

Reference Site Influences Perceived Species Loss in Shade Coffee, But Assemblages in Fact Depend on Landscape Context

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Abstract

Context: Shade coffee plantations are purported to maintain forest biodiversity in agricultural landscapes. Understanding their conservation importance is hindered, however, by the limited taxa studied and failure to account for the landscape context of plantations and quality of reference sites.

Objectives/Research questions: (1) how occupancy of mammals and birds changed from continuous forest to fragmented forest and coffee plantations while statistically controlling for landscape context, and (2) whether mammal and bird communities responded differently to shade coffee with regard to richness and composition.

Methods: We used camera traps to sample ground-dwelling birds and medium- and large-bodied mammals (31 and 29 species, respectively) in shade coffee plantations and two types of reference forest (fragmented and continuous) in Colombia's Western Andes. We used a multi-species occupancy model to correct for detection and to estimate occupancy, richness, and community composition.

Results Shade coffee lacked ~50% of the species found in continuous forest, primarily forest-specialist insectivorous birds and forest-specialist and large-bodied mammals, resulting in different species composition between coffee and forest assemblages. Coffee plantation birds were generally a unique subset of disturbance-adapted specialists, whereas mammals in coffee were mostly generalists encountered across land uses. Forest fragments had species richness more similar to shade coffee than to continuous forest. Species sensitive to shade coffee responded negatively to isolation and disturbance at the landscape scale.

Conclusions: Studies comparing coffee with relictual forest fragments may overestimate the conservation value of shade coffee. Conservation of biodiversity in shade coffee landscapes will be ineffective unless these efforts are linked to larger landscape-level conservation initiatives.

Introduction

Conversion of forest to agriculture is the leading cause of the tropical deforestation crisis, with more than 2.2 million km² of tropical forests having been cut since the 1950s (Gibbs et al. 2010, Laurance et al. 2014). Because over 60% of known terrestrial biodiversity occurs in tropical forest, deforestation for agriculture is a major driver of species loss and endangerment (Dirzo and Raven 2003; Tracewski et al. 2016). Nonetheless, negative impacts of this habitat conversion are thought to be mitigated in agroforestry systems (i.e., production systems where crops are grown under tree cover), and agroforestry is widely advocated as a means of balancing biodiversity conservation and agricultural production (Bhagwat et al. 2008; Clough et al. 2011; Jha et al. 2014). Among tropical agroforestry systems, coffee grown under shade trees (shade coffee) is one of the most widespread and economically important crops that provides structurally complex vegetation, extensive canopy cover, and other forest-like characteristics that could support native species in agricultural landscapes (Rappole et al. 2003; Mertens et al. 2018). Shade coffee mitigates habitat loss and fragmentation for some species by providing food resources,

facilitating movement, and enhancing landscape connectivity (Muriel and Kattan 2009; Cassano et al. 2012; Ramirez-Villegas et al. 2013). However, in spite of the decades-long research interest in shade coffee and increasing acceptance of it as high quality habitat, extensive uncertainty remains, even within the taxa studied, about the value of coffee landscapes for biodiversity (Philpott et al. 2008; Jha et al. 2014; Caudill and Rice 2016).

The equivocal results regarding suitability of shade coffee as wildlife habitat may be driven in part by the limited consideration of the landscape context of coffee plantations. Also, the quality of forested reference sites and landscape context of these sites shape conclusions. Studies of biodiversity in shade coffee traditionally have assessed species richness and habitat variables within specific land use categories (i.e., shade coffee vs. sun coffee and/or forest), often as a basis for coffee certification standards for individual coffee farms (Estrada et al. 2006; Caudill and Rice 2016). Perhaps because of this farm focus, the landscape context of shade coffee has received relatively little attention, even though diversity and composition of plant and animal communities are known to be influenced by landscape composition and configuration (Laurance and Laurance 1999; Lindenmayer et al. 2002; Caudill and Rice 2016). For example, landscapes comprise habitats that differ in resource availability, and high-quality habitats may support populations that spill over into low-quality habitats (Rand et al. 2006; Gilroy and Edwards 2017). Habitat fragmentation and isolation, and the level of human disturbance on the landscape, also affect the ability of species to move between patches, access resources, and persist over the long term (Wilson et al. 2016). The few studies of coffee within a landscape context indicate that landscape-level factors are relevant to interpreting patterns of biodiversity and deserve more study. For instance, forest cover in the landscape surrounding coffee farms has been linked to species richness at the site and matrix type influences extinction thresholds of wildlife (Bali et al. 2007; Gordon et al. 2007; Boesing et al. 2018a). In addition, forest quality in reference sites will influence researchers' perceptions of loss or maintenance of species in coffee plantations. In many cases, reference sites are disturbed or fragmented forest patches near coffee farms that hold only a fraction of the original biodiversity (e.g., Arellano et al. 2005; Gordon et al. 2007; Saldaña-Vázquez et al. 2010). A full assessment of the conservation value of shade coffee farms for native species requires comparisons with well-conserved forest, as well as incorporation of landscape context.

In this study, we evaluated suitability of shade coffee as habitat for two animal groups; ground-dwelling birds, which are characterized as sensitive to habitat degradation and good indicators of habitat quality (Kupsch et al 2019, Powell et al 2015) and medium- and large-bodied mammals, a group highly sensitive to forest loss and fragmentation (Laurance et al 2000, Lino et al 2019). To our knowledge, ground-dwelling avifauna has not been studied in shade coffee plantations globally and research on mammals in coffee is limited. Our research was conducted in the tropical Andes of Colombia, which have been subjected to intense deforestation driven by the expansion of coffee; Colombia is the fourth largest coffee producer worldwide (Armenteras et al. 2011; ICO 2020). This deforestation is particularly concerning because the tropical Andes are a global hotspot of avian and mammalian species diversity and endemism, including many poorly known species threatened by habitat loss (Schipper et al. 2008). We addressed two main questions: (1) How does occupancy of ground-dwelling birds and mammals

change from continuous forest (reference sites) to disturbed forest fragments (alternative reference sites) and shade coffee plantations, while controlling for landscape context? (2) Do ground-dwelling bird and mammal communities differ in their responses to shade coffee with regard to richness, occupancy, and community composition? Based on their sensitivity to land-use change, we expected ground-dwelling birds and mammals, particularly large-bodied species, to exhibit lower occupancy and taxonomic diversity in shade coffee than in forest, and that this pattern would be exacerbated in areas with large amounts of human disturbance and mitigated on coffee farms closer to continuous forest. In addition, we predicted that differences in richness and composition between forest and coffee would be higher for continuous forest than for forest fragments. Finally, we predicted that ground birds would be more sensitive than mammals to land-use change, because birds exhibit greater habitat specialization and sensitivity to fragmentation (Ducatez et al. 2014; Keinath et al. 2017).

Methods

Study area

The study was conducted in the Serranía de los Paraguas region of the Western Andes of southwestern Colombia in the Valle del Cauca Department (Fig. 1). The Serranía encompasses ~ 232,000 ha, composed of hyper-wet Chocóan forest on the west-facing slopes and montane forest more typical of the tropical Andes on the eastern slopes. Our study area was located on the eastern slope in El Cairo municipality (4°45'39"N, 76°13'21"W), between 1250 and 2700 m.a.s.l. This region is part of the Coffee Cultural Landscape of Colombia, a UNESCO World Heritage Site, and recently was categorized by the Colombian National Parks System as a *protected area with sustainable use of natural resources* (IUCN Category VI; IUCN 2020; UNESCO 2020). This landscape contains a network of ~ 70 privately protected areas (or Natural Reserves of the Civil Society), known as the Reserve Network of Northern Valle del Cauca, of which around half include shade coffee plantations.

The study landscape comprised a mosaic of forest fragments embedded in a matrix of mixed agriculture, primarily shade coffee and cattle pasture, with continuous forest present on the ridgetops. The coffee system supports moderate canopy cover (30–60%) in which more than 80% of the tree species are native, but shade tree diversity is low and mostly planted. Based on photographs acquired by our cameras, some mammals such as tayras (*Eira barbara*), agoutis (*Dasyprocta punctata*) and crab-eating foxes (*Cerdocyon thous*) feed on plantain fruits within coffee plantations. Forested areas in this landscape comprise patches of old secondary forest (typically 20+ years of regrowth) regenerating from pasture or abandoned coffee plantations and, at higher elevations, continuous old-growth forest that connects with the Chocó lowlands to the west (Fig. 1). The topography is steep, with up to 90% slope at higher altitudes.

Focal bird and mammal communities

The potential species pool in this landscape includes approximately 30–35 species of ground-dwelling birds. These bird species, like Andean bird species in general, have “shoestring” ranges within narrow elevational bands, resulting in high beta diversity over the altitudinal gradient (Kattán et al. 2006). Of the

expected species at our study elevations, 8 were thought to occur only below 2000 m and 4 only above 2000 m. If there were an altitudinal gradient in species richness in our study landscape, it should therefore be highest at lower elevations in the absence of human disturbance. However, forest fragmentation and disturbance can shift the width of elevational ranges of Andean species (Ocampo-Peñuela and Pimm 2015), and we found some species both above (e.g., *Leptotila plumbeiceps* and *L. verreauxi*) and below (e.g., *Turdus fuscater*) expected elevations at multiple sites. From the species pool for birds, one species (Chestnut wood-quail, *Odontophorus hyperythrus*) is listed by the IUCN (2020) as Near-Threatened (Appendix A, Table S1), but the ecology and conservation status of many species in our study area are barely known (Greeney et al. 2008).

We expected to detect around 32 mammal species in this altitudinal range of the eastern slope of the Western Andes (Solari et al. 2013). Elevational turnover is less pronounced for mammals than birds in this region (Patterson et al. 1998), and all potential species occur across the entire elevational range of our study area. As with birds, the ecology of many mammals in this region is poorly known (Schipper et al. 2008), but many more species are listed by the IUCN (2020) as of conservation concern: 3 Vulnerable, 5 Near-Threatened, and 2 Data Deficient (Appendix A, Table S2).

Camera trap surveys

We used camera traps to sample birds and mammals in shade coffee plantations and two types of reference forest (forest fragments and continuous old-growth forest) between July 2016 and July 2018. Forest fragments were owned and managed by individual smallholders and generally were part of shade-coffee farms. Therefore, we deployed cameras in fragments and coffee plantations simultaneously at the same sites based on a stratified random sample design by primary land-use type. Each site represented one to four nearby coffee farms containing an agricultural mosaic of shade coffee, forest fragments and pasture ($N=13$ sites at 1250–1900 m elevation, black triangles in Fig. 1). Continuous Andean forest sites were located along ridgetops and connected to the continuous Chocoran forest ($N=11$ sites at 1600–2700 m, black circles in Fig. 1). These sites were private forested landholdings that were primarily or completely made up of old-growth forests. To ensure that all samples were within the same landscape, all continuous forest sites were located on the east slope of the Andes no more than 8 km from fragment and coffee plantation sites. The minimum distance among all sites was 1 km.

Our sites ranged in area from 3–39 ha for coffee farms and from 20–700 ha for forested landholdings. The number of cameras at each site varied with site area (range = 4–26) for a total of 340 cameras across the 24 sites, and stratified sampling within sites resulted in 57 cameras in shade coffee plantations, 127 in fragmented forest, and 156 in continuous forest. Camera locations ranged in elevation from 1293 to 2518 m (Mean \pm SD = 1810 \pm 312 m). Cameras were placed a minimum of 100 m apart and deployed for at least one month at each site (Mean \pm SD = 39 \pm 8 days). We attached cameras to trees ~ 30–40 cm above the ground and did not use baits or lures. All cameras (Browning Trail Cameras, Browning BTC- 5 HD Strike Force) were equipped with motion-activated sensors, and we programmed cameras to take four photographs each time the camera was triggered. We considered consecutive records of the same species to be temporally independent if they were separated in time by at least 24

hours. Cameras within a site were not spatially independent for mammals and some birds because of their large home ranges, and we addressed this lack of independence with a random effect of site in our multi-species occupancy model. Also, we parameterized the detection sub-model to account for variation in camera trapping effort. In our study, occupancy should be interpreted as a measure of habitat use for mammals because species with large home ranges likely moved in and out of our sites during sampling (MacKenzie et al. 2006; Tobler et al. 2015).

For analyses of mammals, we included all species that triggered our cameras except small rodents and marsupials (< 200 grams), which were unidentifiable with cameras. For birds, we only used captures of species that are wholly or partially ground-dwelling, defined *a priori* based on natural history information on foraging and nesting habits in *Birds of the World* (Billerman et al. 2020) and expert opinion. Major families included tinamous (Tinamidae), guans (Cracidae), quail (Odontophoridae), doves (Columbidae), antpittas (Grallaridae), and thrushes (Turdidae).

Calculation of landscape variables

To characterize the landscape context of our survey sites, we used remote sensing to classify land use across our study landscape and then calculated landscape-level variables that measured the amount of forest cover (not including shade coffee), degree of isolation, and intensity of human disturbance for each camera location. First, we generated a land use map using a supervised classification with 10-m resolution performed on a Sentinel-3 image acquired through the Google Earth Engine platform (see Appendix B for classification methods). Using this map, we then calculated the following landscape-level variables in ArcMap 10.7 (Esri; Redlands, CA): (1) Percentage of forest, which was the percent of total land cover comprising forest within a 1-km buffer around each camera. We also calculated this variable for a 500-m buffer, but this measure was highly correlated with the 1-km buffer and was not used in analyses. (2) Distance to continuous forest, which we considered a measure of isolation. We calculated the distance to continuous forest as the straight-line distance from each camera location to the nearest edge of a polygon that encompassed continuous old-growth forest. This polygon was built by merging adjacent pixels of the forest class in the land-use map (Appendix B, Figure S1). Strips of forest less than 100 m wide were not included as continuous forest. (3) Human disturbance, represented by an index of human access and influence. We calculated this index using a cost-distance analysis of ease of human access to any grid cell in the study area based on distance to roads, distance to towns (weighted by population), and ease of human movement in the three broad land-use types in our landscape (forest, coffee plantations, and pasture). We used the Summed Point Influence Tool 1.0 beta for these calculations (Fisher and Didier 2012; see Appendix C for detailed methods).

Sampling vegetation and elevation at camera sites

To account for effects of local vegetation on species detectability at camera locations, we sampled vegetation structure around each camera. Variables included: (1) canopy cover calculated as the average of four measures of percent canopy cover taken with a vertical canopy densiometer (Geographic Resources Solution, GRS-Densitometer) at 5 m from each camera in the four cardinal directions, and (2)

understory vegetation density calculated by counting the number of 25-cm segments of a 2-m pole obscured by vegetation while standing 10 m away from the pole in front of the camera. We also determined the elevation of each camera with a GPS (Garmin GPSMAP 64s).

Multi-species occupancy model

We used a multi-species occupancy model (Kéry and Royle 2016; Devarajan et al. 2020), implemented in a Bayesian framework, to measure the influence of land-use type (term used for simplicity to represent shade coffee plantations, secondary forest fragments, and older continuous forest) and landscape context on camera-level richness and occupancy of ground-dwelling birds and mammals. In this model, species occupancy is modeled hierarchically to distinguish true absence of a species from non-detection (Royle and Dorazio 2008; Tobler et al. 2015). This framework offers advantages over traditional approaches for inference about species richness and occupancy by accounting for both species-level effects of land-use type and landscape context, as well as aggregated effects of these variables on the full community. This leads to increased precision in estimates of species richness by improving occupancy estimates for all species, including those with low detection rates (Russell et al. 2009).

We constructed the model with the program JAGS (R2Jags: Plummer 2017) implemented in R, which uses Markov Chain Monte Carlo (MCMC) simulation to estimate parameters based on a posterior distribution. We analyzed bird and mammal datasets separately (See model specifications and the final code in Appendix D). We assessed statistical significance of occupancy covariates based on whether 95% credible intervals of beta estimates overlapped 0 and based on visual assessments of violin plots.

Analysis of species richness

We determined species richness for birds and mammals at the camera level and by land-use type for shade coffee and the two types of reference forest. Camera-level richness was calculated within the multi-species occupancy model using a data augmentation approach. We calculated species richness by land-use type using a rarefaction approach because the number of cameras differed across the three land uses. These rarefaction analyses were performed with the package *iNEXT* (Hsieh et al. 2016), which uses a bootstrap resampling method (bootstrap replicates = 100) and extrapolation sampling curves to estimate an asymptotic species richness. We used the median realized presence/absence (Z) matrix of the multi-species occupancy model, which is an estimate of the observed presence/absence matrix corrected for detection (Dorazio and Royle 2005; Dorazio et al. 2006), as the input for our calculation of richness by land-use type. The Z matrix and the matrix based on naïve occupancy were nearly identical (mismatch between pairs of values = 0.8% for birds, 0.2% for mammals;).

Comparison of species composition between shade coffee and reference forests

To visualize differences in composition of communities among land-use types, we used non-metric multidimensional scaling (NMDS), which measures differences in composition as the variance of distances between the centroids for each land use (i.e., NMDS space). This analysis used a site-by-

species presence-absence matrix. To avoid circularity in our analyses, we used the naïve presence-absence matrix and converted it to a pairwise dissimilarity matrix using the Jaccard dissimilarity index in the R package *vegan* (Oksanen et al. 2016). We subsequently tested for significant differences in community composition across land-use types with a Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2017) performed with the function *adonis* in the *vegan* package. Because overall differences in composition were significant, we ran a *post-hoc* permutational pairwise test of significance between land-use types using the *RVAideMemoire* package (Hervé 2020).

Results

Overall species richness

Over two years of camera trap sampling, we obtained 918 independent records of 31 species of ground-dwelling birds and 1029 records of 29 species of terrestrial mammals (Appendix A). In analyses, we only included species with two or more independent records (i.e., captures at a camera at least 24 hours apart), and thus, we modeled richness and occupancy with data from 26 species of birds and 27 species of mammals. Our multi-species occupancy model estimated a total richness of 39 species of birds (SD = 3.9, 95% Bayesian confidence interval [BCI] = 32–46) and 33 species of mammals (SD = 2.6, 95% BCI = 30–40), which is slightly higher than the known number of ground birds (~ 34) and mammals (~ 32) for this region.

Species richness at the level of cameras and land-use type

Estimates of species richness (S_{est}) for bird and mammal communities were substantially lower for coffee plantations than for forest, but the magnitude of these differences depended on the type of reference forest. At the camera level, mean richness of birds in coffee plantations was less than half the mean richness in continuous forest, but richness in forest fragments was more similar to richness in coffee than in continuous forest (Fig. 2a). Similarly, richness of ground-dwelling birds estimated for land-use types with rarefaction curves was more than 50% lower in shade coffee ($S_{est} = 15$) than in continuous forest ($S_{est} = 35$), whereas differences were smaller between shade coffee and forest fragments ($S_{est} = 18$, Fig. 2c). In contrast to birds, species richness of mammals in coffee plantations was lower than richness in both forest fragments and continuous forest. At the camera level, mean richness of mammals in coffee plantations was about 30% lower than richness in fragments and continuous forest (Fig. 2b). For land-use types, mammal richness differed more between coffee plantations ($S_{est} = 17$) and continuous forest ($S_{est} = 31$) than between coffee and forest fragments ($S_{est} = 20$, Fig. 2d). Confidence intervals of rarefaction curves for coffee and continuous forest did not overlap; for coffee plantations and forest fragments, confidence intervals overlapped little in the range of sampling conducted in coffee plantations (i.e., 57 cameras, Fig. 2d).

Rarefaction curves demonstrated that richness remained low in coffee plantations for both taxa even when extrapolated to the higher number of camera traps sampled in forest (Fig. 2). Species richness

estimates were only slightly higher than raw species counts, with bird richness in continuous forest exhibiting the greatest difference (raw species richness: birds - continuous forest N = 29, forest fragments N = 16, shade coffee N = 14; mammals - continuous forest N = 29, forest fragments N = 19, shade coffee N = 15).

Species occupancy in coffee plantations, forest fragments, and continuous forest

For both taxa, occupancy probability was lower in shade coffee plantations compared to continuous forest for most species (mean $\beta < 0$; Fig. 3), including 73% of bird species and 85% of mammal species. In contrast, only 58% of bird species exhibited a lower probability of occupancy in forest fragments compared to continuous forest, and mammals were equally likely to respond positively or negatively to forest fragments (Fig. 3). Species responding positively to coffee and forest fragments included disturbance adapted doves (*Leptotila verreauxi*, *L. plumbeiceps*; Columbidae) and thrushes (*Turdus ignobilis*, *Catharus aurantiirostris*; Turdidae). Functional groups that responded negatively to shade coffee also generally responded negatively to fragmented forest. These consisted primarily of large-bodied species that consume fallen fruits (*Nothocercus* spp.; *O. hyperythrus*) and leaf-litter-foraging insectivores, including tapaculos (*Scytalopus* spp.), antthrushes (*Formicarius rufipectus*, *Chamaeza turdina*), a leaftosser (*Sclerurus mexicanus*), antpittas (*Grallaria flavotincta*, *G. [rufula] alvarezii*), and a wren (*Cyphorhinus thoracicus*). For mammals, only the agouti and common opossum (*Didelphis marsupialis*) exhibited a higher probability of occupancy in shade coffee compared to continuous forest (Fig. 3). The agouti and other generalist species, such as tayra, crab-eating raccoon (*Procyon cancrivorous*), and jaguarundi (*Puma yaguaroundi*), also showed higher probability of occupancy in fragments than in continuous forest. Functional groups of mammals that responded negatively to fragments, particularly large-bodied species (> 12 kg) and forest specialists, also responded negatively to shade coffee. Twelve mammal species were not detected in shade coffee. This group included all large-bodied mammals (red-brocket deer, *Mazama americana*; collared peccary, *Pecari tajacu*; Andean bear, *Tremarctos ornatus*; jaguar, *Panthera onca*; puma, *Puma concolor*) and all other forest specialists except three small cats. Smaller forest specialists not detected in coffee comprised herbivores (mountain paca and pacarana, *Cuniculus taczanowskii* and *Dinomys branickii*), carnivores (Colombian weasel, *Mustela felipei*), and omnivores, notably all Procyonids except the crab-eating raccoon. These included species of low conservation concern with broad geographic ranges (South American coati, *Nasua nasua*; kinkajou, *Potos flavus*) as well as range-restricted, near-threatened species (olinguito, *Bassaricyon neblina*; Western mountain coati, *Nasuella olivacea*, IUCN 2020). Both coatis were commonly recorded in continuous forest in our study area (Appendix A, Table S2). The ocelot (*Leopardus pardalis*), margay (*Leopardus wiedii*), and, to a lesser extent, oncilla (*Leopardus tigrinus*), were recorded infrequently in shade coffee (1, 2, and 7 independent records, respectively; Appendix A), but commonly in both forest types.

Species responses to land use versus landscape variables

Bird and mammal occupancy responded strongly to both land-use type and landscape context (Fig. 4). On average, occupancy of species found in continuous forest declined in coffee plantations (mean of median β s: birds = -1.17, mammals = -0.75) and in fragmented forest (mean of median β s: birds = -0.94, mammals = -0.46; Fig. 4a, b). Occupancy of these species also declined with increasing distance to continuous forest (mean of median β s: birds = -0.77, mammals = -0.58). This variable represented the strongest landscape-level effect on both taxa and effect size was twice as large as for other landscape context covariates. The amount of forest within a 1-km buffer and human disturbance had smaller negative effects on occupancy of both groups (mean of median β s: 1-km buffer - birds = -0.28, mammals = -0.03; human disturbance - birds = -0.23, mammals = -0.28).

When we examined the subset of taxa that occurred in coffee plantations, responses to land use and landscape variables differed from the set of species that occurred in forest. Taxa found in coffee plantations were generally less sensitive to landscape context. For birds, mean occupancy of species that occurred in coffee was greater in coffee plantations and fragments than in continuous forest (mean of median β s: coffee = 0.35; fragments = 0.44; Fig. 4c). In contrast to this finding, mammals that used coffee plantations had lower occupancy in coffee than in continuous forest (mean of median β s = -0.24) but, as with birds, their occupancy was greater in forest fragments than in continuous forest (mean of median β s = 0.42; Fig. 4d). With respect to landscape variables, birds and mammals that occupied coffee plantations responded negatively to all covariates, though effect sizes were smaller than for species that occurred in forest. For mammals in particular, mean effect sizes were near zero and species had only ~ 50% chance of responding negatively to distance to continuous forest (mean of median β s: mammals = -0.07; birds, -0.25) and amount of forest in a 1-km buffer (mean of median β s: mammals = -0.05; birds = 0.28).

Changes to community composition

For birds and mammals, community composition was distinctive for continuous forest and coffee, and composition of fragmented forest was intermediate and partially overlapped with that of coffee (Fig. 5). The NMDS showed that forest-restricted and at-risk species occurred primarily within continuous forest, whereas coffee plantations contained generalist species and forest visitors. Overall differences in species composition among the three land-use types, as well as all pairwise comparisons, were significant (PERMANOVA – birds: $F_{(2,32)} = 8.43$, $p < 0.001$; mammals: $F_{(2,32)} = 15.7$, $p < 0.001$; *post-hoc* PERMANOVA test – continuous forest-coffee, $p_{birds} = 0.002$, $p_{mammals} = 0.0015$; forest fragments-coffee, $p_{birds} = 0.01$, $p_{mammals} = 0.005$; forest fragments-continuous forest, $p_{birds} = 0.0015$, $p_{mammals} = 0.0015$).

Discussion

Our results indicate that shade coffee plantations do not provide quality habitat for most ground-dwelling birds and mammals in this Andean landscape. Species richness, at both camera and land-use levels, was lower in shade coffee than in continuous forest (Fig. 2). Differences in richness were accompanied by significant shifts in community composition of birds and mammals between forest and shade coffee

(Fig. 5), and species that were sensitive to land-use type (i.e., continuous forest versus forest fragments or coffee plantations) also were sensitive to landscape context, particularly isolation from continuous forest and degree of human disturbance (Fig. 4). Observed effects of shade coffee on biodiversity, however, were contingent upon both the type of reference site used and taxon under study. Forest fragments embedded in the agricultural matrix showed reduced species richness for both taxa, and nearly equal to that of shade coffee for birds. Thus, studies using fragmented forest as reference sites are likely to underestimate impacts and overestimate conservation value of shade coffee. There also were important differences between avian and mammalian responses to shade coffee: birds in coffee plantations tended to be a unique subset of disturbance-adapted specialists (e.g., *Leptotila* doves), whereas mammals that persisted in coffee plantations were generalists and non-forest species encountered in all land use types. Overall, our results highlight the importance of considering landscape context, integrity of reference forests, and a greater diversity of sensitive taxa in assessing the conservation value of shade coffee.

Shade coffee communities: persistence of species insensitive to landscape-level factors

Species richness of mammals and birds was 50% lower in shade coffee plantations than in continuous forest, indicating that shade coffee does not provide adequate habitat for many forest-restricted species of mammals and birds in the Western Andes. This result contrasts with previous findings showing similar richness in forest and shade coffee for small-bodied and volant mammals (e.g., Estrada et al. 2006; Caudill et al. 2014; Mertens et al. 2018), but parallels studies that documented reduced mammal diversity in lowland cacao agroforestry landscapes (Cassano et al. 2014). For birds, shade coffee sometimes has equal species richness to forest patches, and often equal or higher densities of migratory species (Greenberg et al. 2000; Tejeda-Cruz and Sutherland 2004; Bakermans et al. 2009). Disparities between our results and these studies likely can be explained by our focus on sensitive subsets of the mammal and bird communities, as well as our relatively intact reference sites.

Bird and mammal community composition differed markedly between forest and shade coffee at our site in the western Andes (Fig. 5), as reported in some other studies (Harvey and González Villalobos 2007; Leyequién et al. 2010; Buechley et al. 2015; Mertens et al. 2018). For birds, this represented species turnover driven by loss of insectivorous, forest-restricted ground and understory species, a group particularly sensitive to disturbance of vegetation structure and loss of specific foraging microhabitats (Philpott and Bichier 2012; Powell et al. 2015; Stratford and Stouffer 2015). Changes to leaf litter structure and the leaf-litter arthropod community may preclude effective foraging in shade coffee understory (e.g., Armbrrecht et al. 2005). Most birds observed foraging in shade coffee plantations use the relatively intact canopy stratum rather than the highly disturbed understory (Latta and Wunderle 1998; Jones et al. 2002). For mammals, compositional changes reflected fewer forest specialists and large-bodied mammals (all species with body mass > 12 kg were absent) and increased occurrence of smaller habitat generalists, a common trajectory with land-use change and human disturbance across the tropics (Beca et al. 2017; Rovero et al. 2019). In addition to direct impacts of forest loss with conversion to coffee

plantations, this conversion may impact mammals by altering prey availability or increasing hunting pressure or human-wildlife conflict (Cullen et al. 2000; Woodroffe et al. 2005). Mammals also may perceive plantations to be riskier habitat given their general proximity to human homes and roads (Quiroga et al. 2016; Amit and Jacobson 2018).

The subset of birds and mammals sensitive to forest conversion to coffee plantations was also sensitive to the landscape context of a site (Fig. 4). Distance to continuous forest and human disturbance in the local landscape were important factors in site occupancy and functional diversity for birds and mammals. These results agree with emerging evidence suggesting that degree of isolation from nearby forest is a key driver of bird and mammal diversity in agroforestry systems, as in forest fragments (Bali et al. 2007; Anand et al. 2008; Cannon et al. 2019). For birds, there is strong evidence that greater amounts of forest cover in proximity to shade coffee plantations, and in fragmented tropical landscapes in general, increases avian species richness, particularly of forest specialists and insectivores (Raman 2006; Leyequién et al. 2010; Boesing et al. 2018a). Equivalent data are scarce for mammals, but distance to a forested protected area was shown to be the strongest predictor of mammal species richness in coffee plantations in the Western Ghats of India (Bali et al. 2007). Many forest-restricted species likely persist in agroforests as 'spillover' from nearby forest habitat (Boesing et al. 2018b).

The importance of considering forest reference site quality when evaluating agroforestry systems

Our conclusions about suitability of shade coffee habitat for wildlife were dependent upon the forest reference site: continuous, old-growth forest contained double the species richness of coffee plantations, whereas fragmented secondary forest patches in the agricultural matrix were more similar to shade coffee in richness. Most species of conservation concern (Near Threatened or Vulnerable, IUCN 2020) also were associated with continuous forest. Thus, forest fragmentation, successional stage and other reference site characteristics determine conclusions drawn from forest-coffee comparisons, with biased inference about suitability of shade coffee resulting from use of forest reference sites that do not contain the full community of interest. This issue is important because many studies of biodiversity in shade coffee plantations and other agricultural landscapes use nearby relictual forest patches as reference sites (e.g., Arellano et al. 2005; Gordon et al. 2007; Saldaña-Vázquez et al. 2010), and few studies of shade coffee have considered or statistically controlled for effects of the quality or landscape context of reference forest (Caudill and Rice 2016). However, many tropical vertebrates are as sensitive to fragmentation as they are to conversion to shade coffee, with specific functional groups such as insectivorous birds, large-bodied species, and forest specialists being more negatively affected (Bregman et al. 2014; Keinath et al. 2017). Forest fragments are adversely impacted by forest edges and human disturbance (e.g., selective logging and hunting) further compounding negative effects of declining patch size (Aubad et al. 2008; Pfeifer et al. 2017). Fragment assemblages represent impoverished and compositionally distinct communities, dominated by generalist and non-forest species (Carrara et al. 2015; Beca et al. 2017; Keinath et al. 2017; this study), and thus have limited utility as reference sites.

Taxon-specific responses to agroforests

Our study identified distinct responses for ground-dwelling birds and mammals, both in terms of how biodiversity was lost and which species remained in shade coffee. For mammals, species richness was lower in shade coffee than in both types of reference forest, whereas, for ground-dwelling birds, fragment reference sites were equally species-poor as coffee plantations. Many of the birds in coffee plantations represented disturbance-adapted woodland or shrubland specialists, with similar functional roles, and were not found in either type of reference forest (e.g., *Leptotila* doves, *Turdus* and *Catharus* thrushes). By contrast, mammal species that persisted in shade coffee generally represented medium-bodied, non-forest and generalist species also encountered in both reference forest types (e.g., *D. marsupialis*, *Dasypus novemcinctus*, *D. punctata*, *C. paca*, *C. thous* and *E. barbara*). This pattern may be largely explained by differences in habitat specialization across taxa. Globally; birds exhibit greater habitat specialization than mammals (Ducatez et al. 2014), and tropical forests birds are closely tied to specific microhabitats related to their specialized resource use (Marra and Remsen 1997; Stratford and Stouffer 2015). Habitat specialists are sensitive to habitat disturbance and fragmentation (Devictor et al. 2008; Keinath et al. 2017; Kellner et al. 2019); thus, many ground-dwelling, forest-restricted birds are unlikely to persist in shade coffee and forest fragments in our system. The literature also suggests that shade coffee bird communities are dominated by disturbance-adapted and generalist species (Tejeda-Cruz and Sutherland 2004; Komar 2006). For mammals, about half the species on this landscape were forest specialists, and these species were largely absent from shade coffee. However, coffee plantations also were missing wide-ranging habitat generalists, such as the jaguarundi (*P. yagouaroundi*) and puma (*P. concolor*), which may be sensitive to other threats such as retaliation killing for depredation on livestock and pets. Understanding of how large mammals interact with shade coffee plantations is minimal (but see Daily et al. 2003; Cruz-Lara et al. 2004; Caudill and Rice 2016) in spite of the fact that large mammals are considered highly vulnerable to extirpation in disturbed landscapes (Morrison et al. 2007). Clearly, the contrasting patterns, as well as magnitude, of response that we documented for birds and mammals supports the need to fill large remaining taxonomic gaps by diversifying the number and types of species studied in shade coffee plantations.

Conservation implications

Our study demonstrates that to advance biodiversity conservation in shade coffee agroforestry systems, we should consider the following: 1) Efforts to conserve biodiversity in regions with shade coffee will be ineffective unless these are linked to larger landscape-level conservation initiatives that conserve surrounding forest (Chandler et al. 2013; Caudill and Rice 2016). Currently, biodiversity conservation in coffee plantations is primarily focused on the farm level, likely because certification of coffee farms is the primary conservation management tool. Conservation initiatives at this scale are inadequate to protect all biodiversity (Tschardt et al. 2015). Our work demonstrates that even in landscapes with remnant forest and the full complement of native species, shade coffee plantations contain a small subset of the original taxonomic diversity, comprising primarily habitat generalists and disturbance-tolerant species common in secondary forest fragments. Forest-restricted species of ground-dwelling birds and mammals, including leaf-litter insectivores and large-bodied species, are missing from coffee plantations. This larger set of species is strongly impacted by landscape-level factors such as isolation

from continuous forest and human disturbance. In our region, protection of the large continuous forest that connects the Andes with the Chocó is critical for persistence of the diverse fauna of this coffee-forest mosaic. Maintenance of connectivity between forest fragments and continuous forest will also help reduce the effective distance to this continuous forest. 2) The full impacts and biodiversity value of shade coffee can only be understood with comparative datasets from intact forest reference sites as a baseline. By comparing fauna in shade coffee to remnant or highly degraded forest, the benchmark of success is a half-empty forest. We recommend that future studies in shade coffee landscapes explicitly account for the landscape context of reference sites and that, where possible, primary forest sites be used as reference communities. We acknowledge that in many regions such reference sites no longer exist; in this case, historical species lists may be the best alternative.

Declarations

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Ethics approval: Our research has been approved by University of Florida's animal care ethics committee (IACUC Study No. 201408440) and review board for research with human subjects (landowner interviews, IRB Protocol No. 15U0661).

Data availability and material (data transparency): Data supporting the findings of this study are presented in the article and supplementary materials. Nevertheless, field data on species presence-absence and specific information for sites are available from the first author upon reasonable request.

Code availability: The code for the hierarchical multispecies occupancy is provided in the supplemental material.

Authors' contributions: MJBD designed the study, collected the data. HHJ and LCB assisted with study design. MJBD, HHJ, and KMM analyzed the data. MJBD and HHJ wrote the manuscript with input from LCB. All authors edited the manuscript.

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Figures

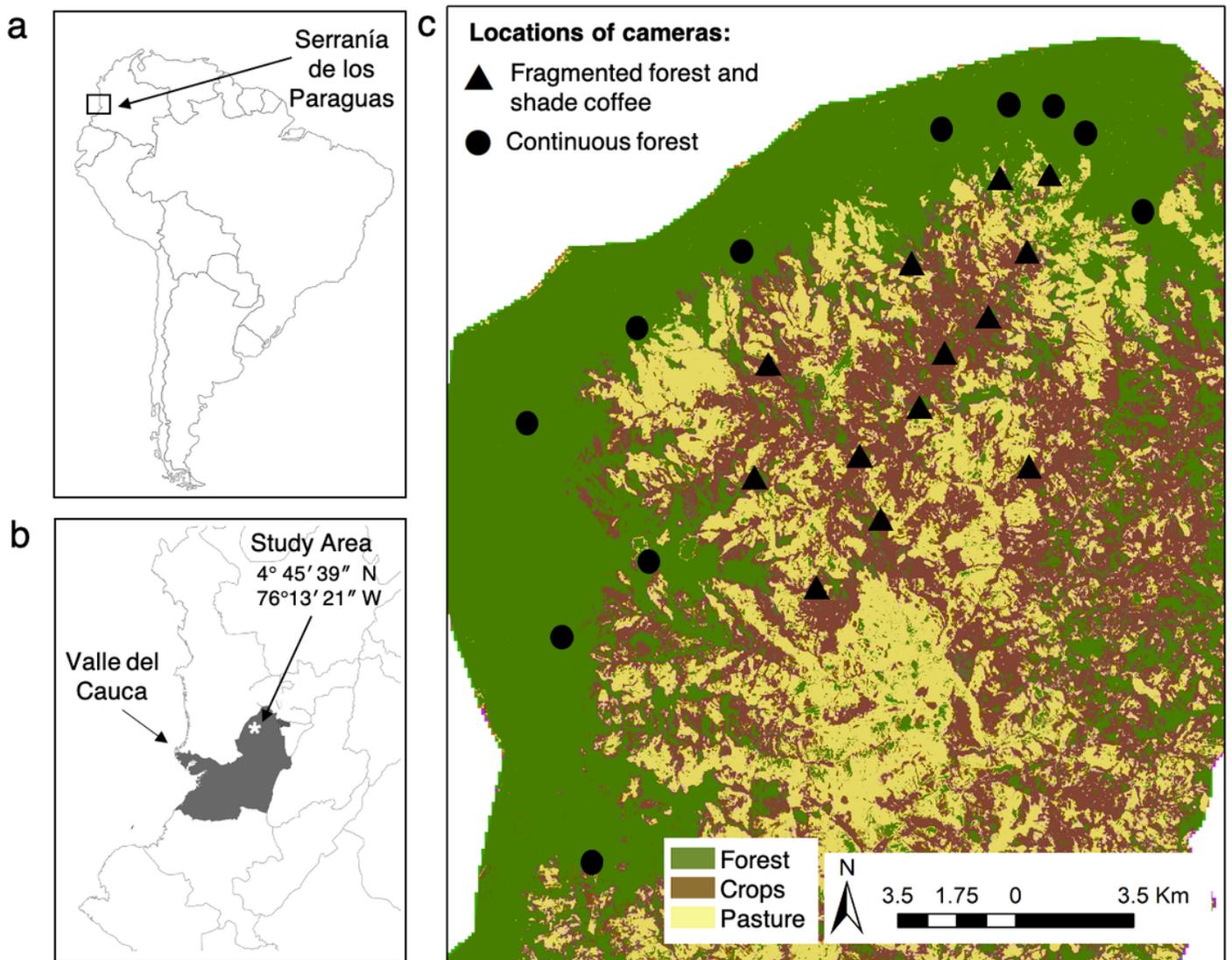


Figure 1

Study area in the Serranía de Los Paraguas region of the Western Andes of Colombia. Black triangles represent groups of cameras (sites) within shade coffee and forest fragment land-use types; black circles represent groups of cameras within the continuous forest land-use type. Each site contained 4 - 26 camera traps, depending on site size. Cameras at each site were activated for ~ 39 days between July 2016 and July 2018.

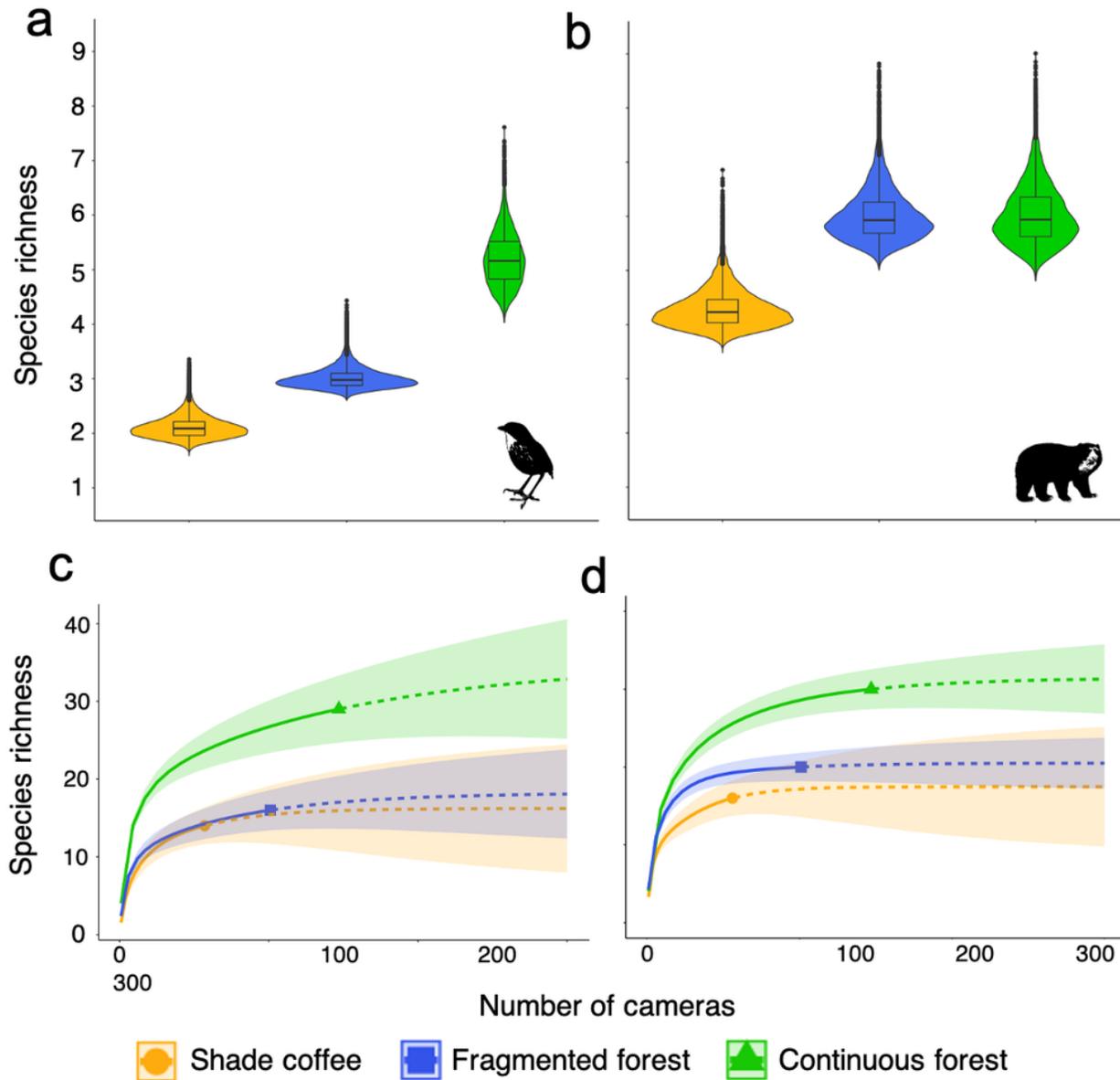


Figure 2

Species richness of birds and mammals in shade coffee, forest fragments and continuous forest calculated at the camera level (a, b) and for land-use types (c, d) in the Serranía de Los Paraguas region of the Western Andes of Colombia. Violin plots show the shape of the posterior distribution of mean species richness at the camera level for a) ground birds and b) medium- and large-bodied mammals. Black boxes represent the interquartile range (middle 50% of the distribution) and the tails represent

credible intervals of the posterior distribution. Camera-level estimates of richness were obtained with a hierarchical multi-species occupancy model. Rarefaction curves for c) birds and d) mammals show estimated species richness at the level of land-use type as a function of the number of camera traps deployed. To facilitate comparisons of species richness among land-use types, extrapolations extend to the total number of camera traps. Shaded areas represent 95% Bayesian confidence intervals.

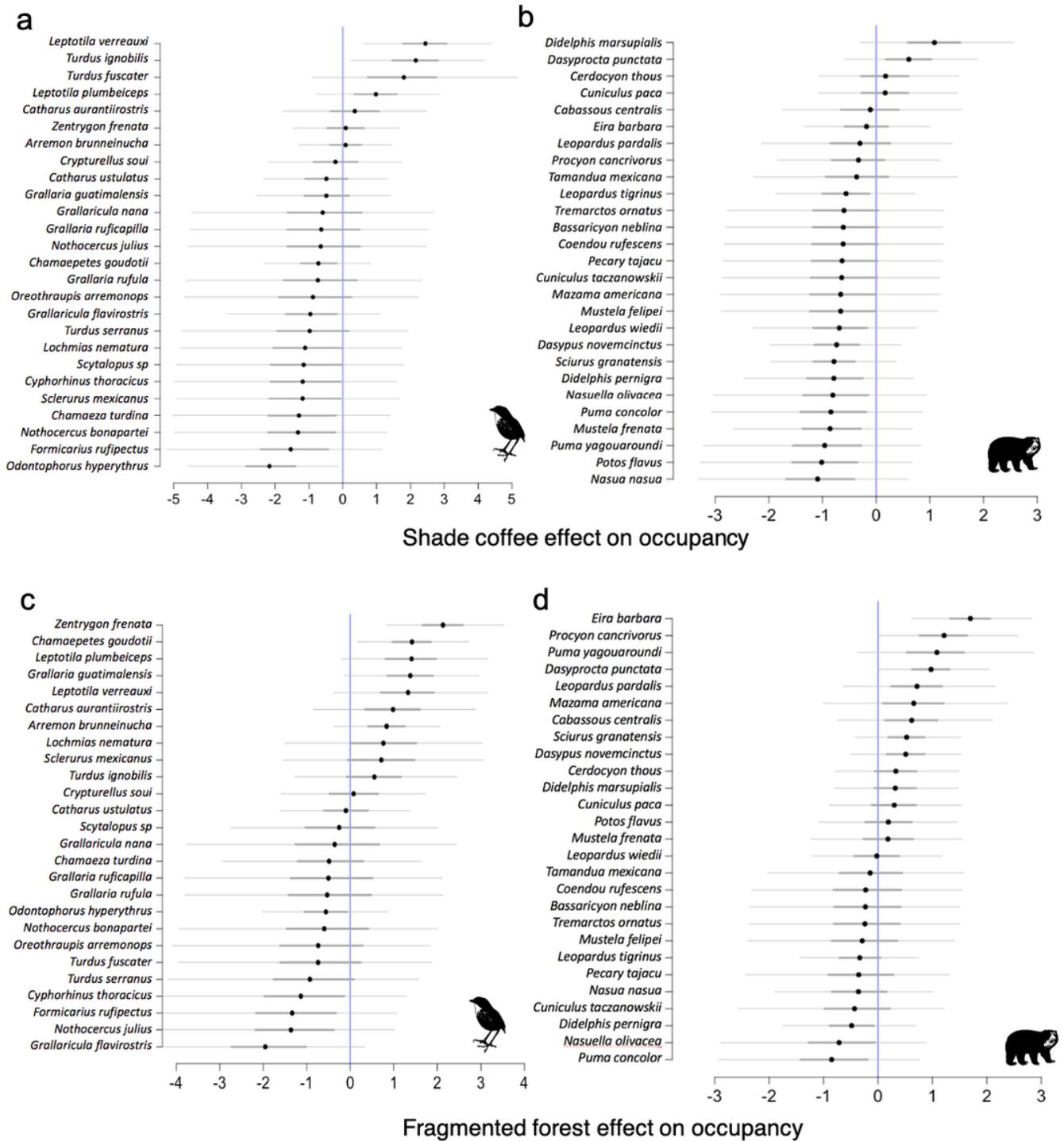


Figure 3

Caterpillar plots showing effects of land-use type on avian (a, c) and mammalian (b, d) occupancy in the Serranía de Los Paraguas region of the Western Andes of Colombia. Plots show the standardized median beta coefficients and Bayesian credible intervals for changes in occupancy from continuous forest to shade coffee (a, b) and from continuous forest to forest fragments (c, d). Negative values indicate that occupancy declined between continuous forest and coffee plantations or forest fragments. The 95% Bayesian credible intervals are shown in light grey and 50% Bayesian credible intervals are in dark grey.

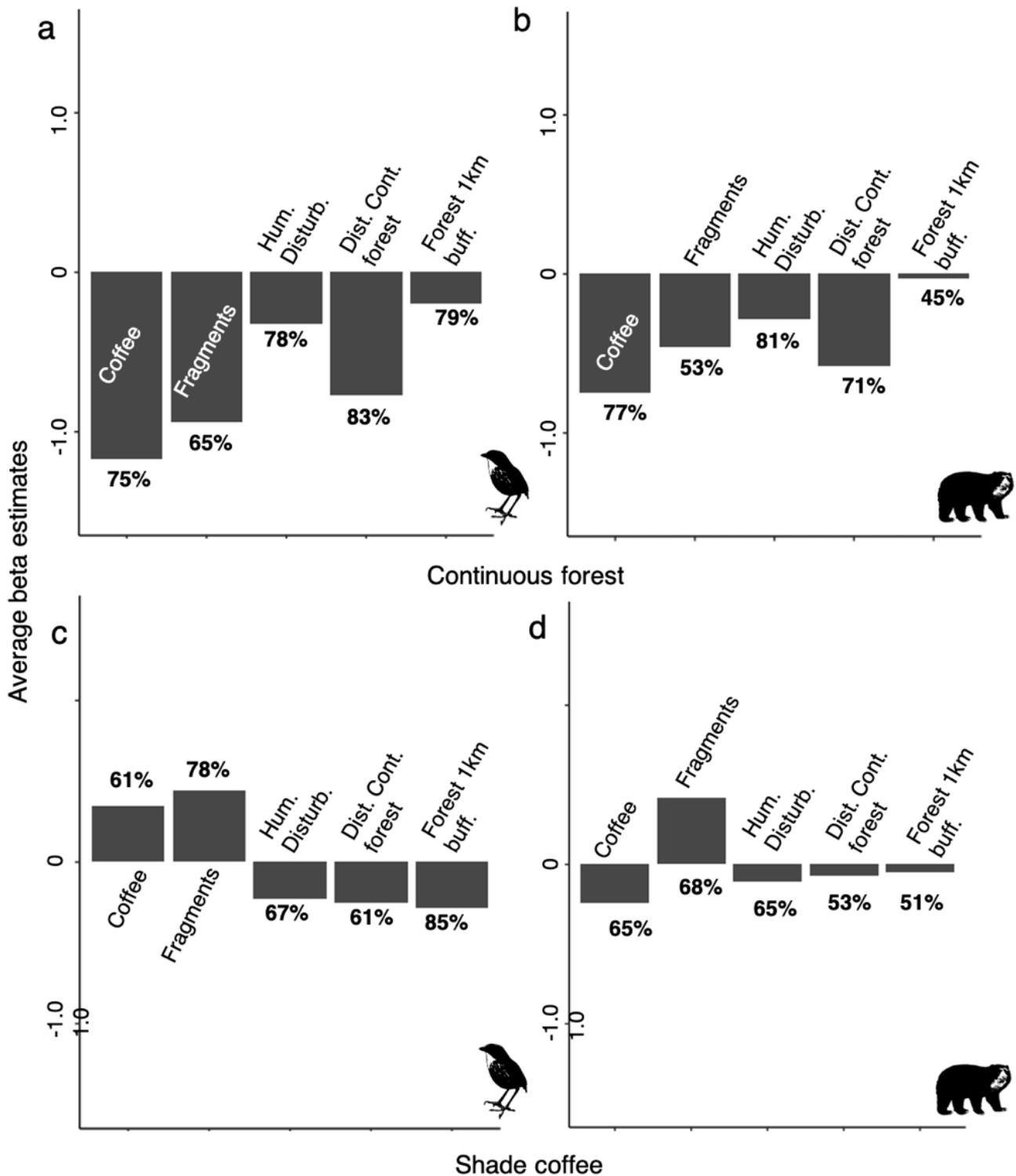


Figure 4

Mean beta coefficients for birds and mammals in continuous forest (a, b) and in shade coffee plantations (c, d) in the Serranía de Los Paraguas region in the Western Andes of Colombia. Data represent all species recorded in these land-use types, including species that were present in other land-use types as well. Coefficients are shown for the change in occupancy from continuous forest to coffee and continuous forest to fragments and for three landscape-context covariates. Numbers associated with each factor show the percent of the posterior distribution (across all species) in the same direction (positive or negative) as the mean.

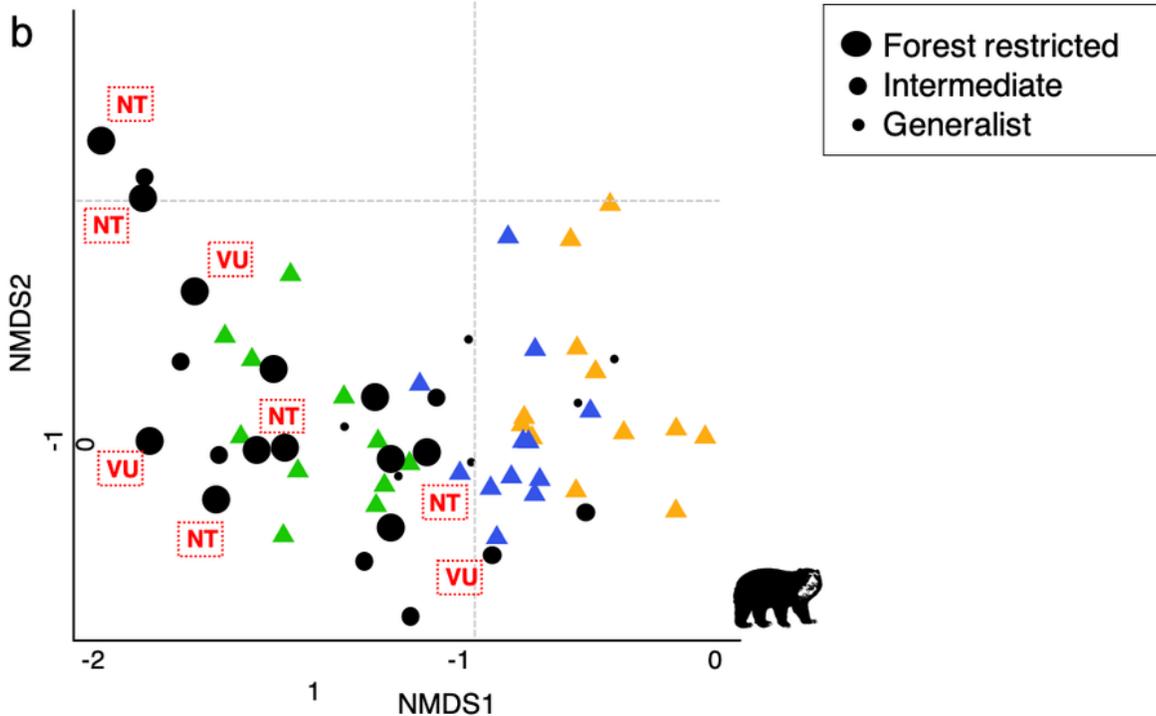
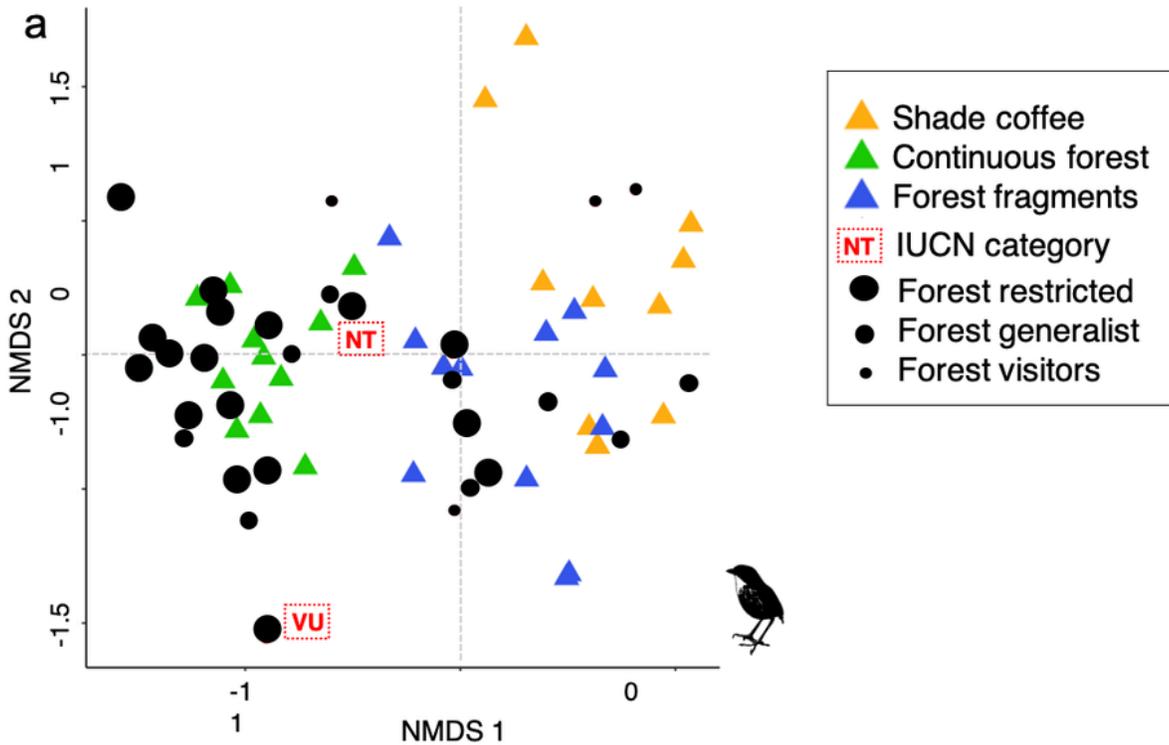


Figure 5

Non-metric multidimensional scaling (NMDS) ordination plot of avian (a) and mammalian (b) community composition across land-use types in the Serranía de Los Paraguas region of the Western Andes of Colombia. Colored triangles correspond to land-use type within a site (e.g., all species recorded in coffee at one site). Circles correspond to species, with point size representing the level of forest dependence. Symbols with letters represent the global IUCN Red List threat category for species listed as vulnerable (VU) or near threatened (NT); species without abbreviations are globally assessed as “least concern”. NMDS, birds stress = 0.011, mammals stress = 0.099.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementBedoyaetal2021.docx](#)