


Human disturbance impacts on rainforest mammals are most notable in the canopy, especially for larger-bodied species

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Abstract

Aim: Community-level assessments of how biodiversity responds to disturbance within forest habitats are often biased towards terrestrial-based surveys. However, recent research suggests that arboreal communities of several indicator groups (ants, amphibians, beetles and butterflies) are more susceptible to human disturbance than their terrestrial counterparts, but what about wildlife at higher trophic levels? We assess responses to disturbance, from forest floor to canopy, of a key conservation flagship group: medium to large rainforest mammals.

Location: The Manu Biosphere Reserve, southeast Peru.

Methods: We deploy both arboreal and terrestrial camera traps to directly compare the response of arboreal and terrestrial mammal communities to rainforest degradation and disturbance.

Results: We show that the arboreal mammal community is more susceptible to habitat disturbance than the terrestrial community. Furthermore, the largest-bodied arboreal species, which are major seed dispersers, showed the greatest negative response to forest disturbance. The strongest predictors of occupancy probability for arboreal communities were focal tree connectivity and canopy cover, whereas surrounding forest loss and canopy height were the strongest predictors of terrestrial community occupancy, although these also had effects similar in size and magnitude on the arboreal community.

Main conclusions: Conservation conclusions drawn from camera-based studies focused on the terrestrial realm likely underestimate the impact of rainforest degradation to arboreal communities and on arboreal rainforest biodiversity in general. We highlight the importance of implementing arboreal research methods, capable of investigating conservation implications of anthropogenic disturbance across all vertical strata, for accurate conservation assessments and improving rainforest management and restoration strategies.

KEYWORDS

camera traps, degradation, forest, Neotropics, primates, stratification

1 | INTRODUCTION

The drastic rate and scale of degradation of the world's natural places has led us into the current era, the Anthropocene (Johnson et al., 2017). In light of the intense threats arising from a growing human population and demand for resources (e.g., habitat fragmentation, destruction and unsustainable harvesting of bushmeat), understanding how global biodiversity responds to forest degradation is essential to predict how ecosystems structure and function will change (Sala & Sala, 2009), and for the development of appropriate conservation measures. This represents a particular challenge in tropical forests; complex ecosystems that represent somewhere between a half to two-thirds of the world's terrestrial biodiversity, yet receive a relatively small proportion of research attention (Stroud & Feeley, 2017). One of the focal conservation priority groups are the medium to large mammals; important for seed dispersal, herbivory, a source of protein for local communities and often used as a flagship group to drive conservation policy for many other less well known groups or species (Brodie, Helmy, Brockelman, & Maron, 2009).

Despite forest disturbance being widely regarded as detrimental to tropical biodiversity as a whole (e.g., Gibson et al., 2011), recent evidence suggests that tropical mammals may be resilient to some intermediate forms of habitat modification, such as selective logging of tropical forests (Gibson et al., 2011; Putz et al., 2012; Tobler et al., 2018). However, the majority of assessments conducted to date either rely on terrestrial camera traps (e.g., Roopsind, Caughlin, Sambhu, Fragoso, & Putz, 2017; Wearn et al., 2017), which under-represent arboreal species, or on ground-based transect techniques (e.g., Carrillo, Wong, & Cuarón, 2000; Lopes & Ferrari, 2008), which are typically biased towards large, conspicuous, diurnal species and often miss cryptic and nocturnal arboreal species (Bowler, Tobler, Endress, Gilmore, & Anderson, 2017; Kays & Allison, 2001; Whitworth, Braunholtz, Huarcaya, Macleod, & Beirne, 2016). Ground-based transect techniques have demonstrated that large-bodied primates are more susceptible to human disturbance (especially from hunting) than their smaller-bodied counterparts, likely due to their size and slow reproductive rates (Carrillo et al., 2000; Lopes & Ferrari, 2008; Sampaio, Lima, Magnusson, & Peres, 2010), however very little is known about the responses of arboreal mammal communities as a whole (Kays & Allison, 2001). The inherent bias in survey techniques targeting mammal communities has thus far kept the challenge of characterizing community-level responses to forest degradation in complex tropical rainforest environments beyond the reach of conservation science. Failure to fully characterize arboreal and terrestrial community responses could lead to under or over-estimation of the true biodiversity impacts of rainforest disturbance, potentially leading to inappropriate and/or ineffective conservation management and policy approaches to address the issue.

The bias towards the study of terrestrial mammal communities using cameras and diurnal primates from ground-based transects is not surprising given the difficulties researchers face in accessing the canopy (Kays & Allison, 2001; Lowman, Devy, & Ganesh, 2013). However, addressing this bias is important for three key reasons:

First, arboreal communities play critical roles for healthy ecosystem function, including seed dispersal, pollination services, predator-prey balances and folivory (Kays & Allison, 2001; Lowman, 2009). Second, arboreal biodiversity makes up a considerable proportion of overall community biomass (Kays & Allison, 2001), and a comparable if not greater proportion of overall community diversity (Fagan et al., 2006; McClearn et al., 1994). Third, for ants, amphibians, beetles and butterflies, where terrestrial and arboreal communities have been directly compared, arboreal fauna have proven to be more sensitive to habitat disturbance (Klimes et al., 2012; Tregidgo, Qie, Barlow, Sodhi, & Lee-Hong Lim, 2010; Whitworth et al., 2016; Whitworth, Villacampa, Serrano Rojas, Downie, & MacLeod, 2017). If medium to large arboreal mammal species respond to disturbance in the same way as terrestrial species, then the conclusions based on terrestrial communities are applicable to the whole medium-large mammal community. However, if arboreal mammals show differential sensitivity to anthropogenic disturbance, we may be dramatically under or over-estimating the impact of disturbance to tropical mammal communities.

Here, we use both arboreal and terrestrial camera traps to directly compare the response of arboreal and terrestrial mammal communities to rainforest disturbance. While the benefits of terrestrial camera traps for understanding community-level responses have been well documented (Rowcliffe & Carbone, 2008; Srbek-Araujo & Chiarello, 2005; Tobler, Carrillo-Percestequi, Leite Pitman, Mares, & Powell, 2008; Tobler, Carrillo-Percestequi, Zúñiga Hartley, & Powell, 2013; Tobler, Hartley, Carrillo-Percestequi, & Powell, 2015), only recently has arboreal camera trapping become feasible at greater scale; thanks to improvements in battery life, reduced cost and memory capacity (Bowler et al., 2017; Whitworth et al., 2016). Consequently, to date there have been no direct comparisons using camera traps to test whether terrestrial and canopy mammal communities respond to rainforest disturbance in a similar way—although previous work has compared arboreal camera trapping with terrestrial transects (e.g., Bowler et al., 2017, Whitworth et al., 2017). In this study, we use multispecies occupancy models, which are well suited to analysis of camera data at the community level (Tobler et al., 2015) and for assessing species-specific responses to varying levels of forest disturbance (Bowler et al., 2017; Sollmann et al., 2017; Tobler et al., 2018), to answer the question of whether arboreal rainforest mammals show a greater sensitivity to forest habitat degradation compared with their terrestrial counterparts.

2 | METHODS

2.1 | Site description

This study was carried out in the Manu Biosphere Reserve, a UNESCO and IUCN World Heritage Site in south-eastern Peru, designated for the global conservation importance of its Amazonian rainforest biodiversity and thought to be the world's most species rich terrestrial conservation hotspot. Six locations that reflected the diverse land uses of the reserve were surveyed:

two locations were within core protected locations (one pristine within the national park and one privately owned regenerating forest area) and four locations with no strict formal protection (three native community territories and one a community of non-indigenous settlers). See Text S1 for comprehensive site descriptions and Figure 1 for a map of the study locations.

2.2 | Camera trapping

All fieldwork was conducted during the dry seasons of 2015 and 2016. A total of 168 camera stations were established, 80 of which had both terrestrial and arboreal cameras and 88 of which had just arboreal cameras (to account for the lower detection probabilities

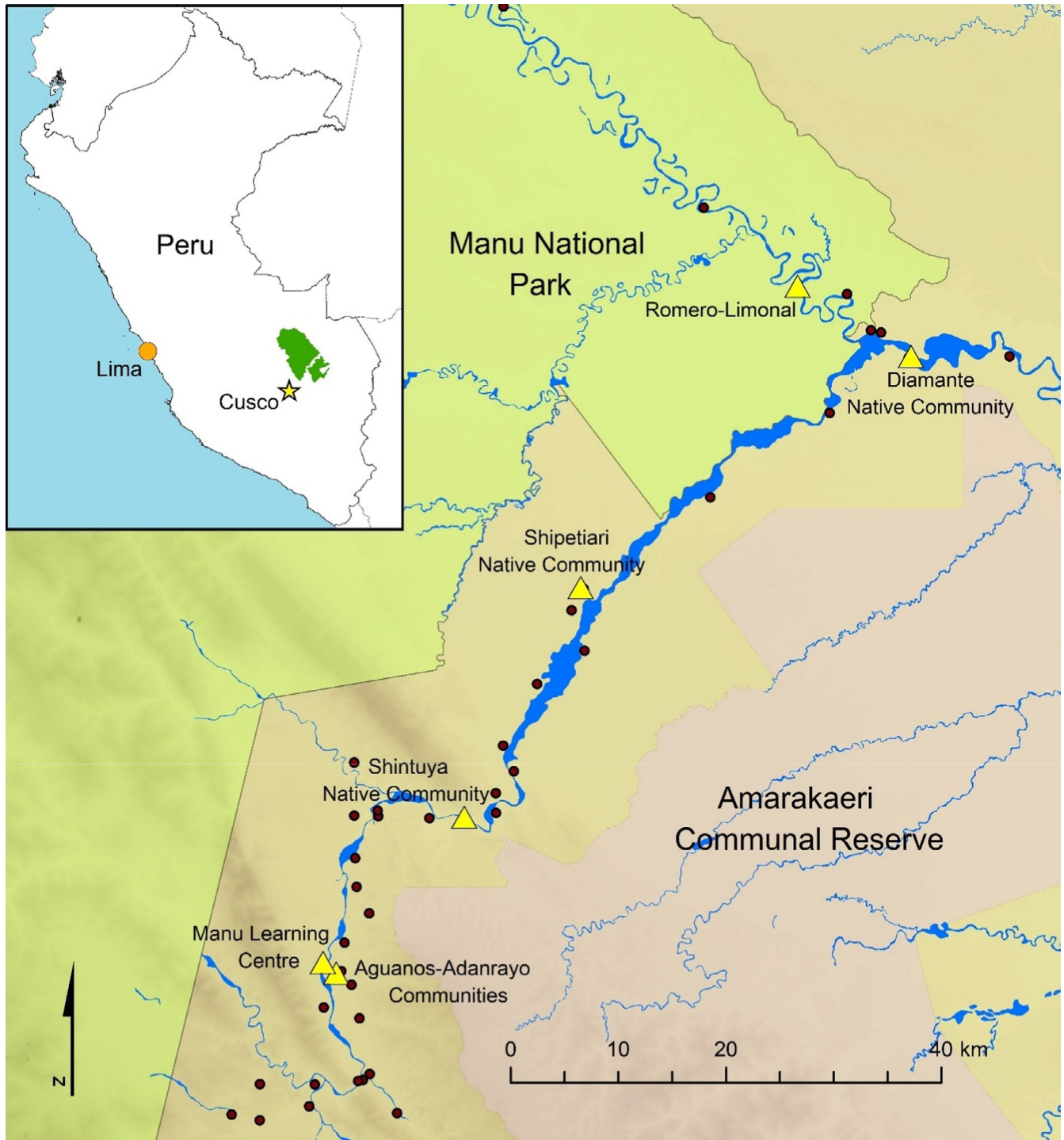


FIGURE 1 Map of the survey sites (as shown by yellow triangles) within the Manu Biosphere Reserve. Other communities and lodgings are represented by red circles, major rivers in blue, and the two major protected areas (Manu NP and Amarakaeri CR) indicated. Inset is the location of the Manu BR to the north-east of Cusco, in south-eastern Peru. For a detailed description of each of the survey sites, see Appendix materials Text S1

TABLE 1 Session and strata-specific survey effort and estimated species richness (with 95% credible intervals)

Site	Year	Terrestrial					Arboreal				
		Effort (camera days)	Sites	Sp. Obs.	Sp. Est.	95% CI	Effort (camera days)	Sites	Sp. Obs.	Sp. Est.	95% CI
Aguanos	2016	1,421	10	17	19.5	17–22	2,142	19	11	15.9	13–19
Diamante	2015	1,329	9	17	19.2	17–22	2,019	14	11	15.5	12–19
Diamante	2016	1,411	10	20	21.6	20–24	1,972	15	19	20.0	19–22
MLC	2015	1,559	10	20	21.8	20–24	2,867	18	15	17.6	15–20
MLC	2016	1,519	10	23	23.7	23–25	2,550	19	17	18.6	17–21
Romero	2015	1,432	9	24	24.6	24–26	2,967	18	17	19.2	17–22
Romero	2016	–	–	–	–	–	1,058	8	13	17.1	14–20
Shintuya	2015	1,307	9	15	19.0	16–22	2,217	16	16	18.8	16–21
Shipetiari	2016	1,275	10	23	23.9	23–26	2,572	18	16	17.8	16–20
Total		11,253		26			20,364		24		

of arboreal traps); (Bowler et al., 2017), totalling 248 camera traps. Of these, 40 in 2016 and 40 in 2015 were terrestrial camera traps, placed 30–40 cm from the ground and 88 cameras in 2016 and 80 in 2015 were placed in the canopy at different heights (average camera height = 17.3 m; min = 3.5 m, max = 30 m). All cameras were Bushnell #119438, #119676C and #119736C models. Each camera was set to capture 14 s of video, with a thirty second interval between captures. Arboreal Camera traps were strapped to the main trunk of the tree ideally looking over horizontal limbs. Arboreal cameras were located >250 m apart and terrestrial cameras >500 m apart. Cameras were established in April and May and retrieved in September and October in both years. Thirty-eight cameras which functioned for fewer than 18 days (due to the camera failing, becoming obscured or shifting into a position unlikely to detect animals, or being stolen) were removed from the analysis as they failed to reach the three six-day session threshold required for the occupancy analysis, resulting in resulting in a total of 210 cameras (145 arboreal and 77 terrestrial) considered in this analysis. Each of the nine arboreal sampling sessions accrued >1,000 camera trap nights, the threshold required to adequately capture the arboreal mammal community in tropical rainforest (Table 1; Bowler et al., 2017). All videos were reviewed, and all mammals and birds were identified to species, where possible. Videos were sorted into hierarchical folders based on year, site, station and species then exported for data analysis with associated metadata (time and date of detection) using Microsoft PowerShell software for analysis in the R statistical environment (R Core Team, 2013).

2.3 | Characterizing forest disturbance

In order to characterize forest disturbance at each of the camera stations, we measured eight key features of the forest that are known to vary with anthropogenic or natural disturbance (Whitworth et al., 2016, 2017). Six of the eight features related to physical forest structure: average canopy height, canopy cover, understorey shrub density, density of trees (>5 cm DBH), 2000–2014 forest cover loss

and focal tree connectivity. The final two features were distance to the nearest navigable river (to account for any effect of changes in habitat or hunting associated with riparian systems), and distance to nearest community (which is often used as a proxy for hunting pressure in the tropics (e.g., Levi et al., 2011; Oliveira, Fragoso, Overman, Luzar, & Levi, 2016; Roopsind et al., 2017)). The physical characteristics of forest structure were measured based on methods in Whitworth et al. (2016) and Whitworth et al. (2017), using the following procedures: “canopy height” was estimated as the average height of two trees considered to reflect the canopy height in the immediate vicinity of each camera station measured using a laser hypsometer; “canopy cover” was taken by a standard observer (AW) by using a 10 cm² square and estimating the canopy coverage within the square at eight points circling the base of the tree (an average of all eight estimates was taken); “shrub density” was estimated by two observers 10 m apart with a one metre pole marked every 10 cm with orange tape held one metre from the ground—the number of tapes that could be observed were recorded (where 11 observed tapes = completely open understorey; 0 tapes observed = completely closed understorey); “density of trees (>5 cm DBH)” was estimated as the number of trees with a diameter of greater than 5 cm at breast height (DBH) in a 10 × 2 m wide survey strip; “forest cover loss 2000–2014” was calculated as the amount of forest lost within a 250 m radius around each survey site using data from the forest watch loss assessment (Hansen et al., 2013). Finally, “focal tree connectivity” was assessed by a single observer (AW) for consistency using the following scoring system: 0 = a stand-alone tree with no points of entry (where “point of entry” is defined as referred to a continuous connecting path, via overlapping limbs or lianas, from the focal tree to an adjacent tree); 1 = tree with at least a single point of entry from an adjoining tree; 2 = at least two points of entry from adjoining trees from different directions; 3 = at least 3 points of entry from adjoining trees in different directions; 4 = at least 3 points of entry from adjoining trees from different directions and access points up and down the tree running to the ground from extensive vines and lianas; 5 = surrounded and connected on all sides

with ≥ 4 points of entry and extensive vine and liana routes. The distance from each camera station to nearest navigable river and nearest community were estimated in ArcMap10.3.

We checked for covariance in the disturbance features (see Text S2), as covariance can lead to spurious type one or type 2 errors (Crawley, 2012). Distance to the nearest navigable river and shrub density were treated as independent covariates as they were weakly correlated with other parameters (correlation coefficients < 0.4). As all the remaining factors (canopy cover, canopy height, density of larger trees, distance from community, tree connectivity and forest loss) showed marked covariance between one or more of the other features (correlation coefficients > 0.4), we used multi-variate factor analysis to extract a single explanatory factor to represent overall habitat disturbance for each camera station to use in the analysis—referred to as the “disturbance factor” from this point forwards. The disturbance factor represented 45% of the variation in the data set and was 2.7 times more informative than any single factor alone (an eigenvalue of 2.69). The factor loadings of each feature were consistent with higher rainforest disturbance: low canopy cover, low tree connectivity, higher forest cover loss, lower canopy height, low density of trees > 5 cm DBH and high forest recent forest loss resulted in higher “disturbance factor” scores (see Figure 2; Text S2). In order to determine the relative contribution of each covariate to the disturbance factor, we also applied each of the co-varying explanatory terms independently in separate occupancy model runs.

2.4 | Data analysis

To determine the effect of anthropogenic disturbance on terrestrial and arboreal mammal communities, we implemented strata-specific, multi-session, multispecies Royle–Nichols occupancy models, developed for community-level analysis of camera trap data (Tobler

et al., 2015). Each model contained three nested hierarchical levels: (a) session-level community (all species occurring at an area in a given session); (b) station-level community (the occurrence of species at a given camera site) and; (b) the detection process. For a full description of the occupancy approach, see Text S3. All occupancy models contained the disturbance factor or one of the co-varying disturbance features, and river distance as explanatory variables on occupancy probability. For explanatory variables on detection probability, the arboreal models included camera height and tree connectivity, and the terrestrial models included shrub density.

Models were run in JAGS using the R2Jags package (Su & Yajima, 2015) in the R statistical environment. Models were run with three chains with 50,000 iterations, a burn-in of 30,000 iterations and a thinning ratio of 50. Model convergence was assessed through inspection of the resultant Markov Chain Monte Carlo (MCMC) chains. Model fit was assessed using Pearson's residuals (observed residuals vs. model-simulated residuals). The significance of the explanatory variables was assessed through examining their 95% credible intervals. Potential relationships between species-specific responses to anthropogenic disturbance and body mass obtained from (Emmons & Feer, 1997) were assessed using linear models. We deal with species that used both arboreal and terrestrial strata by including them in each model separately, as including them in the different strata could reveal novel ecological information. For example, species which operate in multiple strata may change the degree to which they use a given strata with anthropogenic disturbance. Throughout the results and discussion, we use the common names of all species for ease of communication. The corresponding Latin names are presented in the supplementary materials (arboreal species see Text S4; terrestrial species see Text S5).

3 | RESULTS

In total, 4,928 records representing 26 observed species were gathered from terrestrial cameras (Text S5), and 2,574 records representing 24 observed species from arboreal cameras (Text S4). Considered together, this community represents 46 species. Overall survey efforts were 20,364 arboreal camera trap nights across 145 camera stations, and 11,253 terrestrial camera trap nights across 77 camera stations (see Table 1). The highest mean estimated species richness of the terrestrial community came from the protected site within Manu National Park (Romero = 24.6) and the highest estimated arboreal richness was from one of the native community sites (Diamante = 20.0). Session-level estimated species richness was negatively associated with average forest disturbance score for both arboreal and terrestrial communities (Text S6). Of the current known mammalian assemblage of the region, just eight medium- to large-bodied mammals were undetected within this study (listed in Text S7; determined using Whitworth, Downie, Downie, May, Villacampa, & Macleod, 2016), all of which are patchily distributed or principally associated with aquatic habitat, and as such are often missed from most mammal inventories within tropical forests.

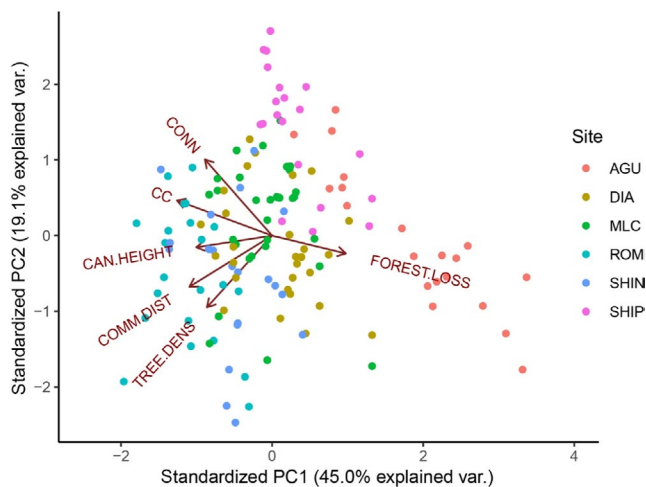


FIGURE 2 The structural disturbance factor loadings from the PCA; component 1 across the x-axis and component 2 along the y-axis. Low canopy cover (CC), low tree connectivity (CONN), higher forest cover loss (FOREST.LOSS), lower canopy height (CAN.HEIGHT) and low density of trees > 5 cm DBH (TREE.DENS) = high forest disturbance. Colours represent the different survey site groupings

3.1 | Detection probabilities

The detection probabilities of seven arboreal species were significantly influenced by the height at which cameras were located from the ground (Figure 3a; Text S8): dwarf squirrel, spider monkey and kinkajou all increased with increasing camera height, whereas squirrel monkey, saddleback tamarin, Amazonian red squirrel and large-headed capuchin detection probability decreased with increasing camera height. The relationship with detection probability and focal tree connectivity was weaker, with just two arboreal species having significantly lower detection probabilities in trees with higher levels of connectivity (Figure 3b): night monkey and titi monkey. We found no support for understory shrub density influencing terrestrial mammal detection probabilities (Figure 3c; Text S9).

3.2 | Occupancy probabilities

Both the arboreal and terrestrial communities showed a decline in occupancy with increasing forest disturbance at the community-level; however, the relative effect size was greater for the arboreal community (Figure 4a; Text S10) than the terrestrial community (Figure 4b; Text S11). On average, the mean occupancy of the arboreal community declined by 64% from the lowest to the highest values of the disturbance factor, whereas the terrestrial community's mean species occupancy declined by 10%. The community-level divergence between arboreal and terrestrial responses was underpinned by heterogeneity in species-specific responses to disturbance (Figure 5; Text S9 and S11). Within the arboreal community, four species (17%) showed significant declines in occupancy in response to the disturbance factor: Peruvian woolly monkey, white-fronted capuchin, brown titi monkey, common opossum, and a further eight species were close to significant (~50% of the community overall; Figure 5a; Text S9). In contrast, the species-specific effect sizes of the disturbance factor were small and non-significant for all terrestrial species (all beta estimates <0.063; Figure 5b; Text S11). There was a clear relationship between body mass and the mean effect of structural disturbance for arboreal species; larger arboreal species had more negative responses to increasing disturbance in comparison with smaller species, whereas there was no such relationship occurred for terrestrial species (Figure 6). Decomposition of the disturbance factor into its individual components suggests that focal tree connectivity made the greatest contribution to the disturbance factor for the arboreal community (greater connectivity resulted in higher community-level occupancy), followed by a positive effect of canopy cover, then a negative effect of forest loss and a positive effect of canopy height (see Table 2). For the terrestrial community, recent forest loss had the largest, negative, effect on community occupancy probability, followed by a positive effect of canopy height. The effects of both recent forest loss and canopy height were similar in magnitude and in the same direction for both

terrestrial and arboreal communities (Table 2). The effect of distance to nearest community was neutral for both arboreal and terrestrial communities.

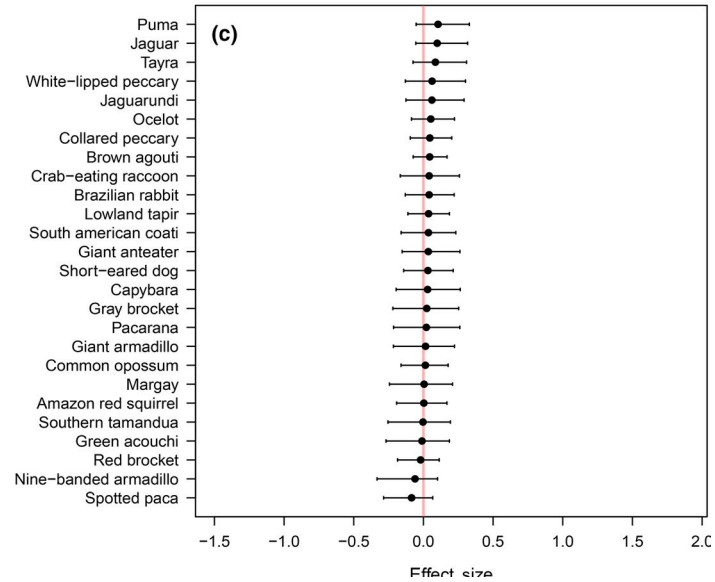
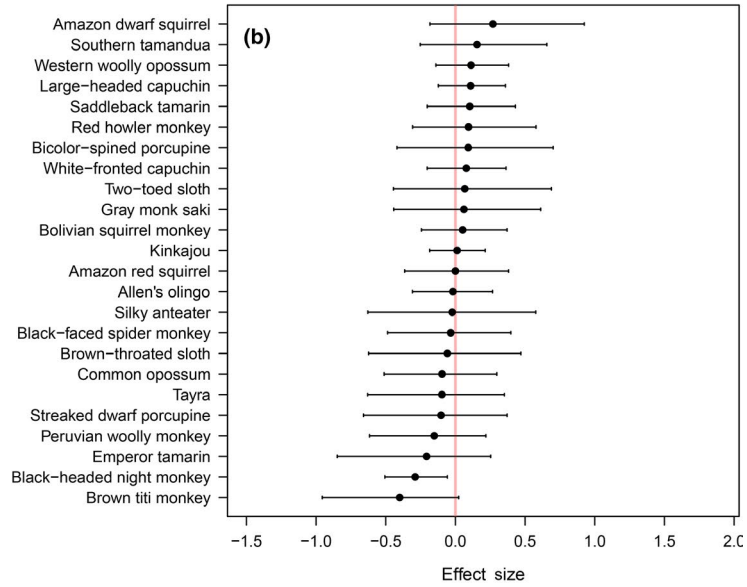
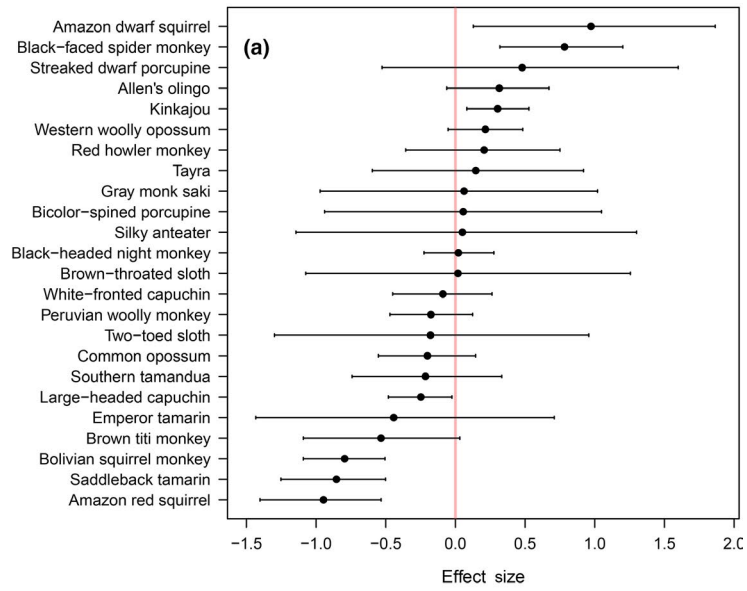
Further decomposition of the disturbance factor covariates to species-level responses highlights some general trends. For the arboreal strata, focal tree connectivity had a positive effect on all species in the community (Text S12) and was significant for 15 species (63%). Increasing canopy cover had a positive effect on all species, 12 of which were significant (50%). While we found no significant effect of community distance for single species, the three largest primate species (spider, woolly and howler monkeys) which are often targeted by hunters showed the greatest positive increase in occupancy with increasing distance from community. In the terrestrial community, tapir and paca both showed a small yet significant increase in occupancy in forest with greater canopy height (Text S13), a measure often associated with forest maturity. The only other significant effects at the species-level for the terrestrial community were of tapir, collared peccary and common opossum responding negatively to greater levels of recent forest loss.

Distance to the nearest navigable river influenced the occupancy probability of several species: increasing river proximity had a negative effect on the occupancy probability of Peruvian woolly monkey and a positive effect on smaller monkeys (titi, squirrel and night), Amazonian red-squirrels and kinkajous (Figure 7a). In the terrestrial community, collared peccary, puma and Brazilian rabbit occupancy probabilities increased near to navigable rivers (see Figure 7b).

4 | DISCUSSION

We present compelling evidence that arboreal mammal communities are more impacted by several key aspects of forest disturbance and degradation than their terrestrial counterparts, particularly species of a larger body size. Consequently, terrestrial camera trap assessments of mammalian responses to forest disturbance likely do not generalize to the arboreal community. While it is challenging to fully separate the roles of structural habitat change from hunter-mediated impacts without manipulative experiments or detailed hunting surveys, the sensitivity of arboreal communities appears to be largely driven by reduced opportunities for movement in the arboreal realm. The current bias in camera trap research studies to terrestrial mammals is likely to lead conservation practitioners and policymakers to underestimate the true biodiversity impacts of anthropogenic disturbance on medium to large rainforest mammals, ultimately resulting in conservation monitoring and management approaches that fail to maximize effective biodiversity recovery across strata. Camera trap case studies from other rainforest regions comparing mammal responses from both terrestrial and arboreal communities should be carried out to determine the generality of these patterns. We discuss the factors

FIGURE 3 The effect size of camera trap height (a) and tree connectivity (b) on mean detection frequency of arboreal mammals and the effect size of shrub density (c) on the mean detection frequency of terrestrial mammals. Where: black points represent mean β -estimates and black lines represent 95% credibility intervals



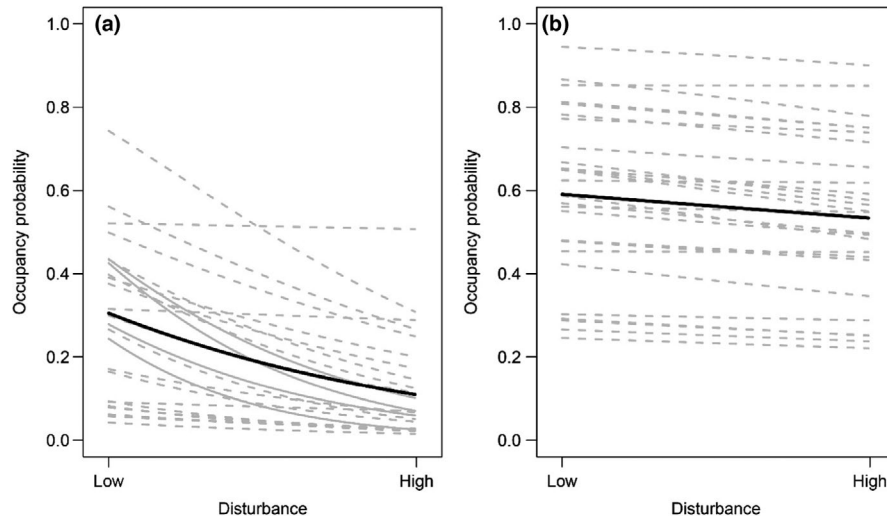


FIGURE 4 Change in occupancy probability with degree of structural forest disturbance for arboreal species (a) and terrestrial species (b): solid black lines represent the average community change in occupancy, grey lines represent individual species (solid lines grey lines = species that showed a significant change in occupancy in relation to forest disturbance, dashed lines = non-significant relationships)

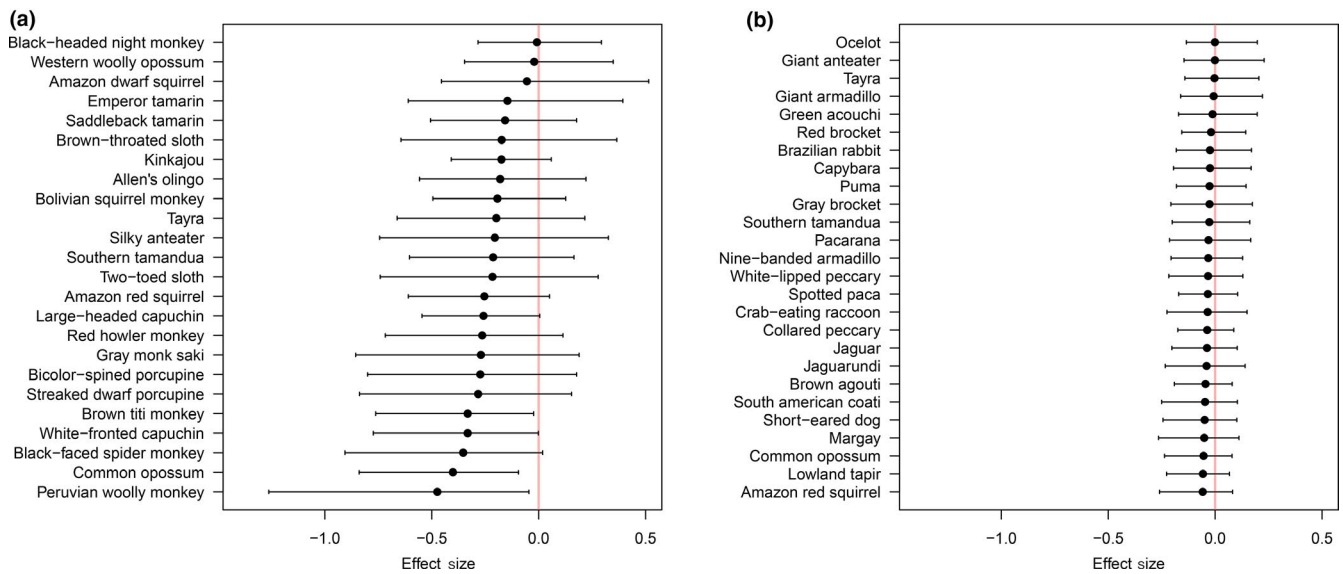


FIGURE 5 Species-specific effects of the forest disturbance factor on arboreal (a) and terrestrial (b) communities. Where: black points represent mean β -estimates and black lines represent 95% credibility intervals

driving our results and the implications for conservation management strategies of rainforests and the mammalian communities they support below.

Whereas the effects of rainforest disturbance were weakly negative on the occupancy of species within the terrestrial community, the arboreal community showed a much stronger response. All species responded negatively, while large-bodied species showed markedly reduced occupancy with increasing forest disturbance. The large-bodied species most sensitive to forest disturbance include the endangered *Atelines*, the Peruvian woolly monkey and black-faced spider monkey. This finding corroborates previous transect-based assessments that have also highlighted impacts of forest

disturbance on large-bodied diurnal primates (Carrillo et al., 2000; Lopes & Ferrari, 2008; Sampaio et al., 2010). *Ateline* primates in particular are known to be major dispersers of large-seeded hardwood trees that contribute disproportionately to the biomass of tropical forests (Peres et al., 2016). The loss of larger-bodied arboreal species and subsequent cascading breakdown in ecological interactions (Ceballos, Ehrlich, & Dirzo, 2017) poses a significant risk to carbon storage potential of degraded tropical forests (Bello et al., 2015). Furthermore, local communities are often dependent on the resources provided by large-seed dispersed plants and trees moved around by bigger species (Koné, Lambert, Refisch, & Bakayoko, 2008). Larger-bodied frugivores in addition to being capable of

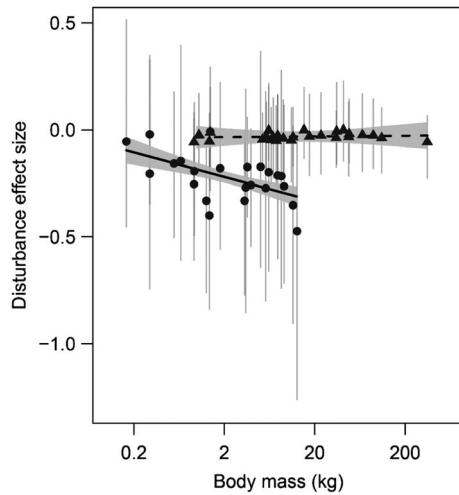


FIGURE 6 The relationship between log body mass and forest disturbance effect size for arboreal (circles) and terrestrial (triangles) mammals. Black lines represent the model predictions (solid = arboreal; dashed = terrestrial); grey lines represent the 95% credible intervals around the mean forest disturbance effect size; and the grey polygons represent the 95% confidence intervals of the regression on mean estimates

consuming larger fruits are also more likely to deposit seeds away from the parent plant and at greater distances (Wotton & Kelly, 2012).

Our work is consistent with previous evidence that suggests degradation impacts are particularly severe for species of ecological importance (Brodie et al., 2015); major seed dispersing tropical rainforest architects, and that the largest of these are most at risk (Fritz, Bininda-Emonds, & Purvis, 2009). Although it is known that large mammalian apex predators and large-bodied frugivores are often missing from highly degraded areas (Meyer et al., 2016), we suggest that large-bodied arboreal species are the most vulnerable group of all to forest degradation, even within large intact landscapes.

The reasons underpinning the increased sensitivity of larger arboreal species to structural disturbance likely involves a combination of species-specific traits (e.g., low reproductive rates, phylogeny, diet, home-range, etc.), hunter preferences, and their dependence on intact forest structure and food availability (Cardillo et al., 2005). Our arboreal camera results align with those of Bowler et al. (2017),

with distance from community having a positive effect on the occupancy of the three largest primates, and it is known that large-bodied arboreal species are targeted by hunters in the Manu region (Ohl-Schacherer et al., 2007). Teasing apart the relative contributions of structural habitat changes and hunting are difficult in observational studies as they typically co-vary in tropical systems; however, the community-level effect size of focal tree connectivity was substantially larger than distance to nearest community, a commonly used proxy for hunting pressure. This suggests that the physical structure of the forest is a major determinant of arboreal species occupancy probabilities, at least within this landscape. Focal tree connectivity had the largest effect size at the community level (twice as influential as any other individual factor), suggesting that forest areas with multiple connection routes to other trees, and lianas connecting the different vertical layers, generally had higher levels of occupancy of arboreal wildlife than lower connectivity areas. This importance of structural connectivity for arboreal wildlife has recently been showcased via the importance of natural canopy bridges over forest dissecting linear infrastructure (Gregory, Carrasco-Rueda, Alonso, Kolowski, & Deichmann, 2017; Gregory, Carrasco Rueda, Deichmann, Kolowski, & Alonso, 2014). This suggests that it is not enough for conservation management approaches to just target reductions in hunting pressure to restore ecological functions; they should also ensure that networks of larger trees capable of facilitating arboreal pathways and vertical space are conserved or, in already impacted areas, are regrown and reconnected as quickly as possible to support recovery of complete arboreal rainforest mammal communities.

Furthermore, if hunting was the major driving force behind the responses observed in the arboreal realm, why would the terrestrial mammal community be relatively insensitive to forest disturbance parameters, as many terrestrial species are also actively targeted by hunters (Ohl-Schacherer et al., 2007). We believe that this adds weight to the conclusion that the increased sensitivity to disturbance in the arboreal community detailed here is related to the effects of changes to the greater multi-dimensional area and structural complexity of the arboreal realm. It is important to note that distance to nearest community did not explain much variation in community-level occupancy in either strata, despite a wealth of literature detailing this key driver of mammal species composition

Covariate	Arboreal			Terrestrial		
	Mean	L95%	U95%	Mean	L95%	U95%
Disturbance factor	-0.226	-0.749	0.236	-0.031	-0.203	0.149
Connectivity	0.406	-0.064	0.909	-0.003	-0.178	0.181
Canopy cover	0.218	-0.042	0.493	-0.057	-0.196	0.085
Forest loss	-0.152	-0.773	0.350	-0.116	-0.302	0.047
Tree density	-0.097	-0.273	0.081	-0.019	-0.238	0.182
Canopy height	0.071	-0.280	0.405	0.079	-0.186	0.322
Community distance	-0.005	-0.344	0.317	-0.017	-0.219	0.176

TABLE 2 Summary of community-level occupancy parameters; these are then mean effects of each of the different covariates at the community level; for both arboreal and terrestrial communities

Note. Upper and lower 95% confidence intervals are shown.

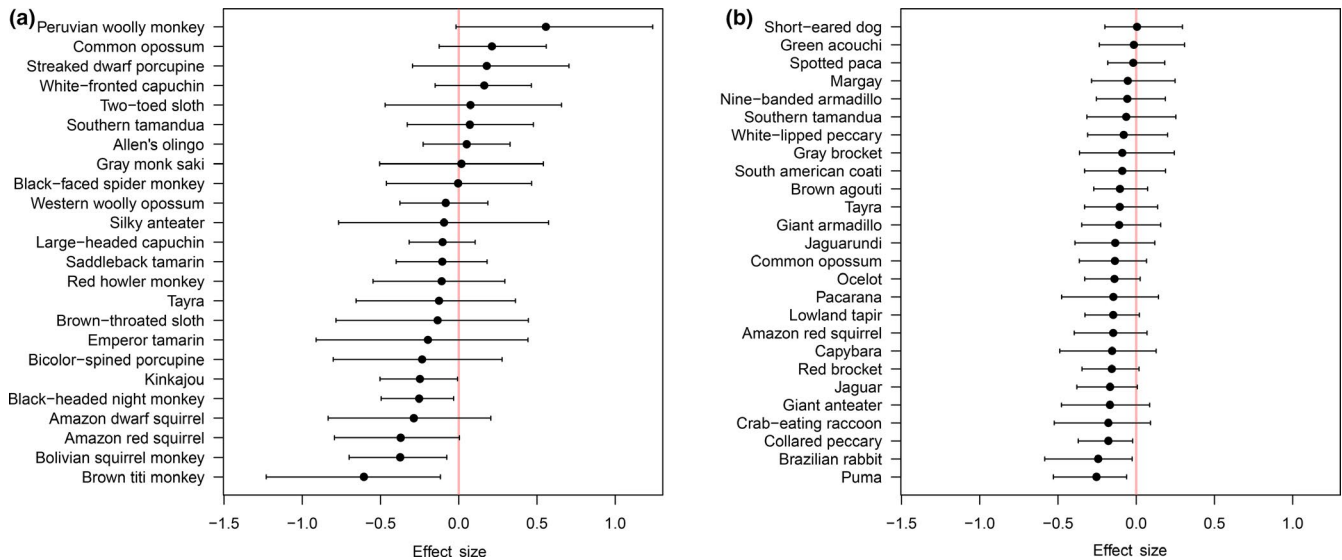


FIGURE 7 Species-specific effects of the distance to nearest navigable river on arboreal (a) and terrestrial (b) communities. Where: black points represent mean β -estimates and black lines represent 95% credibility intervals

(e.g., Oliveira et al., 2016; Roopsind et al., 2017). This could be due to our use of several locations that were completely protected from any hunting activity, likely weakening the overall effect of distance to community as a proxy for hunting, and all sites being well-connected to surrounding forests, therefore reducing potentially synergistic effects of hunting and fragmentation. Furthermore, given the reliance on river transport in the region, Euclidean distance to community may not be the best proxy of hunting pressure or accessibility. Interestingly, the effects of forest loss and canopy height were of a similar magnitude and direction in both strata, suggesting that some disturbance parameters do operate in similar fashion between vertical levels.

The occupancy probability of several species (both terrestrial and arboreal) were affected by the distance to the nearest navigable river. Where positive, this likely reflects species-specific affinities to riparian habitat types and food resource availability. Where negative, as is the case for the Peruvian woolly monkey, this is could also be due to increased hunting activity closer to river edges where canoe access for hunters is greatest. These reduced occupancies of larger, arboreal species close to communities or hunter access areas, likely facilitates competitive release of smaller non-hunted primates, such as squirrel, titi and night monkeys, that show an affinity to riparian habitat for key food resources (Rosin & Swamy, 2013).

Arboreal camera trapping remains in its infancy; thus, several caveats remain to be addressed in the future. Firstly, arboreal habitats are structurally more complex than the terrestrial strata, making the factors influencing the detection process in the arboreal and terrestrial realms different. For example, increasing camera deployment height strongly influences the detection probability of several species, both negatively (e.g., black-mantled tamarin) and positively (e.g., black-faced spider monkey); this is not surprising given previous work finding vertical stratification evidence in Neotropical forests (e.g., Grelle, 2003). This suggests that studies looking to characterize

community-level responses to disturbance need to deploy cameras at different heights to maximize the detection probabilities of all species, whereas studies looking to examine species-specific responses may want to target specific strata (e.g., upper canopy for spider monkeys and lower canopy for saddle-backed tamarins). Arboreal camera trapping could also be used to detect fine-scale changes in strata use in response to extrinsic factors such as habitat disturbance (e.g., Pozo-Montuy & Serio-Silva, 2007). Secondly, although we make comparisons defined by strata (arboreal vs. terrestrial), future work should explore if other species groupings, such as guild or phylogenetic relationships, share common responses between strata. Such information could be important for conservation strategies targeting specific at-risk groups of vertebrates or predicting the risk status of un-censused species. Finally, we suggest that further work should investigate the potential impacts of species that utilize both arboreal and terrestrial realms. For example, the common opossum showed a significant reduction in occupancy with increasing forest disturbance in the arboreal strata, despite being known by many as a particularly robust, generalist species. However, it is quite plausible a given species could show strata-specific response to habitat disturbance. For species which are not adept at jumping or swinging between features with poor connectivity, such as common opossums, their occupancy in the arboreal realm may be drastically affected by a lack of connectivity between trees and reduced canopy cover, and thus constrained to a more terrestrial lifestyle.

Although disturbance within Manu is active and increasing, the scale compared to other human-modified systems is relatively small. Consequently, large contiguous forest patches surround many of the communities and study sites that we surveyed. Whereas terrestrial species can move easily through these heterogeneous landscapes, larger-bodied arboreal species depend on structurally intact forest habitat for movement (with high connectivity and canopy cover; to escape hunters and reach appropriate foraging sites). These results

suggest that, where possible land-sparing rather than land-sharing should be prioritized as the most beneficial strategy to conserve complete intact community assemblages of rainforest mammals, which includes species using the canopy (Edwards et al., 2014) that require well-connected intact systems of arboreal highways. When land-sharing is the most relevant conservation solution, we recommend active rainforest conservation management strategies to focus on the preservation and regrowth of large, well-connected trees. Such features can act as hubs for the facilitation of movement, provide essential sleeping sites and food resources, and ensure preservation of the complete range of vertical levels to provide enough space for stratification of faunal communities. This is imperative, especially as vertical differences in wildlife communities are more marked than those that over horizontal gradients (Nakamura et al., 2017).

5 | CONCLUSIONS

To date, the majority of conservation assessments reporting weak or neutral impacts of anthropogenic disturbance on non-volant mammal communities have been based on data from terrestrial camera traps (Roopsind et al., 2017; Wearn et al., 2017) or have highlighted the threats to diurnal conspicuous primates from evidence gathered via ground-based human observations (Romero, Timm, Gerow, & McClearn, 2016). Our findings, along with those surveys made from the ground, suggest that larger-bodied arboreal rainforest mammals are more sensitive to structural forest degradation than smaller-bodied arboreal and terrestrial species. Camera trap conservation assessments that detect little impact to terrestrial species are likely under-estimating impacts of rainforest disturbance on the whole medium-large mammalian community. As such, terrestrial camera trap studies should either be paired with transects that are effective in detecting large diurnal primates, or also use arboreal cameras to detect nocturnal and cryptic species currently missed by both terrestrial and transect census techniques.

This greater sensitivity of arboreal communities to forest disturbance suggests there is a need to reprioritize various aspects of current rainforest conservation policy and management. Specifically, these results indicate that greater consideration should be given to land-sparing rather than land-sharing to ensure the protection of existing connected wilderness areas that can support complete three-dimensional community assemblages. Further, we recommend a shift to more active regeneration approaches that focus upon improving upper canopy structure and connectivity in existing degraded areas. Finally, we recommend that future studies aim to exploit novel research methods (such as arboreal camera traps) in order to fully understand the conservation implications of anthropogenic disturbance across all vertical strata and for rainforest conservation strategies in general. Importantly these efforts should be paired with assessments to quantify and disentangle the scale and intensity of hunting impacts from those of structural degradation through selective logging of

potentially key arboreal highway networks that are essential for arboreal mammal wildlife movements.

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DATA ACCESSIBILITY

Data underpinning the analyses will be available once accepted and available by Enlighten data storage service.

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BIOSKETCH

Andrew Whitworth has been working in tropical forests of Latin America for over 10 years, in Ecuador, Peru and currently, Costa Rica. The majority of this has been spent in the field and an increasing portion of this time within the rainforest canopy. In the year 1917 William Beebe stated that "... another continent of life remains to be discovered, not upon the Earth, but one to two hundred feet above it, extending over thousands of square miles." As a Royal Geographical Society, Scientific Exploration Society and National Geographic Society explorer, Andrew could not agree more, even 100 years on.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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