Abundance of Panamanian dry-forest birds along gradients of forest cover at multiple scales

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Abstract: Community structure and species' abundances may be strongly correlated to patterns of forest cover, although such patterns are poorly known for tropical dry-forest birds, especially for those in Panamanian dry forests. Birds were distance-sampled during point counts in five dry-forest fragments in Panama. Distance from point count to forest edge and forest coverage at three spatial scales (500, 1000 and 2000-m radius) were compared as covariate predictors of the abundance of avian species and guilds. Each covariate was selected in at least two models of species or guild abundance. Abundance patterns were consistent with previously reported habitat associations for only two of seven open-habitat or forest-preferring species that showed forest cover-abundance relationships. Null models best described the abundance of all forest species and the subset of uncommon forest species. Thus many of these species appear insensitive to the forest-cover gradients studied. Total abundance of open-habitat-preferring species increased in dry forests with increasing forest coverage within 500 m, suggesting that the relationship between their abundance and vegetation structure are spatial-scale and habitat dependent. Nectarivores had lower abundance as forest cover within 1000 m increased, supporting previous claims that this group is tolerant of forest edges.

Key Words: abundance modelling, edge effects, feeding guild, fragmentation, land-use

INTRODUCTION

Tropical bird distribution and abundance patterns are often correlated to anthropogenic variation in forest cover (Gillespie 2000, Restrepo & Gomez 1998, Shahabuddin & Kumar 2006, Stouffer & Borges 2001). Researchers, however, are only beginning to describe such abundance patterns for tropical dry-forest birds (Gillespie 2000, Shahabuddin & Kumar 2006). Few data have been published that characterize the structure and fauna of Panamanian dry forests (but see Griscom *et al.* 2007). Additionally, the spatial scales at which abundance patterns correlate to tropical forest cover are poorly known (but see Pearman 2002 for scale of diversity patterns). Two goals of this study are to discover (1) species' traits that mediate the relationship between forest cover and abundance, and (2) the spatial scale of such relationships. This information may lead to insights into the mechanisms that underlie abundance patterns (Levin 1992, McGill *et al.* 2006).

Spatial variation in Panamanian dry-forest bird communities might differ from that of tropical rain-forest bird communities for several reasons. Many Central American dry forests have been extremely fragmented and reduced in area for decades (Gillespie *et al.* 2000). Extant fauna may be less sensitive to habitat fragmentation and edge effects than fauna found in more extensive and recently fragmented forests (Restrepo & Gomez 1998, Stouffer & Borges 2001). Additionally, dry-forest avifauna might be less sensitive to variation in land cover and forest edges (Laurance *et al.* 2002) due to the large seasonal fluctuations in environmental conditions within dry forests, which have long (4–6 mo) and intense dry seasons and deciduous vegetation of reduced stature relative to vegetation of wetter forests (Holdridge *et al.* 1971).

We employ a statistical model of local abundance along environmental gradients that accounts for detection error at greater distances from the observer and random Poisson error in counts (Royle *et al.* 2004). This model diverges from traditional distance-sampling methods (Buckland *et al.* 2001) in several key ways. Traditional distance-sampling models often sacrifice fine-scale spatial

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information. Many sample points are lumped together to estimate abundance across sample sites where birds were detected (i.e. abundance conditioned on detection, Buckland *et al.* 2001). In the method of Royle *et al.* (2004), local abundance is estimated using all sample points, instead of only those where birds were detected. Thus the unconditional consideration of abundance in the model of Royle *et al.* (2004) is more biologically realistic, especially within a single habitat type, where absence is but the case when local abundance approaches zero.
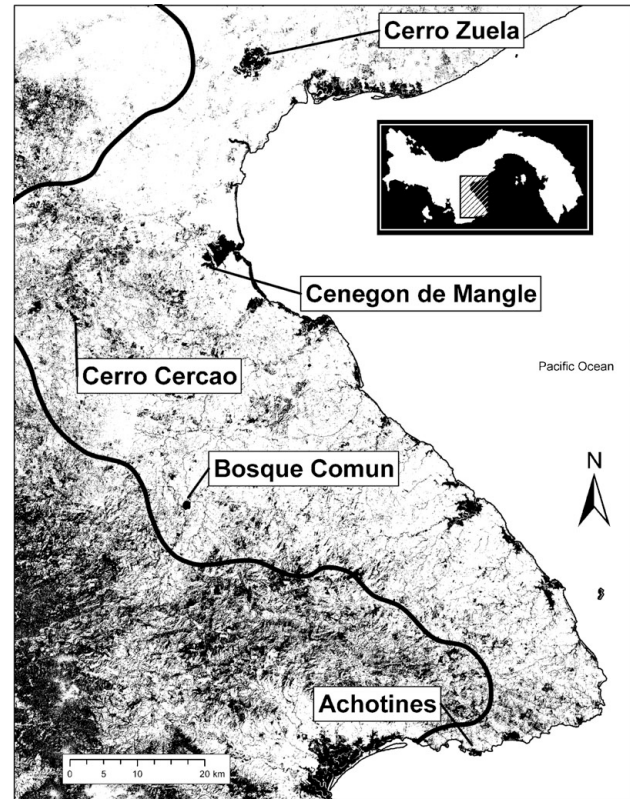
We test four major predictions about how the abundance of Panamanian dry-forest birds changes along two types of spatial gradient of forest cover: per cent forest cover at three scales and distance to forest edge. First, we hypothesize that the abundance of forest-preferring species increases in dry-forest interiors and where forest coverage is high. We hypothesize secondly, however, that many species of dry-forest birds do not show abundance variation along gradients of forest cover and distance to forest edge, in contrast to avifauna of wet forests where nearly all common species may exhibit such patterns (Stouffer & Borges 2001). Third, we predict that in dry forests the abundance of habitat generalist species commonly found in open habitats declines along gradients of increasing distance to forest edge and forest coverage. As insectivores have been reported to be the feeding guild most sensitive to anthropogenic change in dry forests (Shahabuddin & Kumar 2006), we predict that insectivore abundance is positively correlated to forest cover and distance to forest edge.

Figure 1. Map of the study region showing forest coverage, with an inset map of Panama with the study region indicated. Study fragments are indicated. The thick black line represents the approximate limit of Panamanian dry forests. The more extensive forests near river mouths are mostly mangroves. Data are taken from Landsat ETM+ scenes from 2001–2002.

METHODS

Study sites

The Panamanian tropical dry forest region covers $\sim$5100 km^2 (Olson *et al.* 2001). This region is isolated from more extensive Latin American dry forests to the north (Costa Rica) and south (Ecuador) along the coast of the Pacific Ocean. As of 1992, the dry-forest municipalities of Los Santos, Herrera and Coclé provinces (where study sites were located) had 0.8% forest coverage (Autoridad Nacional del Ambiente, http://www.anam.gob.pa/Sif%202002/index.htm).

In November and December 2004 we conducted a search for fragments of tropical dry forest using ground surveys, aerial photographs (Instituto Geográfico Nacional of Panama), satellite imagery, and scientist and resident contacts. Forest fragments were selected for study based on their relatively large size, level of protection, and/or accessibility. The five fragments studied, ranging in size from 80 to 1115 ha, represent nearly all of the largest and best-protected remaining fragments of tropical dry forest in Panama (Figure 1, Appendix 1).

For reference, vegetation structure was measured at a randomly located 0.1-ha plot within each fragment following the method of Gentry (1982, Appendix 1). Mean annual precipitation at sites ranged from 1134–1702 mm y^{-1} (Panama: Dirección de Estadística y Censo 1970–2002), placing sites within the tropical dry-forest life zone of Holdridge *et al.* (1971). The matrix surrounding forest fragments was composed principally of cattle pasture, with smaller areas of crops, mangroves and secondary scrub growth.

Forest cover

Forest fragment edges were identified using aerial photography and ground surveys with a GPS unit (Brunton Inc.). Maps of forest coverage of the region were created using Landsat ETM+ images from 2001–2002 with pixels of 30 × 30 m (U.S. Geological Survey Global Landcover Facility). We created ground-truthed training sites. Using GIS software (Idrisi Andes), we then

classified pixels using standardized minimum distance to class mean and also based on ground observations and aerial photography. The map of forest cover correctly classified 92% of random forest sample sites. We used GIS software (Arc GIS, ESRI) to calculate the percentage of land covered by forest within 500 m, 1000 m and 2000 m of each bird sampling location. We also calculated the distance from each forest point count (the location of the observer) to the nearest forest edge. In calculating these metrics we did not distinguish between dry forest and mangrove forests that adjoined two of the fragments.

Bird sampling

During May and June 2005, the peak breeding season for birds in lowland Central America (Stiles & Skutch 1989), an experienced observer (J. R. Lasky) distance-sampled birds from point counts (Buckland *et al.* 2001). Counts lasted 10 min (Hutto *et al.* 1986), during which time all individual birds identified by sight or sound within a radius of 50 m and their distance from the counting point estimated to the nearest 5 m were recorded. After counts were completed, distances were placed into four bins for statistical analyses: 0–12.5, 12.5–25, 25–37.5 and 37.5–50 m. Distance estimation by the observer was verified before counts began by comparing distance estimates to actual measurements of distance to stationary singing birds. To avoid counting the same individual twice, multiple individuals of the same species were recorded only if all were observed simultaneously. Point counts were located at least 100 m apart and 100 m from the forest edge. Thirty point counts were conducted in each fragment. Only non-aquatic and diurnally active species were counted. We completed counts within 2 h of sunrise and conducted counts over two periods of three consecutive days at each of the five fragments, alternating between fragments every 3 d.

Data analyses

Species habitat affinities are often reported qualitatively and represent expert opinion of general habitat-abundance relationships across entire countries (Ridgely & Gwynne 1989, Skutch 1954, Stiles & Skutch 1989, Wetmore 1965). These affinities have successfully predicted patterns of forest bird diversity relative to forest cover in Costa Rican and Nicaraguan dry-forest reserves (Gillespie & Walter 2001), although related patterns of abundance and their scale are unknown. Based on habitat associations reported in the literature (Ridgely & Gwynne 1989, Skutch 1954, Stiles & Skutch 1989, Wetmore 1965) and the expertise of an ornithologist with

over 15-y experience throughout Panama (G. Angehr, pers. comm.), we divided species habitat associations into three main categories: species primarily found in forest and woodland habitats, species primarily found in open habitats (e.g. grasslands, savanna), and intermediate species falling into neither preceding category. In order to determine if the abundance of uncommon forest birds varied with landscape structure, we lumped the abundances of those forest species detected fewer than 15 times (i.e. too few to model species-specific abundance). We also classified species into dietary guilds (insectivore, insectivore–frugivore, frugivore, granivore, omnivore and raptor), based on feeding habits reported in the literature (Poulin *et al.* 1994, Skutch 1954, Stiles & Skutch 1989, Trainer & Will 1984, Wetmore 1965). The abundances of insectivore–frugivores, which mostly consume insects, were combined with the abundances of insectivores for analysis. Additionally, the abundances of nectarivore–frugivores were included in nectarivore abundance.

In order to account for sampling error that results from imperfect detection and random error in a Poisson process, we employed the Poisson and negative binomial regression models of Royle *et al.* (2004) that model distance decay in detection probability and the effects of local environmental covariates on local abundance. The distance sampling method assumes that detection probability decays over distance from the observer (Buckland *et al.* 2001). The model of Royle *et al.* (2004) estimates biologically interpretable, species-specific parameters for detection probability, mean local abundance, the effect of covariates on abundance, and in the case of the negative binomial, an over-dispersion parameter.

All models and statistical tests were executed with the open-source software R (R Development Core Team, www.r-project.org). We logarithmically transformed distances from point count to forest edge data and logit-transformed per cent forest cover in order to make covariate distributions more normal. All covariates were scaled to have mean equal to 0 and standard deviation equal to 1.

Using Akaike's Information Criterion (AIC), we compared null models of abundance with models containing each covariate of forest cover or the distance from the observer's location in the point count to nearest forest edge. Null abundance models estimated parameters for detection and fragment mean abundance, but did not include parameters for forest cover. Abundance was modelled for species and functional groups found in at least four of the five forest fragments and detected at least 15 times. Because there were 30 point counts within each of five dry-forest fragments, we estimated a mean abundance for each fragment in all models to account for block effects. For species that were found in only

Table 1. Selected models of log abundance and model parameters for dry-forest bird species and group abundances, with the habitat, diet guild, and number of detections (N) of each species or group. The model column gives the type of forest cover parameter in the abundance model selected by AIC, or 'null' if a model without a forest cover parameter was selected, and the error distribution of the selected model in parentheses. Parameters are α_1, the slope of the transformed and scaled covariate effect, and k, the negative binomial over-dispersion parameter. Null abundance models (without a parameter for forest cover, α_1) were selected for the species and groups below. The other α parameters are fragment mean abundance (individuals ha^{-1}; A = Achotines, B = Bosque Común, C = Cerro Cercao, M = Cenegón de Mangle and Z = Cerro Zuela). If species did not occur at a site, N/A is written. Habitat preferences are F = forest/woodland, I = intermediate and O = open habitats. Guild abbreviations are ins = insectivore, fru = frugivore, nec = nectarivore, gra = granivore, omn = omnivore and rap = raptor.

Species or group	Model	α_1	k	α_A	α_M	α_B	α_C	α_Z	Habitat	Guild	N
Leptotila verreauxi	2000 m (Pois.)	−0.86		0.10	1.71	1.13	0.80	0.99	I	gra	102
Brotogeris jugularis	Distance (Neg.B.)	−0.49	14.11	1.16	0.18	2.24	2.90	2.77	I	omn	93
Lepidopyga coeruleogularis	Distance (Pois.)	0.56		1.62	5.82	1.52	1.61	2.27	O	nec	17
Amazilia edward	1000 m (Pois.)	−1.82		6.68	1.09	6.02	8.60	2.73	O	nec	33
Thamnophilus doliatus	2000 m (Pois.)	−0.69		0.08	1.31	0.65	0.94	0.55	I	ins	50
Elaenia flavogaster	500 m (Pois.)	0.31		N/A	0.57	0.19	0.04	0.13	O	ins/fru	23
Tolmomyias sulphurescens	2000 m (Pois.)	1.57		4.19	N/A	N/A	2.41	1.80	F	ins/fru	68
Myiodynastes maculatus	2000 m (Neg.B.)	2.37	5.04	1.74	0.58	0.83	0.17	0.91	I	ins/fru	28
Thryothorus rufalbus	2000 m (Pois.)	−1.74		0.80	N/A	2.62	0.29	0.10	F	ins	53
Vireo flavoviridis	Distance (Neg.B.)	−0.51	1.89	2.27	0.42	0.39	0.42	0.91	I	ins/fru	42
Polioptila plumbea	1000 m (Pois.)	−0.84		3.72	0.28	4.31	2.77	2.12	F	ins	85
Euphonia leuteicapilla	Distance (Neg.B.)	0.30	1.17	0.11	0.42	1.26	N/A	1.49	O	fru	54
Nectarivores	1000 m (Pois.)	−0.57		12.34	22.66	21.11	17.15	13.35			134
Open-habitat preferring	500 m (Neg.B.)	0.15	1.01	14.96	30.20	9.37	9.36	13.59			473
Piaya cayana	Null (Pois.)			0.65	1.94	1.14	0.98	0.48	I	ins/rap	32
Melanerpes rubricapillus	Null (Pois.)			0.70	1.64	1.75	0.83	2.22	I	ins/fru	61
Camptostoma obsoletum	Null (Pois.)			N/A	0.29	0.86	0.14	1.02	I	ins/fru	32
Lophotriccus pilaris	Null (Pois.)			3.10	4.29	3.20	4.29	3.30	F	ins/fru	182
Pitangus sulphuratus	Null (Neg.B.)		2.70	0.24	0.43	0.13	0.36	0.18	O	ins/fru	22
Megarhynchus pitangua	Null (Neg.B.)		1.28	0.99	0.61	2.07	1.92	3.01	I	ins/fru	112
Myiozetetes similis	Null (Neg.B.)		4.46	1.19	1.41	0.60	1.47	0.74	O	ins/fru	36
Tyrannus melancholicus	Null (Neg.B.)		2.28	3.66	1.52	2.20	3.19	0.56	O	ins/fru	59
Chiroxiphia lanceolata	Null (Neg.B.)		0.59	0.37	N/A	5.42	6.50	5.42	F	fru	235
Frugivores	Null (Neg.B.)		0.50	1.22	3.00	10.05	8.45	10.53			349
Insectivores	Null (Neg.B.)		0.19	21.37	34.12	27.50	19.32	36.02			1257
Forest preferring	Null (Neg.B.)		0.25	10.93	5.27	22.19	18.94	15.13			730
Uncommon forest preferring	Null (Neg.B.)		1.15	1.22	0.47	2.01	1.71	1.13			110

four of the five forest fragments, we excluded sample points from the fragment where it was absent because we cannot stably estimate a parameter that results in a mean log abundance equal to zero. Non-linear minimization of deviance was used to estimate parameter values to maximize joint likelihood of the data across all sites (Royle *et al.* 2004).
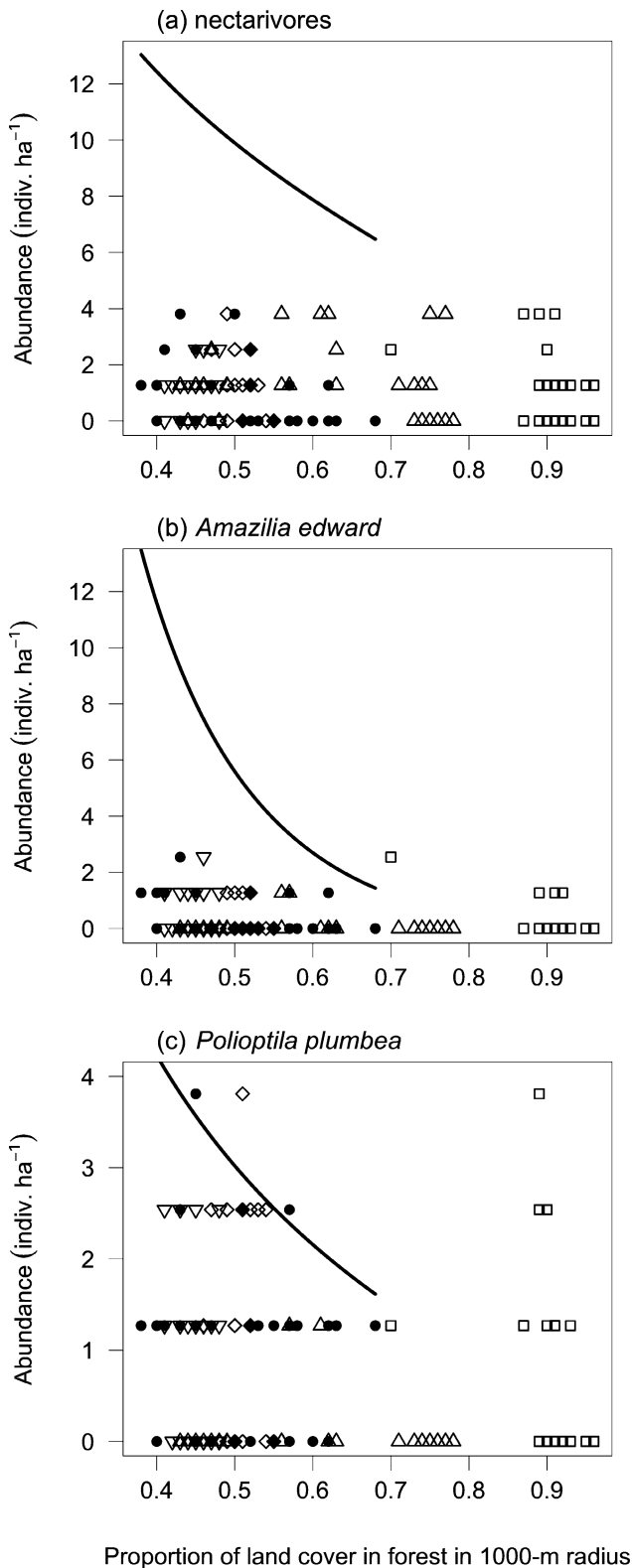
Models selected based on AIC that included a parameter for forest cover or distance from point count to forest edge were tested for spatial autocorrelation in the deviates ($-2 \times$ log(likelihood)) at each sample site, corresponding to autocorrelation in the data not predicted by the model. Using the Mantel test, a Euclidean distance matrix of the site-specific deviates was compared with a Euclidean distance matrix of the geographical distance between sites. The null hypothesis that geographical distance is not correlated to deviate distance was tested among the sample sites of each fragment ($\alpha = 0.05$). A goodness-of-fit test using parametric bootstrapping was used to verify that the model's likelihood did not deviate significantly from its respective Poisson or negative binomial distribution ($\alpha = 0.05$).

RESULTS

We observed a total of 2117 individual birds and 71 species at 150 point counts (Appendix 2). Models of local abundance were compared for each of the 21 species (totalling 1429 individuals) that occurred in at least four of the five forest fragments and were detected at least 15 times (Table 1).

Nectarivore abundance decreased as forest coverage within 1000 m increased (Table 1, Figure 2). For open-habitat species, abundance slightly increased as forest cover within 500 m increased (Figure 3), while a null model of abundance was favoured for total forest-preferring birds and total forest-preferring birds of species detected fewer than 15 times (Table 1). Null models were also selected for frugivore and insectivore abundances. Granivores were comprised almost wholly of *Leptotila verreauxi,* so we did not model the abundance of this group. We detected very few raptors and did not model the abundance of this group.

Of the 21 species for which we modelled abundance, models incorporating a habitat spatial structure covariate

(a) nectarivores

(b) *Amazilia edward*

(c) *Polioptila plumbea*

Proportion of land cover in forest in 1000-m radius

Figure 2. Estimated abundance relationships with forest coverage within a 1000-m radius of the sample points for total nectarivores (a), *Amazilia edward* (b), and *Polioptila plumbea* (c). Count values for each patch are shown, converted from raw individuals per count to individuals ha^{-1} (circles = Achotines, triangles pointing up = Cenegón de Mangle,

were selected for 12 species, five of which had habitat effects of the opposite sign as expected based on habitat association groups (Table 1). The distance to forest edge and three forest cover covariates were all selected in at least one species abundance model (Figures 2–5). Three of the five species of forest-habitat birds, four of seven species of open habitat, and five of nine intermediate habitat species with sufficient detections to model species abundance had non-null abundance models selected.

Mantel tests for spatial autocorrelation among deviates from the likelihood models showed no significant spatial autocorrelation ($\alpha = 0.05$) in all but two instances: at the Achotines fragment for *Leptotila verreauxi*, and at the Cerro Zuela fragment for *Tolmomyias sulphurescens*. Because of the rarity of these instances and the fact that these fragments comprise a small proportion of the total observations for these species (2% of *L. verreauxi* and 17% of *T. sulphurescens* observations), we give no further consideration to spatial autocorrelation.

DISCUSSION

Habitat-affinity groups were very poor predictors of correlations between abundance and gradients of distance to forest edge and forest cover. The abundances of total forest birds, of total uncommon forest species, and of some forest species did not decline along such gradients, while the abundances of some open habitat species did decline along such gradients. Although we expected total forest-bird abundance to decline with decreasing forest cover and distance to forest edge, we expected many species of dry-forest bird would not respond to such gradients. Overall, the abundances of only 33% of bird species with sufficient detections to model decreased with decreased forest cover and distance to forest edge. In dry forests in Costa Rica and Nicaragua, 55% of forest-preferring bird species were restricted to the five forest reserves over 1000 ha out of eight in total, while only 8% were restricted to the three smaller reserves (Gillespie 2000). The relative insensitivity of Panamanian dry-forest birds could be due to the spatiotemporal scale of deforestation and fragmentation in the heavily deforested Panamanian dry-forest region. The time lapse after major deforestation in the region, which occurred at least 20 y before our study (Autoridad Nacional del Ambiente, http://www.anam.gob.pa/Sif%202002/index.htm), may have

diamonds = Bosque Común, triangles pointing down = Cerro Cercao, squares = Cerro Zuela). The estimated abundance curves are shown for Achotines and the range of variation in forest coverage for sample points there. Note that mean abundance parameters are estimated for each patch, the curves only show estimates for Achotines.

(a) open habitat spp.

(b) *Elaenia flavogaster*

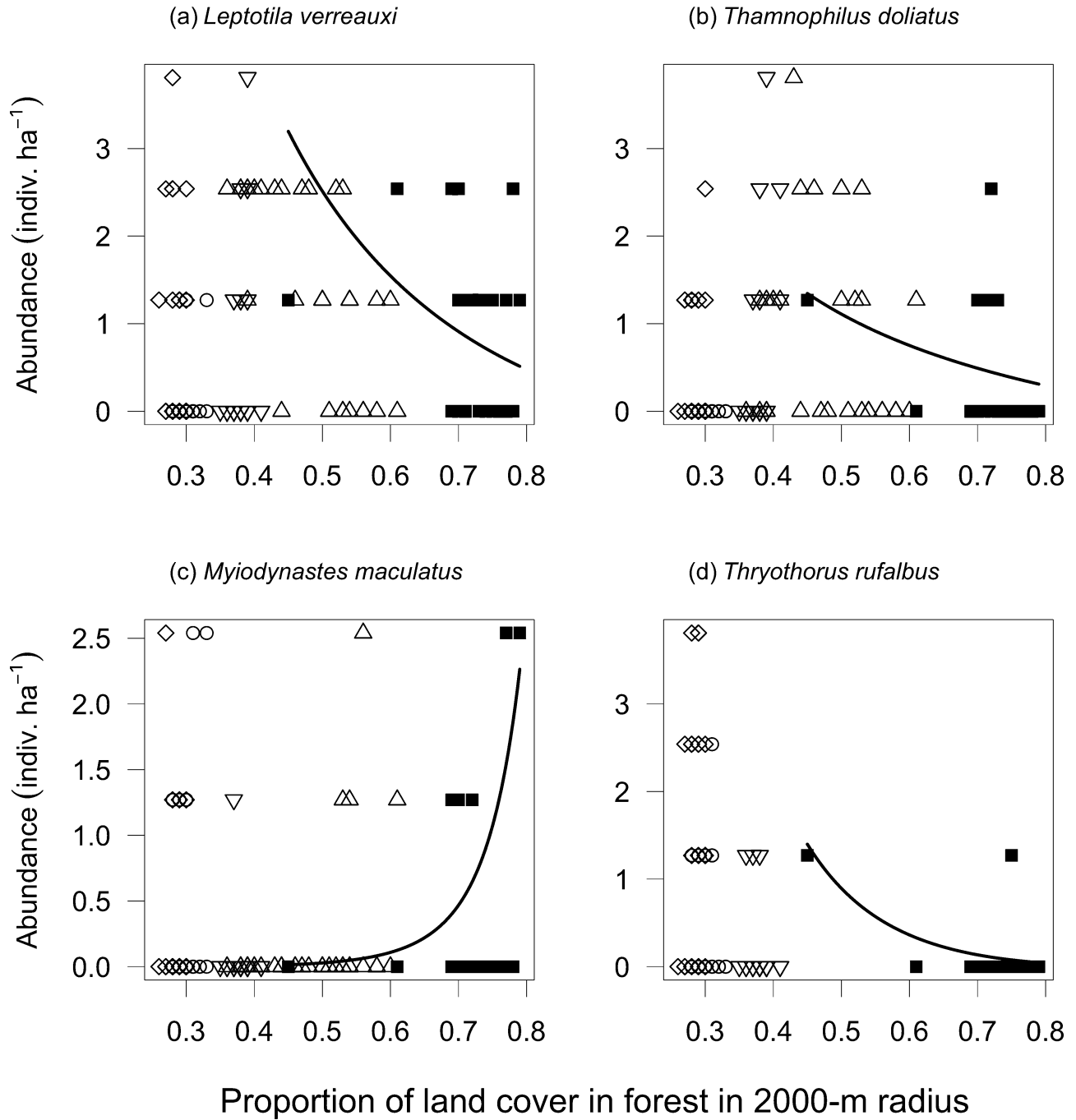Proportion of land cover in forest in 500-m radius
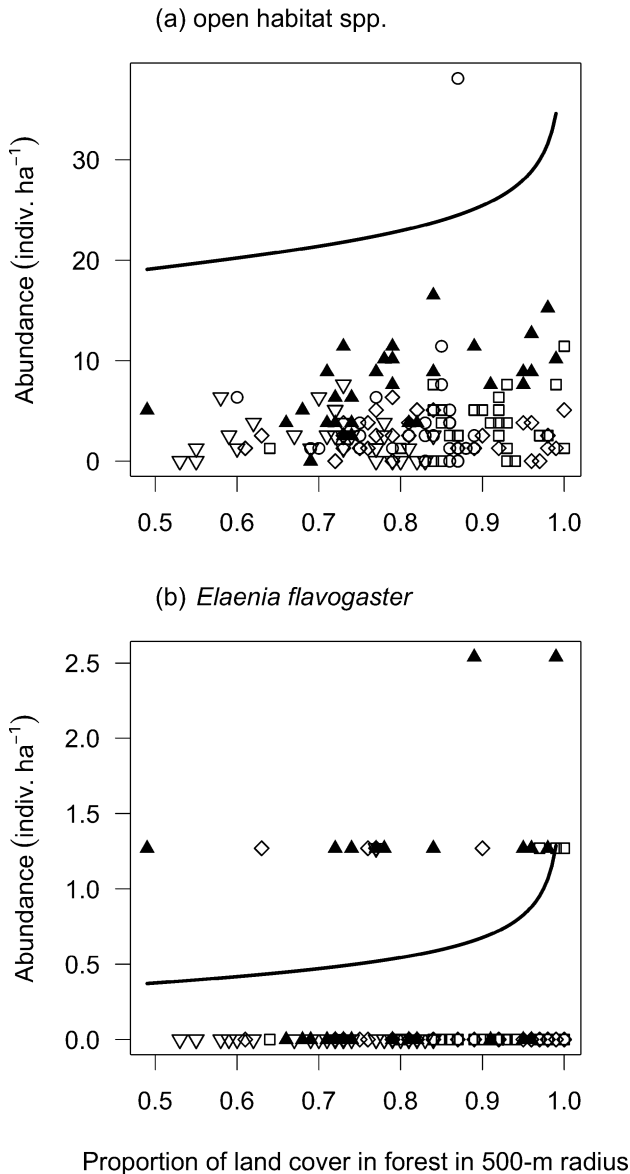
Figure 3. Estimated abundance relationships with forest coverage within a 500-m radius of the sample points for total open-habitat species (a) and *Elaenia flavogaster* (b). Count values for each patch are shown, converted from raw individuals per count to individuals ha^{-1} (circles = Achotines, triangles pointing up = Cenegón de Mangle, diamonds = Bosque Común, triangles pointing down = Cerro Cercao, squares = Cerro Zuela). The estimated abundance curves are shown for Cenegón de Mangle and the range of variation in forest coverage for sample points there. Note that mean abundance parameters are estimated for each patch, the curves only show estimates for Cenegón de Mangle.

weakened correlations between abundance and variation in forest cover. Restrepo & Gomez (1998) found that lower abundances of certain guilds at new forest edges (<12 y old) did not occur at old edges (>40 y old). The dry-forest region in Panama is heavily deforested, even relative to deforested dry regions elsewhere in Central America (Gillespie 2000), and the only large

tract of dry forest is located at Cerro Zuela (Figure 1). As a result, species sensitive to extensive habitat loss and fragmentation may have already gone extinct in the region, leaving behind more generalist species that tolerate a wide range of conditions (Owens & Bennett 2000). None of the species we recorded is restricted to undisturbed primary forest, which does not exist in the dry-forest region of Panama. *Manacus vitellinus*, reported as occurring in the study region and being sensitive to deforestation in 1989 (Ridgely & Gwynne 1989), was not recorded in the 9 mo J. R. Lasky spent in the field in many dry-forest fragments, nor in riparian forests near Achotines (Griscom *et al.* 2007), and may be extirpated from Panamanian dry forests. Continuous monitoring of the region's avifauna would determine if populations of other forest-preferring species are in decline, although total forest cover in the region appears to have stabilized (Autoridad Nacional del Ambiente, http://www.anam.gob.pa/Sif%202002/index.htm).

While it has been established that open-habitat species are also found within dry forests (Ridgely & Gwynne 1989), an increase in their abundance within dry forests as forest coverage increases has not been reported. We classified species as having open-habitat affinities based on literature that described abundance patterns across all habitat types at national scales, while our data describe abundance patterns within dry forests. The unexpected patterns we observed may be due to the difference in scale and the range of habitat variation studied, as the environmental factors most closely related to abundance variation may change across spatial scales (Diez & Pulliam 2007). Composition of adjoining matrix habitats likely played little role in affecting the abundance patterns observed, as nearly all forest was bordered by active pasture with small vegetable plots, except for a rice paddy bordering ∼500 m of the edge of Cerro Zuela. Future research should determine how the demographic processes of these open-habitat species vary from dry forests to adjacent scrub and agricultural fields.

Nectarivores were the only feeding guild for which the selected abundance model contained a parameter for variation in forest cover or distance to forest edge. As forest coverage within a 1000-m radius of sample points increased, nectarivore abundance decreased. Patterns of nectarivore abundance may be related to floral resource density (Cotton 2007). Floral resources may be more abundant in wet-forest edges than interiors (Linhart *et al.* 1987), which may explain the apparent lack of sensitivity to forest fragmentation in trochilid nectarivores (Gillespie 2000, Pearman 2002, Petit *et al.* 1999, Restrepo & Gomez 1998, Stouffer & Bierregaard 1995a). Increases in forest coverage could decrease forest edge habitat and floral resources and create the pattern we observed. However, the estimation of abundance of highly mobile

(a) *Leptotila verreauxi*

(b) *Thamnophilus doliatus*

(c) *Myiodynastes maculatus*

(d) *Thryothorus rufalbus*

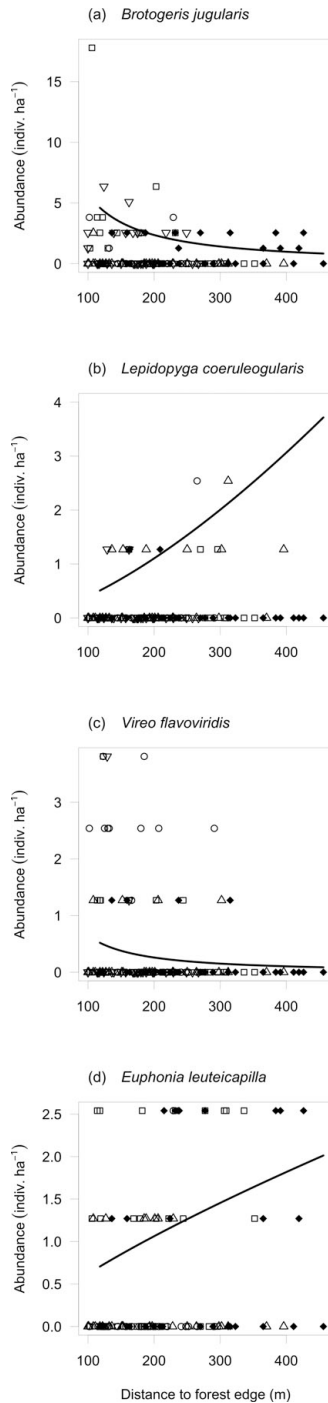## Proportion of land cover in forest in 2000-m radius

Figure 4. Estimated abundance relationships with forest coverage within a 2000-m radius of the sample points for *Leptotila verreauxi* (a), *Thamnophilus doliatus* (b), *Myiodynastes maculatus* (c), and *Thryothorus rufalbus* (d). Count values for each patch are shown, converted from raw individuals per count to individuals ha^{-1} (circles = Achotines, triangles pointing up = Cenegón de Mangle, diamonds = Bosque Común, triangles pointing down = Cerro Cercao, squares = Cerro Zuela). The estimated abundance curves are shown for Cerro Zuela and the range of variation in forest coverage for sample points there. Note that mean abundance parameters are estimated for each patch, the curves only show estimates for Cerro Zuela.

trochilids is notoriously difficult. Past estimates of trochilid abundance using mist-netting in Panamanian wet forests ($\sim$2 individuals ha^{-1}, Robinson *et al.* 2000) are much lower than our estimates (Table 1), possibly reflecting counting individuals in multiple point counts. However, we have no reason to believe our estimates are biased

relative to variation in forest cover at the scales studied. Additional research should determine which specific demographic processes vary spatially for the abundance-forest cover correlations we found.

The abundances of most individual insectivore species and lumped insectivores were not correlated to

(a) *Brotogeris jugularis*

(b) *Lepidopyga coeruleogularis*

(c) *Vireo flavoviridis*

(d) *Euphonia leuteicapilla*

Distance to forest edge (m)

Figure 5. Estimated abundance relationships with distance to forest edge from the sample points for *Brotogeris jugularis* (a), *Lepidopyga coeruleogularis* (b), *Vireo flavoviridis* (c), and *Euphonia leuteicapilla* (d). Count values for each patch are shown, converted from raw individuals per count to individuals ha^{-1} (circles = Achotines, triangles pointing up = Cenegón de Mangle, diamonds = Bosque Común, triangles pointing down = Cerro Cercao, squares = Cerro Zuela). The estimated abundance curves are shown for Bosque Común and the range of variation in distance to forest edge for sample points there. Note that mean abundance parameters are estimated for each patch, the curves only show estimates for Bosque Común.

forest cover gradients. In Indian dry forests, however, insectivores were the only guild that showed negative correlations to localized anthropogenic disturbance (Shahabuddin & Kumar 2006). This result, however, is not necessarily contradictory to ours, as we focused on large-scale gradients of forest cover. In wet forests insectivores are often the avian guild most sensitive to forest edges (Laurance 2004, Şekercioğlu *et al.* 2002, Stouffer & Bierregaard 1995b), but the most sensitive group of insectivores, the terrestrial insectivores, is depauperate in Central American dry forests (Gillespie 2000).

Species abundances and distributions may be affected by both habitat loss and habitat fragmentation, which often occur simultaneously (Fahrig 1997, Trzcinski *et al.* 1999). Of the five species abundance models with negative effects of deforestation or fragmentation, two had lower abundances closer to forest edges (i.e. a measure of fragmentation), while the others declined with decreasing forest coverage (i.e. a measure of habitat loss). Because the abundances of so few species declined along such gradients, we cannot evaluate whether habitat loss or forest fragmentation plays a larger role in altering bird communities in dry forests (Fahrig 1997).

This study is the first to model bird abundance along gradients of forest cover and distance to forest edge in Latin American dry forests. We have shown how the abundances of 12 bird species and two functional groups vary within Panamanian dry forest along gradients of forest cover, while the abundances of nine species and three functional groups did not significantly vary along the gradients studied. In general, species' habitat preferences were poor predictors of spatial patterns of abundance, possibly because of the long history of deforestation in the region that may have already resulted in the local extinction of sensitive species. The use of distance sampling and Poisson and negative binomial regression to site-specific environmental covariates represents a technical advance in understanding spatial variation in abundance (Royle *et al.* 2004). Studies of bird community abundance patterns (such as ours) provide a richer understanding of spatial ecology than do studies of simpler presence/absence patterns.

ACKNOWLEDGEMENTS

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Appendix 1. Study forest fragment characteristics. Vegetation data are from a series of transects covering 0.1 ha (Gentry 1982).

Site	Elevation (m asl)	Dry forest fragment area (ha)	Effectively protected?	Mean ± SD annual precipitation (mm)	Basal area (m² ha⁻¹)	Trees ≥ 10 cm dbh (ind. ha⁻¹)	Trees ≥ 10 m height (ind. ha⁻¹)
Achotines	33	95	Yes	1702 ± 230	26.5	410	430
Bosque Común	138	132	Yes	1630 ± 346	33.7	550	620
Cerro Cercao	109	80	No	1461 ± 333	18.5	480	500
Cenegón de Mangle	20	237	No	1134 ± 272	10.8	190	70
Cerro Zuela	117	1115	No	1504 ± 301	19.7	330	220

Appendix 2. Species (AOU 1998, Banks *et al.* 2006) recorded during point counts in five fragments (A = Achotines, B = Bosque Común, C = Cerro Cercao, M = Cenegón de Mangle and Z = Cerro Zuela). Species are listed in the order of the AOU check-list. Total counts for each fragment where they were detected, habitat preference, and foraging guild are shown. Guild abbreviations are ins = insectivore, fru = frugivore, nec = nectarivore, gra = granivore, omn = omnivore, rap = raptor and sca = scavenger. Habitat abbreviations are F = forest preferring, I = intermediate habitat preferring and O = open habitat preferring.

Species	A	M	B	C	Z	Habitat	Guild
Tinamidae							
Tinamus major			1			F	omn
Crypturellus soui				7		F	omn
Cracidae							
Ortalis cinereiceps		2		2	2	I	fru
Cathartidae							
Coragyps atratus		1	2			O	scav
Accipitridae							
Accipiter bicolor			1			F	rap
Buteogallus subtilis	1					I	rap
Buteo magnirostris		2		2		O	rap
Falconidae							
Milvago chimachima		9	4	2		O	rap
Columbidae							
Patagioenas cayennensis	6					I	fru
Zenaida asiatica		1				O	gra
Columbina talpacoti		9			1	O	gra
Claravis pretiosa		2			8	I	gra
Leptotila verreauxi	2	34	21	15	20	I	gra
Psittacidae							
Aratinga pertinax		4		6	12	O	omn
Brotogeris jugularis	11	2	20	25	35	I	omn
Amazona ochrocephala		22			25	I	omn

Appendix 2. Continued.

Species	A	M	B	C	Z	Habitat	Guild
Cuculidae							
Piaya cayana	4	12	7	6	3	I	ins/rap
Coccyzus minor					1	F	ins/rap
Crotophaga sulcirostris		28				O	ins/fru
Strigidae							
Glaucidium brasilianum	2	6				I	ins/rap
Trochilidae							
Chlorostilbon assimilis		1				O	nec
Lepidopyga coeruleogularis	2	8	2	2	3	O	nec
Amazilia edward	9	2	7	10	5	O	nec
Amazilia tzacatl	6		4		1	I	nec
Momotidae							
Momotus momota			4	1		F	omn
Picidae							
Melanerpes rubricapillus	6	14	15	7	19	I	ins/fru
Campephilus melanoleucos	1					F	ins
Furnariidae							
Xiphorhynchus picus		4			2	F	ins
Xiphorhynchus susurrans	7		13		13	F	ins
Thamnophilidae							
Thamnophilus doliatus	1	19	9	13	8	I	ins
Tyrannidae							
Camptostoma obsoletum		4	12	2	14	I	ins/fru
Phaeomyias murina		38			14	O	ins/fru
Capsiempis flaveola		4			1	I	ins/fru
Tyrannulus elatus					5	I	ins/fru
Elaenia flavogaster		14	5	1	3	O	ins/fru
Elaenia chiriquensis		1		1	2	O	ins/fru
Sublegatus arenarum	1	6			1	I	ins/fru
Lophotriccus pilaris	31	43	32	43	33	F	ins/fru
Poecilotriccus sylvia					7	I	ins
Todirostrum cinereum		1				I	ins
Tolmomyias sulphurescens	21		25	12	10	F	ins/fru
Myiarchus panamensis		1			2	O	ins/fru
Pitangus sulphuratus	4	7	2	6	3	O	ins/fru
Megarhynchus pitangua	13	8	27	25	39	I	ins/fru
Myiozetetes similis	8	9	4	10	5	O	ins/fru
Myiodynastes maculatus	10	5	5	1	7	I	ins/fru
Tyrannus melancholicus	20	8	12	16	3	O	ins/fru
Pachyramphus cinnamomeus	1					I	ins/fru
Pachyramphus polychopterus		4	3			F	ins/fru
Tityra semifasciata	1		2			F	ins/fru
Pipridae							
Chiroxiphia lanceolata	5		70	86	74	F	fru
Vireonidae							
Vireo flavoviridis	21	4	4	4	9	I	ins/fru
Hylophilus flavipes		19			12	I	ins/fru
Hylophilus aurantiifrons					30	I	ins/fru
Hylophilus decurtatus	9		7			F	ins/fru
Cyclarhis gujanensis		25	3		17	I	ins
Corvidae							
Cyanocorax affinis	1		1	6	5	F	omn
Troglodytidae							
Thryothorus rufalbus	11		36	4	2	F	ins
Sylviidae							
Ramphocaenus melanurus				6		F	ins
Polioptila plumbea	25	2	28	18	15	F	ins
Turdidae							
Turdus grayi	1		2			I	ins/fru
Parulidae							
Basileuterus rufifrons					31	I	ins

Appendix 2. Continued.

Species	A	M	B	C	Z	Habitat	Guild
Incertae Sedis							
Coereba flaveola		20				I	fru/nec
Thraupidae							
Thraupis episcopus			14	1	1	I	fru/nec
Cyanerpes cyaneus					10	I	fru/nec
Emberizidae							
Volatinia jacarina		15			7	O	gra
Arremonops conirostris				2		I	omn
Cardinalidae							
Saltator conirostris		20			14	I	ins/fru
Icteridae							
Quiscalus mexicanus	50	14				O	omn
Psarocolius decumanus	1		2	7		F	omn
Fringillidae							
Euphonia luteicapilla	2	7	21		24	O	fru