Landscape-level tree cover predicts species richness of large-bodied frugivorous birds in forest fragments

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ABSTRACT

Large-bodied frugivorous birds play an important role in dispersing large-sized seeds in Neotropical rain forests, thereby maintaining tree species richness and diversity. Conversion of contiguous forest land to forest fragments is thought to be driving population declines in large-bodied frugivores, but the mechanistic drivers of this decline remain poorly understood. To assess the importance of fragment-level versus local landscape attributes in influencing the species richness of large-bodied (>100 g) frugivorous birds, we surveyed 15 focal species in 22 forest fragments (2.7 to 33.6 ha, avg. = 16.0 ha) in northwest Ecuador in 2014. Fragment habitat variables included density of large trees, canopy openness and height, and fragment size; landscape variables included elevation and the proportion of tree cover within a 1 km radius of each fragment. At both the individual species level, and across the community of 12 species of avian frugivore we detected, there was higher richness and probability of presence in fragments with more tree cover on surrounding land. This tendency was particularly pronounced among some endangered species. These findings corroborate the idea that partially forested land surrounding fragments may effectively increase the suitable habitat for forest-dwelling frugivorous birds in fragmented landscapes. These results can help guide conservation priorities within fragmented landscapes, with particular reference to retaining trees and reforesting to attain high levels of tree cover in areas between forest patches.

Abstract in Spanish is available with online material.

Key words: BirdLife International Important Bird Area; Chocó biogeographic zone; Ecuador; IUCN Red List; seed dispersal.

Tʜᴇ ᴅᴇɢʀᴇᴇ ᴛᴏ ᴡʜɪᴄʜ ᴘᴀᴛᴄʜ ᴠᴇʀsᴜs ʟᴀɴᴅsᴄᴀᴘᴇ ᴄʜᴀʀᴀᴄᴛᴇʀɪsᴛɪᴄs ɪɴꜰʟᴜᴇɴᴄᴇ sᴘᴇᴄɪᴇs ʀɪᴄʜɴᴇss ᴀɴᴅ ᴅɪᴠᴇʀsɪᴛʏ represents a long-standing question in tropical ecology and conservation biology (Thornton *et al.* 2011). In the case of forest fragmentation, research has historically focused on patch-level effects (*e.g.*, fragment size). However, a growing body of research shows that characteristics of the surrounding landscape, which includes 'matrix' habitat as well as nearby forest fragments, can have a strong impact on richness and community composition in fragments (Cardoso da Silva *et al.* 1996, Levey *et al.* 2005, Prevedello & Vieira 2010). This has led to the hypothesis that 'habitat amount' at the local landscape level may be a better predictor of species richness in fragmented landscapes than patch-level characteristics (Fahrig 2013, but see Hanski 2015). Distinguishing between these alternatives is important because species management and conservation requires knowledge of mechanistic drivers of frugivore decline in fragmented landscapes. If patch-level fragment properties dominate, then protecting large, high-quality individual patches of forest may maximize conservation success. However, if local landscape-level processes are more important,

then conserving habitat, regardless of spatial configuration, may be the most effective conservation strategy.

Resolving the impacts of local versus landscape factors on species richness is particularly important for large-bodied frugivorous birds, a guild sensitive to habitat loss and forest fragmentation (Ribon *et al.* 2003, Uezu *et al.* 2005, Ribeiro da Silva *et al.* 2015). Endemic species in the tropics, with narrow ranges, are often at an even greater risk of extinction (Ribon *et al.* 2003, Uezu *et al.* 2005, BirdLife International 2016). Large frugivores consume the fruits of many tree species and distribute their seeds, thereby promoting seedling recruitment and tree species richness and diversity (Wunderle 1997, Almeida-Neto *et al.* 2008, Ribeiro da Silva *et al.* 2015). This relationship is particularly important for large-seeded plants that rely on larger dispersers for effective dispersal (Galetti *et al.* 2000, Holbrook & Smith 2000). Consequently, understanding the relative impact of environmental variables at patch versus landscape scales on frugivore occurrence and richness in fragmented landscapes represents a priority for tropical ecology.

Habitat characteristics within fragments that are likely to influence avian frugivore species richness include canopy height and openness, density of large trees, and fragment size (Trzcinski *et al.* 1999, Uezu *et al.* 2005), while relevant landscape variables

include surrounding tree cover or elevation (Chaves-Campos 2004, Levey *et al.* 2005). At the patch scale, smaller fragments may lack adequate resources to support frugivorous birds (Rolstad 1991), thereby increasing the probability of local extirpation (Marini 2001, Durães *et al.* 2013). In forests with relatively open canopies, light infiltration can stimulate plant growth and increase habitat complexity and food availability (Hubbell *et al.* 1999, Durães *et al.* 2013, Peters *et al.* 2016), whereas more extensive disturbance can negatively impact tree density and height (Aleixo 1999, Gray *et al.* 2007).

Among landscape variables, elevation explains patterns of frugivorous bird richness among fragments in some cases (Almeida-Neto *et al.* 2008), but not others (*e.g.*, Galetti *et al.* 2000, Chaves-Campos 2004). Characteristics of the landscape surrounding fragments may also influence occurrence patterns (Loiselle & Blake 1993, Prevedello & Vieira 2010). For example, when surrounding areas consist of pastures or agricultural lands with little to no tree cover, forest-associated bird species often avoid these areas (Laurance *et al.* 2002). In contrast, partial tree cover, small forest patches, or scattered trees in the areas surrounding fragments may help support bird species in fragments (Cardoso da Silva *et al.* 1996) by facilitating inter-fragment travel, providing refuge, and offering food resources (Cardoso da Silva & Tabarelli 2000, Ewers & Didham 2006). As few studies have concurrently addressed the impact of these fine-scale versus landscape-scale environmental factors on large-bodied frugivorous birds, there is a need to better understand their relative impact on species richness of this ecologically important guild.

To address this need, we evaluated the relative importance of patch-level versus local landscape attributes in influencing the occurrence and richness of large-bodied frugivorous birds in forest fragments in northwest Ecuador. Many of the 15 avian frugivores we evaluated for presence and species richness are threatened (Table 1; Carrasco *et al.* 2013, BirdLife International 2016). We expected occurrence and richness in fragments to be influenced by both patch and landscape variables, with the prediction that occurrence and richness would be lower in smaller fragments with reduced surrounding tree cover. We also reasoned that these effects would be more pronounced for threatened species. Finally, to improve sampling design, we modeled how survey characteristics (*e.g.*, time of day) are associated with the probability of detecting frugivore species.

METHODS

STUDY AREA.—From August to December 2014, we conducted transect surveys in 22 forest fragments in and around the Mache-Chindul Ecological Reserve (REMACH), northwest Ecuador (0°47′N, 79°78′W; Fig. S1). REMACH is a BirdLife International Important Bird Area (BirdLife International 2016) and is part of the Chocó biogeographic zone, a globally recognized conservation priority (Myers *et al.* 2000). The fragments we surveyed are remnants of primary tropical rain forest that has experienced extensive deforestation from the 1960s to present (Dodson & Gentry 1991). Fragments ranged in size from 2.67 to 33.62 ha

(avg. = 15.97 ± SD 9.87 ha; Table S1) and in elevation from 135 to 592 m asl (avg. = 345 ± 157 m asl, Table S1). Lands surrounding fragments were typically comprised of a mixture of cattle pastures, small-scale plantations (*e.g.*, cacao [*Theobroma cacao*], teak [*Tectona grandis*], bananas [*Musa* spp.]), and partially forested areas. Our 5-mo sampling period corresponds with the regional dry season when fruit production for many tree species is relatively high (J. Karubian, unpubl. data). We did not measure fruit availability in this study, and it is possible that differences in fruit abundance between fragments may have skewed our results. However, we consider this unlikely because there was no relationship between any of the environmental variables we measured, which indicates that there was no systematic bias in the relationship between fruit availability and our response variables.

BIRD SURVEYS.—Surveys were conducted individually by either J.O. or L.B. along 500 m transects that started at the forest edge and ran toward the center of each fragment. Transects were linear in larger fragments, but in smaller fragments that could not accommodate a single, linear transect, we angled transects back and forth or divided the transect into smaller, parallel sections separated by >50 m to achieve a total transect distance of 500 m. Observers walked the length of the transect at a steady pace and recorded the presence of 15 'focal' species of large-bodied (>100 g) and forest-dependent (BirdLife International 2016) frugivorous birds known to inhabit our study area (Table 1; Carrasco *et al.* 2013). We include psittacids because some parrots are occasional dispersers of viable seeds (Blanco *et al.* 2016), although we found qualitatively similar results when excluding psittacids from analyses. Two thirds of our focal species are threatened at the national or global level, or both, and approximately one-half are endemics (BirdLife International 2016; Table 1).

Within each fragment, six surveys were conducted during mornings (range of start times: 0606 h–1010 h; mean ± SD: 0747 h ± 50 min, Table S1) and afternoons (1205 h–1730 h; 15:17 ± 63 min, Table S1), for a total of 12 surveys per fragment within a 20-d period. We generally conducted two surveys consecutively (*i.e.*, one walking from fragment edge to center, and the second survey returning back along the same transect), waiting approximately 30 min between the end of the first survey and the start of the second. We avoided surveying the same fragment in both the morning and afternoon within the same day, and we randomized the survey order across a subset of five fragments. A single survey lasted 48 min on average (SD ± 14 min; range = 28 to 99 min, Table S1). If focal species were heard or sighted within the fragment boundary, we noted the species as present in the fragment. During surveys, we also recorded rain, fog, and wind intensity as none or moderate; surveys were not conducted during extreme weather.

PATCH-LEVEL VARIABLES.—Fragment attributes included tree density, canopy openness, canopy height, and fragment size. We measured density of large trees (defined as >50 cm diameter at breast height; dbh), as well as canopy openness and height, in each of 100 contiguous 5 × 5 m plots along the 500 m transect. We

TABLE 1. *Species information for focal frugivore species surveyed in 22 forest fragments in northwest Ecuador in 2014 as part of this study. Ecuadorian and international IUCN conservation and endemic status to either the Chocó or Tumbesian regions are from BirdLife International (2016). Detections refer to the number of surveys in which the species was seen or heard at least once, during 264 total surveys, and occurrence is the probability of a species being detected in a fragment. Detection probability is the probability of detecting the species during one average survey, if the species is truly present at the site (95% credible interval available in Appendix S4a).*

Common name	Scientific name	Ecuador status	IUCN status	Endemic	Mass (g)	Detections	Occurrence	Detection probability
Red-lored Amazon	*Amazona autumnalis*	EN	LC	No	416	0	0.00	–
Mealy Amazon	*Amazona farinosa*	LC	NT	No	626	28	0.59	0.13
Chestnut-fronted Macaw	*Ara severus*	LC	LC	No	343	15	0.50	0.06
Crimson-rumped Toucanet	*Aulacorhynchus haematopygus*	LC	LC	No	171	10	0.27	0.05
Long-wattled Umbrellabird	*Cephalopterus penduliger*	EN	VU	Yes	534	3	0.14	0.02
Great Curassow	*Crax rubra*	EN	VU	No	4133	0	0.00	–
Rufous-headed Chachalaca	*Ortalis erythroptera*	VU	VU	Yes	632	18	0.50	0.08
Crested Guan	*Penelope purpurascens*	EN	LC	No	2060	0	0.00	–
Bronze-winged Parrot	*Pionus chalcopterus*	VU	LC	No	210	16	0.41	0.06
Blue-headed Parrot	*Pionus menstruus*	LC	LC	No	251	2	0.09	0.02
Red-masked Parakeet	*Psittacara erythrogenys*	VU	NT	Yes	151	13	0.46	0.06
Pale-mandibled Araçari	*Pteroglossus erythropygius*	VU	LC	Yes	278	54	0.91	0.19
Purple-throated Fruitcrow	*Querula purpurata*	LC	LC	No	110	48	0.55	0.28
Choco Toucan	*Ramphastos brevis*	VU	LC	Yes	412	84	1.00	0.29
Chestnut-mandibled Toucan	*Ramphastos swainsonii*	VU	NT	No	665	62	0.86	0.26

Ecuador status (LC, Least Concern; VU, Vulnerable; EN, Endangered); IUCN status (LC, Least Concern; NT, Near Threatened; VU, Vulnerable).

estimated canopy openness using the method of Brown *et al.* (2000) that assigns a size index (1–25) to the largest canopy gap over each 5 × 5 m plot; larger values indicate larger canopy gaps. Canopy height was measured as the height in meters of the tallest tree over each plot using a Simmons digital rangefinder. Within each plot, we also counted the number of large trees, which along with canopy openness and canopy height, is a useful indicator of forest quality in our study area (Durães *et al.* 2013). Forest structure measurements from each plot were averaged across each transect to provide a single mean value for each fragment. Finally, we estimated the fragment size in hectares using manually mapped borders of each fragment in QGIS (QGIS Development Team 2012).

LOCAL LANDSCAPE VARIABLES.—Landscape variables included elevation and proportion of tree cover in the nearby lands surrounding each fragment. More specifically, surrounding tree cover in this study represents the total available forest habitat in a 1 km radius, which could include small clusters of trees, portions of surrounding forest fragments, tree plantations or some combination thereof. Due to limitations of remote sensing imagery, we were not able to distinguish among these land-use types. To quantify the proportion of surrounding tree cover in a 1 km radius surrounding each fragment, we used the Global Forest Watch dataset (Hansen *et al.* 2013), which includes datasets of tree canopy cover for the year 2000 and forest cover loss between 2000 and 2013, following the methods of Browne and Karubian (2016). As there is no contemporary map of tree cover available in the Global Forest Watch dataset, we began with the

map of tree cover for the year 2000. We classified 30 × 30 m grid cells across our study area as either forest or non-forest based on whether there was >95 percent tree canopy cover in the year 2000 (Hansen *et al.* 2013). We then produced a contemporary tree cover map of our study area by converting grid cells to non-forest if the cell had forest loss between 2000 and 2013 (Hansen *et al.* 2013), which generally properly assigned areas known to be cleared for agriculture 3–5 yr ago and areas surrounding forest boundaries as non-forest (Browne & Karubian 2016). Tree cover in a 1 km radius around fragments ranged from 38 to 77 percent (Table S1). Elevation was taken with a handheld GPS in each 5 × 5 m plot along transects, and averaged to obtain a single value per fragment.

SPECIES RICHNESS AND COMMUNITY COMPOSITION ANALYSIS.—To assess the relative importance of our patch-level versus local landscape attributes in influencing the richness of large-bodied frugivorous birds in forest fragments, we used multiple linear regression with a Gaussian error distribution. We calculated species richness in each fragment as the sum of all species observed at least once. We started with a full model that contained species richness as the response variable and all six predictor variables: tree cover surrounding fragments, fragment area, density of large trees, elevation, canopy height, and canopy openness. We ensured the model met all linear model assumptions using the 'gvlma' package (Pena & Slate 2014) in R (R Core Team 2016). Next, using an all-subset model averaging approach, we created models for all possible combinations of predictor variables, eliminating models with little or no support (*i.e.*, $\Delta AICc > 10$ compared to

the top-ranked model; Burnham & Anderson 2002). We calculated model-averaged coefficients across remaining models by averaging coefficient estimates for each predictor for only the models in which they are present (i.e., conditional model averaging; Burnham & Anderson 2002, Symonds & Moussalli 2011). Model averaging was done using the 'MuMIn' package (Bartón 2016) in R 3.3.1 (R Core Team 2016). To test the relationship between frugivore community composition and the six predictor variables, we used multiple regression on distance matrices (Legendre et al. 1994, Lichstein 2007), assessing significance via permutation (N = 9999) in the 'ecodist' R package (Goslee & Urban 2007). We used the Sørensen index to calculate frugivore community similarity between forest fragments and Euclidian distances to calculate environmental distance matrices.

OCCURRENCE MODELING FRAMEWORK.—To assess the relationship between patch-level and local landscape attributes on the occurrence (i.e., the probability of being detected in a fragment) of individual frugivore species, we used a multi-species, hierarchical logistic regression. We modeled occurrence as a linear combination of our six predictor variables (above). Parameter estimates at the species level were linked to the community level (e.g., across all frugivores in the study) via a hyper-parameter, which assumes that each species-level parameter estimate comes from a normal distribution with a community-level mean and standard deviation (model formulation detailed in Appendix S1, Zipkin et al. 2009, 2010, Burton et al. 2012). This is the same as treating species-level parameters as random effects. The advantage of this approach is that the sharing of information across species improves precision on parameter estimates, especially for rare species that 'borrow strength' from more common species (Appendix S2A vs. S2C, Zipkin et al. 2009, Iknayan et al. 2014). Incorporating community-level hyper-parameter in our model allowed us assess strength and direction of covariate effects at the community level; without the hyper-parameter, the model was unable to reliably estimate parameters for many species (Appendix S2A vs. S2c).

Initially, we attempted to use a multi-species occupancy model to estimate probability of occurrence, while accounting for imperfect detection, where a species is not detected but actually present at a site (Royle & Dorazio 2008, Zipkin et al. 2009, Burton et al. 2012). However, due to numerous species with low numbers of detections and low detection probability, accounting for imperfect detection caused large uncertainty in parameter estimates with many parameters; in particular, the estimated effect of elevation showing extreme sensitivity to prior distributions and posterior distributions concentrating toward prior distribution boundaries (Zipkin et al. 2009, Appendix S2A vs. S2B). This inability to account for imperfect detection in our occurrence models, which has the effect of conservatively underestimating the true occurrence of frugivore species in fragments, suggests that results from this aspect of the study should be interpreted considering this known bias. We included these results under the rationale that having conservative occurrence estimates for rare species is better than having no data at all (see Banks-Leite et al.

2014), especially given the fact that many of these species are threatened with extinction and little is known about their conservation status in forest fragments.

To assess the relative importance of each covariate on community-level occurrence, we estimated a latent Bernoulli inclusion parameter for each covariate (model formulation detailed in Appendix S1, Dellaportas et al. 2002, Burton et al. 2012, Mutshinda et al. 2013) that will tend toward 1 if there is evidence that the parameter is important for having an effect (regardless of the direction) on the occurrence of all frugivore species in the community, and toward 0 if it is unimportant. This is a useful metric because species may have diverging responses to the same covariate and the inclusion parameter allows the estimation of the overall importance, regardless of the direction of the effect. Following Mutshinda et al. (2013), a posterior inclusion probability of ≥0.75 signals an important predictor, while values ≤0.25 suggest an unimportant predictor.

DETECTION PROBABILITY MODELING FRAMEWORK.—In an effort to improve future sampling methodology, we modeled detection probability (i.e., probability of detecting a species during a survey at a site where the species is present) for each species to determine factors that maximize detection probability and thus the efficiency of sampling. As mentioned above, we did not integrate our estimates of detection probability with occurrence estimates in our main analyses, as would be done in a traditional occupancy model; these results are available in Appendix S2b and S2d. Following a similar framework as the occurrence model (a multi-species, hierarchical logistic regression), we modeled detection probability as a linear combination of the following variables: survey duration, survey start time, and binary categories of fog, wind, and rain conditions (Table S1). As in the occurrence model, species-level effects were linked to community-level effects via hyper-parameters (Appendix S1), and we assessed the importance of each covariate on detection probability using inclusion parameters. To assess the certainty that a species not detected was absent in a fragment, we calculated P^*, which is defined as the probability of detecting a species during n surveys with detection probability p, following the formula $P^* = 1 - (1 - p)^n$ (Kéry 2002, Kéry & Schaub 2012).

MODEL ANALYSIS.—We fit the occurrence and detection models to our data using a Bayesian framework in JAGS (Plummer 2003). A total of 9000 samples from posterior distributions of each parameter were taken from three Markov Chain Monte Carlo (MCMC) chains that ran for 300,000 iterations after a burn-in of 15,000 iterations, thinning samples every 100 iterations. We used vaguely non-informative priors for all parameters and hyper-parameters (model code available in Appendix S3). We assessed chain convergence by visual assessment of chain traceplots and ensuring that the Gelman–Ruben statistic ('Rhat') was <1.1 for all parameters (Kéry & Schaub 2012). Prior to all analyses (including the linear regression on species richness), we checked for collinearity among explanatory variables, and VIF (variance inflation factor) values were all <2.4, below the VIF = 3 threshold

suggested by Zuur *et al.* (2010). Pairwise correlations between explanatory variables were all |R| < 0.60 (Table S2). We then mean centered and scaled covariates by dividing by one standard deviation to aid in comparison of regression coefficients and model convergence (Schielzeth 2010). The range, mean, and standard deviation of covariates are in Table S1. To assess how occurrence estimates varied by species conservation status, we tested for differences in average occurrence among IUCN and Ecuadorian conservation categories and endemic and non-endemic species with a non-parametric Kruskal–Wallis test.

RESULTS

SPECIES RICHNESS AND COMMUNITY COMPOSITION.—Across 22 fragments, we observed 12 of the 15 total focal frugivore species (range: 3–10 species per fragment, mean ± SD: 6.3 ± 1.7; Table 1). Species richness had a strong positive relationship with surrounding tree cover (Fig. 1), which was the strongest predictor

of all variables assessed (Table 2). In contrast, fragment area, the density of large trees, elevation, canopy height, and openness were weakly and not significantly related to richness (Fig. 1; Table 2). The multiple regression on distance matrices explained a significant amount of variation in frugivore community similarity (R^2 = 0.26, P < 0.001). Fragments that were similar in elevation, forest cover, and canopy openness had a more similar frugivore community than would be expected by chance (P < 0.05 for all, Fig. S2).

OCCURRENCE.—Occurrence among the 22 sampled fragments ranged widely across species (0.00–1.00, Table 1). Notably, the Chocó Toucan (*Ramphastos brevis*), Pale-mandibled Araçari (*Pteroglossus erythropygius*), and Chestnut-mandibled Toucan (*Ramphastos swainsonii*) were found in >85 percent of fragments (Table 1). In contrast, the Blue-headed Parrot (*Pionus menstruus*) and Long-wattled Umbrellabird (*Cephalopterus penduliger*) were found in <15 percent of fragments (Table 1). Three of our 15
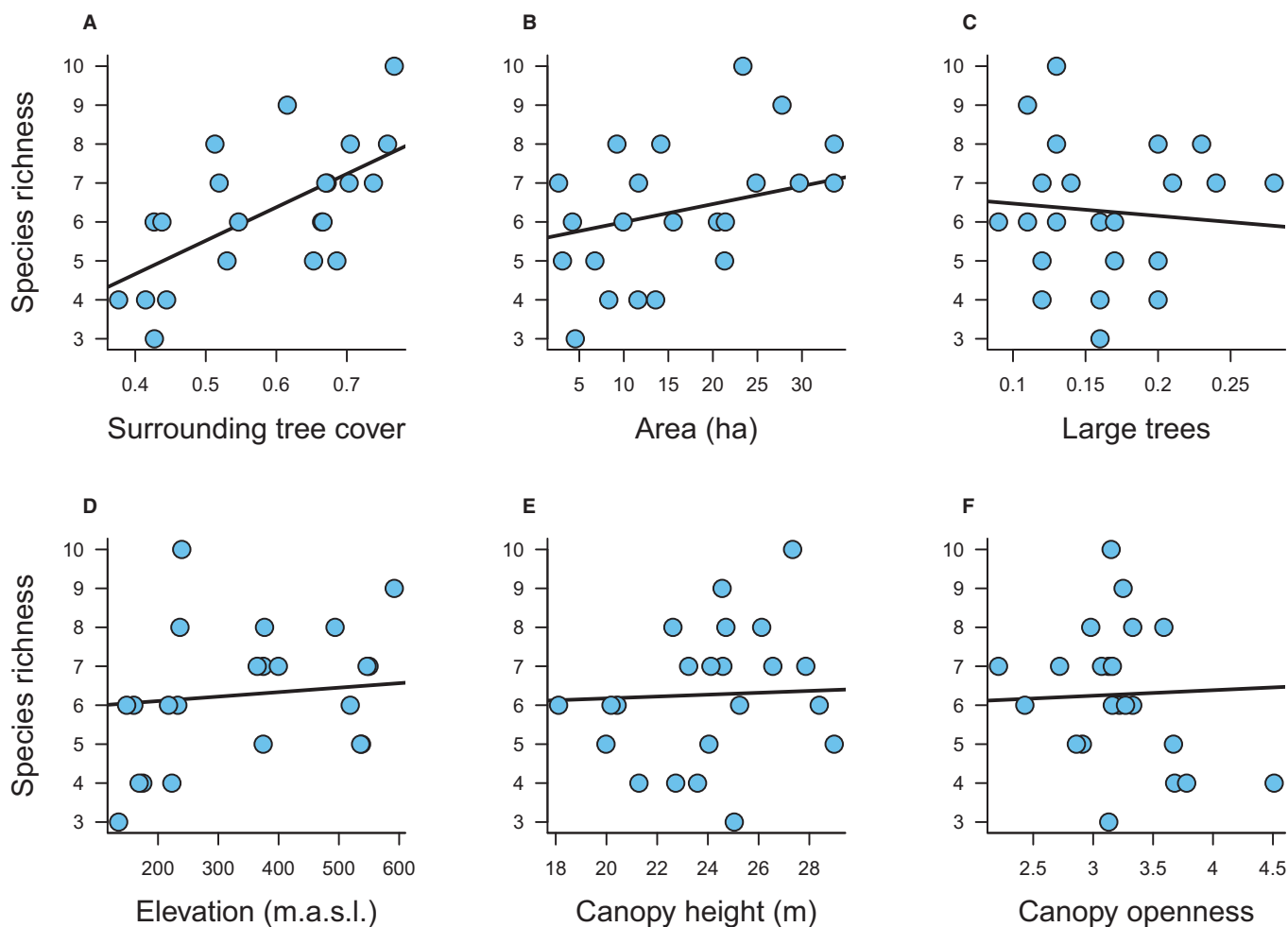

FIGURE 1. Frugivore species richness in 22 forest fragments in northwest Ecuador in relation to (A) proportion of surrounding tree cover in 1 km radius, (B) fragment area (ha), (C) density of large trees (ind/25 m²), (D) elevation (m.a.s.l.), (E) canopy height (m), and (F) canopy openness. Circles show observed number of species in each fragment and solid black line shows model-averaged predictions (Table 2).

focal species (20%) were never detected in study fragments: the Great Curassow (*Crax rubra*), Crested Guan (*Penelope purpurascens*), and Red-lored Amazon (*Amazona autumnalis*) (Table 1).

Frugivores considered Endangered (EN) in Ecuador had significantly lower mean occurrence than 'Vulnerable' (VU) or 'Least Concern' (LC) species (χ^2 = 8.5, df = 2, *P* = 0.01, Fig. 2). Frugivores in the IUCN VU category had lower average occurrence than frugivores in the LC and 'Near Threatened' (NT) categories, but this difference was not statistically significant (χ^2 = 2.3, df = 2, *P* = 0.31, Fig. 2). There was no difference in mean occurrence between endemic and non-endemic species (χ^2 = 2.0, df = 1, *P* = 0.16, Fig. 2).

TABLE 2. *Standardized model-averaged coefficients of multiple linear regression of frugivore species richness on habitat and fragment characteristics in 22 forest fragments in northwest Ecuador. Shown are the parameter estimates, standard error (SE), P value, and variable importance (i.e., the sum of the Akaike weights over models including the covariate) averaged across N = 37 models with a ΔAICc < 10 compared to the top-ranked model. P values < 0.05 are shown in bold. Complete details on individual models are available in Table S3 and the mean and standard deviation (SD) of covariates for back-transforming standardized coefficients are shown in Table S1.*

	Estimate	SE	*P* value	Importance
Intercept	6.273	0.298	<0.001	–
Forest cover in 1 km radius	**1.084**	**0.355**	**0.004**	**0.931**
Area (ha)	0.457	0.426	0.309	0.286
Large trees (ind/25 m^2)	0.180	0.364	0.642	0.181
Elevation (m.a.s.l.)	−0.156	0.319	0.648	0.178
Canopy height (m)	0.068	0.382	0.868	0.162
Canopy openness	0.070	0.346	0.850	0.161

At the community level, both surrounding tree cover and elevation were important predictors of frugivore occurrence, with an inclusion probability of ≥0.92 for both (Table 3). There was only weak support for fragment area, density of large trees, canopy height, and canopy openness being predictors of occurrence across the community (Table 3). At the community level, the mean response to surrounding tree cover was consistently positive, with occurrence probability increasing with increasing tree cover around the fragment (Table 3). The mean response to elevation was lower and standard deviation higher than the response to tree cover, indicating variation in species-specific responses to elevation (Table 3).

At the species level, all species showed a positive relationship between mean probability of presence and tree cover, consistent with community-level effects (Appendix S2A). In contrast, and consistent with community-level effects, there was a variable response between species presence and elevation (Appendix S2A). The Rufous-headed Chachalaca (*Ortalis erythroptera*) showed a significant negative relationship with elevation, while the Long-wattled Umbrellabird and Mealy Amazon (*Amazona farinosa*) showed the strongest, although non-significant, positive relationships (Appendix S2a). No species had significant relationships between probability of occurrence and fragment area, canopy height, density of large trees, or canopy openness (Appendix S2A), consistent with low inclusion probabilities of these covariates in community-level effects (Table 3).

DETECTION.—Because of very low detection probabilities (<0.30, Table 1), the *P** analysis revealed that 12 surveys were not sufficient to obtain a high level of certainty of detecting some species if they were present (Fig. S3). The Chocó Toucan, Chestnut-mandibled Toucan, and Purple-throated Fruitcrow (*Querula purpurata*)
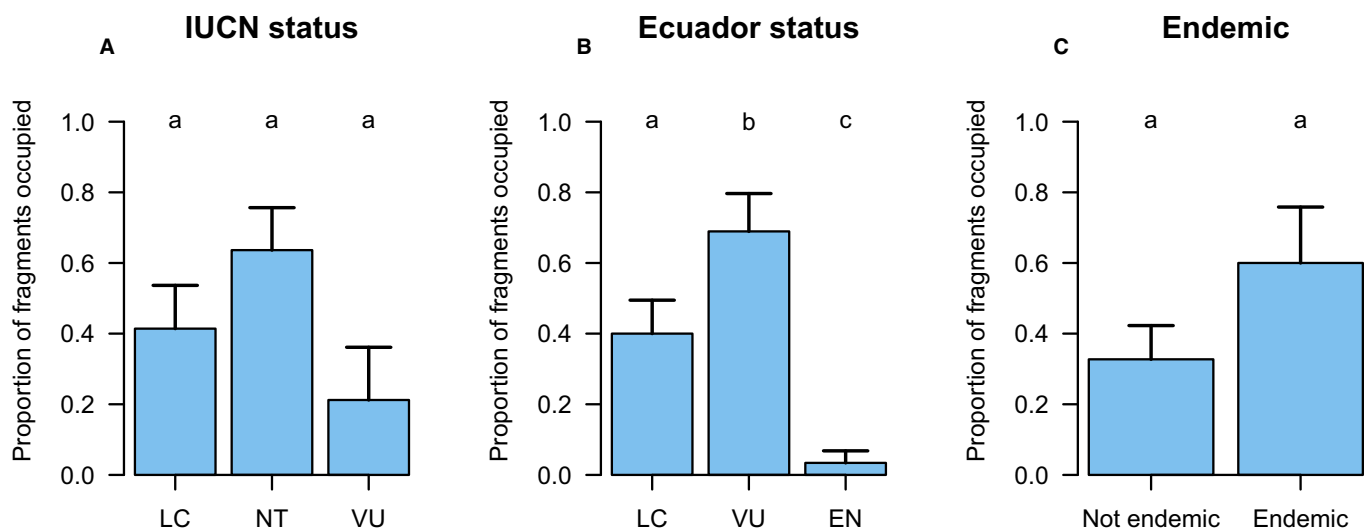

FIGURE 2. Proportion of 22 forest fragments (mean + standard error), where large-bodied frugivores separated by (A) IUCN status, (B) Ecuador conservation status, and (C) endemism status were detected at least once. Ecuadorian and international IUCN conservation and endemic status to either the Chocó or Tumbesian regions are from BirdLife International (2016). Small letters indicate significant differences among categories. IUCN status (LC, Least Concern; NT, Near Threatened; VU, Vulnerable); Ecuador status (LC, Least Concern; VU, Vulnerable; EN, Endangered).

TABLE 3. *Community-level inclusion probability and parameter estimates on frugivore occurrence and detection. Shown is the inclusion probability, a metric of variable importance, with values closer to 1 suggesting stronger support for the covariate being an important predictor of either occurrence or detection across the 12 detected species in the frugivore community, while values closer to 0 suggest the opposite (see Methods). The inclusion parameter estimates the importance of a covariate, regardless of the direction of the effect. Inclusion estimates ≥0.75 are shown in bold. Also provided are the community-level posterior mean, standard deviation (SD), and 95% credible intervals (CI) associated with the parameter effect. The posterior mean provides the magnitude and direction of the response of the frugivore community as a whole to the covariate. Species-level parameter estimates for each covariate are available in Appendix S2A.*

	Inclusion probability	Mean	SD	95% CI
Occurrence model				
Tree cover in 1 km radius	**0.92**	**0.54**	**0.30**	**−0.03, 1.14**
Area	0.12	0.24	0.24	−0.21, 0.73
Large trees	0.03	−0.13	0.20	−0.50, 0.26
Elevation	**0.93**	**0.17**	**0.40**	**−0.62, 0.97**
Canopy height	0.04	0.05	0.21	−0.35, 0.48
Canopy openness	0.16	0.05	0.27	−0.50, 0.57
Detection model				
Start time	**0.91**	**−0.23**	**0.10**	**−0.42, −0.03**
Survey duration	**0.92**	**0.12**	**0.10**	**−0.09, 0.33**
Rain	**0.76**	**−0.26**	**0.09**	**−0.43, −0.06**
Wind	**0.94**	**−0.11**	**0.14**	**−0.40, 0.16**
Fog	0.17	0.13	0.10	−0.07, 0.34

had the highest probabilities of detection (Table 1), and 8–10 surveys were sufficient to achieve high certainty (95%) of detecting the species at least once when it was present (Fig. S3).

At the community level, frugivores were more likely to be detected during surveys with earlier start times and clear conditions (Table 3). The effects of survey duration and wind conditions were weaker and less consistent, indicated by mean posterior estimates closer to 0 and the 95% CIs overlapping with 0 (Table 3). Species-level responses to survey conditions are available in Appendix S4A. Most detections across species were visual (69%), while 31 percent of detections were auditory. Incorporating imperfect detection in occurrence models produced qualitatively similar species-level parameter estimates for each covariate (*e.g.*, Appendix S2A vs. S2B).

DISCUSSION

Among 15 species of large-bodied frugivorous bird that we sampled in northwest Ecuadorian forest fragments, species richness, community composition, and occurrence were all significantly and positively associated with the proportion of tree cover surrounding each fragment. As such, this study suggests that richness of this guild may respond more to this regional landscape

factor than to within-fragment attributes such as fragment area or forest structure.

LANDSCAPE ATTRIBUTES.—Tree cover within a 1 km radius of study fragments may promote species richness among frugivorous birds by providing additional fruiting tree resources, as many fruit-eating birds consume fruit in isolated trees outside of fragments (Uezu *et al.* 2005, but see Laurance *et al.* 2002). For instance, in Brazil only 3 of 47 forest-dependent, frugivorous bird species were observed in pastures without trees, yet 18 of the same 47 species were observed in fields with scattered fruiting shrubs and trees (Cardoso da Silva *et al.* 1996). Similarly, for other Neotropical avifauna, such as nocturnal birds, neighboring forested landscapes may promote increased species diversity and richness within fragments (Sberze *et al.* 2010).

Additionally, the presence of trees across the landscape may facilitate animal movement between otherwise isolated fragments (Pizo & dos Santos 2011, McConkey *et al.* 2012). Land surrounding our study fragments held 38 to 77 percent of tree cover, and this habitat may have supported movement into, and out of, fragments, including fragments likely too small to support resident populations. Our fragments averaged only 16 ha in size, and all 12 focal species we detected were present in fragments smaller than 10 ha; seven species were observed in our smallest fragment of 2.7 ha. In contrast, forest fragments smaller than 50 ha surrounded by a non-forested landscape commonly lack large-bodied frugivorous birds (Uezu *et al.* 2005, Ribeiro da Silva *et al.* 2015). Although we did not assess movement, it is probable that many of the birds we detected utilized a wider network of habitat beyond the fragment where observed (Chaves-Campos 2004, Karubian *et al.* 2012, Karubian & Durães 2014). All birds we studied are forest-dependent species (BirdLife International 2016), and tree cover outside of fragments accounted for the increase of one additional frugivore species per 13 percent additional surrounding tree cover.

Tree cover within surrounding local landscape, be it comprised of individual trees, scattered clusters, or even the edge of a nearby fragment, provides an additional perspective on the concept of 'travel corridors' (Levey *et al.* 2005). In our study area, we suggest that additional tree habitat may serve as 'stepping stones' that provide connectivity between fragments. Consequently, maintaining or restoring tree cover in areas outside of fragments may increase frugivorous bird presence and movement at the landscape scale (Simberloff *et al.* 1992, Prugh *et al.* 2008, Mendenhall *et al.* 2011), which facilitates gene flow (Sezen *et al.* 2009, Pizo & dos Santos 2011) and regeneration (Peters *et al.* 2016) among tree species whose seeds these frugivores disperse. Additional study of connectivity between fragments and external habitats would enhance conservation planning for large-bodied frugivorous birds (Cardoso da Silva & Tabarelli 2000, Ewers & Didham 2006, Laurance 2008).

Elevation was also related to frugivore presence in our study, yet its effects were inconsistent. Elevation had no relationship with overall species richness, yet elevation was an influential

factor at the individual species and community level. Some species occurred in predominately high elevation sites, while others were more common at low altitudes, with community composition of fragments at similar elevations being more similar than fragments at different elevations. The differences in individual species' trends highlight the need to preserve habitat across the elevational range we studied (135 to 592 m) to accommodate different species' habitat preferences, particularly at higher elevation sites that support species such as the Long-wattled Umbrellabird, Mealy Amazon, and Blue-headed Parrot. The importance of these higher elevation sites is emphasized by expected upward range shifts of many animals associated with climate change (Chen *et al.* 2011). Finally, it is important to consider that our study did not account for seasonal effects that could affect birds' elevational range patterns in response to breeding requirements (Loiselle & Blake 1993), food availability (Galetti *et al.* 2000, Chaves-Campos 2004), or severe weather events (Boyle 2011).

Local attributes.—Despite the generally strong influence of fine-scale habitat attributes on forest avian communities (Durães *et al.* 2013), we did not find associations between the density of large diameter trees, canopy height, or canopy openness and frugivore richness or presence, with the exception of similarity in canopy openness among fragments being related to frugivore community similarity. Despite variation across our fragments, differences in these parameters were apparently insufficient to affect bird species presence. Tree density did not affect frugivore presence or community structure in our study, which is consistent with a study in Brazil in which bird frugivore abundance did not differ between non-logged and selectively logged forests that experienced a 10 percent decrease in tree density (Aleixo 1999). Although differences in sampling habitat prevents direct comparisons of absolute tree density or composition between these studies, these results suggest other factors beyond tree density per se, such as fruit resources (Loiselle & Blake 1993, Chaves-Campos 2004), may be important for predicting frugivore presence and abundance.

Conservation implications and recommendations.—Although small omnivorous birds appear more important than large specialized frugivores in accelerating forest regeneration in deforested lands (Carlo & Morales 2016), large frugivorous birds are key in promoting tree regeneration and diversity in forest fragments and successional forests by providing dispersal to seeds too large to be dispersed by small frugivores (Cardoso da Silva *et al.* 1996, Dehling *et al.* 2016). Our data that suggest landscape tree cover promotes large frugivorous bird persistence is particularly important for our study area located in the Chocó biogeographic zone, one of the world's top 25 priority regions for protection of biodiversity (Myers *et al.* 2000). We observed fewer endangered species compared to species of least concern. Of species endangered in Ecuador, we did not observe three species at all (Crested Guan, Red-lored Amazon, and Great Curassow) and observed a fourth species (Long-wattled Umbrellabird) only three times. Conversely, 59 percent of our observations were of toucans (Ramphastidae), a group relatively resilient to habitat disturbances, capable of using a variety of forest and non-forest habitats, and that consumes a wide range of food items (Galetti *et al.* 2000, Graham 2001), but that can also be threatened by hunting (Holbrook & Loiselle 2009). As over 25 percent of avian frugivores are extinction-prone globally, particularly forest-dependent and large-bodied birds (Pimm & Raven 2000, Sekercioglu *et al.* 2004, Gray *et al.* 2007), our findings should be used to slow the loss of frugivorous birds via management that increases or maintains tree cover across the landscape (Mendenhall *et al.* 2011, McConkey *et al.* 2012, Peters *et al.* 2016).

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DATA AVAILABILITY

The data used in this study are archived at the Figshare Digital Repository (https://doi.org/10.6084/m9.figshare.4968014.v1).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Occurrence and Detection model formulation.
APPENDIX S2. Parameter estimates of occurrence model for 12 frugivore species detected in 22 forest fragments in northwest Ecuador.
APPENDIX S3. Example JAGS model code in for hierarchical multi-species occurrence and detection model of 12 frugivore species in 22 forest fragments in northwest Ecuador.
APPENDIX S4. Parameter estimates of detection model for 12 frugivore species detected in 22 forest fragments in northwest Ecuador.
FIGURE S1. Map of study area and 22 forest fragments surveyed for frugivorous birds in northwest Ecuador.
FIGURE S2. Community similarity of frugivore communities.
FIGURE S3. Species-level P* analysis to determine the level of certainty in the number of surveys necessary to detect a species at least once for a given number of surveys if present in a fragment.

TABLE S1. *Summary statistics on 22 forest fragments in northwest Ecuador sampled for avian frugivores and summary statistics for transect surveys.*

TABLE S2. *Pairwise correlations between covariates included in occurrence and detection models.*

TABLE S3. *AIC model selection table of a multiple linear regression of habitat and fragment characteristics on nocturnal bird species richness.*

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