



Original research article

Oil palm expansion drives avifaunal decline in the Pucallpa region of Peruvian Amazonia

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HIGHLIGHTS

- First study examining effect of oil palm on avian diversity in Western Amazonia.
- Less than 5% of captured species were common to forest and oil palm habitats.
- Bird species richness, evenness and abundance higher in forest than in oil palm.
- Insectivorous and frugivorous birds most affected by oil palm conversion.
- Oil palm plantations represent particularly poor habitat for Amazonian birds.

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ABSTRACT

Oil palm is one of the world's most rapidly expanding crops, replacing humid forests across tropical regions. Studies examining the effect of this land conversion on biodiversity have tended to focus predominantly on Southeast Asia, where the majority of the world's oil palm is produced. Because the Amazon possesses the greatest area of suitable land for oil palm expansion, oil palm is considered an emerging threat to Amazonian biodiversity. This is the first study to examine how oil palm agriculture affects avian diversity within the context of Western Amazonia. We used mist nets to conduct avifaunal surveys of forest and oil palm habitat in the Pucallpa region of Peruvian Amazonia. Bird species richness, species evenness, and overall abundance were all significantly higher in the forest than in oil palm habitat. Strikingly, less than 5% of all captured species were common to both forest and oil palm habitat. The species absent from the oil palm plantations were disproportionately habitat specialists, forest interior birds, birds with high sensitivity to disturbance, and insectivores and frugivores. The results suggest that oil palm is particularly poor habitat for Amazonian birds, and that the species that are persist on them are of lower conservation value. Given the apparent lack of diversity on oil palm plantations, preventing further conversion of forests to oil palm should be prioritized.

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1. Introduction

Despite covering only a small fraction of the Earth's surface, tropical humid forests are thought to be home to over 50% of the world's species (Myers, 1988). Agricultural expansion is the primary driver of deforestation in tropical regions, and one

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of the greatest threats to global biodiversity (Geist and Lambin, 2002). Each year, millions of hectares of primary forest are destroyed to meet rising demands for food, timber, and other natural resources (Donald, 2004; DeFries et al., 2010; Gibbs et al., 2010; Foley et al., 2011; Wilcove et al., 2013). African oil palm (*Elaeis guineensis*), a palm native to West and Central Africa, is one of the most rapidly expanding crops, and a leading cause of deforestation in tropical lowland areas around the world (Koh and Wilcove, 2008; Turner et al., 2008; Miettinen et al., 2012; Carlson et al., 2013). Over the past 40 years, global production of oil palm has increased exponentially and continues to expand by 250,000 hectares each year (Danielsen et al., 2009; Koh and Wilcove, 2008). Worldwide, oil palm accounts for one tenth of permanent cropland (Koh and Wilcove, 2008).

In tropical countries with weak environmental regulations, large areas of primary and secondary forests have been cleared to make way for oil palm plantations (Danielsen et al., 2009; Fitzherbert et al., 2008; Turner et al., 2008; Wilcove and Koh, 2010). Koh and Wilcove (2008) found that from 1990 to 2005 more than 50% of oil palm expansion in both Malaysia and Indonesia came at the expense of old growth and secondary forests. Gutiérrez-Vélez et al. (2011) found that high-yield oil palm expansion in the Ucayali region of Peru involved forest conversion 75% of the time.

Much of agricultural expansion in the next 40 years is expected to occur primarily in Latin America and Sub-Saharan Africa where land is readily available (Tilman et al., 2001). Yet the vast majority of published studies that have looked at the impacts of oil palm on biodiversity have focused on Southeast Asia (Fitzherbert et al., 2008; Danielsen et al., 2009; Wilcove et al., 2013; Abram et al., 2014). The recent increase in plans for oil palm expansion by domestic and foreign corporations in the Brazilian Amazon has caused concern among conservationists that oil palm may soon emerge as a serious threat to Amazonian forests and its biodiversity (Butler and Laurance, 2009; Lees et al., 2015).

As the country with the fourth largest area (45.8 million hectares) of forested land suitable for oil palm agriculture, Peru may be particularly under threat (Stickler et al., 2007). The Amazon Basin contains the second-highest avian species richness in the world (Orme et al., 2005), and Peru has one of the highest avian diversities of any country, with 1822 species, 173 of which are threatened (INEI, 2005). Rainforests in Peru are thought to contain 44% of all known tropical bird species, and one study recorded over 300 different bird species in just one 100-hectare area of Peruvian Amazonia (White et al., 2005; Terborgh et al., 1990).

Existing studies that have compared bird communities in forest and oil palm plantations have found significant reductions in species richness and dramatic changes in bird assemblages. A meta-analysis of existing studies that compare diversity between forest and oil palm found that vertebrate species richness in oil palm plantations is only 38% of what it is in forests (Danielsen et al., 2009). In Thailand, at least 60% of forest birds disappeared following conversion of forest to oil palm, including virtually all of the threatened species (Aratrakorn et al., 2006). In Malaysia, forest birds declined by 77% when oil palm plantations replaced primary forests, and 73% when oil palm replaced logged forests (Koh and Wilcove, 2008). In Sumatra, ten years after conversion of a primary forest to an oil palm plantation, only 5%–10% of birds previously recorded in forest were still present (Danielsen and Heegaard, 1995). Senior et al. (2013) re-analyzed data of several published studies on oil palm and biodiversity and found that overall avian species richness was reduced by 43% following conversion of forest to oil palm. A recent study that examined the potential effects of oil palm on avian diversity in the Brazilian Amazon found that oil palm plantations hosted impoverished avian communities with similar species composition to that of cattle pastures (Lees et al., 2015).

The objective of the present study is to investigate how conversion of forests to oil palm agriculture affects bird species richness, abundance, and composition in the Pucallpa region of Peruvian Amazonia. We asked four questions: (1) Does bird species richness differ in forest and oil palm habitat? (2) Does overall abundance and relative (i.e. species-specific) abundance of birds differ in forest habitat and oil palm habitat? (3) How does the functional diversity of bird assemblages (i.e. feeding guilds) in the forest differ from that in oil palm? and (4) How are “vulnerable” bird species affected by conversion to oil palm? We used sensitivity to disturbance, habitat specialization, adaptation to forest interior, and endemism as proxies for “vulnerability” because they are factors correlated with increased extinction risk (Sekercioglu et al., 2004). This is the first study to investigate the effects of oil palm agriculture on avian diversity in Western Amazonia.

2. Material and methods

2.1. Study area

This study was conducted under Permit No. 33089 from the Dirección de Gestión Forestal y de Fauna Silvestre (DGFFS) of Peru's Ministry of Agriculture (MINAG). The study took place in the department of Ucayali within the province of Coronel Portillo. The study area was located west of Pucallpa at 74° West and 8° South (Fig. 1), within the watershed of the Rio Aguaytía. Pucallpa is the largest city in the department of Ucayali and the second most populous Amazonian city in Peru, with an estimated 350,000 residents. It is located within the Amazon Basin on the Ucayali River, the main transportation thoroughfare in Peruvian Amazonia, and its natural vegetation cover is humid tropical evergreen forest (White et al., 2005; Uriarte et al., 2012; Porro et al., 2015). Pucallpa has an average elevation of 150 m above sea level, an average annual temperature of 25.7 °C, and an average humidity of 80% (White et al., 2005; Lojka et al., 2008). It receives between 1800 and 3000 mm of rainfall per year, occurring bimodally from February to May and September to November. Dry months are June–August and December–January (Fujisaka and White, 1998).

Logging and small-scale shifting cultivation that relies on slash-and-burn practices are the primary causes of deforestation in Peruvian Amazonia (Labarta et al., 2008; Lojka et al., 2008). In contrast with Brazilian Amazonia,

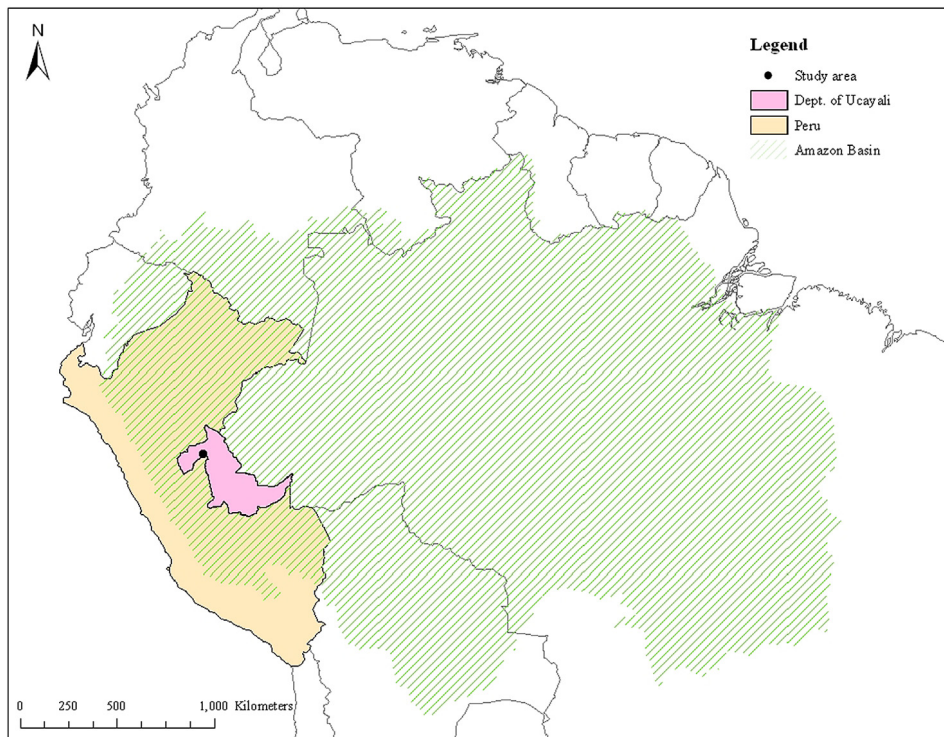


Fig. 1. Location of study area in the department of Ucayali, Peru.

deforestation in Peruvian Amazonia takes place on a smaller scale and tends to follow a linear pattern, occurring primarily along roads and rivers (Oliveira et al., 2007). This trend has been particularly evident in the Pucallpa region. In the 1970s, the Frederico Basadre road (843 km) connecting Pucallpa to Lima was paved, causing a major influx of settlers and prospectors that have transformed the landscape at an alarming rate (Imbernon, 1999; Fujisaka et al., 2000; Uriarte et al., 2012; Porro et al., 2015). From 1999 to 2001, 64% of all forest disturbance and deforestation in Peruvian Amazonia took place in this single region, and Pucallpa now holds the title of the largest center for logging and milling operations in Peruvian Amazonia (Oliveira et al., 2007; Putzel et al., 2008). Pucallpa has little undisturbed forest remaining, and its landscape is characterized by a mosaic of secondary forests, pasture, fallows, and agricultural crops (Lojka et al., 2008). Oil palm in Peru is largely concentrated in the two Amazonian regions of Ucayali and San Martin (Gutiérrez-Vélez et al., 2011). The impacts of human disturbance and land-use change on forest ecology and biodiversity in this region are poorly understood, in part because the Ucayali basin is so understudied biologically (T.S. Schulenberg, pers. comm.)

2.2. Study design

In order to locate areas that accurately represent forest and oil palm habitat, we consulted vegetation classification images (Fig. 2). Forest study sites were separated from oil palm study sites by approximately 25 km. The areas were deemed similar in terms of elevation (approximately 150 m above sea level), distance from a major freshwater source (approximately 20 km), and original vegetation cover.

Birds were chosen as a study subject because: (1) The species-level taxonomy and ecology of birds is better known than any other taxonomic group (Stotz et al., 1996; Sekercioglu et al., 2004; Child et al., 2009); (2) Birds can be easily detected, identified, and surveyed. They are typically diurnal, active throughout the year, and either visually or audibly conspicuous (Robinson et al., 2004; Padoa-Schioppa et al., 2006). Unlike most other living organisms, bird species can generally be easily and reliably identified based on color patterns, and can be sampled using relatively simple methods such as mist-netting and point counts. (Stotz et al., 1996); (3) Across species, birds cover many ecological roles and carry out numerous activities that benefit humanity (e.g. pollination and pest control; Padoa-Schioppa et al., 2006, Sekercioglu et al., 2004); (4) Birds occur across a wide array of landscapes representing varying levels of human impact, and species-level responses to disturbance are highly diverse (Koh, 2008a; Child et al., 2009; Robledano et al., 2010); (5) Birds are effective indicators of patterns and trends among other taxa (Stotz et al., 1996); in fact, birds have proven to be good predictors of the responses of other taxa to oil palm conversion (Edwards et al., 2014); (6) Birds are capable of attracting public support for conservation because they are charismatic and “popular” (Robinson 2004, Robledano et al., 2010); and (7) In the Neotropics, a high degree of specialization, limited home ranges, and vulnerability to habitat disturbance make birds particularly useful for identifying

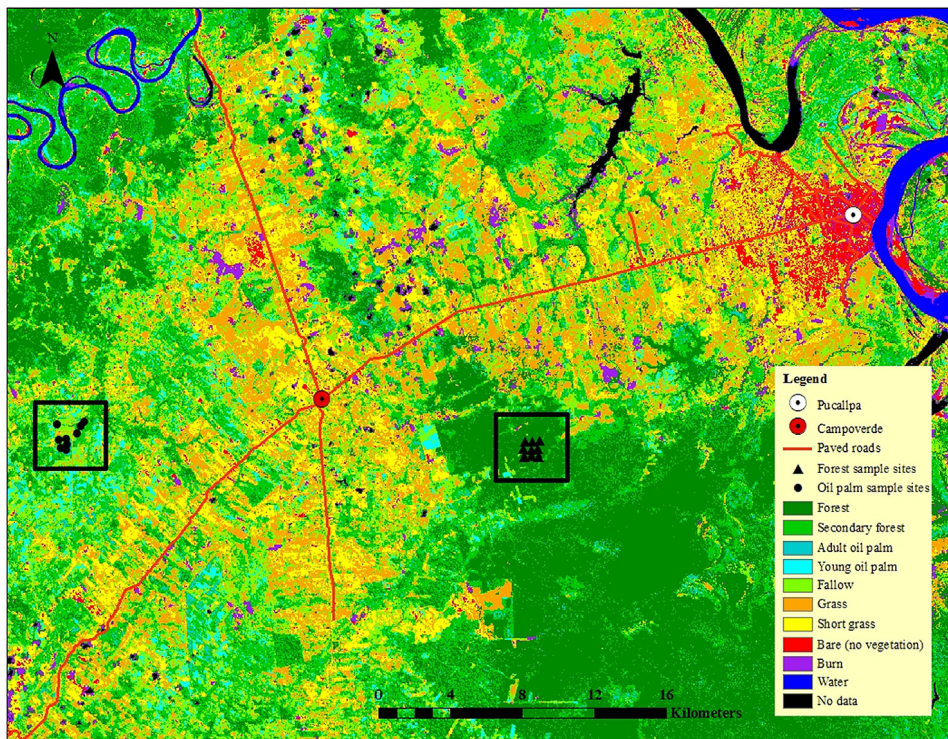


Fig. 2. Vegetation classification map of the study area (used with permission from V. Gutiérrez-Vélez). Forest sample sites are located within a 2 km by 2 km area of an unprotected, “disturbed” forest ~22 km west of Pucallpa at $74^{\circ}42'0.778''\text{W}$, $8^{\circ}30'1.044''\text{S}$. Oil palm sample sites are located within a 2 km by 2 km area of an oil palm plantation ~45 km west of Pucallpa at $74^{\circ}55'57.877''\text{W}$, $8^{\circ}29'39.978''\text{S}$.

biological communities or localities in need of conservation action (Stotz et al., 1996; Robinson et al., 2004; Edwards et al., 2010).

Birds were sampled at a total of 18 sample sites; 9 sample sites within a 2 km² area in a large contiguous forest, and 9 sample sites within a 2 km² area in an oil palm plantation. Sample sites were located at evenly-spaced intervals along randomly chosen transects, with no bias towards factors that might influence capture rate like topography, gaps in the canopy, or locations of fruiting trees (Blake and Loiselle, 2001). GPS points for all sample sites were recorded in UTM coordinates (Zone 18S, reference WGS 1984) and photographs were taken of the site-specific vegetation (see Supplementary materials). In both habitats, a minimum of 400 m between sample sites was achieved (after Derlindati and Caziani, 2005). Similar studies deemed 200 m (Peh et al., 2006) and 250 m (Edwards et al., 2010) sufficient for the spatial separation of sample sites.

In the forest habitat, sample sites were located within a 2 km by 2 km area of an unprotected, disturbed forest ~22 km west of Pucallpa at $74^{\circ}42'0.778''\text{W}$, $8^{\circ}30'1.044''\text{S}$. The term “disturbed” is used because the forest was affected by selective logging and subsistence hunting. During sampling of the forest, both chainsaw and gunshots were frequently heard. Sample sites were arranged along three transects in a grid-like fashion.

In the oil palm habitat, sample sites were located within a 2 km by 2 km area of an oil palm plantation called *Plantación Sais Tupac*, located ~45 km west of Pucallpa at $74^{\circ}55'57.877''\text{W}$, $8^{\circ}29'39.978''\text{S}$. According to local accounts the historic land cover in this area consisted of a large, contiguous forest. This particular plantation was chosen because: (a) It was embedded within a matrix of other oil palm crops of varying ages; (b) It was relatively large in comparison with many of the smallholder-managed oil palm crops in the area; (c) The study plantation contained mature trees of uniform height and age (planted approximately 25 years ago), and were approaching the age at which the palms are typically cut down, burnt, and replaced with young palm plants (Fitzherbert et al., 2008). Immature oil palm plantations are considered “transient habitats” for wildlife and would therefore not have been useful for this analysis (Koh, 2008a); (d) The plantation was heterogeneous with several creeks running through it, small fragments of original forest cover where the land was too low to plant, and significant undergrowth in several of the independently-owned parcels. Since biodiversity is thought to increase with structural complexity of plantations (Najera and Simonetti, 2010a,b), it was thought that this particular palm plantation might be more “bird friendly” than a typical homogeneous oil palm monoculture. Sample sites in the oil palm habitat were also arranged along three transects, though not in the same grid-like pattern that was achieved in the forest.

Edge effects are thought to have the highest impact on birds within 100–200 m from the forest edge (Robinson et al., 2004; Laurance et al., 2000; Fuller, 2000). In order to avoid the potential influence of edge effects, all sample sites in the

forest habitat were located at least 400 m from the forest edge, and all sample sites in the oil palm habitat were located at least 200 m from the plantation edge. Infrequently used dirt roads, forest fragments, pasture, and younger oil palm crops constituted the edges of this particular plantation.

2.3. Avifaunal surveys

Surveys were conducted in the dry season over two months (July and August 2010) using the same sampling method in both habitats and across all samples. Fieldwork was carried out exclusively by the primary researcher and a Peruvian field biologist with expertise in Neotropical birds. Daily weather conditions of temperature and precipitation did not differ significantly during the days of forest surveys and oil palm surveys, and was therefore not considered to be a factor influencing captures. However, it is worth noting that due to increased sun exposure, the microclimate of the plantation was consistently hotter than that of the forest. [Ramdani et al. \(2014\)](#) has demonstrated how local surface temperatures increase with oil palm expansion.

Birds were sampled using ground-level mist-nets (12 m × 2.6 m with a 36 mm mesh). Mist netting was chosen as a survey method because it minimizes errors in species identification, reduces bias in observers' ability to detect and identify birds, and allows for the marking of captured individuals ([Blake and Loiselle, 2001](#); [Martensen et al., 2008](#)). It is considered to be more effective than point counts for sampling small, cryptic, and non-vocal understory birds, but less effective for sampling large-bodied and canopy species ([Derlindati and Caziani, 2005](#); [Blake and Loiselle, 2001](#)). Mist-netting allows for identical sampling of sites, although there are limitations when comparing habitats with different environmental characteristics. For example, sun exposure in open habitats can make mist-nets more visible to birds ([Levey, 1988](#)) and birds in disturbed habitats tend to fly at a lower height where they are captured more readily ([Blake and Loiselle, 2001](#)).

In both habitats, 18 mist nets were opened at 9 independent sample sites. At each sample site, the GPS waypoint that had been previously marked on the map served as the point of origin for a straight, continuous net-line of 9 mist-nets going North–South, and another straight net-line of 9 mist-nets going East–West, for a total of 216 m of mist-net coverage. The nets were arranged in this fashion in order to avoid any bias arising from the direction in which the birds were flying. Trails and pathways were always cleared at least two days prior to sampling in order to avoid scaring birds, and mist-nets were erected one day prior to sampling and left closed for the night. In the forest habitat, mist-nets were placed directly in the center of a ~2 m-wide pathway that we had previously cleared for them. In the oil palm habitat, instead of placing mist-nets in the center of the pathway between the rows of oil palm trees, we placed them flush with the rows of trees so they would remain hidden beneath the shade of the palms.

Each site was sampled for a single day. Nets were opened slightly prior to 0600 and closed at 1200 on each day of sampling. General weather conditions were recorded, and temperature measurements were taken at 0600, 0900, and 1200. We banded all captured birds with an aluminum band containing a unique code number and the words "PERU www.corbidi.org". Since we did not have the paper bands necessary to mark hummingbirds (Trochilidae), a small triangle was cut on one of their right covert feathers in order to facilitate recognition of recaptures. Species were identified using the revised and updated version of the field guide "Birds of Peru" ([Schulenberg et al., 2010](#)) and digitally photographed in front of a markerboard containing their banding number. Wing chord, weight, and other measurements were taken before birds were released back into the wild (see Supplementary Materials).

Birds that possessed plumage or soft parts that did not conclusively match what was depicted or described in the field guide were photographed from all angles. Post-field season, these photographs were brought to the American Natural History Museum and compared against the specimens in the ornithological collections to determine the species. Peruvian bird expert Tom Schulenberg assisted with particularly difficult species identifications.

2.4. Data analysis

The software program EstimateS v.8.2 ([Colwell, 2009](#)) was used to construct sample-based rarefaction curves based on the total number of individuals captured and their abundances per site. Species accumulation curves were rarefied and the *x*-axis was rescaled to the number of individuals to account for differences in abundance levels and sampling effort, thereby allowing for appropriate comparison of observed and expected species richness between the two habitats ([Gotelli and Colwell, 2001](#); [Gotelli, 2008](#)).

"True" species richness for the two habitats was based on the average of four nonparametric richness estimators produced by EstimateS: (1) first order jackknife richness estimator (JACK1) (2) Chao 1 richness estimator (CHAO1), (3) abundance-based coverage (ACE), and (4) BOOTSTRAP (after [Barlow et al., 2007](#)). These estimators quantify the number of bird species that were not detected by the mist-net surveys but may have been present in the habitat. They also use patterns in the numbers of singletons and doubletons (birds captured only once and twice, respectively) to determine completeness of sampling effort ([Gotelli and Colwell, 2001](#); [Meredith, 2008](#)). While they are not exact, these estimators compare well to observed species richness in localities where near-complete inventories exist ([Gotelli and Colwell, 2001](#)). *T*-tests were performed to determine if habitat type had significant effects on observed and expected species richness.

Similarity indices, calculated using EstimateS v.8.2 ([Colwell, 2009](#)), were used to determine similarity in species composition both within and between habitats. Sørensen's Classic Incidence-based Index, based on raw presence/absence

data, was used to determine overall similarity between the two habitats. It is calculated as $\frac{S_{12}}{.5(S_1 + S_2)}$, where S_1 and S_2 represent the total number of species unique to each habitat, and S_{12} is the number of species common to the two habitats. Chao's Abundance-based Sørensen's Index, based on statistical estimates of shared species, was used for pairwise comparisons between (1) all site-pairs within the forest habitat (2) all site-pairs within the oil palm habitat (3) all site-pairs where one site is in the forest habitat and one site is in the oil palm habitat. This similarity index corrects for incomplete sampling effort (i.e. undetected species) when estimating the probability that two randomly chosen individuals from any given site-pair will be a member of a species that is common to both sites (Chao et al., 2006).

T-tests were performed to determine if there were significant differences in overall abundance between the two habitats. Rank abundance curves were created using relative abundances of species and used to compare species evenness between the two habitats.

Because of small sample sizes, Fisher's exact tests were used to determine significant effects of habitat type on bird feeding guilds, foraging strata, and various measures of vulnerability. Patterns among migratory vs. resident birds were not analyzed, as most species in the region are permanent residents (Schulenberg et al., 2010). The four species that were identified only to the family level were excluded from these analyses because it was impossible to definitively place them in categories without knowing the species. They were, however, included in the feeding guild analysis since the unknown species' diet could be inferred from family-level information. Fisher's exact tests and *t*-tests were conducted using the statistical package R.

Species were categorized as "habitat specialists" if they depend exclusively on one habitat type—tropical lowland evergreen forests. Species were categorized as "non-specialists" if they are found in 2 or more of the 41 habitat types defined by Stotz et al. (1996). Species were categorized as "Amazon endemics" if their geographic range was restricted to Northern Amazonia, Southern Amazonia, or both. Species were designated to categories of "sensitivity to disturbance", foraging strata, and adaptation to edges based on Stotz et al. (1996). Species were assigned to feeding guilds based on species-specific information compiled by Terborgh et al. (1990) and Barlow et al. (2007). Feeding guild information for species not included in either of those studies was taken from del Hoyo et al. (1992) or Schulenberg (2010).

Stotz et al. (1996) has identified 62 species that are exclusive to tropical lowland evergreen forests in Southern Amazonia. These species are fairly common, easily detectable, and highly vulnerable to habitat disturbance. When taken as a whole, they comprise a "complete ecological assemblage" for this habitat in this zoogeographic region. The presence of all (or at least the majority) of the species on this list is thought to be an indication that a given habitat is "pristine" (Stotz et al., 1996). The presence of these indicator species in forest and oil palm habitat was examined.

3. Results

A total of 262 individuals of 64 species from 18 families (Table 1) were recorded during 1986 mist-net hours of sampling in the two habitats. Total sampling effort was 1158 mist-net hours in the forest and 828 mist-net hours in the oil palm plantations, where mist-net hours are calculated as number of nets \times number of hours operated (Ralph et al., 1993). As a general rule, we sampled one site per day with 18 mist-nets. However, sampling effort was ultimately lower in the oil palm habitat than the forest habitat due to logistical complications. We accounted for the difference in sampling effort between the two habitats through rarefaction of species accumulation curves (Gotelli and Colwell, 2001) and by standardizing abundance data per 100 mist-net hours (Derlindati and Caziani, 2005).

We recorded a total of 24 recaptures; however, many of these were the same individuals that were recaptured multiple times on the same day or at the same site. We only recaptured 14 birds (4.8% of total captures) at *different* sample sites. Since all 13 recaptured individuals in the forest were either woodcreepers (Furnariidae) or antbirds (Thamnophilidae), we suspect that the recapture rate was being driven by highly mobile species whose movement patterns are closely tied to the movements of army ant swarms (Willis and Yoshika, 1978). The single individual that we recaptured at a different site in the oil palm plantation was *Glaucis hirsutus*. Only first-time captures were included in data analysis.

Strikingly, only 3 species (5%) of the 64 recorded species were common to the forest and oil palm habitats: *Sporophila angolensis*, *Phaethornis atrimentalis* and *G. hirsutus*. 44 species (69%) were recorded only in the forest habitat and 17 species (26%) were recorded only in the oil palm habitat. We recorded 8 bird families only in the forest: Tinamidae, Motomotidae, Bucconidae, Formicariidae, Furnariidae, Cotingidae, Pipridae, and Turdidae. We recorded Psittacidae and Cuculidae only in the oil palm crop, but it should be noted that we definitively observed Psittacids flying in the canopy in the forest habitat. We captured almost exclusively resident birds, with the exception of two Austral migrants, *Elaenia spectabilis* and *Myiophobus fasciatus*. We included these birds in all analyses because they are seasonal residents that spend most of the year (March–October) in Peru (Schulenberg et al., 2010).

3.1. Species richness

Observed species richness (MauTau) decreased from 47 ± 7.3 (95% C.I.) in the forest habitat to 20 ± 6.0 in the oil palm habitat. Observed species richness was significantly higher in the forest than in the oil palm habitat (*t*-test, $t_{10,78} = 4.71$, $p = 0.00067$) (Figs. 5 and 7(a)). Estimated "true" species richness, based on the mean of four nonparametric species richness estimators, was also significantly higher in the forest habitat than the oil palm habitat (*t*-test, $t_{13,40} = 4.91$, $p = 0.00026$)

Table 1

List of species captured in forest and oil palm sites, and associated capture data. Species naming and ordering follows that of the South American Classification Committee (SACC) of the American Ornithologist's Union (AOU) (Remsen et al., 2015).

| Species | | Habitat | | Numbers | |
|------------------------------------|-----------------------------|---------|----------|---------|-------|
| | | Forest | Oil palm | Sites | Birds |
| <i>Crypturellus soui</i> | Little Tinamou | 1 | | 1 | 1 |
| <i>Geotrygon montana</i> | Ruddy Quail-Dove | 5 | | 3 | 5 |
| <i>Columbina talpacoti</i> | Ruddy Ground-Dove | | 1 | 1 | 1 |
| <i>Claravis pretiosa</i> | Blue Ground-Dove | | 3 | 2 | 3 |
| <i>Crotophaga ani</i> | Smooth-billed Ani | | 1 | 1 | 1 |
| <i>Florisuga mellivora</i> | White-necked Jacobin | 2 | | 2 | 2 |
| <i>Glaucis hirsutus</i> | Rufous-breasted Hermit | 1 | 27 | 9 | 28 |
| <i>Threnetes leucurus</i> | Pale-tailed Barbthroat | 5 | | 5 | 5 |
| <i>Phaethornis atrimentalis</i> | Black-throated Hermit | 4 | 4 | 5 | 8 |
| <i>Phaethornis hispidus</i> | White-bearded Hermit | | 4 | 4 | 4 |
| <i>Phaethornis philippii</i> | Needle-billed Hermit | 10 | | 6 | 10 |
| <i>Phaethornis superciliosus</i> | Long-tailed Hermit | 2 | | 1 | 2 |
| <i>Amazilia lactea</i> | Sapphire-spangled Emerald | | 8 | 5 | 8 |
| <i>Trogon viridis</i> | Green-backed Trogon | | 2 | 1 | 2 |
| <i>Trogon rufus</i> | Black-throated Trogon | 1 | | 1 | 1 |
| <i>Momotus momota</i> | Amazonian Motmot | 1 | | 1 | 1 |
| <i>Bucco macrodactylus</i> | Chestnut-capped Puffbird | 1 | | 1 | 1 |
| <i>Malacoptila rufa</i> | Rufous-necked Puffbird | 4 | | 2 | 4 |
| <i>Brotogeris cyanoptera</i> | Cobalt-winged Parakeet | | 1 | 1 | 1 |
| <i>Thamnophilus aethiops</i> | White-shouldered Antshrike | 2 | | 1 | 2 |
| <i>Megascictus margaritatus</i> | Pearly Antshrike | 2 | | 2 | 2 |
| <i>Isleria hauxwelli</i> | Plain-throated Antwren | 3 | | 1 | 3 |
| <i>Pygiptila stellaris</i> | Spot-winged Antshrike | 1 | | 1 | 1 |
| <i>Myrmotherula axillaris</i> | White-flanked Antwren | 1 | | 1 | 1 |
| <i>Myrmoborus myotherinus</i> | Black-faced Antbird | 5 | | 3 | 5 |
| <i>Myrmeciza atrothorax</i> | Black-throated Antbird | | 10 | 5 | 10 |
| <i>Gymnopithys lunulatus</i> | Lunulated Antbird | 11 | | 6 | 11 |
| <i>Hylophylax naevius</i> | Spot-backed Antbird | 7 | | 3 | 7 |
| <i>Willisornis poecilinotus</i> | Common Scale-backed Antbird | 4 | | 4 | 4 |
| <i>Phlegopsis nigromaculata</i> | Black-spotted Bare-eye | 7 | | 3 | 7 |
| <i>Fornicarius colma</i> | Rufous-capped Antthrush | 2 | | 2 | 2 |
| <i>Certhiasomus stictolaemus</i> | Spot-throated Woodcreeper | 3 | | 3 | 3 |
| <i>Dendrocincla merula</i> | White-chinned Woodcreeper | 11 | | 6 | 11 |
| <i>Dendrocincla fuliginosa</i> | Plain-brown Woodcreeper | 6 | | 4 | 6 |
| <i>Glyphorhynchus spirurus</i> | Wedge-billed Woodcreeper | 7 | | 3 | 7 |
| <i>Xiphorhynchus elegans</i> | Elegant Woodcreeper | 7 | | 6 | 7 |
| <i>Xiphorhynchus guttatus</i> | Buff-throated Woodcreeper | 2 | | 2 | 2 |
| <i>Xenops</i> — | (Spp. unidentified) | 1 | | 1 | 1 |
| <i>Synallaxis rutilans</i> | Ruddy Spinetail | 7 | | 4 | 7 |
| <i>Elaenia spectabilis</i> | Large Elaenia | | 5 | 1 | 5 |
| <i>Cnipodectes subbrunneus</i> | Brownish Twistwing | 3 | | 3 | 3 |
| <i>Myiophobus fasciatus</i> | Bran-colored Flycatcher | | 2 | 2 | 2 |
| <i>Tyrannus melancholicus</i> | Tropical Kingbird | | 1 | 1 | 1 |
| <i>Rhytiptera simplex</i> | Grayish Mourner | 1 | | 1 | 1 |
| <i>Myiarchus tuberculifer</i> | Dusky-capped Flycatcher | 2 | | 2 | 2 |
| <i>Myiarchus ferox</i> | Short-crested Flycatcher | | 1 | 1 | 1 |
| <i>Lipaugus vociferans</i> | Screaming Piha | 1 | | 1 | 1 |
| <i>Lepidothrix coronata</i> | Blue-crowned Manakin | 3 | | 3 | 3 |
| <i>Pipra fasciicauda</i> | Band-tailed Manakin | 4 | | 3 | 4 |
| <i>Machaeropterus regulus</i> | Striped Manakin | 1 | | 1 | 1 |
| <i>Machaeropterus pyrocephalus</i> | Fiery-capped Manakin | 2 | | 1 | 2 |
| <i>Dixiphia pipra</i> | White-crowned Manakin | 9 | | 5 | 9 |
| <i>Microcerculus marginatus</i> | Scaly-breasted Wren | 2 | | 2 | 2 |
| <i>Troglodytes aedon</i> | House Wren | | 1 | 1 | 1 |
| <i>Cantorchilus leucotis</i> | Buff-breasted Wren | | 4 | 2 | 4 |
| <i>Turdus leucops</i> | Pale-eyed Thrush | 1 | | 1 | 1 |
| <i>Tachyphonus surinamus</i> | Fulvous-crested Tanager | 3 | | 2 | 3 |

(continued on next page)

(Figs. 3 and 4). Sampling effort yielded between 55.0% and 77.8% (median = 72.5%) of the estimated “true” species richness in the forest habitat, and between 58.9% and 64.8% (median = 61.7%) in the oil palm habitat. In both habitats, the species rarefaction curves showed signs of reaching their asymptotes (Gotelli and Colwell, 2001).

Overall similarity between forest and oil palm habitat based on Sørensen's Classic Incidence-based index is 9%. Mean similarity of pairwise comparisons based on Chao's Abundance-based Sørensen's index, is 47% for all site-pairs within the forest habitat, 46% for all site-pairs within the oil palm habitat, and 2% for all site-pairs where one site is in the forest habitat

Table 1 (continued)

| Species | | Habitat | | Numbers | |
|--|-----------------------------|------------|------------|---------|-------|
| | | Forest | Oil palm | Sites | Birds |
| <i>Ramphocelus carbo</i> | Silver-beaked Tanager | | 22 | 5 | 22 |
| <i>Sporophila angolensis</i> | Chestnut-bellied Seed-Finch | 1 | 1 | 2 | 2 |
| <i>Sporophila murallae</i> | Caqueta Seedeater | | 1 | 1 | 1 |
| Unidentified species | | | | | |
| <i>Unknown spp.</i> , - F. Pipridae | | 1 | | 1 | 1 |
| <i>Unidentified spp.</i> 1- F. Thamnophilidae | | 1 | | 1 | 1 |
| <i>Unidentified spp.</i> 2- F. Thamnophilidae | | 1 | | 1 | 1 |
| <i>Unidentified spp.</i> - F. Tyrannidae | | | 1 | 1 | 1 |
| Totals: numbers of birds captured | | 162 | 100 | | |
| Totals: species counts | | 47 | 20 | | |
| Total of 64 species captured (60 conclusively identified) | | | | | |

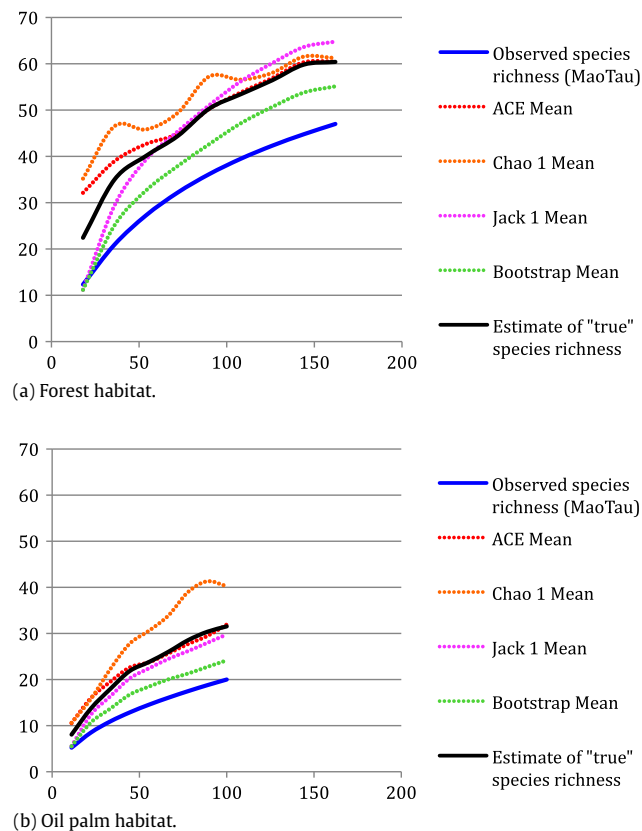


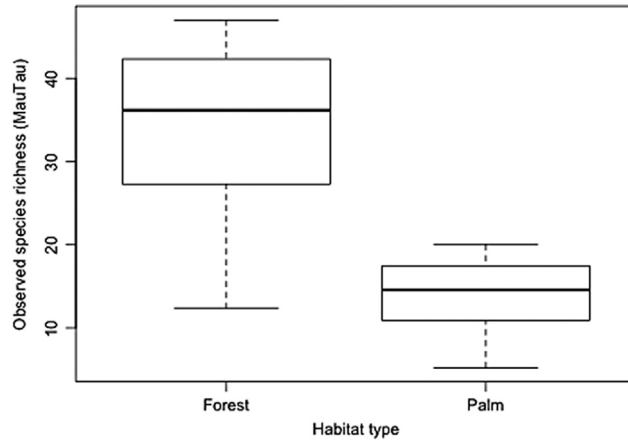
Fig. 3. Species rarefaction curves show the observed species richness (MauTau), rescaled to number of individuals. Estimates of "true" species richness, based on mean of four commonly used nonparametric richness estimators (ACE, Chao 1, Jack 1, and Bootstrap) in (a) Forest habitat and (b) Oil palm habitat.

and one site is in the oil palm habitat. As expected, the between-habitat similarity values are notably less than the within-habitat similarity values.

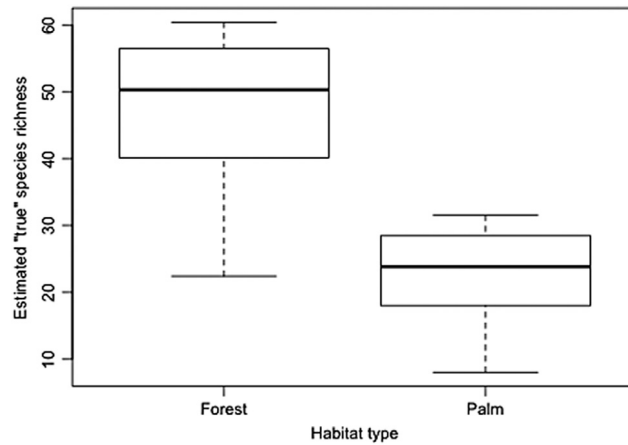
3.2. Abundance

3.2.1. Overall abundance

To properly compare bird abundances between the two habitats, we standardized sampling effort by captures per 100 mist-net hours (after [Derlindati and Caziani, 2005](#)). Overall abundance (the average number of individuals across all species per 100 mist-net hours) is 14.7 ± 3.6 in the forest habitat, and 14.0 ± 13.6 in the oil palm habitat ([Fig. 5](#)). The number of individual birds per 100 MNH was not significantly different between the two habitats (t -test, $t_{19,13} = 0.14$, $p = 0.89$) ([Fig. 6\(a\)](#)). However, at Site 1 of the oil palm plantation, an entire mixed-species flock flew into our mist-nets between 0600



(a) Observed species richness ($t_{10.78} = 4.71, p = 0.00067^*$).



(b) Estimated "true" species richness ($t_{13.40} = 4.92, p = 0.00026^*$).

Fig. 4. Boxplots of (a) Observed species richness (MauTau), and (b) Estimated "true" species richness in forest and oil palm habitat. * denotes statistical significance ($p < 0.05$) of t -test.

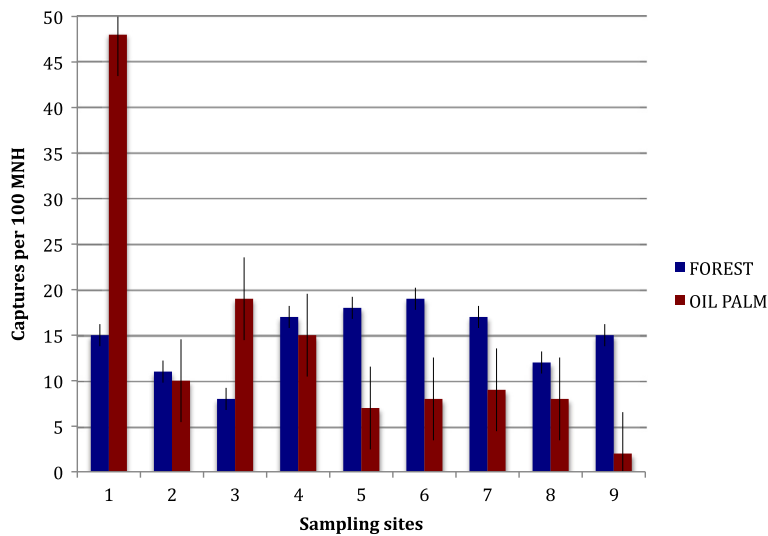
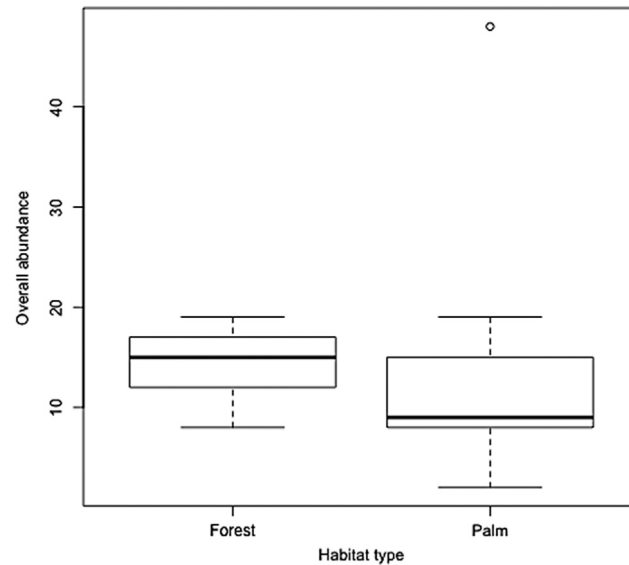
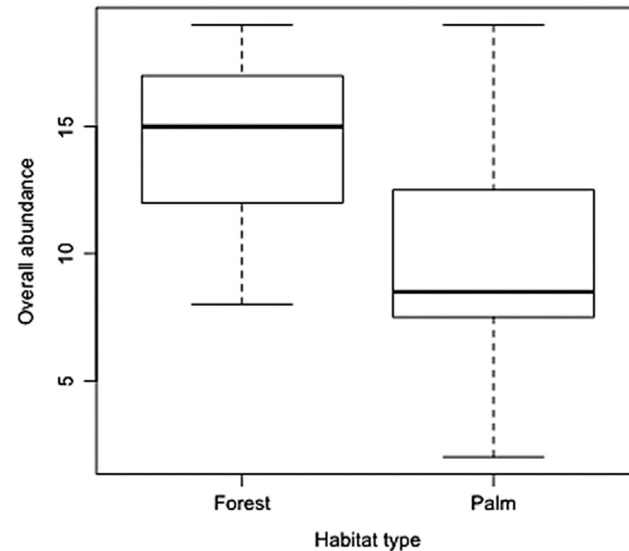


Fig. 5. Overall abundance at each sample site in forest and oil palm habitats. Captures per site have been standardized per 100 mist-net hours to account for differences in sampling effort between the two habitats.



(a) Including all sample sites ($t_{19,13} = 0.14, p = 0.89$).



(b) Excluding site 1 from the oil palm plantation ($t_{12,41} = 2.24, p = 0.044^*$).

Fig. 6. Boxplots of overall abundance in forest and oil palm habitats (a) Including all sample sites, and (b) Excluding site 1 from the oil palm plantation. Outliers are represented by an open dot. * denotes statistical significance ($p < 0.05$) of t -test.

and 0800. This rare event is indicated by the extreme outlier in Fig. 6(a). When Site 1 is excluded from analysis, abundance in the oil palm habitat is 9.8 ± 5.2 , and the difference in overall abundance between the two habitats is significant (t -test, $t_{12,41} = 2.24, p = 0.044$) (Fig. 6(b)).

3.2.2. Relative abundance

Rank abundance curves (Fig. 7) show that species evenness was higher in the forest (slope = -0.19) than in the oil palm habitat (slope = -0.89). In the oil palm habitat, the two most common birds (*G.hirsutus* and *Ramphocelus carbo*) accounted for 49% of the 100 individuals captured; whereas, in the forest habitat, the two most common birds (*Dendrocincla merula* and *Gymnopithys lunulatus*) accounted for only 13.6% of the 162 individuals captured. Because only three species were common to the two habitats, it was not possible to analyze differences in species-specific capture frequency between forest and oil palm habitats.

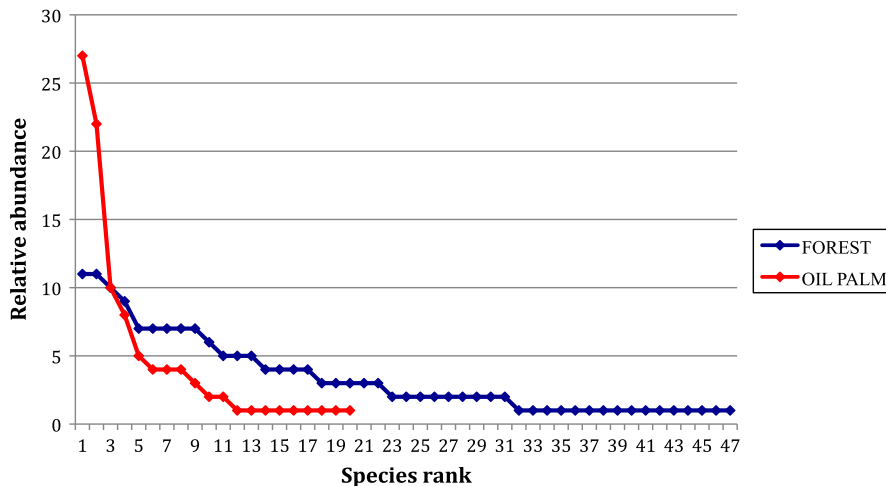


Fig. 7. Rank abundance curves for species captured in forest and oil palm habitats from July 22, 2010 to August 25, 2010. Slope of the forest curve is -0.19 and slope of the oil palm curve is -0.89 .

Table 2

Species richness and relative abundance of birds in different feeding guilds for birds captured in forest and oil palm sites from July 22, 2010 to August 25, 2010. Four species that were only identified to the family level are excluded. Species were assigned to feeding guilds based primarily on Terborgh et al. (1990) and Barlow et al. (2007).

| Feeding guild | Forest | | Oil palm | |
|--------------------------|-------------|-----------|-------------|-----------|
| | No. species | No. Inds. | No. species | No. Inds. |
| <i>Frugivore</i> | 7 | 25 | | |
| Arboreal | 6 | 20 | | |
| Terrestrial | 1 | 5 | | |
| <i>Granivore</i> | 2 | 2 | 5 | 7 |
| Arboreal | | | 2 | 2 |
| Terrestrial | 2 | 2 | 3 | 5 |
| <i>Insectivore</i> | 26 | 103 | 7 | 20 |
| Antfollower | 4 | 33 | | |
| Arboreal gleaner | 5 | 14 | 3 | 6 |
| Arboreal sallier | 9 | 23 | 3 | 4 |
| Trunk/bark gleaner | 4 | 17 | | |
| Terrestrial gleaner | 4 | 16 | 1 | 10 |
| <i>Nectarivore</i> | 6 | 24 | 4 | 43 |
| <i>Arboreal omnivore</i> | 3 | 5 | 3 | 29 |
| Totals | 44 | 159 | 19 | 99 |

3.3. Functional diversity

Three feeding guilds recorded in the forest habitat were conspicuously absent from the oil palm habitat: (1) frugivores (*Lipaugus vociferans* and Pipridae spp.) (2) bark-gleaning insectivores (*Glyphorhynchus spirurus*, *Xenops* spp., *Xiphorhynchus guttatus*, *Xiphorhynchus elegans*), and (3) antfollowers (*D. merula*, *G. lunulatus*, *Phlegopsis nigromaculata*, and *Willisornis poecilinotus*) (Table 2). There was a significant difference in feeding guild composition between the two habitats (Fisher's exact test, $p = 0.013$) (Table 3(e)). It seemed likely that the significant value was due largely to the high frequencies of frugivores and insectivores in the forest habitat. Thus, we conducted additional Fisher's tests, each of which excluded one of the guilds. In all cases, there persisted in being a significant difference in feeding guilds between the two habitats except when both insectivores and frugivores were excluded (Fisher's exact test, $p = 0.50$). This suggests that habitat type has a significant effect on frugivores and insectivores, but not on granivores, arboreal omnivores, and nectarivores. There were also significant differences in foraging strata between the two habitats (Fisher's exact test, $p = 0.013$) with more understory and understory/midstory foragers in the forest than in the oil palm habitat (Table 3(f)).

3.4. Avian vulnerability

There were a significantly higher number of bird species with "sensitivity to disturbance", as defined by Stotz et al. (1996), in the forest than in the oil palm plantation (Fisher's exact test, $p < 0.0001$) (Table 3(a)). There were a significantly higher proportion of habitat specialists in the forest than in the oil palm plantation (Fisher's exact test, $p = 0.00054$) (Table 3(b)).

Table 3

Population data and effects of habitat type on avian: (a) Sensitivity to disturbance, (b) Habitat specialization, (c) Edge-adaptedness (d) Endemism (restricted to Amazonia) (e) Feeding guild, and (f) Foraging strata, for species captured in forest and oil palm sites from July 22, 2010 to August 25, 2010. Four species that were only identified to the family level were excluded from all but the feeding guild analysis.

| | | a. Sensitivity to disturbance ($p < 0.0001^*$) | | | | Total | | | | |
|---------|----------|--|----------------------------|-------------|-------------------------|-------------------|---------------------|--------|-------------------------------|-------|
| | | Low | Medium | High | | | | | | |
| Habitat | Forest | 6 | 16 | 22 | 44 | | | | | |
| | Oil palm | 15 | 4 | 0 | 19 | | | | | |
| | Total | 21 | 20 | 22 | 63 | | | | | |
| | | b. Habitat specialization ($p = 0.00054^*$) | | | Total | | | | | |
| | | Specialist | Non-specialist | | | | | | | |
| Habitat | Forest | 22 | 22 | | 44 | | | | | |
| | Oil palm | 1 | 18 | | 19 | | | | | |
| | Total | 23 | 40 | | 63 | | | | | |
| | | c. Edge-adaptedness ($p = 0.0018^*$) | | | Total | | | | | |
| | | Edge-adapted | Interior only | | | | | | | |
| Habitat | Forest | 3 | 41 | | 44 | | | | | |
| | Oil palm | 8 | 11 | | 19 | | | | | |
| | Total | 11 | 52 | | 63 | | | | | |
| | | d. Endemism ($p = 0.080$) | | | Total | | | | | |
| | | Endemic | Non-endemic | | | | | | | |
| Habitat | Forest | 18 | 26 | | 44 | | | | | |
| | Oil palm | 3 | 16 | | 19 | | | | | |
| | Total | 21 | 42 | | 63 | | | | | |
| | | e. Feeding guild ($p = 0.013^*$) | | | | | | | | |
| | | Frugivore | Gramnivore | Insectivore | Nectarivore | Arboreal Omnivore | Total | | | |
| Habitat | Forest | 8 | 2 | 28 | 6 | 3 | 47 | | | |
| | Oil palm | 0 | 5 | 8 | 4 | 3 | 20 | | | |
| | Total | 8 | 7 | 36 | 10 | 6 | 67 | | | |
| | | f. Foraging strata ($p = 0.013^*$) | | | | | | | | |
| | | Terrestrial | Terrestrial/ Understory | Understory | Understory/ Midstory | Midstory | Midstory/ Canopy | Canopy | Forages in ≥ 5 strata | Total |
| Habitat | Forest | 3 | 1 | 18 | 13 | 2 | 5 | 1 | 1 | 44 |
| | Oil palm | 1 | 2 | 6 | 1 | 0 | 2 | 4 | 3 | 19 |
| | Total | 4 | 3 | 24 | 14 | 2 | 7 | 5 | 4 | 63 |

* Denotes statistical significance ($p < 0.05$) of Fisher's exact test.

There were a significantly higher number of edge-adapted species in the oil palm plantation than the forest (Fisher's exact test, $p = 0.0018$) (Table 3(c)). The percentage of Amazonian endemics was notably higher in the forest (40.9%) than in the oil palm plantation (15.8%); however, the difference was not significant (Fisher's exact test, $p = 0.080$) (Table 3(d)). Interestingly, two Amazon endemics – *Malacoptila rufa* and *Megastictus margaritatus* – were not thought to range as far south as the study area, and their presence in this locality represents a new distributional record (Srinivas and Molina Vilca, 2013). Threat status of the species found in the two habitats did not differ, as all 64 species recorded in this study were listed as Least Concern by the World Conservation Union (IUCN, 2010).

In the oil palm habitat, we did not detect a single one of the 62 indicator species defined by Stotz et al. (1996) for tropical lowland forests in Southern Amazonia. In the forest habitat, we documented the following 12 indicator species: *P. philippii*, *M. rufa*, *Dendrocincla fuliginosa*, *D. merula*, *X. elegans*, *Synallaxis rutilans*, *Thamnophilus aethiops*, *M. margaritatus*, *Isleria hauxwelli*, *Myrmoborus myotherinus*, *Formicarius colma*, *Microcerculus marginatus*.

4. Discussion

4.1. Reduced avian diversity and abundance in oil palm

This study revealed that in comparison with forest habitat, oil palm habitat in the Pucallpa region is significantly lacking in species diversity (as measured by both species richness and evenness) and functional diversity (as measured by feeding guild assemblages). Only 5% of the species found in the forest were also found in the oil palm plantation, and the mean similarity for all pairwise comparisons between forest and oil palm sites was only 2%. The species absent from oil palm were disproportionately habitat specialists, forest interior birds, birds with high sensitivity to disturbance, and insectivorous and frugivorous birds. These results suggest that oil palm plantations are particularly poor habitat for Amazonian birds, and

that the species that are persist in them are likely of lower conservation value. The difference in overall abundance of birds (i.e. number of individual birds) between the two habitats was only significant when the site in which we captured the mixed-species flock was omitted from the analysis (Fig. 6). Nevertheless, it is evident from Fig. 7 that the abundance in oil palm was dominated by high numbers of relatively few species. Edwards et al. (2013) also found reduced species evenness in oil palm plantations compared to forest.

The findings of this study are consistent with the existing studies that have compared biodiversity in oil palm plantations and forests. Previous studies have demonstrated that large-bodied animals, species of high conservation value, and species with specialized dietary and habitat requirements are largely absent from oil palm plantations, while simple communities of generalists and non-forest species tend to dominate (Danielsen and Heegaard, 1995; Danielsen et al., 2009; Fitzherbert et al., 2008; Najera and Simonetti, 2010b; Sodhi et al., 2010; Edwards et al., 2013; Senior et al., 2013; Azhar et al., 2014; Lees et al., 2015). The only other study that has examined the effects of oil palm on avian diversity within the context of the Amazon basin (Lees et al., 2015) concluded that oil palm plantations cannot provide habitat for most forest-associated bird species.

The reduced species diversity in oil palm plantations is likely due to several factors. Although tree plantations have a canopy and provide shade, they are incapable of supporting the biodiversity of natural forests because of the structural simplicity of their vertical vegetation. This includes a uniform age and size structure of trees, a lower canopy, and the lack of a dense understory (Peh et al., 2006; Fitzherbert et al., 2008; Sheldon et al., 2010). Importantly, food and nesting sources are largely absent, particularly for habitat or feeding specialists. Oil palm plantations also have a high level of human disturbance as they are routinely harvested and cleared of undergrowth (Sheldon et al., 2010). It is also difficult for long-term assemblages to inhabit them as they are entirely cleared and replanted when they cease to produce high yields (Fitzherbert et al., 2008).

4.2. Differences in bird assemblages

There were significantly fewer insectivorous birds in oil palm than forests. This trend is likely due to their high degree of specialization on arthropod prey. In fact, insectivorous birds are considered to be the most extinction-prone of all feeding guilds (Sekercioglu et al., 2004). The paucity of insectivorous birds on oil palm plantations may be correlated with reductions in insect prey populations. The complete absence of frugivorous birds from the oil palm was likely due to the lack of fruiting trees. Consistent with the findings of this study, Senior et al. (2013) found that insectivores and frugivores were the feeding guilds most affected by conversion of forest to oil palm. Edwards et al. (2013) found that functional diversity of avifauna in oil palm plantations was significantly lower than in logged and primary forest. The disproportionate loss of certain functional groups can have serious ecological consequences (Edwards et al., 2013). The deficiency of frugivorous birds that disperse seeds or nectarivorous birds that pollinate flowers can disrupt plant ecology and can even cause plant extinctions (Sekercioglu et al., 2004).

In the oil palm habitat, we did not detect a single ovenbird (Furnariidae), woodcreeper (Furnariidae), or manakin (Pipridae) species. We recorded 11 antbird (Thamnophilidae) species in the forest, and only one (*Myrmeciza atrothorax*) in the oil palm habitat. In the forest habitat, these large Neotropical bird families (i.e. Thamnophilids, Furnarids, and Piprids) accounted for 57% of all species and 68% of all individuals captured. Thus, their almost complete absence from oil palm plantations is cause for concern. Both Thamnophilids and Furnarids are known to follow swarms of army ants (primarily *Eciton burchelli* and *Labidus praedator*) alone or in mixed-species flocks. Previous studies on fragmentation in the Amazon have revealed that antfollowing birds are an extremely vulnerable ecological guild (Bierregaard et al., 1992; Barlow et al., 2007). They are incapable of persisting in small fragments, and will not cross clearings of 30 m wide (Laurance et al., 2000; Lees and Peres, 2009). As these birds are inextricably tied to the movements of ants, it is worthwhile to examine how ants themselves cope with habitat disturbance. Ants have been shown to have reduced species richness in oil palm plantations (Fayle et al., 2010; Brühl and Eltz, 2010; Senior et al., 2013; Lucey et al., 2014). *E. burchelli* is a forest-adapted species that is highly vulnerable to high surface temperatures. The higher microclimate of more open habitats like pastures and crops acts as a barrier preventing them from leaving forest areas (Meisel, 2006). On the rare occasions in which army ants are seen in agricultural areas, antbirds will not follow them (Barlow et al., 2007).

In the oil palm habitat, the most commonly captured bird was *G. hirsutus*. This species is nectarivorous and feeds exclusively on the specific flowers to which its beak is co-evolved, including *Heliconia*, *Centropogon*, *Pachystachys*, *Passiflora*, *Trichanthera*, and *Costus* spp. (Hinkelmann, 1999). Given the apparent lack of these flowers in the oil palm plantation, the high abundance of *G. hirsutus* was surprising.

4.3. Sampling limitations

The limited temporal and spatial scale of the study should be considered when interpreting the results of this research. In order to draw broader conclusions, future studies would benefit from: (1) Sampling more varied and spatially separated sites such as palm of different ages or forests with different levels of disturbance; (2) Sampling during different seasons, particularly during the wet months of February to May and September to November, since the feeding and breeding behaviors of birds and the presence of certain feeding guilds are known to be tied to phenological events such as the peak

of flowering (Barlow et al., 2007); (3) Sampling over longer time periods in order to discern temporal patterns and trends; (4) Sampling using more than one survey method.

Since both mist-nets and point counts are biased towards birds of particular size or behavior, conducting avifaunal surveys using both methods can lead to more complete estimates of species richness (Pagen et al., 2002). As point counts require expertise of bird vocalizations not possessed by the primary researcher, this was not a viable option in this study. Nevertheless, one study that compared mist-net and point count surveys found that expected species richness was similar between the two survey methods (Derlindati and Caziani, 2005). Another study found that the families that were dominant in this study (i.e. Furnariidae, Thamnophilidae, Tyrannidae) were equally represented by both survey methods (Blake and Loiselle, 2001).

Although mist-net surveys can provide a nearly complete sampling of understory bird communities (Stotz et al., 1996), they are relatively ineffective at capturing large-bodied or canopy birds (Derlindati and Caziani, 2005; Blake and Loiselle, 2001; Pagen et al., 2002). For example, Psittacids and Cotingids are rarely captured by mist-nets because these birds seldom fly at the ground level, and because they can be too large to be entangled by mist-nets with the standard 36 mm mesh (Blake and Loiselle, 2001). During net runs, we witnessed several large-bodied birds (e.g. *Crotophaga ani*) fly into the net, disentangle themselves, and fly away before we reached them. These biases may have important implications since large-bodied species and canopy species are two groups thought to be negatively affected by agricultural conversion (Child et al., 2009; Sodhi et al., 2010).

4.4. Lack of intact forest “control” habitat

The decreasing presence of undisturbed primary forest in the Neotropics makes it challenging to find valid baselines for comparative studies (Barlow et al., 2007). Pucallpa is known to contain very little undisturbed forest (Lojka et al., 2008). As such, this study compared oil palm habitat to a “disturbed” forest instead of a primary forest. Given that the forest “control” in this study was itself a disturbed fragment, its avian community is likely to be impoverished relative to intact Amazonian forests in the region. If we were to compare oil palm habitat against an intact primary forest habitat, it is likely that the differences in biodiversity would be more pronounced.

4.5. Influence of spatial context on biodiversity in oil palm plantations

Farms in the Pucallpa region are generally 22 hectares or less in size and managed by smallholders (Labarta et al., 2008). From 2000 to 2010, low-yield plantations accounted for 80% of the oil palm expansion in this region (Gutiérrez-Vélez et al., 2011). Thus, oil palm in this region contrasts greatly with the large-scale intensive oil palm plantations common in Southeast Asia, some of which are known to span over 20,000 hectares (Donald, 2004). Smallholder plantations have been shown to support higher avian species richness (Azhar et al., 2011) and higher functional diversity (Azhar et al., 2013) than large-scale plantations. Because of the nature of land-use in this part of the Amazon, the oil palm plantation in this study was embedded in a complex matrix that included forest fragments, other oil palm crops of varying ages, agricultural crops, homegardens, and pastures. Different cooperative members independently managed distinct parcels of the study plantation, so there were areas in which the palms were neglected or abandoned, areas that had been burned, areas with significant undergrowth, and areas where the understory was actively cleared. In this study, the bird community found in the oil palm plantation sites was likely influenced by the relatively heterogeneous landscape both within and surrounding the oil palm plantation, and probably did not represent a community that was foraging and breeding exclusively within the plantation confines. In any avifaunal survey, it can be difficult to conclude whether an individual captured is an actual resident of the habitat, or simply a bird in transit (Levey, 1988; Peh et al., 2006).

4.5.1. Plantation-level factors

Eleven of the 20 bird species found in the oil palm plantation were “forest” birds (Stotz et al., 1996). The forest patches and water sources left within the oil palm plantation almost certainly contributed to the presence of these forest species in the oil palm plantation. In fact, we witnessed two species (*Brotogeris cyanopectera* and *Trogon viridis*) flying directly out of forest patches into our mist-nets. Overall, the presence of patches of native vegetation within oil palm plantations correlates positively with biodiversity (Hartley, 2002; Koh, 2008a; Azhar et al., 2013; Gilroy et al., 2015). Importantly, patches can serve as corridors, connecting spatially separated parts of the forest (Edwards et al., 2010). Several studies have found that oil palm plantations that contained significant understory vegetation were able to support higher levels of bird species richness than those without (Aratrakorn et al., 2006; Najera and Simonetti, 2010a; Azhar et al., 2011, 2013). When Najera and Simonetti (2010a) experimentally removed undergrowth, they found that bird species richness declined by 41%. Other factors known to affect the responses of birds to oil palm include the age and size of the plantation trees, percentage of canopy cover (Azhar et al., 2011, 2013), the presence of naturally growing epiphytic ferns on oil palm trees (Koh, 2008b), and human disturbance such as weeding or harvesting (Azhar et al., 2014).

4.5.2. Landscape-level factors

Species assemblages within oil palm plantations are most certainly influenced by proximity to intact forest habitat (Azhar et al., 2011; Gilroy et al., 2015; Lucey et al., 2014). In fact, many birds enter sub-optimal habitat like plantations as “refugees” from nearby forests that are actively disturbed (Sheldon et al., 2010). The presence of natural forests near oil palm plantations are critical to sustain birds in plantations which may still reproduce or feed in the forests (Koh, 2008a). Fragments of forest within the larger landscape can act as buffer zones for more common and disturbance-resistant forest species although they may not ensure the persistence of the most specialized species (Lees and Peres, 2009; Sodhi et al., 2010). Forest fragments can also enable birds to navigate through oil-palm dominated landscapes (Azhar et al., 2013). Koh (2008a) found that the greatest factor influencing bird species richness was the percentage of young secondary forest cover near oil palm plantations. Factors correlated with reduced avian species richness on oil palm plantations include proximity to roads and distance from rivers (Azhar et al., 2014).

5. Conclusions

The expansion of oil palm and its consequences for biodiversity are cause for alarm among conservationists (Koh and Wilcove, 2009; Wilcove et al., 2013). Demand for edible oil is predicted to double in the next 40 years (Corley, 2009), and given the high yield and high value of this crop, oil palm expansion is expected to increase globally (Aratrakorn et al., 2006; Phalan et al., 2009; Butler and Laurance, 2009). Unlike other crops that require large amounts of fertilizers, pesticides, or irrigation, oil palm plantations are not considered to be inherently environmentally harmful (Tilman et al., 2001; Donald, 2004). Rather, oil palm crops cause environmental harm because they result in the destruction of forest habitat (Donald, 2004; Basiron, 2007). Because of the emphasis on short-term economic growth in most tropical regions, oil palm will likely continue to expand at the expense of natural habitats like forests (Koh, 2008a; Wilcove and Koh, 2010; Gutiérrez-Vélez et al., 2011).

The majority of studies that have examined the effect of oil palm on biodiversity advocate preventing further conversion of primary forests to oil palm plantations as a primary conservation strategy (Aratrakorn et al., 2006; Fitzherbert et al., 2008; Phalan et al., 2009; Edwards et al., 2010; Wilcove and Koh, 2010; Sodhi et al., 2010; Azhar et al., 2011; Moura et al., 2013; Wilcove et al., 2013; Lees et al., 2015). Although protecting large tracts of contiguous forest is priority, preventing the conversion of secondary forests, logged forests, and forest fragments is also important. In many cases, logged forests do not differ significantly from primary forests in their species richness (Danielsen and Heegaard, 1995; Waltert et al., 2004; Koh and Wilcove, 2008; Sodhi et al., 2010; Edwards et al., 2013; Moura et al., 2013; Edwards et al., 2014) although species composition might be quite distinct (Barlow et al., 2007; Edwards et al., 2014). Forest-dwelling species are often capable of persisting in logged forests, but are virtually absent from oil palm plantations (Danielsen and Heegaard, 1995; Wilcove and Koh, 2010).

Although existing plantations can indeed be made more hospitable to wildlife through various modifications, even the most “wildlife-friendly” oil palm plantations are a poor substitute for forest habitat (Edwards et al., 2010). Since oil palm is a more efficient land-use than cattle or soy, the most promising way to reconcile demand for oil palm with conservation priorities may be to encourage the expansion of oil palm onto currently deforested or degraded lands (Koh, 2008a; Koh and Wilcove, 2008; Phalan et al., 2009; Butler and Laurance, 2009; Gutiérrez-Vélez et al., 2011; Garcia-Ulloa et al., 2012; Smit et al., 2013; Gilroy et al., 2015). Smit et al. (2013) has developed a methodology which can be used to identify degraded lands suitable for oil palm expansion.

Given the high rate of habitat loss in the tropics, tropical conservationists are often faced with the challenge of where to direct limited conservation funds. In order to maximize the use of these resources, it is imperative to understand the nature and extent of change associated with habitat loss and land-use change. Peruvian Amazonia is included in almost every global biodiversity index as a top priority for conservation (Brooks et al., 2006) and yet there have been no studies to date on how oil palm expansion may threaten vertebrate diversity in this region. One of the irreversible consequences of these anthropogenic changes is the extinction of species (Tilman et al., 2001; Sekercioglu et al., 2004). Currently 21% of all extant bird species are threatened with extinction, primarily due to habitat loss (Sekercioglu et al., 2004). Human disturbance often has predictable effects on species with similar characteristics, even across different taxa and geographic regions (Danielsen and Heegaard, 1995; Sheldon et al., 2010). Thus, the responses of birds to the conversion of forest to oil palm plantations can be useful for identifying biological communities or habitat localities in need of conservation action.

Although there are strong parallels between the effects of oil palm agriculture on biodiversity in the Amazon and Southeast Asia, the nature of oil palm agriculture in the two regions differs significantly, as does their ecological, socio-economic, and political context. Quantitative studies demonstrating the impacts of oil palm on biodiversity in the Neotropics are essential to encourage evidence-based development policies (Gilroy et al., 2015). The present study contributes towards a growing body of literature that aims to understand how conversion of tropical forests to oil palm plantations affects biodiversity, but is the first to explore this topic in Western Amazonia.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.06.005>.

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