Forest fragmentation and loss reduce richness, availability, and specialization in tropical hummingbird communities

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ABSTRACT

Hummingbirds are important pollinators of many native Neotropical plants but their abundance and diversity in landscapes dominated by intensive human uses such as agriculture have rarely been examined, despite such land-uses prevailing in the tropics. We examined how tropical deforestation affects hummingbird community structure in premontane forest patches embedded in a tropical countryside of Coto Brus Canton, Costa Rica. We captured hummingbirds in fourteen landscapes representing a gradient in patch size and forest amount, and tested for the effects of these variables on (1) hummingbird captures at flowers (pollinator availability); (2) species richness; and (3) filtering of functional traits. After accounting for sampling effects, both hummingbird availability and species richness declined by 40% and 50%, respectively, across the gradient in deforestation that we observed (9–66% forest within 1000 m). Focal patch size was the strongest predictor, even after statistically accounting for the amount of forest and matrix composition of landscapes. These reductions in availability and richness were well predicted by functional traits; morphologically specialized species with the capacity to transport long-distance outcrossed pollen and low functional redundancy within the pollinator network showed the greatest sensitivity to landscape change. We hypothesize that declines in hummingbird availability, diversity, and functional traits are important mechanisms driving the observed pollen limitation of ornithophilous flowers in fragmented tropical landscapes. Efforts to conserve large forest patches and enhance matrix permeability are critical for maintaining forest hummingbird communities and pollination services under current and predicted deforestation regimes.

Abstract in Spanish is available with online material.

Key words: Costa Rica; forest fragmentation; habitat loss; pollinator availability; species richness; tropical hummingbirds.

DECLINING POLLINATION SUCCESS ACROSS MULTIPLE ECOSYSTEMS AND PLANT LIFE HISTORY TRAITS HAS LED TO CONCERN ABOUT THIS CRITICAL ECOSYSTEM FUNCTION (Kremen et al. 2002, Aguilar et al. 2006, Eckert et al. 2010). Habitat loss and fragmentation, by decreasing the availability of native pollinators, are often implicated as primary drivers of these pollination declines (Aguilar et al. 2006, Eckert et al. 2010). Such pollinator declines have received a great deal of attention, particularly with respect to agricultural crops (Potts et al. 2010). However, concern over the status of pollinators extends beyond species of strict economic interest (Winfree et al. 2011). Availability of animal pollinators is critical for pollination of ~81% of the world's plant species (Ollerton et al. 2011) and despite the lack of causal links, parallel declines in plants and their pollinators (Biesmeijer et al. 2006) underscore the need for better understanding of pollinator responses to ongoing landscape alteration. This is particularly true in the tropics where pollinator diversity is highest and land-use change is occurring at the greatest rates (Hansen et al. 2013).

Though the asymmetric structure of mutualistic networks is thought to contribute stability in the face of environmental change (Memmott et al. 2004, Bascompte et al. 2006), recent empirical evidence suggests that this theoretical buffering capacity may be overestimated and even small changes in composition of the pollinator community can have important impacts on pollination rates (Brosi & Briggs 2013, Fründ et al. 2013). Reduced pollinator availability (Potts et al. 2010) can increase competition among flowers for limited pollination services, decrease visits, and subsequently reduce pollination success (Eckert et al. 2010). Pollinator diversity per se is also important to pollination systems; in a global study of pollinator effectiveness, Garibaldi et al. (2013) found that fruit set increased and became less variable with increasing pollinator diversity.

Understanding the responses of pollinator abundance, richness, and functional traits (Mouillot et al. 2013, Maglianesi et al. 2015) to landscape changes is an essential step in predicting potential impacts to pollination webs. Pollinator characteristics such as foraging specificity, foraging behavior, and body size have all been shown to influence pollination success (Ghazoul 2005) and not all floral visitors are likely to be equally effective for a particular plant species (Fenster et al. 2004, Betts et al. 2015). For example, floral specialist pollinators are expected to deliver both larger quantities and quality of pollen (Aizen & Harder 2007). Spatial patterns of foraging also impact pollination since pollinators exhibiting territorial foraging strategies may move pollen over

relatively short distances leading to high selfing rates, whereas traplining pollinators that forage over longer distances should increase outcrossing rates (Ohashi & Thomson 2009). Similarly, larger-bodied pollinators often move pollen longer distances than smaller species (Greenleaf et al. 2007) and/or have lower levels of functional redundancy within the system (Dalsgaard et al. 2008).

Functional traits associated with higher outcrossing rates are likely to be among those most vulnerable to landscape changes. The 'specialization disturbance hypothesis' (Vazquez & Simberloff 2002) predicts that specialized species (both in habitat and diet) should be especially susceptible to anthropogenic disturbances (Clavel et al. 2011, Aizen et al. 2012), but evidence for this has been mixed (Vazquez & Simberloff 2002, Biesmeijer et al. 2006). Under this hypothesis, specialist pollinators, particularly those with large body sizes, should need to move further than generalists in order to acquire the necessary resources (Stiles 1978). If the foraging and dispersal movements of such species are constrained by habitat loss and/or fragmentation, they will be the first to be extirpated from degraded landscapes.

Because of their capacity for long-distance movements in inclement weather conditions, hummingbirds are important pollinators for a large number of Neotropical plant species (Bawa 1990). Ten to 30% of plants in tropical communities are estimated to be hummingbird pollinated (Feinsinger 1983, Stratton 1989). However, models of effects of landscape change on hummingbirds have proven difficult to generalize (Lindell et al. 2006). Previous work on the susceptibility of hummingbird community structure to landscape alteration has shown a remarkable resilience to landscape alteration – at least in comparison to other groups (e.g., ground-foraging insectivores; Stouffer & Bierregaard 1995b, Pearman 2002). This has been attributed to hummingbirds' capacity to use nectar resources in regenerating forest areas (Borges 2007) and their relatively high vagility (Moore et al. 2008). However, most studies to date have been conducted in landscapes where forest regeneration between remnant fragments is common (Stouffer et al. 2006). It is now well-known that the condition of the intervening land that exists between forest fragments has a strong impact on biodiversity responses to land-use change (Taylor et al. 1993, Prevedello & Vieira 2010, Driscoll et al. 2013). Given that most tropical deforestation results in forest fragments embedded within more permanent intensive agriculture or pasture (i.e., a high-contrast non-forest matrix; DeFries et al. 2010, Laurance et al. 2014), there is a great need to test the influence of forest loss and fragmentation in such landscapes.

Our objectives were to (1) test whether tropical deforestation reduces the availability and richness of hummingbird pollinators; and (2) test whether functional traits associated with foraging specialization (e.g., body size, bill shape, foraging behavior; Maglianesi et al. 2014) effectively predict fragmentation-induced changes to hummingbird community structure. In our tropical forest system, foraging movements of several morphologically specialized species are sensitive to fragmentation (Hadley & Betts 2009, Volpe et al. 2014). Such species tend to be 'trapliners' in that rather than engaging in territorial defense, they move long distances across landscapes to acquire resources (Gill 1988). If landscape-sensitive movement behavior scales up to influence patch occupancy by these species, fragmentation should impose a strong filter on morphological specialization (i.e., bill size and shape), body size, and foraging mode (i.e., territorial vs. traplining) of the pollinator community. Therefore, we predict that both availability and species richness of specialized pollinators will be reduced in small forest patches, particularly when little forest remains within the landscape. To our knowledge, ours is the first replicated study to conduct such tests in predominantly agricultural landscapes that represent one of the most common tropical deforestation regimes.

METHODS

STUDY AREA.—The study was conducted in an (~31,000 ha) area of Coto Brus Canton in southern Costa Rica (8°47'7″ N, 82°57'32″ W) surrounding the Organization for Tropical Studies Las Cruces Biological Station. The study region is composed of 43.2% Pacific premontane tropical forest and spans an elevation gradient from 300 to 1500 m a.s.l. The agricultural matrix was previously forested, but now is dominated by pasture (~80% of the matrix) and shade-coffee plantations. The majority of land clearing occurred from 1960 to 1990 (Zahawi et al. 2015), and remaining forest patches span a range of sizes from <1 to >1000 ha across a gradient in forest amount from 1% to 99% forest within a 1-km radius.

SAMPLE PATCHES.—We used a stratified random sample to select 14 focal landscapes (Fig. 1) representing a gradient in habitat loss (amount of forest) and fragmentation (size of focal patch; sensu Hadley et al. 2014, Hadley & Betts 2016). Landscapes ranged in forest cover from 9% to 66% within 1000 m and focal patch size ranged from 1.7 to >1300 ha (Table S1). We digitized landcover from 2005 to 2014 images (Google Earth 2014) using ArcMap 10.0 (ESRI 2011). We separately quantified the landscape composition of these 14 landscapes within two distances surrounding the focal patch representing roughly one (500 m) and two times the radius (1000 m) of species thought to have among the largest home ranges in the system (Volpe et al. 2016). Composition metrics included the amount of mature tropical forest, regenerating forest (1–3 m tall), agricultural land (primarily coffee/banana plantations), and pasture (Fig. 1). These landscape composition metrics were calculated by summing all the 10 m by 10 m pixels within the two radii above (e.g., forest amount within 1000 m was calculated by using all the area pixels classified as forest within 1000 m). We included matrix floral resource density as an additional composition variable (see 'matrix resources' below for details).

In this system, patch size and forest amount are typically positively correlated with elevation because of historical land clearing practices in the area, a pattern which has proven problematic for interpretation of results from earlier studies (Borgella et al. 2001). Therefore, we stratified sample landscapes across two elevation bands (low: 900–1199 m a.s.l. and high: 1200–1500 m a.s.l.) to avoid confounding with elevation. Under this
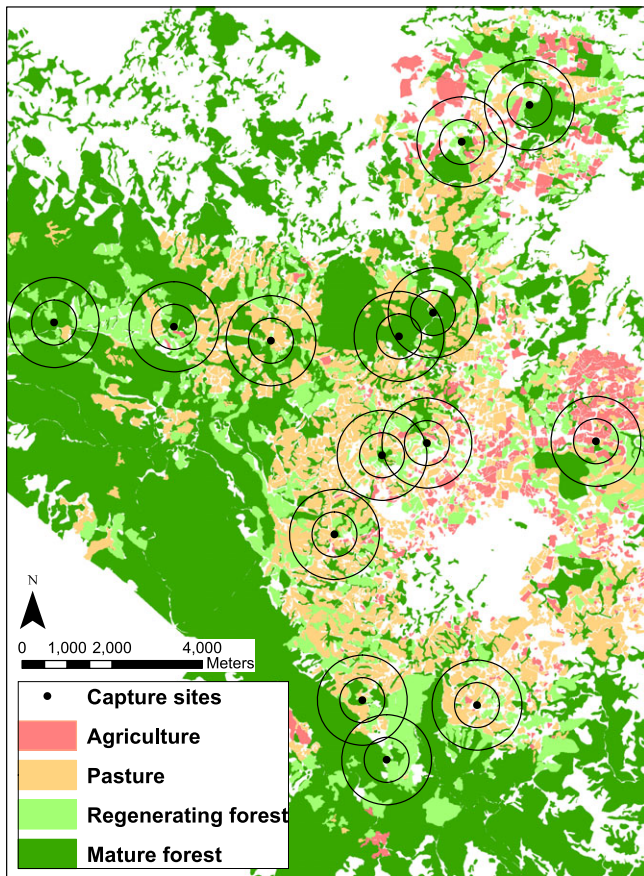
FIGURE 1. Map of the study area in Coto Brus, Costa Rica, showing the hummingbird sampling locations. The two landscape radii (500 m and 1000 m) are outlined by black circles.

design, correlations between elevation and patch size ($r = 0.31$) and elevation and amount of forest within 1000 m ($r = 0.24$) were substantially reduced (for correlations among all landscape-scale predictor variables see Table S2).

HUMMINGBIRD CAPTURES.—We captured hummingbirds in the center patch of each focal landscape from February to March (2010–2011) using standard mistnetting approaches. Ten mist nets (six 12-m and four 6-m) were placed opportunistically at separate locations <3 m in front of understory ornithophilous flowers beginning from a randomly selected point along each patch edge. We placed the nets to representatively sample the ornithophilous understory floral community of the forest patch. Captures in mist nets may not reflect actual abundance of species within all vertical strata of the forest patch (Stouffer & Bierregaard 1995a). However, capture data from nets placed immediately adjacent to understory flowers (<3 m) do indicate the presence and relative availability of pollinators available to pollinate them. Percentages of plants pollinated by hummingbirds are also much higher in the understory than within the canopy (Bawa 1990).

Estimating occupancy and abundance while accounting for imperfect detection is problematic for mist net studies because the assumption of closure between trapping sessions is violated. This is particularly the case for species that move long distances, such as traplining hummingbirds (Rota *et al.* 2009). Our primary focus was to test whether hummingbirds were present at flowers and therefore available as potential pollinators; thus, 'hummingbird availability' is more biologically relevant than even true abundance and is not intended to reflect actual hummingbird densities. We accounted for the potential effect of differential capture rates across patches on species richness using rarefaction (see 'Statistical methods' below).

We held distance to edge constant across patches by consistently sampling at distances <100 m from edges (distance to edge – patch size correlation: $r = 0.278$, $P = 0.34$, distance to edge = 36 ± 22 m [mean $\pm$ SD]). Extent of net arrays (area containing all 10 nets) was also consistent across patch sizes (netting extent – patch size correlation: $r = -0.250$, $P = 0.39$, 0.3 ± 0.21 ha [mean $\pm$ SD]) to avoid the tendency to space nets farther apart in larger patches. We conducted captures between 0530 h and 1230 h during calm and clear conditions. We randomly selected the order in which patches were visited. Each site received three capture visits over the study period. We ensured a minimum of 3 d between capture visits (days between capture visits: 12.8 ± 7.5, 3–31 [mean $\pm$ SD, range]). Total net hours (nh) were 1906.7 with each site receiving an average of 136.2 ± 3.8 nh (mean $\pm$ SD). We used total number of captures per site as a response variable instead of captures/nh since the sampling protocol had consistent effort across sites; results for all analyses were consistent when using either total captures or captures/nh, and since whole numbers of birds are more easily interpreted, we used total captures.

We marked the heads of all captured hummingbirds with colored nail polish using unique color combinations to distinguish recaptures. We identified individuals to species and sex when sexually dimorphic. All hummingbird species within this community have been shown to transfer pollen, but with varying efficiency (Maglianesi *et al.* 2014, Betts *et al.* 2015). We took additional measurements to quantify functional traits including bill length, angle of bill curvature, and body mass which have all been shown to influence foraging specialization (Maglianesi *et al.* 2014). Bill length was measured using digital calipers from where the bill meets the feathers to the tip of the bill (Figure S1A). Body mass was obtained from a digital jeweler's scale. Wing length was the natural wing chord measured using a wing ruler. Bill curvature was calculated as the angle between a horizontal line across the top of the bill and a line running the length of the bill (*sensu* Temeles *et al.* 2009, Appendix S1; Figure S1C). We considered species with body mass heavier than the mean body mass for all species (5.8 g) to be large and lighter species to be small (large species 8.1 ± 1.8 g [mean $\pm$ SD], small species 4.2 ± 0.8 g; Figure S2A). We considered species with longer bills than the mean bill length for all species (23.3 mm) to be long-billed and species with shorter bills to be short-billed (long-billed 25.7 ± 6.8 mm [mean $\pm$ SD], short-billed 22.2 ± 7 mm; Figure S2B). Species with angles of bill curvature >0 were considered to be curve-billed. Foraging strategies were categorized as

either trapliner or territorial. Treating species as representing solely a single strategy (*i.e.*, trapliner/territorial) may simplify foraging roles for a few species that exhibit somewhat more generalized strategies under different contexts (Feinsinger & Colwell 1978). We categorized species under the strategy they use most often based on behavioral observation (Betts *et al.* 2015), published literature (Feinsinger & Colwell 1978), and natural history texts (Fogden & Fogden 2006).

Local vegetation structure, flower abundance, and matrix resources.—To control for the effect of differences in the flowering plant community on hummingbird captures, we censused ornithophilous flowers within a 20-m radius (1256-m^2 sample plot) around each net location. We considered ornithophilous flower species broadly as any flowering plant species visited by hummingbirds according to existing field guides (Zuchowski 2007, Gargiullo 2008), scientific literature (Stiles 1975, Stiles & Freeman 1993, Borgella *et al.* 2001), and any species that local naturalists or the authors had seen hummingbirds using. Each separate flower or flowering inflorescence was counted depending on the logical counting unit for the species. Local vegetation structure (*e.g.*, tree basal area, tree diameter, canopy height, shrub cover) at sampling sites did not differ across our fragmentation gradient (see Appendix S2 for detailed methods and Table A2 for correlation of vegetation structure measures with patch size).

To account for density of floral resources in the non-forest areas around our patches, we counted all ornithophilous flower resources found outside forest within 500 and 1000 m of each patch. Counts were performed by inspecting any non-forest cover types including gardens, fields, or hedgerows for resources available to hummingbirds (Hadley *et al.* 2014). Individual flowers or flower inflorescences were counted on each plant depending on the species. In the case of flowering trees with >100 flowers (*e.g.*, *Erythrina* sp.), flowers were estimated. Resources available outside forest were primarily *Musa* spp., *Heliconia* spp*.*, and *Erythrina* spp. planted along hedgerows, over coffee plantations, or in gardens. We calculated the flowering plant species richness and the density of these resources as the count per area of non-forested land within the two radii. We included these two resource density measures thought to be a good predictors of pollinator abundance/richness (Ebeling *et al.* 2008) as landscape composition variables.

Statistical methods.—We used generalized linear models (GLM, type III sums of squares) to test for effects of landscape configuration (focal patch size) and composition (proportion of mature forest, regenerating forest, agriculture, pasture, and matrix resources in the surrounding landscape [within 500- and 1000-m radii; we only ever included a single scale for each landscape composition metric per model]) on hummingbird availability and species richness. We also looked at how availability and richness of particular sections of the community changed by dividing the species into groups based on life history traits to determine whether species with particular traits are influenced by landscape composition and configuration. The traits included: (1) foraging strategy (trapliner vs. territorial); (2) body size (small vs. large);

(3) bill length (short vs. long); and (4) wing length (short vs. long).

To further quantify landscape filtering on functional traits beyond simply looking at pollinator availability and species richness we quantified the degree to which overall availability of particular functional traits shifts in response to landscape context. We looked at the site-level mean values of bill length, body mass, and bill curvature across measurements taken from all individuals captured in each focal site. We used generalized linear models to test for effects of landscape configuration and composition on the mean trait value found at that site.

To rank landscape composition variables, we first compared univariate models of hummingbird availability and species richness using AIC model selection (Burnham & Anderson 2004). We statistically controlled for potential confounding factors including elevation and the local flowering community, by including them in the models with our landscape variables (*i.e.*, patch size and top composition variables). To test for independent patch-size effects, we statistically controlled for amount of forest within the top-ranked landscape extent (*e.g.*, [availability ~ landscape compostion + patch size]; *sensu* Betts *et al.* 2006b, Hadley & Betts 2016). In all models, residual plots were examined to verify assumptions of normality and constant variance. We log-transformed focal patch size since the biological effects of increasing patch size are expected to be asymptotic (Schmiegelow & Mönkkönen 2002) and log values are most commonly used during species-area studies (Fahrig 2013). We tested for statistical outliers using Cooks distance $Di = 0.75$, influential cut-off $Di > 4/n$. An outlier was detected in mean angle of bill curvature and, therefore, we used robust linear regression (Rousseeuw *et al.* 2013) for this response variable. Robust linear regression is not as vulnerable to violations of normality and influential data points as least-squares estimators and thus allows model assumptions to be met without having to omit outliers (Rousseeuw & Leroy 2003).

Accounting for imperfect detection and sampling effects.—Variability because of sampling can cause biases when estimating occupancy and species richness. Mist-net studies do not allow typical approaches for estimating occupancy and abundance that account for imperfect detection because of the violation of the assumption of closure between trapping sessions (Rota *et al.* 2009). Therefore, we computed measures of species richness using rarefaction. Rarefaction is a resampling method that estimates expected species richness for a given number of sampled individuals, drawn at random from the total sample (Hurlbert 1971). This approach allows comparisons of richness at a standardized sample size, and avoids confounding genuine differences in species richness with differences in sampling effort or mist net detection probability (Willott 2001). We computed rarefaction curves using the R package 'vegan' (Oksanen & O'Hara 2013, Fig. S3). The R package 'ncf' (Bjornstad 2012) was used to test whether spatial autocorrelation in residuals existed, thereby violating the model assumption of independence (Betts *et al.* 2006a). We conducted all statistical tests using R 2.15.1 (R Core Team 2014).

RESULTS

HUMMINGBIRD AVAILABILITY.—In total, we had 516 hummingbird captures representing 19 species (Table S1). Ninety of these individuals were recaptured at least once for a total of 378 unique individual hummingbirds. Total hummingbird captures increased with focal forest patch size (6.3 ± 2.58 [$\hat{\beta}$ ± SE], $P = 0.04$, $r^2 = 0.347$). Total hummingbird availability increased by nearly two times with forest patch size across the gradient we observed (1.7–1359 ha, Fig. 2A). This effect on hummingbird availability remained after accounting for elevation, ornithophilous flower abundance, and species richness of ornithophilous flowers (Table 1). The effect of patch size was also independent of the amount of forest surrounding the patches within 1000 m (scaled log patch size = 13.4 ± 4.6, $P = 0.015$; scaled amount of forest = −7.8 ± 4.6, $P = 0.12$). The availability of large-bodied trapliners and also species with long bills showed the greatest increase with increasing patch size (Table 1). Trapliners increased 2.97 times, large hummingbirds by 3.13 times, and long-billed hummingbirds 3.11 times across the forest patch size gradient. The amount of forest within 1000 m of the focal patch was the top ranked forest amount model from our two landscape extents (Table 1, Table S3), but was not associated with overall hummingbird availability ($\hat{\beta} = 4.1 ± 2.7$, $P = 0.158$, $r^2 = 0.159$). None of the other matrix composition variables (*i.e.*, amount of pasture, regenerating forest, or matrix resource density) influenced hummingbird availability (Table S3).

SPECIES RICHNESS.—Species richness was also strongly negatively influenced by decreases to focal patch size. The slope of the species area curve ($S = cA^z$, where S is the number of species, A is the habitat area, and z is the slope of the species area relationship in log-log space) was $z = 0.21 ± 0.07$, $P = 0.01$, $r^2 = 0.48$) even after accounting for elevation, local ornithophilous flower density, and ornithophilous flower species richness (Fig. 2B, Table 1). These results remained after accounting for differential availability across patches (rarefied species richness z-value = 0.10 ± 0.04,

$P = 0.047$, $r^2 = 0.428$; Table 1; Hurlbert 1971). Life history groups that showed increased species richness with increasing patch size included small, short-billed, territorial hummingbirds (Table 1). Species richness also increased with amount of forest in the surrounding landscape. Increasing amount of agriculture and decreasing amount of forest within 1000 m had negative effects on total species richness (agriculture $\hat{\beta} = -0.18 ± 0.07$, $P = 0.027$, forest $\hat{\beta} = 0.18 ± 0.07$, $P = 0.025$). We were unable to separate the independent contributions of amount of surrounding agriculture and forest, however, AICc model selection (Table S5) suggests that both are influential as the additive effect of both amount of agriculture and forest is ΔAICc < 2 despite penalty for increased model complexity. None of the other matrix composition variables were significant predictors of species richness at either the 500- or 1000-m landscape extents (Table S4).

Amount of forest had no filtering effect on site-level averages of any functional traits we examined (*i.e.*, mean body mass, mean bill length, mean bill curvature, $P > 0.05$). Mean body mass ($\hat{\beta} = 0.3 ± 0.22$, $P = 0.19$, $N = 14$, $r^2 = 0.065$) and mean bill length ($\hat{\beta} = 0.53 ± 0.6$, $P = 0.4$, $N = 14$, $r^2 = -0.019$) also did not scale with patch size. However, mean angle of bill curvature declined 2.2 times from largest to smallest patches (bill curvature; $\hat{\beta} = 1.53 ± 0.55$, $P = 0.017$, $N = 14$; Fig. 3), suggesting that reducing patch size had a filtering effect on morphological specialization.

We did not detect spatial autocorrelation in residuals of models for availability, richness, or functional traits. Using Moran's I correlograms we found no spatial lags with spatial autocorrelation in model residuals of any model ($P > 0.05$, Fig. S4). Typically models for landscape composition variables within the 1000-m landscape extent were ranked higher than models at the 500-m extent (Tables S3 and S4).

DISCUSSION

Total availability of hummingbirds increased nearly two times with forest patch size across the gradient within the 14 focal
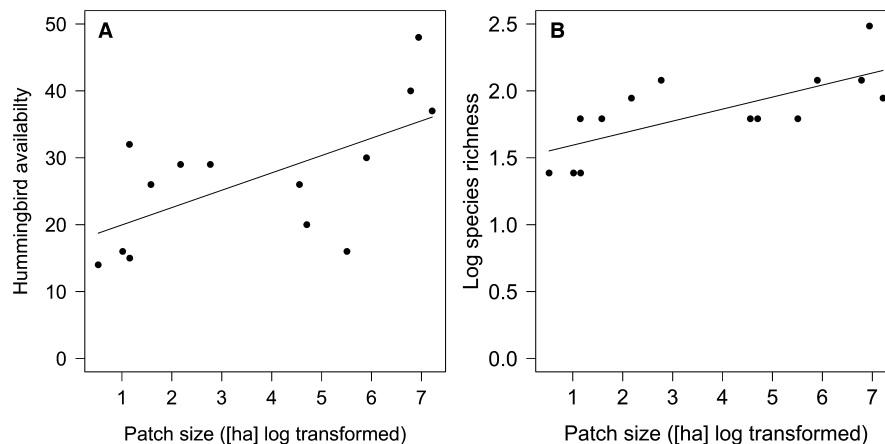

FIGURE 2. Hummingbird availability (A) and log species richness (B) significantly increased with increasing forest patch size, even after accounting for the amount of forest in the surrounding landscape.

TABLE 1. *Effects of landscape- and site-scale variables on the forest hummingbird community. We controlled for potential confounding factors (elevation, flower resources) while examining both patch size and proportion of forest within 1000 m. (A) Effects on captures of hummingbirds (availability); (B) Effects on log species richness; and (C) Rarefied log species richness. Significant relationships ($P < 0.05$) are shown in bold.*

	Log patch size			Elevation			Flower density			Flower species richness			Prop. forest 1000 m*		
	Est	SE	P	Est	SE	P	Est	SE	P	Est	SE	P	Est	SE	P
(a) Availability															
Total	**6.03**	**2.58**	**0.04**	−0.06	2.53	0.98	−2.38	2.87	0.43	−2.06	2.79	0.48	2.89	3.01	0.36
Trapliners	**5.75**	**1.98**	**0.02**	−2.09	1.94	0.31	−1.37	2.20	0.55	−0.66	2.14	0.77	3.09	2.45	0.24
Territorial	0.28	1.59	0.87	2.03	1.56	0.23	−1.01	1.77	0.58	−1.41	1.72	0.43	−0.21	1.54	0.90
Large	**5.78**	**1.90**	**0.01**	0.10	1.87	0.96	−1.29	2.12	0.56	−0.02	2.05	0.99	3.62	2.32	0.15
Small	0.25	1.62	0.88	−0.16	1.59	0.92	−1.10	1.80	0.56	−2.04	1.75	0.27	−0.73	1.54	0.65
Long bill	**5.07**	**1.57**	**0.01**	−0.49	1.54	0.75	−1.27	1.75	0.49	0.39	1.70	0.82	2.98	2.00	0.17
Short bill	0.96	1.70	0.58	0.43	1.67	0.80	−1.11	1.89	0.57	−2.45	1.83	0.21	−0.09	1.67	0.96
Long wing	**5.95**	**1.92**	**0.01**	−0.27	1.88	0.89	−1.27	2.14	0.57	−0.03	2.07	0.99	3.70	2.37	0.15
Short wing	0.25	1.62	0.88	−0.16	1.59	0.92	−1.10	1.80	0.56	−2.04	1.75	0.27	−0.73	1.54	0.65
(b) Richness															
Total	**0.21**	**0.07**	**0.01**	−0.03	0.06	0.65	−0.11	0.07	0.15	0.00	0.07	0.96	0.15	0.08	0.08
Trapliners	0.09	0.11	0.42	−0.04	0.10	0.73	−0.12	0.12	0.33	0.09	0.12	0.46	0.06	0.11	0.59
Territorial	**0.33**	**0.12**	**0.02**	0.00	0.12	0.98	−0.19	0.13	0.19	−0.07	0.13	0.62	0.25	0.13	0.10
Large	0.24	0.14	0.12	−0.04	0.14	0.79	−0.13	0.16	0.45	0.12	0.15	0.47	0.12	0.15	0.43
Small	**0.17**	**0.07**	**0.05**	−0.02	0.07	0.78	−0.08	0.08	0.33	−0.09	0.08	0.29	**0.17**	**0.07**	**0.04**
Long bill	0.20	0.15	0.21	0.07	0.15	0.66	−0.13	0.17	0.47	0.08	0.16	0.64	0.15	0.15	0.36
Short bill	**0.21**	**0.08**	**0.03**	−0.05	0.08	0.54	−0.11	0.09	0.27	−0.05	0.09	0.58	0.17	0.09	0.10
Long wing	0.28	0.14	0.08	−0.14	0.14	0.34	−0.12	0.16	0.48	0.13	0.16	0.43	0.14	0.16	0.40
Short wing	0.17	0.07	0.05	−0.02	0.07	0.78	−0.08	0.08	0.34	−0.09	0.09	0.29	**0.17**	**0.07**	**0.04**
(c) Rarefied richness	**0.10**	**0.04**	**0.05**	0.02	0.04	0.64	−0.05	0.05	0.39	0.00	0.05	0.95	0.09	0.05	0.10

*Proportion of forest within 1000 m and patch size (log) were examined in separate models since they were highly correlated ($r = 0.89$). For the models that include proportion of forest within 1000 m we only show the parameter estimates for proportion of forest although the models did include the three local variables (elevation, local flower density, and species richness).

landscapes we observed. This effect was independent of the amount of forest surrounding the landscape at the two landscape scales, suggesting a negative effect of forest fragmentation per se. In addition to changes in availability, hummingbird species richness (both raw and rarefied) increased with focal patch size and with increasing proportion of forest in the landscape.

Reduced pollinator availability has been shown to have negative effects on plant reproduction in many systems (Eckert et al. 2010). Therefore, reducing hummingbird availability by half in small patches has the potential to limit pollen transfer for ornithophilous plant species in this system. Both small and large species were sensitive to decreasing patch size. However, the fact that large traplining hummingbirds showed the most dramatic declines in availability in small patches supports the hypothesis that hummingbird species with large area requirements are especially sensitive to forest loss and fragmentation. This is of particular concern for plant reproduction since these large trapliners are most likely to move pollen over longer distances and increase outcrossing rates relative to visits by their territorial counterparts (Ohashi & Thomson 2009). In addition, functional traits associated with large trapliners are thought to have the least functional redundancy within the pollinator community (Dalsgaard et al.

2008) and earlier work in this system suggests that their loss may be particularly detrimental (Betts et al. 2015).

We also found that availability of pollinators exhibiting traits associated with floral specialization (i.e., long bills, curved bills) was particularly low in small patches. Given that 40% of the flowering plant species found in this system during the sampling period have curved corollas (Borgella et al. 2001), a strong filtering effect on bill curvature could have negative implications for the stability of pollination networks in fragmented landscapes. Indeed, seed set of the most common flowering plant in this system (Heliconia tortuosa) is strongly associated with availability of large trapliners; seed set increased 37% across the range in trapliner availability that we observed (0.29–1.7 pollinators per net hour; Hadley et al. 2014). Thus, while hummingbirds are thought to be less sensitive to landscape changes than other avian guilds such as understory insectivores (Stouffer et al. 2006), landscape-scale changes to forest amount and configuration may potentially still result in biotic homogenization from replacement of specialists by generalists (Newbold et al. 2014, De Coster et al. 2015) and could have profound implications for pollinator availability and subsequent plant reproduction (Valdivia et al. 2006).
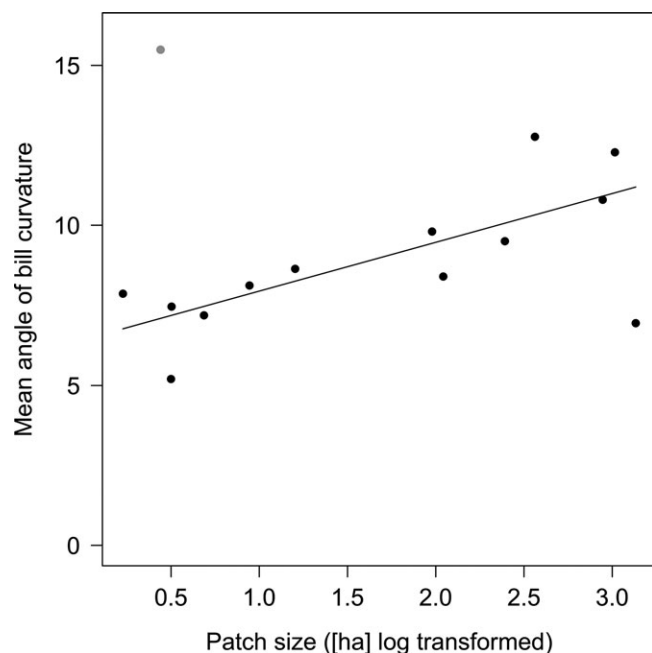
FIGURE 3. Decreasing patch size was associated with a decrease in mean angle of bill curvature of hummingbirds visiting flowers. The solid line shows the modeled relationship between mean degree of bill curvature and log patch size. Filled circles are data points with a statistical outlier shown in grey.

Observed increases in hummingbird availability with focal patch size could result from at least two mechanisms. First, effects of patch size on hummingbird availability could be due to differences in floral resources or vegetation structure in small versus large patches. However, this is unlikely since patch size effects were still present after accounting for both local floral resources and vegetation structure. Alternatively, patch size effects could arise from limitation to daily hummingbird movements. Gap-crossing avoidance (Hadley & Betts 2009, Volpe *et al.* 2014) and increased costs associated with movements in disturbed areas likely reduce daily foraging movements to flowers in small forest patches. This behavior should scale up to reduce captures in small patches.

The declines in species richness that occurred as a result of habitat loss and fragmentation may also influence pollination and network function. Diversity of pollinators has been shown to increase plant reproductive success even in situations where pollinators are otherwise sufficiently abundant (Fründ *et al.* 2013, Garibaldi *et al.* 2013). Diverse pollinator communities are thought to enhance pollination success through a combination of niche complementarity (Albrecht *et al.* 2012), the presence of specific functional groups within the system (Albrecht *et al.* 2012, Fründ *et al.* 2013), and synergistic increases in pollination service through interactions that alter pollinator behavior (Brittain *et al.* 2013, Brosi & Briggs 2013). Long-term stability of pollination networks and resistance to future perturbations are expected to be enhanced by the functional redundancy present in more diverse communities (Burkle *et al.* 2013). Loss of small territorial

hummingbirds may also increase reliance on insect pollinators (Dalsgaard *et al.* 2008). Therefore, we hypothesize that limited hummingbird diversity in small patches could have substantial impacts on sustainability of plant reproduction in fragmented landscapes (Hadley & Betts 2012).

To date, most studies on hummingbird community structure in relation to forest disturbance have found weak negative effects on species richness in the short term (Stouffer & Bierregaard 1995a), or even positive responses at longer temporal scales (Linhart *et al.* 1987, Borges 2007). However, patches in these studies tend to be embedded in more ephemeral, 'softer' matrix types – namely regenerating forest, which often has not only cover from predation but also the nectar resources required by hummingbirds. In contrast, studies on pollinators in landscapes intensively managed for agriculture have tended to report strong, negative impacts of forest loss on pollinator abundance and richness (Winfree *et al.* 2011). In our system, we found no effect of abundance of floral resources outside of the forest patches on availability of hummingbirds to plants within the forest. The lack of influence of matrix resources is perhaps not surprising since many of the forest hummingbird species will not visit highly attractive resources within open areas unless there is connecting forest structure to reach them (Kormann *et al.* 2016). Alternatively, for species accessing resources outside of forest, any positive influence of increased abundance of matrix resources on hummingbird availability could be negated by a subsequent decrease in visits to native flowers occurring within forest; use of matrix resources and non-native flowers has generally been shown to have widespread negative effects on pollinator visitation to native plant species (Morales & Traveset 2009).

Our study region, though agricultural in nature, still retains some of the landscape features that many expect should buffer species against the negative effects of fragmentation (*e.g.*, smaller pasture size, hedgerows, coffee plantations); indeed, recent studies have shown that patch isolation in this tropical countryside has little capacity to explain bat (Mendenhall *et al.* 2014) or bird (Mendenhall *et al.* 2011) species richness. Nevertheless, our results showing reduced species richness of hummingbirds in areas with higher levels of agriculture (*e.g.,* coffee, banana plantations) indicates that such findings depend greatly on the life history traits of the organism under study (Betts *et al.* 2014).

CONCLUSIONS

Our results support a growing consensus that habitat loss and fragmentation result in widespread negative impacts on native pollinator communities (Winfree *et al.* 2011). Both hummingbird availability at ornithophilous plants and species richness of visitors were reduced in small patches and at sites with little surrounding forest. Species of hummingbirds possessing traits associated with long-distance pollen transfer (Ohashi & Thomson 2009) and with low functional redundancy within the network (Dalsgaard *et al.* 2008, Betts *et al.* 2015) appear to show the steepest availability declines, suggesting that reproductive success of plant species dependent on them could be compromised in

fragmented landscapes. Future work should examine how persistence of tropical plant communities may be impacted by both reduced pollinator availability and community homogenization in fragmented landscapes.

These findings add to a growing body of work showing strong negative effects of landscape change on pollinators worldwide (Winfree *et al.* 2011). Tropical forest loss and fragmentation are expected to continue at high rates (DeFries *et al.* 2010, Hansen *et al.* 2013). Our results emphasize the importance of conserving large patches of remaining forest for the functionality of ornithophilous networks even in tropical countrysides characterized by less intensive agricultural development.

ACKNOWLEDGMENTS

DATA AVAILABILITY

Data available from the Dryad Repository: https://doi.org/10.5061/dryad.g4623 (Hadley *et al.* 2017).

SUPPORTING INFORMATION

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

APPENDIX S1. Details of hummingbird traits.

APPENDIX S2. Vegetation structure sampling details.

TABLE S1. *Characteristics of the fourteen sample sites and hummingbird capture data for each patch.*

TABLE S2. *Correlation matrix for all landscape-scale predictor variables.*

TABLE S3. *Model selection results for the effect of landscape composition variables on hummingbird availability.*

TABLE S4. *Model selection results for the effect of landscape composition variables on hummingbird species richness.*

TABLE S5. *Model selection results for the effect of amount of forest versus amount of agriculture within 1000 m on hummingbird species richness.*

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