Do Collared Peccaries Negatively Impact Understory Insectivorous Rain Forest Birds Indirectly Via Lianas and Vines?

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ABSTRACT

Tropical rain forest understory insectivorous birds are declining, even in large forest reserves, yet the mechanisms remain unclear. Abundant large mammals can reshape forest structure, which degrades foraging microhabitat. We used six sites in Nicaragua, Costa Rica, and Panama with varying collared peccary (*Pecari tajacu*) density to test three linked hypotheses: (1) locally declining understory insectivores forage preferentially in liana tangles; (2) vine and liana density, cover, and frequency of dense tangles are lower in the presence of abundant collared peccaries; and consequently (3) abundant collared peccaries are associated with reduced understory insectivorous bird abundance. Three insectivores that declined at La Selva preferentially foraged in liana tangles: Checker-throated Antwren (*Epinecrophylla fulviventris*), Dot-winged Antwren (*Microrhopias quixensis*), and Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*). Vine density, liana cover, liana tangle frequency, and forest cover were lower in the presence of collared peccaries relative to experimental mammal exclosures, with the greatest differences at La Selva Biological Station, Costa Rica. Across sites, five of seven vine and liana measures showed negative, curvilinear relationships with peccary densities. Vine and liana measures peaked at sites with intermediate peccary density, and were low at La Selva. Structural equation models suggest negative indirect effects of the collared peccaries on focal bird densities, mediated by vine and liana density, cover, or tangle frequency. Forest area and rainfall affected both lianas and birds, but collared peccaries also contributed to the reduced abundance of understory insectivores. Indirect effects such as that suggested here may occur even in large, protected forest reserves where large mammal communities are changing.

Abstract in Spanish is available with online material.

UNDERSTORY INSECTIVOROUS BIRDS, A GUILD THAT ACCOUNTS FOR ABOUT 15 PERCENT OF ALL NEOTROPICAL FOREST BIRDS, are declining across the tropics (Sodhi *et al.* 2004, Newmark 2006, Sigel *et al.* 2010, Yong *et al.* 2011, Powell *et al.* 2015). Declines in this guild were first observed in small (1–100 ha) forest fragments and attributed to direct fragmentation effects (Şekercioğlu *et al.* 2002). Yet understory insectivores have declined even within larger reserves (*e.g.*, 10,000 ha Reserva Ducke, Brazil, P.C. Stouffer, unpubl. data), in which frequently invoked mechanisms applicable to small fragments—such as large area needs or edge effects— appear insufficient to explain declines (Stratford & Robinson 2005, Stouffer *et al.* 2011).

Moreover, some bird species have concurrently declined and increased at ecologically similar, proximate sites experiencing the same climatic trends (Sigel *et al.* 2010). For example, several understory insectivorous bird species, including Checker-throated (*Epinecrophylla fulviventris*) and Dot-winged Antwrens (*Microrhopias*

quixensis), declined to near-extirpation at 1600 ha La Selva Biological Station, Costa Rica (Sigel *et al.* 2006, 2010) while persisting at Tirimbina, a 300 ha reserve near La Selva, and concurrently increasing 150–300 percent on the 1550 ha Barro Colorado Island (BCI), Panama (Robinson 2001, B.J. Sigel, unpubl. data).

Even well-protected forest preserves such as La Selva have undergone mammal community changes that we suggest might affect its understory insectivore guild. Trophic downgrading (Estes *et al.* 2011) is implicated in mammal community changes in many otherwise undisturbed tropical forests, typified by the elevated abundance of large frugivores, herbivores, and omnivores (Terborgh *et al.* 2001, Peres & Palacios 2007). Although large vertebrate frugivores and herbivores provide valuable seed dispersal services (Levey *et al.* 2002), in sufficient abundance they may reduce plant biomass and simplify vegetation structure through consumption, trampling, and other behaviors. Indeed, plants—and, consequently, the organisms that depend on them— often exhibit nonlinear responses to herbivory, in which low to moderate levels of herbivory and trampling are beneficial or neutral, but above a threshold, large mammals disturb the vegetation

structure sufficiently to reduce the abundance and richness of birds and other organisms (Foster *et al.* 2014). Understory insectivores, as microhabitat-specialized birds, are likely particularly susceptible to such threshold responses (Marra & Remsen 1997, Côté *et al.* 2004, Stratford & Robinson 2005, Stratford & Stouffer 2013).

Peccaries (Tayassuidae) cause major understory vegetation disturbances (*e.g.*, trampling, rooting, wallowing) in many Neotropical forests (Beck 2006, Queenborough *et al.* 2012). White-lipped peccaries (*Tayassu pecari*)—now mostly extirpated across Central America—are larger-bodied, travel in larger groups, and consume a wider range of seeds than the collared peccaries (*Pecari tajacu*), but both disrupt understory plant communities (Beck 2005, 2006). At La Selva, collared peccaries have increased from near-extirpation in the 1970s to densities up to eight times greater than those in lightly hunted regions of Mexico's Montes Azules Biosphere Reserve ($7.9 \pm 6.0/km^2$; Naranjo *et al.* 2004) and 10 times greater than those in unhunted Amazonian forests ($6.6 \pm 1.3/km^2$; Peres & Palacios 2007, Romero *et al.* 2013, Table 1). Moreover, collared peccary population increases coincided with understory insectivorous bird declines (Sigel *et al.* 2006). Collared peccary activity reduces understory vegetation density in Costa Rica and Panama, including density and cover of vines and lianas (= woody vines; Michel 2012). These in turn provide crucial foraging and nesting microhabitat for many birds, including both Checker-throated and Dot-winged Antwrens (Gradwohl & Greenberg 1980). Despite their known impacts on the vegetation used by birds, the peccaries' potential to impact bird populations indirectly remains unexplored.

To investigate this peccary-bird relationship, we tested a three-part hypothesis: (1) locally declining understory insectivores forage preferentially in liana tangles; (2) vine and liana density, cover, and frequency of dense tangles are lower in the presence of abundant collared peccaries; and consequently; (3) collared peccaries contribute to reduced understory insectivorous bird abundance. We tested these predictions with both experimental and observational methods at six lowland Central American forest reserves, taking advantage of the variation in peccary density as well as pre-existing experimental mammal exclosures.

METHODS

STUDY sites.—We worked at six lowland tropical forest sites in three countries: Refugio Bartola (Nicaragua); La Selva Biological Station and Tirimbina Biological Reserve (Costa Rica); Barro Colorado Island, Gigante Peninsula, and Limbo Hunt Club (Panama; site descriptions in Tables 1 and 2; site map in Fig. S1). All study sites include a mix of old growth and secondary rain forest. At BCI and Gigante, four fenced 30 m × 45 m mammal exclosure —control pairs were built per site in 1993, effectively excluding most terrestrial mammals (described in Royo & Carson 2005, Fig. S1). La Selva's five 20 m × 50 m fenced mammal exclosure —control pairs were built in 1999, but only exclude large terrestrial vertebrates due to the lack of buried fine mesh fencing (Reider *et al.* 2013). All mammal exclosure–control pairs are adjacent, and by thus controlling for soils, forest composition and history, presumably differ primarily in the presence or absence of large terrestrial mammals. All sites are anthropogenically disturbed, and apex predators (jaguar, *Panthera onca*; cougar *Felis concolor*) are rare or extirpated (Timm 1994, Wright *et al.* 1994).

COLLARED PECCARIES.—Collared peccaries (Tayassuidae: *P. tajacu*; hereafter 'peccaries') are a large-bodied (1135 kg), primarily frugivorous native omnivore (Beck 2005). Most other large

TABLE 1. *Characteristics of study sites ranked by estimated collared peccary (P. tajacu) density, including country, latitude and longitude, elevation (meters above sea level), life zone (tropical wet or tropical moist forest; Holdridge et al. 1971), area of the reserve and, where applicable, the continuous forest within which it is embedded, level of protection against poaching, collared peccary density (mean $\pm$ SE/km², range in parentheses) and Relative Abundance Index (RAI mean $\pm$ SE).*

Study site	Country	Latitude longitude	Elevation (m asl)	Life zone	Area (ha) reserve/embedded	Protection level	Collared peccary density (/km²)[a]	Collared peccary RAI
Tirimbina Biological Reserve	Costa Rica	10°25′N 84°8′W	180–220	Wet	340/na	Low	3.0 ± 0.7 (3.0; A)[b]	–
Refugio Bartola	Nicaragua	10°58′N 84°20′W	30–100	Wet	300/260,000	Low	3.7 ± 0.6 (3.7; A)[b]	–
Gigante Peninsula	Panama	9°8′N 79°52′W	25–120	Moist	800/5600	Low	5.2 ± 0.9 (1.0–12.0; AD)[c]	2.9 ± 0.1
Limbo Hunt Club	Panama	9°9′N 79°45′W	35–80	Moist	104/22,104	Low	6.9 ± 3.1 (6.0; ACD)[b]	–
Barro Colorado Island	Panama	9°10′N 79°50′W	25–165	Moist	1562/na	High	12.9 ± 2.0 (1.0–35.0; C)[d]	4.0 ± 0.8
La Selva Biological Station	Costa Rica	10°26′N 84°0′W	35–130	Wet	1611/46,000	High	31.8 ± 9.5 (14.0–65.9; B)[e]	12.1 ± 0.5

m asl, meters above sea level; RAI, Relative Abundance Index (number of photos of unique individuals per 100 camera days).

[a]Collared peccary (*P. tajacu*) density per square kilometer (mean ± S.E). Numbers in parentheses indicate range of published estimates; letters demarcate sites with similar (when shared) or significantly ($\alpha_{(15)} \leq 0.003$) different peccary densities.

[b]Michel (2012).

[c]Wright *et al.* (1999, 2000).

[d]Eisenberg 1980, Glanz 1982, Wright *et al.* (1994, 1999, 2000).

[e]Torrealba-Suárez & Rau 1994, Romero *et al.* 2013.

TABLE 2. *Liana tangle frequency and focal bird species density (number of birds encountered/100 ha) at six lowland Neotropical sites in Nicaragua (Refugio Bartola), Costa Rica (Tirimbina Biological Reserve, La Selva Biological Station), and Panama (Limbo Hunt Club, Barro Colorado Island, Gigante Peninsula).*

Site	Liana tangle frequency[a]	Checker-throated Antwren density (/100 ha)	Dot-winged Antwren density (/100 ha)	Ruddy-tailed Flycatcher density (/100 ha)
Tirimbina Biological Reserve	20.5 ± 3.1% (AB)	28.3[b]	4.4[b]	2.2[b]
Refugio Bartola	18.9 ± 3.4% (AB)	18.4[b]	18.4[b]	12.9[b]
Gigante Peninsula	38.1 ± 4.4% (C)	130–256[b]	168–256[b]	25.6–50[b]
Limbo Hunt Club	25.2 ± 4.3% (BC)	130–166[c]	168–170[c]	33–50[c]
Barro Colorado Island	25.2 ± 3.1% (BC)	256[d]	256[d]	25.6[d]
La Selva Biological Station	13.6 ± 2.3% (A)	1.3[e]	0.6[e]	1.3[e]

[a]Percent of random points with a liana tangle. Estimates are mean ± SE; letters in parentheses demarcate sites with similar (when shared) or significantly ($\alpha_{(15)} \leq 0.003$) different peccary densities.

[b]Estimated based on BCI and Limbo densities.

[c]Robinson *et al.* (2000), N.L. Michel, unpubl. data.

[d]Robinson (2001), W.D. Robinson, unpubl. data.

[e]Sigel *et al.* (2006, 2010); N.L. Michel, unpubl. data.

mammals are rare (*e.g.*, Baird's tapirs, *Tapirus bairdii*; Timm 1994) or extirpated at all of our study sites (*e.g.*, white-lipped peccaries [*Tayassu pecari*], Wright *et al.* 1994, Romero *et al.* 2013). The remaining abundant frugivores, *e.g.*, Central American agoutis (*Dasyprocta punctata*; Kuprewicz 2013), are seed predators and dispersers that do not eat or trample existing vegetation. Therefore, we consider collared peccaries primarily responsible for vegetation effects documented here.

Published collared peccary density estimates at our study sites range from 1.0 to 65.9/km². We calculated grand means (3.0–31.7/km²) and compared sites using ANOVA and Tukey HSD *post-hoc* tests on log-transformed densities. Because BCI and Gigante density estimates were published >15 yr ago, we also calculated Relative Abundance Indices (number of unique photos (>30 min apart) per 100 camera days; O'Brien *et al.* 2003) from 2012 Tropical Ecology Assessment and Monitoring (TEAM) camera trap data (Hurtado & Jansen 2012, Table 1). Camera trap data were only available for TEAM sites (La Selva, BCI, and Gigante). Standard errors were calculated by bootstrap sampling (*N* = 1000 replicates) with replacement (Scheiner & Gurevitch 2001). Medians were compared using Kruskal–Wallis and Nemenyi *post-hoc* tests in R package PMCMR (Pohlert 2014).

FOCAL BIRD SPECIES.—We chose three understory insectivorous birds that declined at La Selva but persisted or increased at our other study sites, and consequently are less abundant at La Selva today: Checker-throated Antwren (*E. fulviventris*), Dot-winged Antwren (*M. quixensis*), and Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*). These species were chosen because they were sufficiently abundant at all sites except La Selva for analysis; are well-studied; and are considered to be representative of other small understory insectivorous birds. Focal species densities were calculated as the number of birds encountered/100 ha (Table 2). Although BCI and Limbo's last published surveys were conducted in 1995, unpublished surveys in the late 2000s suggest

that focal species densities remained steady (N.L. Michel, W.D. Robinson, unpubl. data). Mapping of the focal species trailside observations at Gigante suggested that bird densities there were intermediate between those at BCI and Limbo, and far greater than densities at the wet forest sites (N.L. Michel, unpubl. data). Although the numbers are in some cases imprecise, we have used the best available data; the late-2000s surveys at BCI and Limbo (W.D. Robinson, unpubl. data) and observations by the authors at these sites and Gigante lend credence to the density estimates.

FIELD METHODS.—We assessed foraging microhabitat selection by comparing the vegetation structure at foraging versus randomly selected locations, and the effects of the collared peccaries on vines and lianas by comparing the vegetation structure, (1) between mammal exclosures and paired adjacent controls at La Selva, BCI, and Gigante; and (2) across all study sites (Tables 1 and 2). Fieldwork was conducted during 2008 in Nicaragua, 2008–2009 in Costa Rica, and 2010 in Panama.

We located birds while walking all trails during sunrise to midday, and followed them until we observed a foraging maneuver. No more than two foraging points were recorded per individual or flock daily (≤4 points per individual or flock in total); all foraging points were ≥20 m apart (Marra & Remsen 1997). Birds were often detected >100 m off-trail, reducing trail-edge effects. Up to 23 foraging points were surveyed per species at all sites except Gigante, where foraging data were not able to be collected due to time constraint (sample sizes in Table S1).

We selected up to 80 random microhabitat points per site using stratified random sampling (Table S1). Detailed descriptions of random point selection are provided in the Appendix S1. We assessed foraging microhabitat selection (modified from Marra & Remsen 1997) using 29 habitat variables *a priori* considered important to our focal species (Table 3). Detailed descriptions of the variable collection methods are provided in the Appendix S1.

We created a composite, binary variable ('liana tangle') indicating the presence/absence of a dense vine and liana tangle, defined as ≥20 liana stems and/or ≥25 percent vine and liana cover within the 2-m-radius cylinder (12.6 m²). As we are unaware of any previous definition of 'liana tangle', we selected these categories based on the finding that densities exceeding 30 lianas per 20 m² negatively impact trees (Schnitzer *et al.* 2000). We used this composite variable to indicate the presence of liana tangles from the birds' perspective, as liana density or cover may be low if the bird was foraging near the edge of the tangle. Dense tangles of lianas are known to be important to the Checker-throated and Dot-winged Antwrens (Gradwohl & Greenberg 1980). We also conducted rapid surveys of vine and liana variables only (vine and liana density, cover, liana tangle presence/absence, and forest cover) within 2-m cylinders. These rapid liana surveys were conducted at an additional 60–140 randomly selected points per site, and within experimental mammal exclosures/controls at La Selva, BCI, and Gigante (28 random surveys per plot).

DATA ANALYSIS.—We modeled foraging microhabitat selection independently for each of the three focal bird species with classification trees in CART V6.6 (Salford Systems, San Diego, California, U.S.A.). Classification tree analysis models datasets with categorical response variables (*e.g.*, foraging vs. random), makes no frequency distribution assumptions about the data, and is unaffected by collinearity among predictor variables (Breiman *et al.* 1998). Detailed descriptions of the classification tree analytical methods are provided in the Appendix S1.

We calculated liana tangle frequency (percent of points with a liana tangle) for each focal species and site for foraging and random points, and experimental mammal exclosures and controls; and for each focal species for random points summed across all sites at which it occurred. Standard errors were calculated by bootstrap sampling ($N = 1000$ replicates) with replacement (Scheiner & Gurevitch 2001). Mammal exclosure treatment effects on vine and liana density, tangle presence/absence, and forest cover were analyzed using mixed models with exclosure treatment as a fixed effect, and treatment block as a random effect. Means of samples within exclosure and control plots ($N = 26$) were analyzed to avoid pseudoreplication (Millar & Anderson 2004). Linear and nonlinear models were used to evaluate whether collared peccary density better explained variation in liana response variables across sites than a categorical site predictor. In both cases, Gaussian models were used to analyze log-transformed density and logit-transformed percent cover measures, and binomial models to analyze liana tangle presence/

TABLE 3. *Description of microhabitat variables. All variables measured within nested 2-m- and 10-m-radius cylinders, centered around a foraging or random point, to assess foraging microhabitat selection by three avian understory insectivores (Checker-throated Antwren, Dot-winged Antwren, and Ruddy-tailed Flycatcher) at six lowland Neotropical sites in Nicaragua (Refugio Bartola), Costa Rica (Tirimbina Biological Reserve, La Selva Biological Station), and Panama (Limbo Hunt Club, Barro Colorado Island, Gigante Peninsula). The numbers in parentheses (e.g., 2 m) indicate the cylinders within which the variable was estimated. All percent covers except forest cover were assigned to cover classes: 0%, <5%, 5–15%, 15–25%, 25–35%, 35–45%, 45–55%, 55–65%, 65–75%, 75–85%, 85–95%, >95%. See Appendix S1 for descriptions of microhabitat variable collection methods.*

Variable	Description
Ground cover (2 m, 10 m)	Percent live vegetative cover, 0–0.5 m aboveground
Dead wood cover (2 m, 10 m)	Percent dead woody vegetative cover 0–0.5 m aboveground
Understory cover (2 m, 10 m)	Percent live vegetative cover, 0.5–5 m aboveground
Midstory cover (2 m, 10 m)	Percent live vegetative cover, 5–20 m aboveground
Tree density (2 m, 10 m)	Number of trees (≥ 10 cm dbh[a])
Woody stem density (2 m, 10 m)	Number of woody-stemmed plants (≥1 m tall, ≥1 cm and <10 cm dbh), and nonwoody palms, cyclanths, and Zingiberales (≥1 m tall)
Herb density (2 m)	Number of herbaceous plants (≥20 cm tall and <1 cm dbh, or ≥1 cm dbh and <1 m tall)
Vine density (2 m)	Number of vines (climbing stems <1 cm dbh)
Liana density (2 m, 10 m)	Number of lianas (climbing stems ≥1 cm dbh)
Liana cover (2 m, 10 m)	Percent vine and liana cover, 0–20 m aboveground
Palm cover (2 m, 10 m)	Percent palm and cyclanth cover, 0–20 m aboveground
Zingiberale cover (2 m, 10 m)	Percent Zingiberale cover, 0–20 m aboveground
Aerial leaf litter cover (2 m)	Percent aerial dead leaf litter cover (dead leaves and branches caught in vegetation, often lianas), 0–20 m aboveground
Gap (2 m)	Percent area with no vegetative cover between ground and canopy
Forest cover	Percent total forest cover (from canopy photograph)
Vegetation density	Vegetation density index (see Methods)
Canopy height	Canopy height in m (see Methods)
Litter depth	Litter depth in cm (see Methods)
Liana tangle	Liana tangle present/absent (≥20 lianas and/or ≥25% liana cover within 2 m cylinder)

[a]dbh, diameter at breast height (1.3 m aboveground); vine and liana diameter measured 1.3 m from the rooting point.

absence; model selection was done with Akaike's Information Criterion (Burnham & Anderson 2002). Analyses were conducted in R v. 3.1.1 (R Core Team 2014) with packages lme4 (Bates *et al.* 2014) and nlme (Pinheiro *et al.* 2014).

We constructed structural equation models (Fox *et al.* 2012) to assess the relative effects of collared peccaries and two alternative hypotheses for reduced vine and liana density/cover and focal species abundance across sites: seasonality (annual rainfall) and forest area. Our analyses assessed the roles of both direct and indirect effects, as mediated by vegetative structural elements identified as important predictors of foraging microhabitat use: specifically, vine and liana density, cover, tangle frequency, and forest cover. We transformed all the variables prior to analysis (log for densities; logit for covers and frequencies), and created a composite peccary density variable allowing quadratic effects (density + density^2). We fitted the saturated models with all direct and indirect pathways, used model selection to choose among vegetation variables identified above, then sequentially removed nonsignificant paths from the best-fitting saturated model. The final best-fit model was identified using a combination of root mean square error of approximation (RMSEA) and chi-squared goodness of fit tests, corrected using the Bollen–Stine bootstrap where needed (Fox *et al.* 2012).

RESULTS

DID LA SELVA HAVE A HIGHER COLLARED PECCARY DENSITY THAN OTHER SITES?—Peccary density differed significantly among sites ($F_5 = 5.03$, $P = 0.001$). Peccaries were significantly ($P < 0.05$) more abundant at La Selva than any other site, followed by BCI; both had greater peccary densities than Gigante, Tirimbina, and Bartola (Table 1). Collared peccary Relative Abundance Indices also differed significantly among the TEAM sites ($\chi^2 = 2881.43$, df = 2, $P < 0.0001$): Collared peccaries were $\geq 3 \times$ more abundant at La Selva than BCI ($P < 0.0001$) or Gigante ($P < 0.0001$), reinforcing the pattern from published estimates (Table 1).

DID FOCAL BIRD SPECIES PREFER LIANA TANGLES AS FORAGING MICROHABITAT?—All focal bird species preferentially selected foraging microhabitat with a 2–3-fold higher liana tangle frequency than random (Checker-throated Antwren: $\chi^2 = 44.4$, df = 1, $P < 0.0001$; Dot-winged Antwren: $\chi^2 = 50.5$, df = 1, $P < 0.0001$; Ruddy-tailed Flycatcher: $\chi^2 = 16.3$, df = 1, $P < 0.0001$; Fig. 1).

Checker-throated Antwrens selected foraging microhabitat based on liana tangle presence ($N_{foraging} = 85$, $N_{random} = 228$). Liana tangles were found three times as often in foraging (58%) versus random points (19%). Among foraging points without a liana tangle, Checker-throated Antwrens selected foraging microhabitat with <35.5 lianas within a 10-m radius (Fig. 2A). The optimum tree correctly classified 89 percent and 45 percent of foraging and random points, respectively (relative error: 0.88, ROC: 0.74). All measures of vine and liana density and cover, and aerial leaf litter cover had high variable importance scores, supporting the finding that Checker-throated Antwrens based foraging microhabitat selection on vine and liana abundance (Table S2).
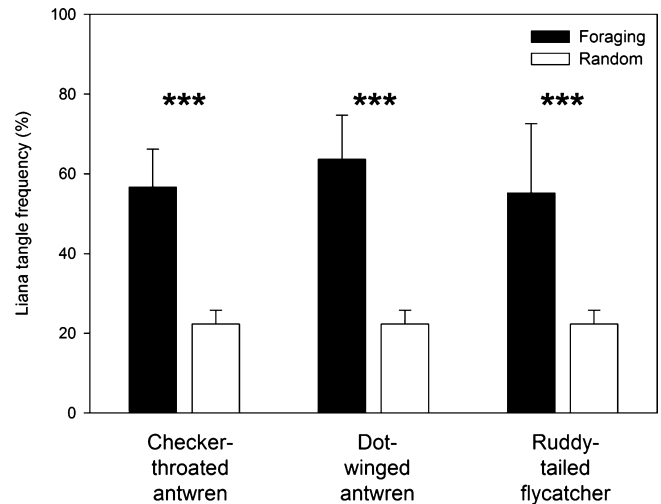

FIGURE 1. Liana tangle frequency at foraging and random points for Checker-throated Antwren, Dot-winged Antwren, and Ruddy-tailed Flycatcher. *P* values from Chi-squared tests. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Dot-winged Antwrens based foraging microhabitat selection on liana cover, midstory cover, and woody vegetation ($N_{foraging} = 68$, $N_{random} = 172$). Nearly two-thirds (65%) of foraging points had high (>25%) liana cover within a 2-m radius, versus 18 percent of random points. The remaining foraging points had low (≤65%) midstory cover, >6.5 woody stems within a 2-m radius, and <198.5 woody stems within a 10-m radius, whereas most (55%) random points had >65 percent midstory cover (Fig. 2B). The optimum tree correctly classified 87 percent and 68 percent of foraging and random points, respectively (relative error: 0.95, ROC: 0.73). Liana tangle presence, vine and liana cover and density, and aerial leaf litter cover had high variable importance scores (Table S2).

Ruddy-tailed Flycatchers selected foraging microhabitat based on vine density, aerial leaf litter cover, and understory cover ($N_{foraging} = 32$, $N_{random} = 252$). Over three-quarters (78%) of foraging points were distinguished by high vine density (>7.5 vines within a 2-m radius) and high (>6.25%) dead woody ground cover within a 10-m radius. Foraging points with low vine density had high aerial leaf litter cover. Conversely, most random points (56%) had <6.25 percent dead woody ground cover within a 10-m radius (Fig. 2C). The optimum tree correctly classified 97 percent and 62 percent of foraging and random points, respectively (relative error: 1.10, ROC: 0.68). Liana tangle presence, vine and liana cover and density, and aerial leaf litter cover had high variable importance scores, supporting the finding that Ruddy-tailed Flycatchers also chose foraging microhabitat based on vine and liana abundance (Table S2).

WERE ABUNDANT COLLARED PECCARIES ASSOCIATED WITH REDUCED VINE AND LIANA DENSITY AND COVER?—Liana tangle frequency was significantly greater within experimental mammal exclosures across all sites with exclosures ($\beta = 3.00 \pm 0.88$ SE, $t = 3.42$, $N = 26$,
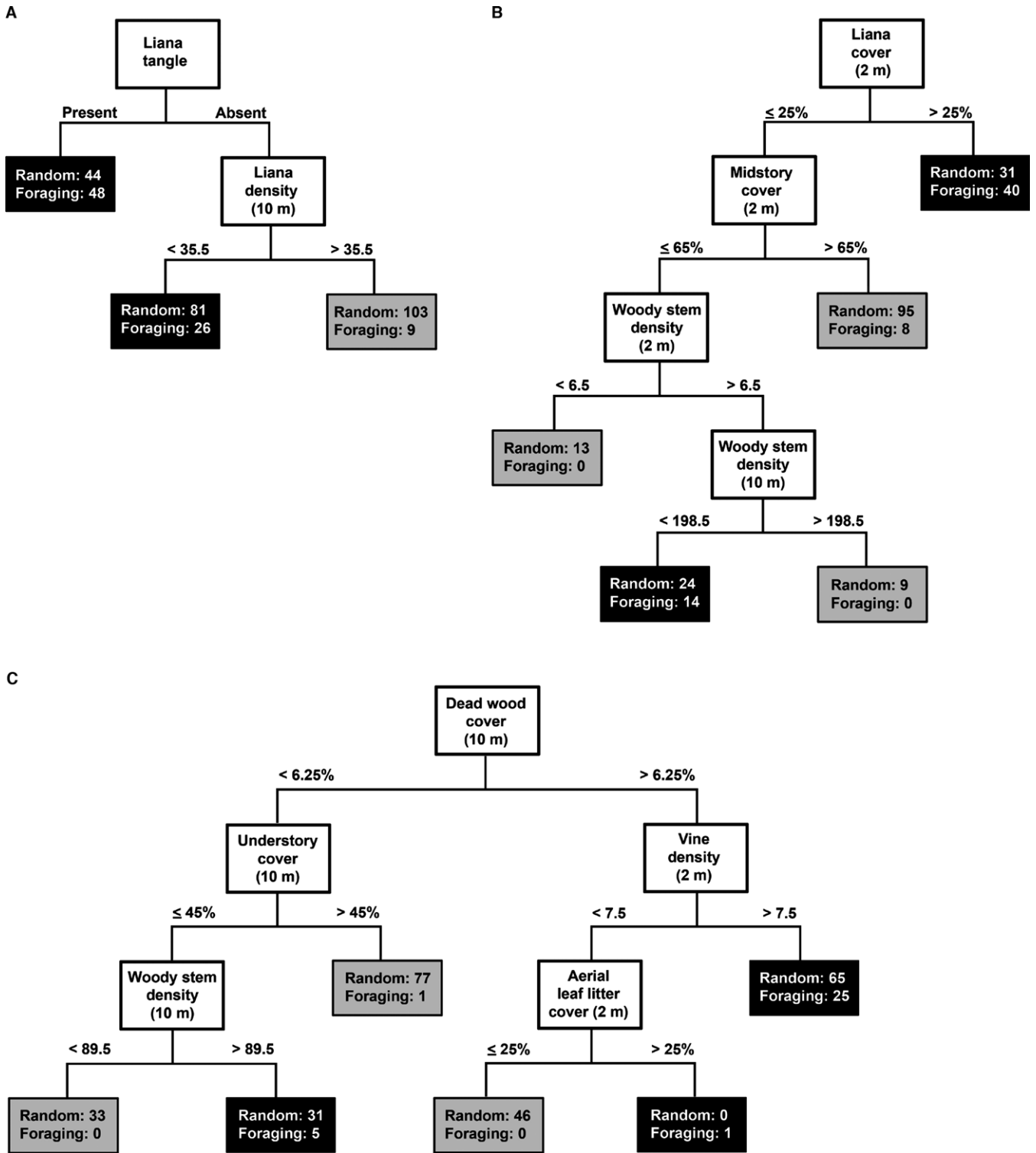
FIGURE 2. Optimal classification tree distinguishing foraging and random microhabitat for (A) Checker-throated Antwren (*E. fulviventris*), (B) Dot-winged Antwren (*M. quixensis*), and (C) Ruddy-tailed Flycatcher (*T. erythrurus*) at four lowland Neotropical sites in Nicaragua (Refugio Bartola), Costa Rica (Tirimbina Biological Reserve), and Panama (Barro Colorado Island, Limbo Hunt Club). Splitting variable codes appear within white boxes (see Table S2); numbers (text) below the splitting boxes show the values (states) of each variable where the split occurred. Numbers inside terminal nodes indicate the number of random and foraging points included. Shading indicates the designated class for each terminal node (black = foraging microhabitat, gray = random microhabitat).

$P = 0.005$), with a 133 percent increase (*i.e.*, 57% reduction in the presence of peccaries relative to mammal exclosures) at La Selva, where peccaries were most abundant (Table 4; Fig. 3A). Vine density ($\beta = 5.58 \pm 1.95$ SE, $t = 2.86$, $N = 26$, $P = 0.01$; Fig. 3B), liana cover ($\beta = 4.57 \pm 1.69$ SE, $t = 2.71$, $N = 26$, $P = 0.02$; Fig. 3D), and forest cover were also significantly greater within exclosures across sites ($\beta = 0.88 \pm 0.38$ SE, $t = 2.30$, $N = 26$, $P = 0.02$; Fig. 3E), but not liana density (Table 4; Fig. 3C).

Across sites, many vine and liana response variables showed curvilinear threshold relationships (quadratic/cubic) with collared peccary density, with peaks at intermediate peccary density and reduced vine and liana density and cover at high peccary densities (Table 4; Fig. 3). Within- and among-site variation in liana density (2 m and 10 m), liana cover (2 m), forest cover, and aerial leaf litter cover (but not liana tangle presence or vine density) was explained as well or better by a curvilinear response to collared peccary density, as by a categorical site predictor variable (Table 4). Meancollared peccary density explained up to 92 percent of the variation in site-level mean vine and liana density, cover, and forest cover (Fig. 3).

WERE ABUNDANT PECCARIES ASSOCIATED WITH REDUCED UNDERSTORY INSECTIVOROUS BIRD ABUNDANCE?—Structural equation models suggest that the collared peccaries had significant negative indirect effects on the abundance of all three focal bird species across sites (Fig. 4). The best-fitting model for Checker-throated Antwrens ($\chi^2 = 35.14$, $P_{\text{Bollen-Stine}} = 0.75$, RMSEA = 0.51) indicated that collared peccaries had significant ($P < 0.05$) negative indirect effects on bird abundance (-0.16) mediated by liana density (10 m). Both forest area (-0.47) and rainfall (-1.63) also had negative direct effects on Checker-throated Antwren abundance, and annual rainfall had negative indirect effects mediated by both liana density and liana tangle frequency (Fig. 4A).

The optimal model for Dot-winged Antwrens ($\chi^2 = 20.74$, $P_{\text{Bollen-Stine}} = 0.91$, RMSEA = 0.42) showed that the collared peccaries had both negative direct (-1.60) and indirect (-1.68) effects on bird abundance mediated by forest cover. Rainfall had negative indirect effects on Dot-winged Antwren abundance mediated by both liana cover (2 m) and forest cover, but forest area was not retained in the best model (Fig. 4B). The optimal model for Ruddy-tailed Flycatchers ($\chi^2 = 0.42$, $P = 0.94$, RMSEA = 0.00) indicated that the collared peccaries had both negative direct (-0.13) and indirect (-0.10) effects on bird abundance mediated by vine density (2 m). Rainfall had negative direct effects on Ruddy-tailed Flycatcher abundance (-1.06), but forest area was not retained in the best model (Fig. 4C).

DISCUSSION

Our findings generally support the hypotheses: the three focal species foraged preferentially in liana tangles; vine and liana density and cover were lower in the presence of collared peccaries relative to the experimental mammal exclosures; and liana density, cover, and forest cover exhibited negative curvilinear relationships with collared peccary density across sites. The structural equation models suggested that collared peccaries have negative direct and indirect effects on the abundance of all focal bird species. Other factors, including forest area and rainfall modeled here (Fig. 4), also had negative direct and indirect effects on focal bird species abundance. Yet our findings reveal that after accounting for alternative hypotheses, abundant collared peccaries were associated with the reduced availability of a key foraging substrate, vine and liana tangles, and thus appear to have contributed to the reduced abundance of these understory insectivores.

Our findings are drawn from the data collected during a brief window following 40 yr of increasing collared peccary abundance (Romero *et al.* 2013) and declining understory insectivorous

TABLE 4. *Model selection table evaluating (A) effects of mammal exclosure treatments within sites (Gigante, BCI, and La Selva), and (B) effects of collared peccary density across sites in explaining variability in liana tangle presence/absence, vine and liana density and cover, forest cover, and aerial leaf litter cover. The best model(s) (AIC ≥ 2.0 below next model) for each response variable are indicated in boldfaced text.*

| Predictor variables	Liana tangle presence	Vine density (2 m)	Liana density (2 m)	Liana cover (2 m)	Forest cover	Aerial litter cover (2 m)	Liana density (10 m)
A. Mammal exclosure							
Treatment × Site	744.0	1849.4	1112.1	2109.9	1721.5		
Treatment + Site	743.5	1843.5	1104.1	2107.1	1719.8		
Treatment	**739.6**	**1840.6**	1106.8	**2101.0**	**1725.5**		
Site	753.2	1872.7	**1098.8**	2122.2	1728.9		
Intercept only	749.2	1869.7	1101.6	2116.1	1734.6		
B. Across sites							
Peccary density + density^2 + density^3	1029.4	2801.6	**1427.8**	556.5	**2436.7**	**617.5**	**783.1**
Peccary density + density^2	1028.6	2800.3	1441.9	**554.7**	2446.7	620.6	786.0
Peccary density	1041.0	2825.2	1537.9	560.0	2475.4	652.5	893.4
Site	**1025.1**	2766.7	1426.6	552.7	2435.0	620.5	786.5
Intercept only	1043.8	2831.4	1539.6	561.0	2503.0	654.3	892.5
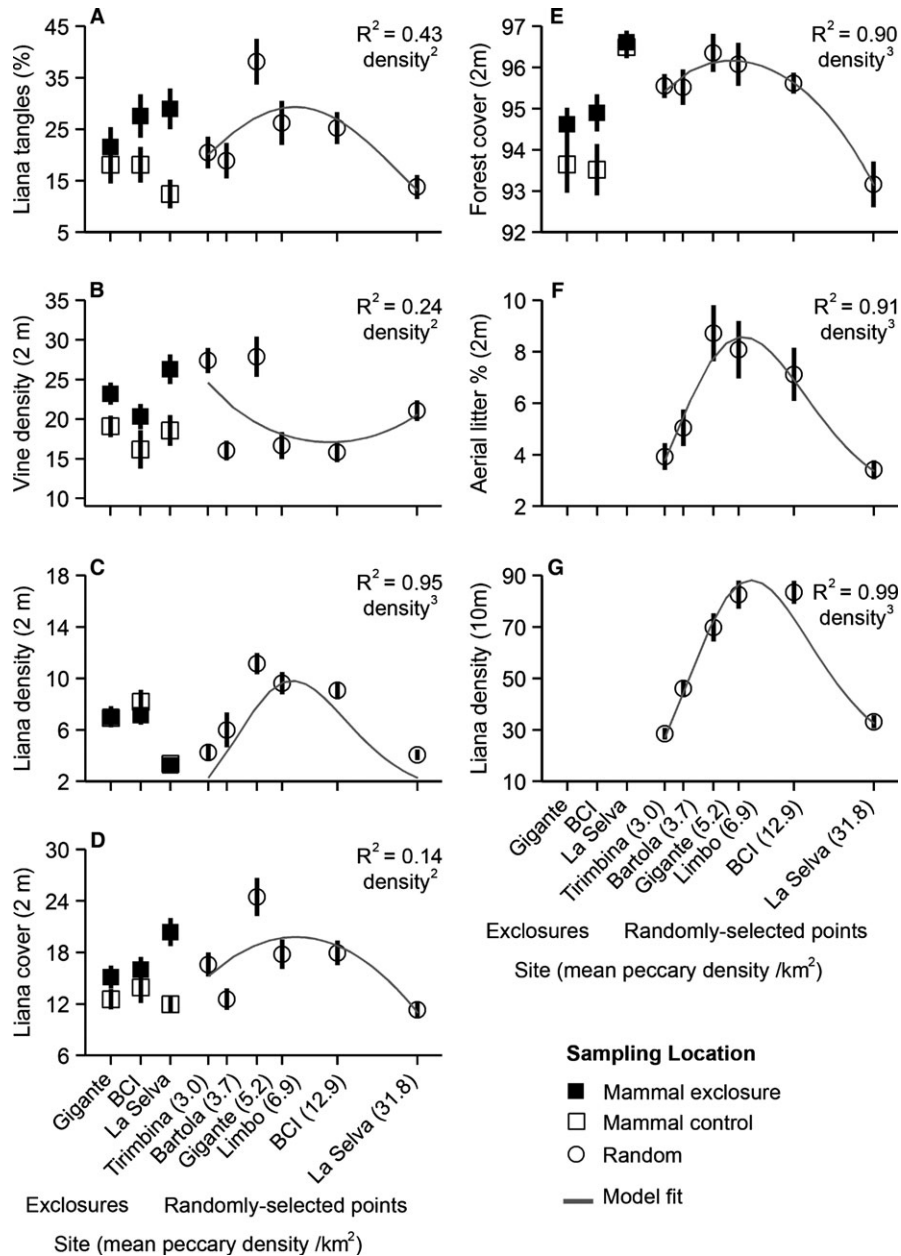
FIGURE 3. Effects of experimental mammal exclosure on, and cross-site differences among, (A) liana tangle frequency, (B) vine density (2 m), (C) liana density (2 m), (D) liana cover (2 m), and (E) forest cover (2 m); and cross-site differences only among (F) aerial leaf litter cover (2 m), and (G) liana density (10 m). Liana response estimates are reported from experimental mammal exclosures and paired controls at Gigante Peninsula, BCI, and La Selva Biological Station; and from randomly selected points at Tirimbina Biological Reserve, Refugio Bartola, Gigante, Limbo Hunt Club, BCI, and La Selva. Bars show standard error; sites are listed in order of increasing mean collared peccary density. Gray lines represent response values predicted by collared peccary density from the best-fitting model; the order of the best-fitting model (density[2], density[3]; see Table 4) is specified.

bird abundance at La Selva (Sigel *et al.* 2006, 2010). As such, we cannot definitely speak for the causes of temporal trends in understory insectivorous bird populations. We also acknowledge that some of the published bird and peccary density estimates were collected >10 yr prior to vegetation surveys, although we validated the historical estimates to the best of our ability using current, unpublished data. Additionally, the cross-site analyses (Table 4; Fig. 3) are correlative; however, they are consistent with

the experimental results showing that vine and liana density, cover, and tangle frequency are significantly greater within the mammal exclosures differing from the adjacent control plots only in the absence of large mammals. Despite these weaknesses, we have compiled a set of findings that, taken together, suggest a role for collared peccaries in understory insectivorous bird declines. Namely, collared peccaries are associated with the reduced availability of preferred foraging microhabitat of birds
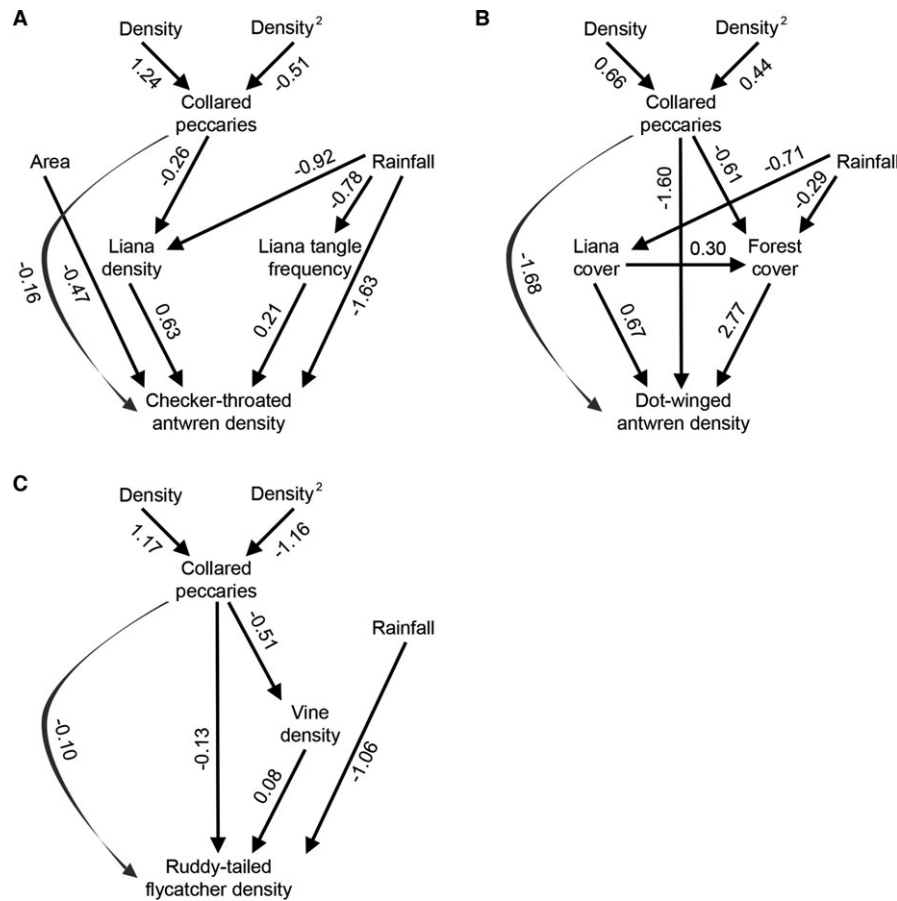
FIGURE 4. Structural equation models for the effects of collared peccary density, forest area, rainfall, and vegetation structure characteristics on (A) Checker-throated Antwren, (B) Dot-winged Antwren, and (C) Ruddy-tailed Flycatcher density at six lowland Neotropical sites in Nicaragua (Refugio Bartola), Costa Rica (Tirimbina Biological Reserve, La Selva Biological Station), and Panama (Limbo Hunt Club, Gigante Peninsula, Barro Colorado Island). We used a composite variable to represent quadratic (density + density^2) effects of collared peccary density (see Methods). Gray curved arrow indicates indirect effects of collared peccaries on bird density mediated by vegetation structure. Standardized path coefficients are shown.

that have declined at a site where collared peccary densities have concurrently increased the most (La Selva). Yet the same bird species have exhibited increasing trends at BCI (Robinson 2001) where collared peccaries have not exhibited a directional trend in abundance (Eisenberg 1980, Glanz 1982, Wright *et al.* 1994, 1999, 2000), and remain abundant at other sites with lower collared peccary densities. Therefore, we suggest that collared peccaries provide one plausible explanation for the spatial variation in population trends of Central American liana-dependent understory insectivorous birds (Robinson 2001, Sigel *et al.* 2006, 2010).

This peccary–liana hypothesis adds to a suite of existing causes proposed to explain declines of tropical understory insectivorous birds. The existing causes likely explain declines of some species or at some locations, *e.g.*, dispersal limitation for extremely fragmentation-sensitive birds or birds in small, isolated fragments (Stouffer *et al.* 2011) and nest predation for species with particularly vulnerable nests or incapable of repeat re-nesting (Young *et al.* 2008, Visco & Sherry 2015). However, area sensitivity does not explain the abundance patterns observed in these species as La Selva—our study site experiencing severe focal species declines—

shares its southern border with the 46,000 ha Braulio Carrillo National Park. Meanwhile, the focal species have persisted at the smaller and more isolated Tirimbina, increased at BCI despite its similar size to La Selva and complete isolation, and have similar nest predation rates at La Selva and BCI (Young *et al.* 2008, Kelley 2011). Indeed, forest area was retained in the best structural equation model for only one species, Checker-throated Antwren (Fig. 4). Although edge effects on prey availability, vegetation structure, microclimate, and nest predation have been implicated in the declines of some tropical forest birds (Laurance 2004, Stratford & Robinson 2005, but see Vetter *et al.* 2013), they are unlikely to explain declines of these focal species at either La Selva (Visco & Sherry 2015) or BCI. The focal species do not avoid, indeed even exploit, forest edges and gaps (Levey 1988, Lindell *et al.* 2007), consistent with their preference for gap-exploiting lianas (Schnitzer *et al.* 2000). Moreover, edge effects typically extend <150 m into forest interior and thus affect <10 percent of forest area in fragments the size of BCI and La Selva (Laurance 2000).

Although climate change may explain declines of montane birds or lowland species isolated from mountains (Şekercioğlu

et al. 2012), it does not explain why these species would decline at La Selva but not at a site within 7 km distance at similar elevation (Tirimbina). Similarly, differences in forest age or structure cannot explain declines of these species in old growth forest at La Selva but not within forest of similar age, structure, and composition at Tirimbina (Guariguata et al. 2000). In what follows we review the strength of the findings supporting each hypothesis and their implications.

PECCARIES ARE ASSOCIATED WITH REDUCED VINES AND LIANAS.— Liana tangle frequency, vine density, liana cover, and forest cover were lower in the presence of peccaries relative to experimental mammal exclosures at all three sites. Although rainfall contributes to liana abundance (DeWalt et al. 2010), peccary density explained as much or more variation in liana density and cover as a categorical site variable that also accounts for other such site differences. The strongest exclosure effects were at La Selva, which is particularly noteworthy since La Selva's mammal exclosures were established 6 yr later than those in Panama, and were surveyed 1–2 yr earlier (2008–2009 vs. 2010), yielding a shorter response time to exclosure treatment. La Selva's mammal exclosures, unlike Panama's, also failed to exclude small seed-predating vertebrates such as rats and agoutis, which may counteract mammal exclosure effects by consuming seeds of nonwind-dispersed lianas such as *Mucuna holtonii* (Kuprewicz 2013). These differences in exclosure design and duration should have resulted in smaller exclosure effect sizes at La Selva than in Panama, yet liana tangle frequency, vine density, and liana cover showed slightly stronger responses at La Selva (Fig. 3). Further experimental studies would help explain these differences.

Peccaries may impact vines and lianas through a combination of trophic (consumptive) and nontrophic (trampling, rooting) effects. Liana stems are typically smaller and have weaker structural protection (*i.e.*, thinner bark, lower wood density) than free-standing trees (Putz 1984), which may increase vulnerability to peccary consumption and trampling. Although many lianas produce woody thorns, these may not deter peccaries, which frequently eat walking palm roots with woody spines (*e.g.*, *Socratea exorrhiza*; Beck 2006). Peccaries may also be drawn to liana tangles for food (*e.g.*, leaves, roots, arthropods; Beck 2005). Peccaries are also major seed predators, but most Neotropical lianas have small, wind-dispersed seeds that are unlikely to be consumed by peccaries (Muller-Landau & Hardesty 2005). Although peccaries reduce leaf litter depth and abundance of some litter arthropods (Michel 2012), terrestrial leaf litter disturbances are unlikely to explain focal species declines as they forage in the forest midstory and canopy (Gradwohl & Greenberg 1980, Sherry 1984).

Our finding that abundant collared peccaries were associated with reduced vines and lianas at La Selva seemingly contradicts a recent study documenting increased liana density and the basal area there during 1999–2007 (Yorke et al. 2013). However, the liana increases described there are smaller than those at other Neotropical sites: 15–20 percent within old growth forest only at La Selva, versus 50–65 percent across BCI (Wright et al. 2004, Ingwell et al. 2010). Moreover, La Selva's liana increases were

primarily due to clonal colonization by large ramets (Yorke et al. 2013) that are presumably less likely to be eaten or trampled by collared peccaries. Thus, we see no inconsistency.

LIANA TANGLES ARE IMPORTANT TO UNDERSTORY BIRDS.—Vines and lianas provide many direct and indirect benefits to birds, including food, nesting sites, and protection from predators (Michel et al. 2015). We suggest that the focal species responded primarily due to the dense vegetation provided by liana tangles. Checker-throated Antwrens forage in dead leaves that accumulate in dense vegetation, while Dot-winged Antwrens and Ruddy-tailed Fly-catchers both use high-energy foraging strategies: gleaning and aerial pursuit, respectively (Fitzpatrick 1980, Gradwohl & Greenberg 1980, Sherry 1984). These strategies are best suited to dense vegetation such as that found in vine and liana tangles, where arthropod densities are often greatest (Dial et al. 2006).

However, reduced liana tangle frequency could affect birds via alternative mechanisms. Lianas account for ≥30 percent of rain forest canopy vegetation (Avalos & Mulkey 1999); consequently, the reduction in lianas by peccaries decreased total forest cover, likely increasing understory light availability and microclimatic variability. Alternatively, liana reduction by peccaries may increase nest predation rates, much as the abundant deer (*Odocoileus* spp.) in North America do by thinning vegetation cover (Allombert et al. 2005, Michel & Sherry 2012). Yet the fact that La Selva's bird declines are most pronounced among insectivores that frequent forest edges and gaps and nest in midstory vegetation suggests that peccary impacts are primarily mediated through arthropod prey availability rather than altered light or predation regimes (Sigel et al. 2006). Further research on understory insectivorous birds' responses to experimental liana manipulation would help identify mechanisms.

APPLICABILITY OF OUR FINDINGS TO OTHER MAMMAL COMMUNITIES AND AVIAN GUILDS.—Our research highlights the potential for large omnivores such as peccaries to contribute to reduced abundance of animals with which they are not trophically linked, through a combination of ricocheting top-down (peccary–liana) and bottom-up (liana–bird) cascades. Although peccaries serve as ecosystem engineers benefiting amphibians (Beck et al. 2010), their effects on other animals are not universally positive. While few ricocheting cascades have been documented in the Neotropics, consumption of canopy leaves by African megafauna (*e.g.*, elephants, giraffes) reduces arthropod, bird, and lizard abundance and diversity (Ogada et al. 2008). A global meta-analysis, including studies from tropical forests (Latin America, Asia, and Africa), showed that high densities of large native mammalian herbivores reduce the abundance and richness of other animals (Foster et al. 2014). Such consequences of large mammal disturbance likely extend beyond the focal species considered in the present study.

Although most of the neotropical research focuses on the consequences of defaunation rather than abundant mammals (Michel & Sherry 2012), we argue that our findings strike a cautionary note for current and future management of tropical forest

reserves. Our study sites, particularly La Selva, are unusual in that apex predators and competing white-lipped peccaries have been lost or greatly reduced due to regional hunting and fragmentation, yet thorough patrolling limits compensatory hunting of collared peccaries while adjacent farms provide supplementary food (Torrealba-Suárez & Rau 1994). However, apex predator loss is a pervasive problem in tropical forests (Estes *et al.* 2011). Most hunted forests today lack predators, herbivores, and omnivores alike (Peres & Palacios 2007, Harrison 2011). Yet if hunting is reduced in other fragmented tropical reserves without concurrent reintroduction or re-colonization of predators, herbivore and omnivore populations may increase, creating the potential for ricocheting trophic cascades such as described here and at Lago Guri (Feeley & Terborgh 2008). Determining the tolerable abundance ranges of such animals to maintain forest health and biological diversity is an important conservation challenge deserving future emphasis.

A recent study of historical and current peccary abundance at La Selva suggests that collared peccaries experienced compensatory population growth following white-lipped peccary extirpation, suggesting that La Selva's collared peccary densities—and, by extension, their effects—are similar to historical levels of the two species combined (Romero *et al.* 2013). Discussions of whether collared peccaries should be considered overabundant at La Selva, and the mechanisms by which they reached today's abundance, are beyond the scope of our study. However, we note that La Selva's collared peccary density (mean: $31.8 \pm 9.5/\text{km}^2$) exceeds the summed density of collared and white-lipped peccaries in both lightly hunted regions of Mexico's Montes Azules Biosphere Reserve ($7.9/\text{km}^2$ and $1.5/\text{km}^2$; Naranjo *et al.* 2004) and unhunted Amazonian sites ($6.6/\text{km}^2$ and $10/\text{km}^2$, respectively; Peres & Palacios 2007), suggesting that collared peccary abundance has progressed beyond compensatory levels. Moreover, collared peccary abundance is substantially greater at La Selva than in any other site of which we are aware, although white-lipped peccaries have long been extirpated from all sites considered here. Although fragmentation may artificially inflate ungulate densities by concentrating animals in a small space and restricting large-scale movements, this is unlikely by itself to explain La Selva's high collared peccary density. Unlike the wide-ranging white-lipped peccaries, collared peccaries maintain and defend relatively small (64–109 ha in northwestern Costa Rica; McCoy *et al.* 1990) year-round territories (Sowls 1984). Moreover, as La Selva is connected to the 46,000 ha Braulio Carrillo National Park while BCI is completely isolated, BCI should have the highest collared peccary densities if fragmentation alone were responsible.

Moreover, other bird species and guilds may be affected by abundant large mammals, including but not limited to collared peccaries. Liana tangles persist in forest canopies for decades after formation (Schnitzer *et al.* 2000), providing a stable long-term habitat feature used by up to 450 species of birds (Michel *et al.* 2015). Several other birds that forage, roost, and/or nest in liana tangles, or that are associated with antwren-nucleus mixed-species flocks, have also experienced moderate to severe declines at La Selva, including White-flanked Antwrens (*Myrmotherula axillaris*), Streak-chested Antpittas (*Hylopezus perspicillatus*), and Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*; Sigel *et al.* 2006, 2010, Michel *et al.* 2015). Tropical understory birds frequently exhibit specialization for other microhabitats, *e.g.*, bamboo (Kratter 1997), and other mammalian herbivores frequently reduce the abundance and richness of tropical and temperate birds via effects on the vegetation structure (Foster *et al.* 2014).

CONCLUSIONS

Our research reveals that native large mammals may, in sufficient abundance, contribute to the declines of birds to which they are not trophically linked, at least within anthropogenically disturbed tropical forest reserves. Moreover, tropical rain forest insectivorous birds, such as the focal species in this study, often limit plant damage by consuming herbivorous arthropods (Michel *et al.* 2014). Our research highlights the importance of maintaining apex predators and monitoring avian and mammalian communities even in relatively large (>1000 ha), protected forest reserves. Conserving large tracts of intact tropical rain forest is necessary, but may not be sufficient, to maintain their biodiversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

APPENDIX S1. Supplemental methods.
TABLE S1. *Number of foraging and random points and liana surveys conducted at each study site.*
TABLE S2. *Variable importance score for all microhabitat variables included in, or considered as surrogates for inclusion in, the optimal*

classification trees modeling microhabitat selection by Checker-throated Antwrens, Dot-winged Antwrens, and Ruddy-tailed Flycatchers.

FIGURE S1. Study site locations, mammal exclosure locations, and land cover in Nicaragua, Costa Rica, and Panama.

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