimizing the opportunity for specialists in other habitats to contribute to richness patterns (Fig. 3).

Disturbed sites consistently clustered separately from intact sites in terms of their species composition, and this difference corresponded to the first axis of variation in nonmetric multidimensional scaling (Fig. 4). 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 (Supporting Information). Thus, in addition to driving species loss, smallholder agriculture drives the disassembly and rearrangement of primary forest communities.

Large numbers of species are disturbance sensitive, with dramatically reduced abundances at disturbed sites (Fig. 5). For example, we detected 137 Screaming Pihas (*Lipaugus vociferans*) at intact sites, and only 1 at disturbed sites. Similarly, we detected 31 *Eschweilera coriacea* (Lecythidaceae) at intact sites and only 1 at disturbed sites. In rarefaction analysis, such species contribute to the species total at disturbed sites, but they are severely harmed by slash-and-burn agriculture.



**Table 1. Results of models for counts of disturbance-sensitive birds and trees summarizing results for the top-performing model (95% CI for the effect size) and for all models within 2 small-sample corrected Akaike information criterion units of the top-performing model (frequency [freq] of inclusion and sign of effect).<sup>a</sup>**

Predictor (definitions)	Birds			Trees		
	freq <sup>b</sup>	sign <sup>c</sup>	95% CI <sup>d</sup>	freq <sup>b</sup>	sign <sup>c</sup>	95% CI <sup>d</sup>
Forest type: upland		–	0.706–0.695		–	3.285–0.002
Forest type: 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 or gap (no closed canopy >5 m tall; % cover within 100 m)	5/11	–		0/6		
Not habitat (water, grass, dirt, buildings; % cover within 100 m)	6/11	–	0.020–0.001	0/6		
Stream (width [m] of incised channel within 100 m)	4/11	+		1/6	+	
Intact 200 (% cover of primary forest within 200 m)	3/11	+		6/6	+	1.491–7.464
Intact 500 (% cover of primary forest within 500 m)	0/11			0/6		
Intact 5000 (% cover of primary forest within 5000 m)	11/11	+	0.417–2.529	0/6		
Primary distance (distance [km] to nearest primary forest)	0/11			1/6	–	
River distance (distance [km] to nearest river >30 m wide)	11/11	–	0.222–0.022	1/6	+	

<sup>a</sup>Forest type was included in all models as a control. All the best-performing bird models had an NB1 negative binomial error structure without 0 inflation. Five of the best-performing tree models (including the best model) had a 0-inflated NB2 negative binomial error structure; 1 had NB2 error without 0 inflation.

<sup>b</sup>Frequency of predictor's inclusion among models within 2 AICc units of the top-performing model.

<sup>c</sup>No predictor for either birds or trees entered multiple models within 2 AICc units of the top-performing model with opposite signs.

<sup>d</sup>The 95% Bayesian CI from the top-performing model, accounting for uncertainty in which species are disturbance sensitive.

Among the 249 bird and 221 tree species for which we detected a significant difference in abundance, 57% and 86% declined at disturbed sites, respectively. Among birds that significantly increased in abundance, fully 39% are common on intact river islands (Rosenberg 1990). Among species without a significant effect, the median total number of individuals detected (across intact and disturbed sites combined) was 2 for birds and 1 for trees, suggesting that lack of significance frequently resulted from low sample size rather than small effect size.

Mixed models revealed a major positive influence of local forest cover and nearby primary forest on the abundance of disturbance-sensitive birds and trees (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. These effects were consistent across all well-performing models and were robust despite uncertainty in which species are disturbance sensitive.

## Discussion

Our results constitute the first large-scale biodiversity assessment of smallholder slash-and-burn agriculture in western Amazonia, and one of the first assessments of biodiversity loss to explicitly consider multiple natural forest types anywhere in the lowland tropics. These features define a key knowledge gap for conservation science because western Amazonia is the epicenter of

terrestrial biodiversity on Earth, harbors multiple forest types, and will face increasing pressure from small-scale agriculture in the future.

Diversity loss, community turnover, and large numbers of declining, disturbance-sensitive species characterize the transition from intact forest to slash-and-burn mosaic. Importantly, much of the loss of regional bird diversity would not be apparent in studies of a single forest type. Slash-and-burn agriculture collapses avian beta diversity among forest types, and this process drives substantial reductions in regional bird diversity. The vast majority of biodiversity comparisons of tropical forest and agriculture have focused on upland forest and therefore missed potential additional biodiversity losses driven by homogenization across forest types (e.g., Daily et al. 2001; Phalan et al. 2011). Andrade and Torgler's (1994) conclusion that slash-and-burn mosaics in the western Amazon support bird diversity on par with primary forest is fully consistent with our own results for upland bird communities (Fig. 3, first panel), but does not reflect overall impacts on regional gamma diversity. Our conclusions are consistent with the observation that smallholder agriculture reduces pairwise avian compositional dissimilarities across biogeographic regions of Costa Rica (Karp et al. 2012, 2017). We expand on these results by showing that homogenization due to smallholder agriculture drives substantial losses of regional gamma diversity. This is not a forgone conclusion, as pairwise dissimilarities do not reliably predict the spatial scaling between alpha and gamma diversity (Baselga 2013). Moreover, our results demonstrate that homogenizing effects are important not only across the widely spaced biogeographic regions and



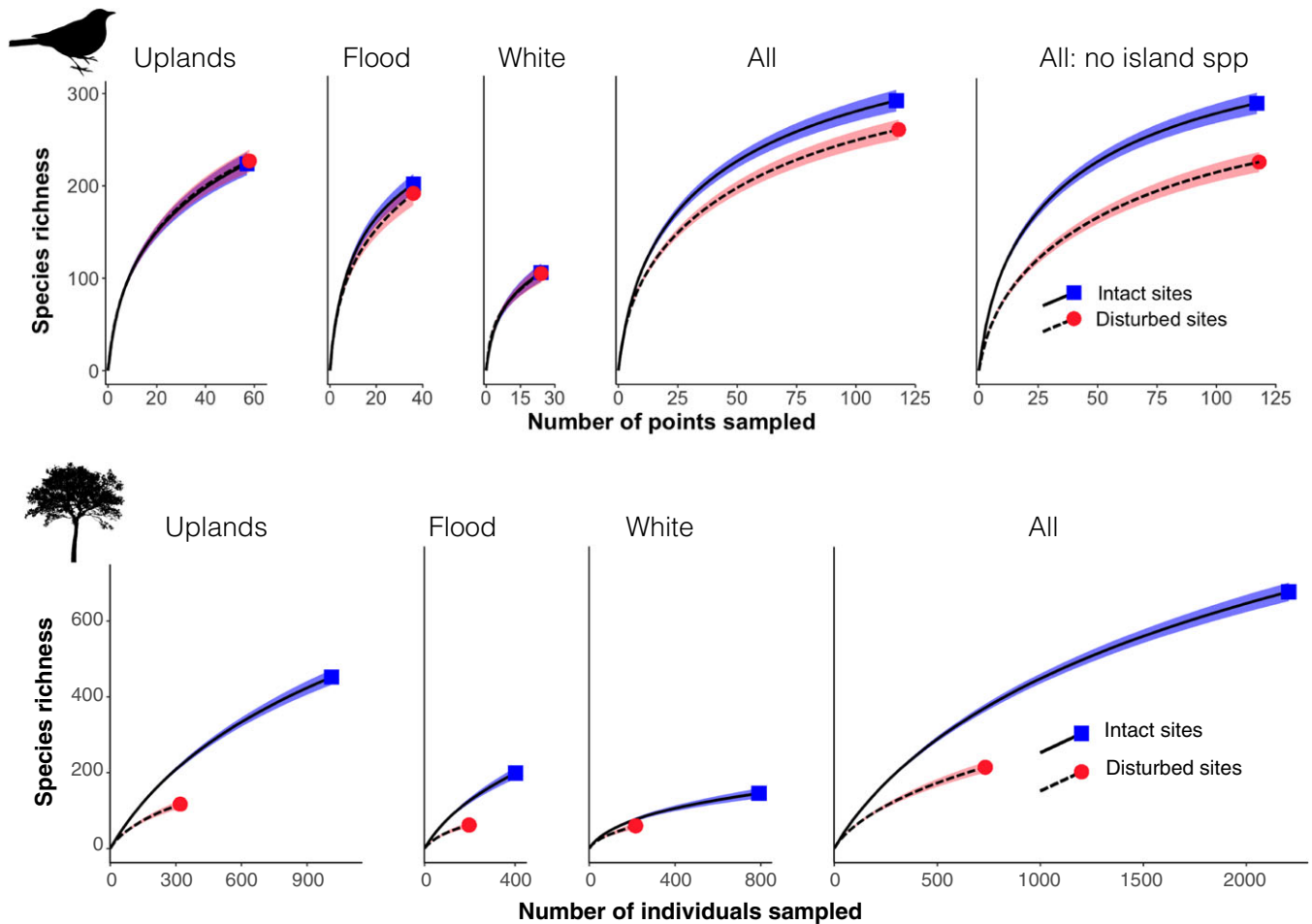


Figure 3. Sample-based rarefaction (mean and 95% CI) for birds and individual-based rarefaction for trees in each forest type separately, all forest types aggregated, and aggregated forest types with river-island species excluded (birds only).

along the steep precipitation gradients studied by Karp et al. (2012, 2017), but also across fine-scale forest habitats of the lowland humid tropics.

We suspect that biotic homogenization across lowland tropical forest types is not unique to western Amazonia. Niche packing and habitat specialization might predispose hyperdiverse assemblages to be sensitive to habitat conversion wherever they occur. Slash-and-burn agriculture impacts forests throughout the tropics (Kissinger et al. 2012), and both Africa and Asia harbor floristically distinctive floodplain forests (Boubli et al. 2004; Theilade et al. 2011) while Asia additionally harbors white-sand forests (Proctor et al. 1983). Peat-swamp forests exist throughout the tropics and have biological affinities to white-sand forests, at least in Amazonia (Díaz-Alván et al. 2017; Draper et al. 2018; Socolar et al. 2018). Thus, processes of biotic homogenization similar to what we observed might be widespread in the lowland tropics globally. Understanding the full impacts of tropical forest disturbance will require spatially extensive sampling

that is comprehensive with respect to regional habitat variation (Solar et al. 2015).

Previous biodiversity comparisons of intact and converted Neotropical forests 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 (Gibson et al. 2011). 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 [e.g., Mayfield & Daily 2005]). However, previous tree inventories in Neotropical agriculture have revealed that primary-forest species are capable of persisting in these landscapes, albeit at low densities (Harvey & Haber 1999; Haggard et al. 2015), and so formal comparisons of abundance and richness using primary-forest controls provide an important quantification of the biodiversity value of these landscapes relative to primary forest. Moreover, trees constitute a critical component of tropical biodiversity, and maintaining tree diversity is essential for the

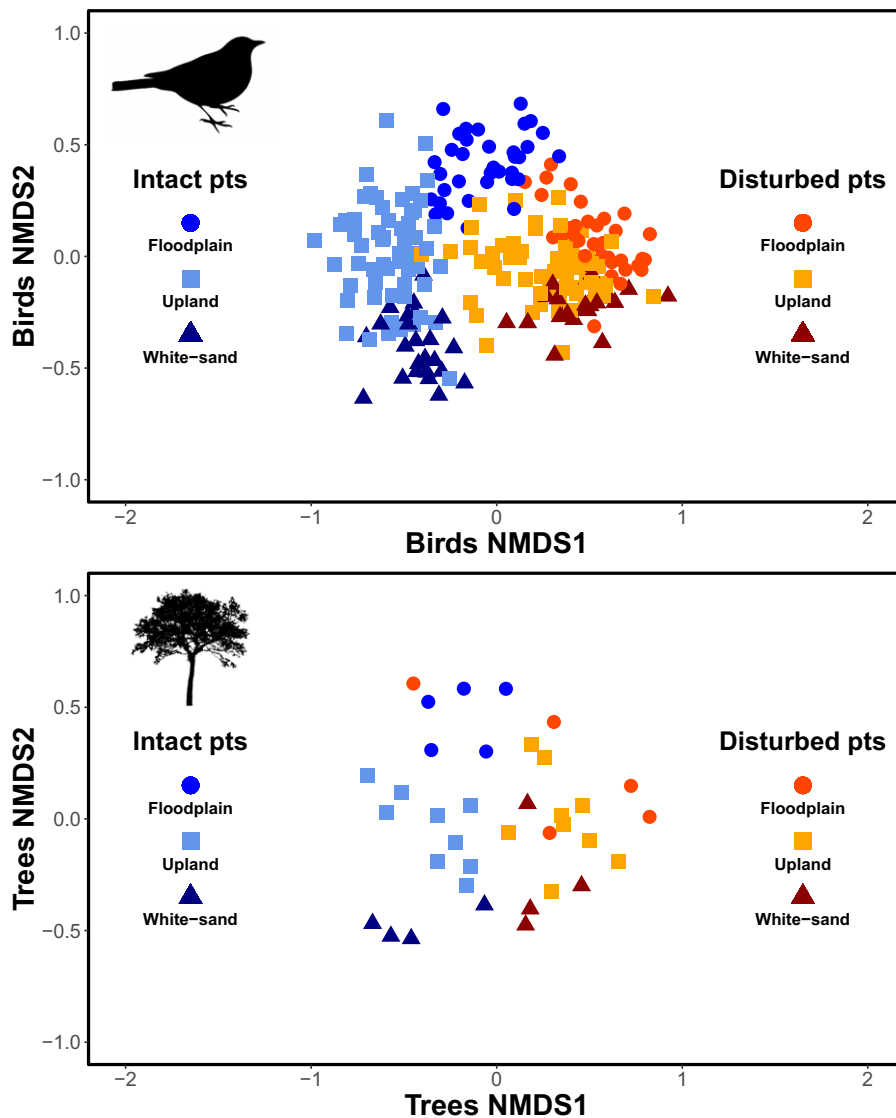


Figure 4. Nonmetric multidimensional scaling (NMDS) based on Raup–Crick dissimilarities for point-scale bird data (stress = 0.21) and site-scale tree data (stress = 0.23).

conservation of a variety of coevolved species (Koh et al. 2004). Finally, we found that agricultural impacts 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. The vast majority of stems were encountered in patches of regenerating secondary forest, so individual-based rarefaction provides a targeted assessment of tree diversity in these second-growth patches compared to primary forest.

A large number of species are disturbance sensitive and decline severely following smallholder conversion. For both birds and trees, secondary forest cover and proximity to primary forest consistently predicted the occurrence of disturbance-sensitive species within the slash-and-burn mosaic. According to our vegetation classifier, the median disturbed point in our data set was surrounded by 19% primary forest at a radius of 0.2 km,

28% at 0.5 km, and 57 % at 5 km and contained 30% closed-canopy secondary-forest cover within a 100-m radius. These figures, coupled with the high heterogeneity of the slash-and-burn mosaics in our system, suggest 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 likely depends on spillover from nearby primary forest into fallow areas.

Overall, our results showed that the continued expansion of smallholder farming will substantially erode western Amazonian biodiversity. However, in the context of one of the most intact and least populated tropical forest landscapes on Earth, we are optimistic that proactive planning can meaningfully conserve regional biodiversity. In particular, our results indicate that careful management of smallholder activities within protected areas will be crucial for them to fulfill their conservation aims. Likewise, our results suggest land-sparing may be

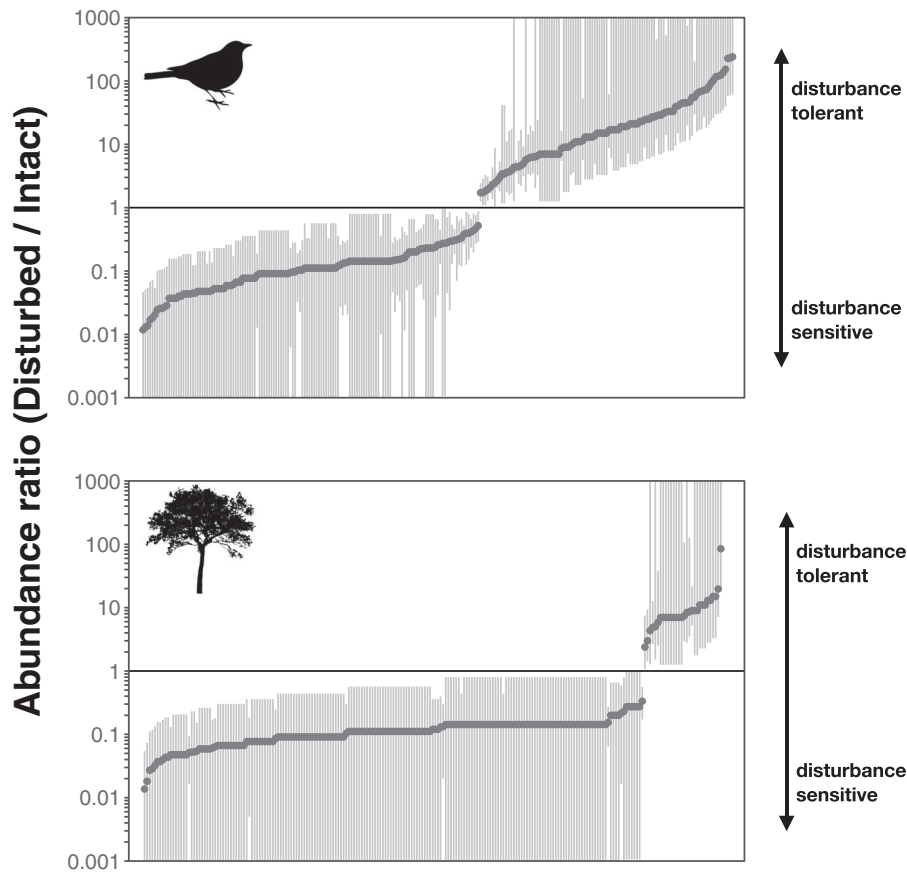


Figure 5. Point estimates and 95% CIs for multiplicative differences in bird and tree species abundance between forest and smallholder agriculture. Only species with CIs (gray bars) that do not overlap 0 are shown.

the most promising approach for harmonizing conservation and regional economic development (Phalan et al. 2011). Because smallholders often gain access to tropical hinterlands following expansions of the road network (Laurance et al. 2014), priorities in the western Amazon are to discourage or prohibit settlement along new hydrocarbons roads and to ensure that these roads are properly decommissioned following the cessation of operations. In Loreto, it is imperative to educate settlers about the difficulty of farming on white sands, the most spatially restricted forest type in the region, both to conserve the diverse white-sands specialist biota and because agriculture here is doomed by the extreme poverty of the soils. It is also crucial to encourage innovative efforts, including efforts inside protected areas, to harmonize conservation objectives with the livelihoods of local people (Pulgar Vidal & Gamboa Moquillaza 2013). Such efforts, including sustainable intensification of smallholder farms and low-impact harvesting of forest products, can potentially provide increased food security to smallholders while sparing forest for conservation and preventing even greater losses of biodiversity that would occur if existing smallholder mosaics were converted to soy monocultures or tree plantations. Importantly, smallholders can be effective conservationists and forest stewards, for example, by securing, protecting, and policing intact Amazonian

forests (Campos & Nepstad 2006) and ensuring that agricultural practices are sustainable without continual expansion into primary forest (Pulgar Vidal & Gamboa Moquillaza 2013).

Biodiversity in smallholder landscapes in Amazonia far exceeds that of industrial agricultural landscapes, and the latter must be regarded as an especially devastating land-use change. Nonetheless, our study highlights the subtler but nonetheless substantial impacts of smallholder agriculture on biodiversity in the western Amazon. Thus, a key challenge will be to ensure that programs promoting sustainable smallholder agriculture in this region are implemented in such a way as to limit rather than promote its expansion. There will be severe biodiversity losses if settlers gain access to the last remaining tropical wildernesses in western Amazonia, no matter how lightly they tread.

## Acknowledgments

We thank F. Draper, F. Hua, Z. Burivalova, A. Washburne, and D. Edwards for input, and P. Saboya, J. Díaz, and D. Lane for sharing extensive knowledge of Amazonian birdlife. For logistical support, we thank C. Rivera, E. Heyman, H. Vásquez, J. Ungvari-Martin, S. Cubas, M. Reis,

D. Chen, Project Amazonas, Explorama Tours, Amazon Refuge Lodge, Otorongo Expeditions, IIAP, Corbidi, J. Paredes, F. Linares, J. Rios, and numerous communities and local guides. We thank the Peruvian government agencies SERNANP and MINAGRI for research permissions. Finally, we gratefully acknowledge funding from the High Meadows Foundation, American Ornithologists Union, American Philosophical Society, and American Museum of Natural History. J.B.S. was supported by an NSF Graduate Research Fellowship.

## Supporting Information

Supplementary methods and results (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. Data and R code are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.nh17p1n>).

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