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Agricultural land in the Amazon basin supports low bird diversity and is a poor replacement for primary forest

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ABSTRACT

The Amazon has a long history of disturbance under subsistence agriculture, but slash-and-burn agriculture is small in scale and has relatively low impact on resident avifauna. More recently, the Amazon has suffered extensive deforestation in favor of cattle ranching and other modern systems of agriculture. Cattle pastures, mechanized agriculture, and even tree plantations have detrimental effects on bird communities, greatly lowering diversity, especially that of primary forest interior specialists. A rising threat to the Amazon is the spread of oil palm plantations that retain few bird species and are not viable alternatives to forest. Embedded within the expanding agropastoral mosaic are forest fragments that have experienced a well-documented loss of diversity. Yet, the matrix can mitigate the recovery of fragmented bird communities depending on the type of secondary regrowth. Connectivity via matrix habitats or forest corridors is critical for the maintenance of forest avifauna. With so many types of land use developing across the Amazon, the "tropical countryside" has potential value for bird diversity. However, evidence suggests that the agropastoral mosaic harbors a small, more homogenized avifauna with few forest species, especially when primary forest is absent from the landscape. For the Amazon Basin's bird life to be conserved into the future, preservation of large tracts of well-connected primary forest is vital. Tropical countryside dominated by agriculture simply cannot sustain sufficient levels of biodiversity.

Keywords: agricultural matrix, avian biology, community ecology, fragmentation, land-use change, oil palm, subsistence agriculture, tropical countryside

La tierra agrícola en el Amazonas mantiene una baja diversidad de aves y es un reemplazo deficiente del bosque primario

RESUMEN

El Amazonas tiene una larga historia de disturbios bajo agricultura de subsistencia, pero la agricultura de tala y quema es pequeña en escala y tiene un impacto relativamente bajo en la avifauna residente. Más recientemente, el Amazonas ha sufrido una gran deforestación para la cría de ganado y otros sistemas modernos de agricultura. Las pasturas para ganadería, la agricultura mecanizada e incluso las plantaciones de árboles tienen efectos negativos en las comunidades de aves, disminuyendo marcadamente la diversidad, especialmente de los especialistas de interior de bosque primario. Una amenaza creciente para el Amazonas es el avance de las plantaciones de palma aceitera que retienen pocas especies de aves y que no son alternativas viables del bosque. Embebidos dentro del mosaico agro-pastoril en expansión están los fragmentos de bosque, que han sufrido una pérdida de diversidad que ha sido bien documentada. A pesar de esto, la matriz puede mitigar la recuperación de las comunidades fragmentadas de aves dependiendo del tipo de crecimiento secundario. La conectividad a través de los hábitats de la matriz o de corredores de bosque es crítica para el mantenimiento de la avifauna del bosque. Con tantos tipos de uso del suelo desarrollándose a través del Amazonas, la "ruralidad tropical" tiene valor potencial para la diversidad de aves. Sin embargo, la evidencia sugiere que el mosaico agro-pastoril alberga una avifauna pequeña y homogeneizada con pocas especies de bosque, especialmente cuando el bosque primario está ausente del paisaje. Para conservar a futuro las aves de la cuenca amazónica, es vital preservar grandes espacios de bosque primario bien conectados. La ruralidad tropical dominada por agricultura simplemente no puede mantener niveles suficientes de biodiversidad.

Palabras clave: agricultura de subsistencia, cambio de uso del suelo, ecología de comunidades, fragmentación, matriz agrícola, palma aceitera, ruralidad tropical

INTRODUCTION

The Amazon Rainforest is almost as famous for its deforestation as it is for its wildlife. Over 780,000 km^2 (19%) of primary rainforest has been cleared in the Amazon since 1970, with 9,762 km^2 cut down in 2019 alone. Even though the deforestation rate has generally declined in the past 15 yr, since 2015 deforestation has spiked again (INPE 2019). Deforestation provides timber and other natural resources while clearing the land for agriculture and other practices (Donald 2004, Defries et al. 2010, Gibbs et al. 2010).

Cattle pasture is the largest agricultural land use in the Amazon, followed by bananas, beans, cassava, coffee, maize, rice, and soybeans (Simon and Garagorry 2006, Peres et al. 2010). Most agricultural expansion has been in southwestern Amazonia, particularly in the Brazilian states of Rondônia, Mato Grosso, and Pará, a region known as the "arc of deforestation" (Cochrane et al. 1999; Figure 1). Here, cropland is becoming increasingly favored, with soybean fields replacing the predominant pastures as well as primary forest (Brown et al. 2005, Morton et al. 2006, Barona et al. 2010, Macedo et al. 2012). Newly constructed roads such as BR-163 have exacerbated forest conversion by increasing access to the forest (Soares-Filho et al. 2004, Fearnside 2007). Roraima and Acre (the states immediately north and east of the arc of deforestation, respectively; Figure 1) are also likely to see a shift away from slash-and-burn farming to agroforestry and permanent cropland, with expected increases in deforestation in the future (Fujisaka et al. 1996, Smith et al. 1996, Wearn et al. 2012).

The Brazilian state of Amazonas (Figure 1) is far less disturbed than the southern and eastern states. Agriculture there is largely restricted to the land immediately adjacent to rivers and lakes where slash-and-burn agriculture is prevalent (Johns 1991, Borges 2007),

FIGURE 1. A map of the Amazon Ecoregion (enclosed by green border). Deforestation (Hansen et al. 2013) is shown in pink and the "arc of deforestation" is outlined. The map was created using ArcGIS Pro software by Esri. ArcGIS Pro is the intellectual property of Esri and is used herein under license. Copyright © Esri. All rights reserved.

but soybean and oil palm are seeing increases there as well (Simon and Garagorry 2006, Butler and Laurance 2009). Where the Amazon approaches the Andes in Peru and Ecuador, higher elevations favor coffee (Aerts et al. 2017) and Peru is also seeing large increases in oil palm plantations (Gutiérrez-Vélez et al. 2011, Srinivas and Koh 2016). In the Colombian and Bolivian Amazon, illicit crops such as coca and cannabis are a continuing cause of deforestation (Alvarez 2002, Murad and Pearse 2018).

With so many different types of land use, a complex agropastoral mosaic is emerging that has the potential to offer varying opportunities for biodiversity (Hughes et al. 2002, Şekercioğlu et al. 2007, Şekercioğlu 2009). As deforestation continues, policy makers and conservation scientists will be faced with decisions on how best to conserve the Amazon's diverse flora and fauna while providing food and income for locals (Phalan et al. 2011). Now is the time for critical land-use decisions, before it is too late for Amazonia's biodiversity, especially given the recent Amazon fire crisis (Barlow et al. 2020).

Subsistence Agriculture

The state of Amazonas is far from the arc of deforestation and here human access is limited, populations are relatively low, and swidden/fallow farming reflects a more historical way of life (Arroyo-Kalin 2012). Small communities lining the rivers, lakes, and few roads eke out a subsistence living based largely on a slash-and-burn rotation of land use. Small sections of forest, perhaps 1–5 ha in size, are cut and burned and then planted with crops such as manioc, beans, or rice. These plots are maintained for a few years before being left fallow, at which point the farmers move on. From the fallow land grows "capoeira," a low scrub of fast-growing trees such as *Vismia* and *Cecropia* intermixed with herbaceous plants. In this fashion, local communities can rotate their land usage with little need to encroach further into the forest (Johns 1991). The resulting landscape forms a localized mosaic of crops, capoeira, and forest.

A handful of studies have characterized the effect of slash-and-burn agriculture on bird communities, with an emphasis on the secondary forest that regenerates in fallow patches (Johns 1991, Andrade and Rubio-Torgler 1994, Borges 2007). These studies provide an important contrast with those in more intensive agricultural land uses. Johns (1991) conducted bird point counts around Tefé Lake, Amazonas, in cultivated land, capoeira, a small forest fragment (35 ha), and logged and unlogged forest. Observing 235 species, he showed that the highest bird species richness occurred in regenerating capoeira. Roughly 39% of the species detected used cultivated land (mostly manioc crop) with an additional 33% using capoeira. However, when controlling for transect lengths, by far the most species per kilometer were detected in the forest fragment whereas capoeira and cultivated land showed similar species richness (both higher than unlogged forest). Only 26% of the species detected were confined to primary forest and just 8% were restricted to unlogged primary forest. With increased disturbance, terrestrial species and bark- and foliage-gleaning insectivores decreased whereas sallying species, insectivore/frugivores, and granivores increased. Thus, the study demonstrated that the more disturbed habitats could support a reasonable proportion of species but still lacked representatives of important forest guilds.

Andrade and Rubio-Torgler (1994) carried out a similar study along the Mirití-Paraná River in southwestern Colombia. The authors used mist netting to characterize the bird communities along a gradient of regenerating vegetation where slash-and-burn practices had led to a patchwork of crop plots, secondary growth, and primary forest (the authors did not assess the bird communities of the crop plots themselves). Over almost a year, the authors captured 103 species and demonstrated that old secondary growth (5–20 yr old) was more similar in species composition to rainforest understory than to young secondary growth (<5 yr old). 47.5% of species were associated with secondary regrowth of which 18.4% were confined to this habitat. Only 4.8% of species were restricted to forest understory. However, proportionally, there were more rarely caught species in the latter habitat. With increased regeneration, understory insectivores increased, especially ant-followers, which were infrequent in disturbed habitat. Sallying insectivores were caught more frequently in regrowth, as were nectarivores, which made use of abundant *Heliconia* flowers. Although the relative proportions of different feeding guilds changed with the level of forest regeneration, Andrade and Rubio-Torgler argued that the scale of disturbance was small enough to preclude the colonization of species, such as granivores, that are more commonly found in highly disturbed habitat. The similarity between old secondary regrowth and undisturbed understory suggests that regrowth soon (>10 yr old) resembles the dynamic open patches created by natural phenomena (treefalls, river edges; Wunderle et al. 2004) within undisturbed forest. Yet, as mist nets do not sample canopy species, it is difficult to generalize from these studies to the entire community, although canopy species are more edge tolerant.

More recently, Borges (2007) surveyed birds along the lightly populated Jaú River in Jaú National Park, Amazonas, where swidden agriculture has left patches of secondary forest. He detected 150 bird species and found that secondary forest in general had higher species richness than primary forest, and medium-to-old (7–35 yr old) secondary forest in particular had similar species richness to primary forest. The richness of secondary forest was augmented by species more typically found in open areas and igapó flooded forests. Frugivore/insectivores and nectarivore/insectivores (i.e. species with mixed diets) were more associated with secondary growth, perhaps reflecting the prevalence of certain resources (e.g., *Heliconia* flowers), but insectivore specialists (e.g., ant-followers and mixed-species flock members) were closely tied to primary forest. Taken together, these studies reveal a relatively low negative impact of slash-and-burn agriculture, perhaps even a positive effect as richness is bolstered by the addition of species from more open habitats where secondary growth mirrors the natural dynamics of the forest. It seems likely that this form of agriculture, which has persisted to varying extents since pre-Columbian times (Arroyo-Kalin 2012), is a relatively sustainable land-use practice for Amazonian birds.

Modern Agricultural Land Use

In recent decades, the Amazon rainforest has been shaped by a multitude of land uses. The biggest cause of deforestation has been the conversion of forest to cattle pastures (Morton et al. 2006), but food crops such as soybeans (Brown et al. 2005, Nepstad et al. 2006, Barona et al. 2010), illegal crops (Alvarez 2002, Murad and Pearse 2018), and plantations of coffee, bananas, pine, and eucalyptus (Canaday 1997, Barlow et al. 2007b) comprise important agricultural land uses within the Amazon. The demand for these crops is rising in response to growing markets, especially in Asia (Tobias et al. 2013). There are surprisingly few studies of how different agricultural land uses have affected Amazonian bird communities and these studies have varied greatly in scope. Canaday (1997) compared bird species richness between coffee plantations and forest at increasing distances from clearings and petroleum company roads in the Cuyabeno Reserve, Ecuador. Despite only conducting 12 three-day surveys, Canaday found a significant decrease in insectivore species richness with increased disturbance. Coffee plantations showed low total species richness although they also received the lowest survey effort and this study was limited in its spatial and temporal replication.

Barlow et al. (2007a) attempted to address some of the methodological shortfalls of other studies by conducting their research over much larger, independent forest areas. Working in the Jari forestry project in the northeastern Brazilian Amazon, Barlow et al. conducted mist netting, point counts and walking transects within large tracts of primary forest, secondary forest (2,682 ha on average), and *Eucalyptus* plantations (1,687 ha on average), spaced many kilometers apart. This enabled them to compare bird species richness in spatially independent, well-replicated forest types without the confounding effect of edge proximity. The authors found that the conservation value of plantations and secondary forest was much lower than that found by other studies (Johns 1991, Andrade and Rubio-Torgler 1994, Blake and Loiselle 2001, Waltert et al. 2005, Beukema et al. 2007, Buechley et al. 2015). Species richness in *Eucalyptus* was just over half that found in primary forests (secondary forests had intermediate values) and community similarity was very low between forest types. These results also showed congruence with other taxa (Barlow et al. 2007a). Foraging guild comparisons revealed that *Eucalyptus* (compared to primary forest) lacked many species of insectivores (e.g., obligate ant-followers, bark searchers), arboreal frugivores/granivores, and habitat specialists. By contrast, *Eucalyptus* did harbor more nectarivores and generalists, especially species more typical of open areas and young secondary forest. Barlow et al. (2007a) thus demonstrated the poor conservation value of extensive *Eucalyptus* monocultures, when controlling for the spillover effect of nearby, higher-quality habitat. However, such large blocks of continuous plantation are relatively rare and agricultural land configuration in the Amazon tends to be more complex.

In order to assess the value of different land uses in more complex landscapes, studies must incorporate large-scale habitat comparisons. Moura et al. (2013) sought to do so by assessing how bird communities differ along a gradient of human agricultural intensity incorporating multiple land uses. Across 36 drainage catchments in 2 regions (Paragominas and Santarém) of Pará, Brazil, the investigators conducted point counts to determine species richness and community similarity. They categorized the land around each transect into 6 types based on disturbance level: primary forest, secondary forest, plantation, small-holder agriculture (manioc plantations and/or fruit trees), cattle pasture, and mechanized agriculture. Agricultural land in the study area supported little more than a third of the regional avifauna, and in very low abundance. In both regions, all agricultural land types were found to contain considerably lower bird species richness than all forest types, especially of forest species. Mechanized agricultural land always had the lowest species richness and plantations and pastures were equally low for Paragominas and Santarém, respectively. Pastures in Paragominas and small-holder land in Santarém were marginally more speciose than other agricultural land, but still well below even secondary forest. Community composition also changed significantly with disturbance level; the only land uses that did not differ from each other were pastures and plantations (in Paragominas) and pastures and small-holder land (in Santarém). Overall, Moura et al. (2013) revealed a trend of decreasing forest bird species richness with decreasing primary forest cover and a decrease in species turnover in more intensive land uses.

Despite the variability in agricultural practices and the scale of investigation, agricultural land consistently supports a small proportion of bird species when compared to primary, and even secondary, forest. The low species richness of cattle pastures and mechanized agriculture is not surprising, as these habitats bear little similarity to primary forest. What may be more surprising, particularly to policy makers, is the low value of plantations such as *Eucalyptus* (Barlow et al. 2007b), coffee (Canaday 1997) and, as we summarize below, oil palm.

Oil Palm

Even though rates of deforestation are decreasing in the Amazon Basin, oil palm (*Elaeis guineensis*) is a new and growing threat to the rainforest. Since its domestication in Central and West Africa, oil palm has become a dominant crop in tropical areas of the world (Fitzherbert et al. 2008), and palm oil is used in a wide range of household consumables and feeds a growing biodiesel market (Koh and Ghazoul 2008). Over the last 40 yr, the crop has seen an exponential increase, rising from 3.6 million ha in 1961 to 18.7 million ha in 2014, expanding by 600,000 ha each year in the last decade (FAO 2017), often at the expense of primary rainforest (Koh and Wilcove 2008, Gutiérrez-Vélez et al. 2011). Southeast Asia in particular has seen a huge increase in land conversion to oil palm (Koh and Wilcove 2008), with subsequent detrimental effects on biodiversity (Aratrakorn et al. 2006, Danielsen et al. 2009, Senior et al. 2013). This crop is increasing in use in Latin America, resulting in the conversion of more forest. In Peru, 72% of oil palm plantations have entailed forest conversion (Gutiérrez-Vélez et al. 2011), and in Brazil there is increased interest in the crop as a lucrative source of income (Butler and Laurance 2009). Oil palm presents a more cryptic danger than other crops because it is viewed by some as less damaging to the ecosystem because plantations superficially resemble forest. The Brazilian state of Pará has even passed a resolution that allows the replacement of forest with "low-impact" oil palm in permanent protection areas and legal reserves on private land (Lees et al. 2015). Yet, there is growing evidence that oil palms hold little value for wildlife (Azhar et al. 2011, Edwards et al. 2013, 2014; Senior et al. 2013, Lees et al. 2015).

Recently, 2 important studies have addressed the impacts of oil palm on Amazonian avifauna (Lees et al. 2015, Srinivas and Koh 2016). Lees et al. (2015) conducted 288 point counts across a mosaic of land uses near Belém, Pará. The study compared species richness and community composition between oil palm plantations, cattle pastures, secondary forest, and primary forest. It found oil palm to be the most species-poor of the 4 land uses, with a third of the species richness of primary forest and just over half the species richness of cattle pastures. This pattern remained when only a subset of forest species was analyzed. When the authors controlled for the distances of plantations and pastures from primary forest, they found the difference in species richness between the 2 agricultural types to be insignificant. To determine the importance of the landscape and vegetation structure on birds, Lees et al. (2015) regressed species richness against various environmental variables. They found that tree species richness was the most important predictor of bird species richness, followed by distance to the nearest forest border, percent forest cover, and tree biomass. Additionally, and perhaps surprisingly, the study demonstrated that older oil palm plantations (>11 yr old) had less than half of the species richness of younger plantations due to the loss of species typically associated with pastures.

On the other side of the Amazon, in Ucayali, Peru, Srinivas and Koh (2016) found similarly bleak prospects for forest birds in oil palm. Following almost 2,000 hr of mist netting, only 5% of the 64 bird species sampled were caught in both forest and oil palm sites, with a community similarity of 2% between habitat types. The species richness in the oil palm plantations was less than half that of the forest sites whereas species evenness and abundance were also significantly lower in oil palm. In particular, the authors found fewer insectivores, frugivores, understory species, disturbance-sensitive species, habitat specialists, interior species, and Amazonian endemics in oil palm. Although this study was limited by the number of true spatial replicates, the findings are not surprising. Furthermore, they are, in some ways, a best-case scenario. The oil palm plantations in the Pucallpa region of Peru are generally much smaller than the vast monocultures of Southeast Asia, and they are embedded within a matrix of other land uses, including forest fragments. Such habitat mosaics may support more diversity than expansive plantations. Even within the study plantation, remaining pockets of forest could have been a source of visiting birds. Thus, if oil palm plantations in the Amazon come to resemble those in the Old World, their effects on Amazonian birds could be more severe. Furthermore, in both studies oil palm was compared to disturbed forest (with both selective logging and hunting reported), which may not represent a true baseline of bird diversity, leading to an underestimation of community differences.

We encourage more research into the effects of oil palm in Amazonia at greater temporal and spatial scales and, in particular, on how different landscape configurations can facilitate the persistence of forest species. However, we expect general results to agree with those found by Lees et al. (2015) and Srinivas and Koh (2016), as well as those found in Southeast Asia (Aratrakorn et al. 2006; Peh et al. 2006; Edwards et al. 2010, 2014; Sodhi et al. 2010; Azhar et al. 2011, 2013). The appearance of oil palm as a forest is highly misleading, as these plantations support few rainforest species; the lack of habitat complexity and resources precludes the persistence of all but the most generalist bird species. Any suggestion that landowners can use oil palm as a viable forest cover on their land should be dismissed and preservation of primary forest should remain the priority (Butler and Laurance 2009, Lees et al. 2015).

Agriculture and Forest Fragments

One of the most obvious features of expanding agriculture is the fragmentation of primary habitats. This has received much attention in the literature, not least because projects such as BDFFP (Biological Dynamics of Forest Fragments Project), near Manaus, explicitly test how fragmentation affects diversity and movement (Ferraz et al. 2003, 2007; Laurance et al. 2004; Antongiovanni and Metzger 2005; Stouffer et al. 2009, 2011; Bregman et al. 2015). We do not review the effects of fragmentation on tropical birds per se (see Fahrig 2003 for a review or the papers above for primary research), but rather how the agricultural matrix can mediate the effects of fragmentation. For some species the matrix can represent an inhospitable sea separating suitable habitats and individuals might be reluctant to cross even small gaps (Develey and Stouffer 2001, Şekercioğlu 2002, Laurance et al. 2004, Laurance and Gomez 2005). Yet for others, the matrix could be an important medium facilitating movement between patches (Stouffer and Bierregaard 1995, Jules and Shahani 2003, Antongiovanni and Metzger 2005).

BDFFP has been used to monitor the role secondary regrowth plays in mediating community changes in forest fragments. Stouffer and Bierregaard (1995) followed the changes in bird communities both before, and up to 9 yr after, fragmentation. Of note was the differential response of the bird community depending on the surrounding matrix. Areas of the forest that had been cleared and burned for pasture supported *Vismia*-dominated regrowth that did little to mitigate the loss of species from fragments, especially ant-followers and mixed-flock species. By contrast, *Cecropia* regrowth, which developed on unburnt land, had a positive effect on the recovering bird community. After 5 yr of isolation, ant-followers began using fragments as small as 1 ha again while the members of mixed-flocks all reassembled by year 9 and even used the *Cecropia* around the fragments when foraging. Moreover, where *Vismia*-surrounded fragments retained a community decreasingly similar to pre-isolation forest, *Cecropia*-surrounded fragments began to resemble the initial community by the end of the study. Yet, despite the success of *Cecropia* in facilitating the return of some guilds, others, such as terrestrial insectivores, failed to return during the study period.

Ten years later in BDFFP, Antongiovanni and Metzger (2005) used playback techniques on 6 focal species to assess the usage of forest fragments and the matrix by 7 understory insectivores. Three species (*Thamnomanes ardesiacus*, *Cyphorhinus arada*, and *Hylophilus ochraceiceps*) failed to use either small fragments or the matrix, 2 species (*Formicarius colma* and *T. caesius*) made infrequent use of fragments and matrix, and 2 species (*Percnostola rufifrons* and *Hypocnemis cantator*) actually benefited from the matrix. Importantly, it appeared that the usage of small fragments was linked to the usage of the matrix as species in the study either used both or neither habitat type. Given that some of these species declined or disappeared from the fragments following isolation and later recolonized, it appears the matrix was vital in facilitating recolonization as those species that did not use the matrix were not found again in fragments. When comparing matrix types, more species recolonized *Cecropia*-surrounded small fragments than *Vismia*-surrounded fragments. This study corroborates evidence that the matrix type affects the persistence and recolonization of bird species in forest fragments (Gascon et al. 1999, Şekercioğlu et al. 2002, Wethered and Lawes 2003, Sisk et al. 2013), and *Cecropia* spp., with their taller, more closed canopy, provide a better medium for species to move through. It is therefore preferable for farmers to refrain from burning large areas of land in favor of a *Cecropia*-based matrix. Additionally, matrix habitats appear to provide foraging opportunities given that the fragments alone were not large enough to sustain moderately sensitive species. Maintaining a permeable matrix is just one way to facilitate connectivity between forest fragments; corridors, stepping stones, and ecotones are all well-known landscape elements that can connect patchy habitats (Şekercioğlu 2009). The landscape is rarely as black and white as "forest" and "matrix"; in reality, land-use mosaics are far more complex (Şekercioğlu and Sodhi 2007).

The Tropical Countryside

We have seen that a multitude of agricultural practices are used throughout the Amazon. In addition, forest fragments and secondary regrowth are scattered across the landscape as well as a network of roads, tracks, and ever-increasing urban areas. This complex mosaic of land use is often referred to as the "tropical countryside" (Mahood et al. 2012). As countryside habitats have increased, so too have studies attempting to quantify their biodiversity value, especially in Central America (Ricketts et al. 2001, Daily et al. 2003, Horner-Devine et al. 2003, Harvey et al. 2004, Karp et al. 2012) where the agropastoral mosaic retains a considerable proportion of forest species (Daily et al. 2001, Hughes et al. 2002, Lindell et al. 2004, Şekercioğlu et al. 2019) and β-diversity (Karp et al. 2012). In the Afrotropics (Kofron and Chapman 1995, Söderström et al. 2003, Naidoo 2004, Waltert et al. 2005) and Southeast Asia (Thiollay 1995, Waltert et al. 2004) results have ranged from a reasonably positive effect of the countryside (Söderström et al. 2003) to negative (Thiollay 1995). In the Amazon, however, there has been considerably less research conducted on the biodiversity value of tropical countryside.

Mahood et al. (2012) took the pessimistic but perhaps realistic stance that in the future the agropastoral matrix may contain negligible forest, and so they attempted to characterize the conservation value of the matrix itself. Moreover, they explicitly examined features of the landscape that favored or reduced species richness. Using data from 325 point counts in the highly deforested Alta Floresta municipality of Mato Grosso, Brazil, the study found that the agricultural matrix supported few forest birds. In an area dominated by cattle pastures, interspersed with scrub, relictual trees, riparian tracts of forest, and small holdings, only 4.3% of detections (20% of species) were of forest species, and none were of forest interior specialists. The remaining detections were either edge-tolerant species (23.1%) or open-country species (72.6%). Mahood et al. tested various habitat variables to determine how they affected species richness. For all habitat-sensitivity groups, the number of relictual trees (excluding palms) was the most important explanatory variable, and was positively associated with species richness. Few other variables made a difference to forest species richness, except perhaps the presence of scrub. For edge and open-habitat species, understory density had a strong positive effect on species richness whereas overhead wires favored edge species and bodies of water favored open-habitat species. Based on these results, the authors forecasted that removing relictual trees would lead to the loss of 81% of forest species (and 43% of edge species) while the additional loss of scrub would remove another 13% of forest species. The importance of both remnant trees and vertical habitat complexity in supporting bird diversity is corroborated by several other studies throughout the tropics (Thiollay 1995; Hughes et al. 2002; Söderström et al. 2003; Peh et al. 2006; Şekercioğlu et al. 2007, 2019; Nájera and Simonetti 2010; Azhar et al. 2013; Muñoz et al. 2013). By explicitly ignoring forested habitats (including forest edge habitats and large tracts of secondary growth) the study failed to detect 66% of the regional species pool, a far worse situation than in other studies (Hughes et al. 2002). The authors suggest that other studies may overestimate the value of tropical countryside by including forested land that provides a source of forest birds (Daily et al. 2001). Alternatively, it is possible that the balance of extinction debt vs. colonization credit could be at different stages in different places (Jackson and Sax 2010), emphasizing the importance of monitoring community dynamics over time.

Many of the studies presented here have documented decreases in localized species richness (α-diversity) in agricultural land but few have analyzed whether these decreases have altered the similarity of species composition across landscapes (β-diversity). de Castro Solar et al. (2015) examined how β-diversity changed across disturbance levels and between sites of similar disturbance in the state of Pará. The study demonstrated that, across taxa (birds, ants, orchid bees, dung beetles, and plants), both α- and β-diversity declined with increased disturbance (from undisturbed primary forest, through disturbed and secondary forest, to cattle pastures and cropland). The contribution of nestedness to β-diversity also increased with disturbance. This suggests biotic homogenization (i.e. species composition; McKinney and Lockwood 1999, Olden and Rooney 2006, Baiser et al. 2012) is more similar across agricultural landscapes than it is across forested landscapes. That said, turnover still contributed considerably to β-diversity, even in agricultural land, indicating a degree of landscape divergence (Laurance et al. 2007). This is likely due to the differential effects of diverse land uses and disturbance intensities on biota. Although the results in this study were largely consistent across taxa, birds did have a noticeably higher β-diversity in agricultural land than did other taxa and the authors suggest that this results from the chance sampling of a subset of agriculturally tolerant species at different sites. Furthermore, β-diversity was higher for birds among cropland sites than among cattle pasture sites, perhaps because mechanized agriculture is more diverse than cattle ranching. It is reassuring that the birds of the agropastoral mosaic are not completely homogenized and that species turnover across agricultural landscapes still contributes to Amazonian γ-diversity (i.e. regional diversity). However, the loss of species turnover across tropical countryside remains an issue, and it is even more vital to conserve forest across landscapes to maintain the Amazon's β-diversity.

CONCLUSION

It is clear that across most agricultural land uses in the Amazon, the tropical countryside harbors a small fraction of the species pool. As deforestation continues, and the agropastoral mosaic expands, the situation for Amazonian birds looks bleak. Furthermore, with the addition of oil palm plantations, the value of the countryside may decline further as more forests are replaced by "pseudoforest" (Butler and Laurance 2009, Lees et al. 2015). Land use is a tradeoff between conserving wildlife and sustaining human populations so how best to partition the land has become a crucial talking point (Phalan et al. 2011). Across Amazonian bird studies, the irreplaceability of primary forest is apparent (Mahood et al. 2012, Moura et al. 2013, Lees et al. 2015) and such habitat should be preserved at all cost (Sodhi et al. 2010). Most other land uses, even secondary-growth forest (Barlow et al. 2007b, Lees et al. 2015), cannot support the diverse forest-interior specialists. Sparing of forest would usually mean intensification of agricultural land in the land-sharing/land-sparing debate (Phalan et al. 2011). However, such a strategy has its own issues as the success of bird species in forest fragments is so contingent on the size, shape, and connectivity of those fragments (Laurance et al. 2002, Lees and Peres 2008, Şekercioğlu et al. 2015). To conserve β-diversity across the Amazon would require a protected area network spanning the basin, preserving large areas of primary forest as sources of forest-dependent diversity while connecting smaller fragments using more permeable matrices, corridors, or stepping stones of forest (Gilroy et al. 2014). Compared to forest-dependent species, the birds supported by tropical countryside tend to be a relatively small number of habitat generalists or open-habitat specialists (McKinney and Lockwood 1999; Mahood et al. 2012; Şekercioğlu et al. 2019) of low conservation concern (Lees et al. 2015). Turnover is also lower across agricultural land uses than between forests (Naidoo 2004, Mahood et al. 2012, Moura et al. 2013) and the dispersive nature of these species means that colonizing suitable habitat is far easier for them than for forest specialists. General declines in bird diversity could impact the ecosystem because of the wide variety of functions that birds provide (Şekercioğlu 2006). Furthermore, birds contribute valuable ecosystem services to humans such as pest control, crop pollination, and disease regulation (Şekercioğlu et al. 2016) and so it is in the interests of farmers to foster bird diversity.

Here, we have shown that studies assessing the effects of agriculture on birds in the Amazon have produced largely negative results and this should send a strong message to conservation managers and policymakers alike. It is a critical time for the conservation of Amazon rainforest birds, as stakeholders decide how best to manage the region for the future. We hope that more people will realize the value of protecting a connected network of primary forest and that the tropical agricultural countryside cannot compensate for native habitat. We urge more research into how birds can use the agropastoral matrix at larger spatial and temporal scales and especially how different land use configurations could maximize biodiversity while meeting agricultural needs.

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