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Lianas maintain insectivorous bird abundance and diversity in a neotropical forest

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Abstract. The spatial habitat heterogeneity hypothesis posits that habitat complexity increases the abundance and diversity of species. In tropical forests, lianas add substantial habitat heterogeneity and complexity throughout the vertical forest profile, which may maintain animal abundance and diversity. The effects of lianas on tropical animal communities, however, remain poorly understood. We propose that lianas have a positive effect on animals by enhancing habitat complexity. Lianas may have a particularly strong influence on the forest bird community, providing nesting substrate, protection from predators, and nutrition (food). Understory insectivorous birds, which forage for insects that specialize on lianas, may particularly benefit. Alternatively, it is possible that lianas have a negative effect on forest birds by increasing predator abundances and providing arboreal predators with travel routes with easy access to bird nests. We tested the spatial habitat heterogeneity hypothesis on bird abundance and diversity by removing lianas, thus reducing forest complexity, using a large-scale experimental approach in a lowland tropical forest in the Republic of Panama. We found that removing lianas decreased total bird abundance by 78.4% and diversity by 77.4% after 8 months, and by 40.0% and 51.7%, respectively, after 20 months. Insectivorous bird abundance and diversity 8 months after liana removal were 91.8% and 89.5% lower, respectively, indicating that lianas positively influence insectivorous birds. The effects of liana removal persisted longer for insectivorous birds than other birds, with 77.3% lower abundance and 76.2% lower diversity after 20 months. Liana removal also altered bird community composition, creating two distinct communities in the control and removal plots, with disproportionate effects on insectivores. Our findings demonstrate that lianas have a strong positive influence on the bird community, particularly for insectivorous birds in the forest understory. Lianas may maintain bird abundance and diversity by increasing habitat complexity, habitat heterogeneity, and resource availability.

Key words: Barro Colorado Nature Monument; birds; Gigante Peninsula; habitat heterogeneity hypothesis; insectivores; lianas; Panama; tropical forest.

INTRODUCTION

The contribution of habitat complexity to the maintenance of species abundance and diversity has a long history in ecology (Huffaker 1958, MacArthur and MacArthur 1961, Lack 1969, Tews et al. 2004, Stein et al. 2014). Greater habitat heterogeneity has been proposed to explain patterns of diversity at local, regional, and global scales, with diversity increasing with spatial habitat heterogeneity (Pianka 1966, Quan and Ricklefs 2007, Hovick et al. 2015). For example, greater spatial

habitat heterogeneity is thought to explain the higher diversity in tropical forests compared to their temperate counterparts, where habitat heterogeneity is presumably lower (Pianka 1966). For animals, habitat heterogeneity is typically provided by the plant community, with more diverse and vertically complex plant communities such as forests providing greater spatial habitat heterogeneity (Lawton 1983, Tews et al. 2004).

One of the major differences between tropical and temperate forest plant communities is the presence of lianas, which can form dense tangles of stems that loop through the forest understory on their path to the canopy (Schnitzer and Bongers 2002, Schnitzer 2018). Lianas increase habitat heterogeneity throughout the vertical profile of tropical forests by increasing

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complexity and structure. For example, measurements using terrestrial and airborne LiDAR, plant area index, and manual leaf harvesting in intact forest and following liana removal experiments have shown that liana stems and leaves add considerable structure and complexity to the understory, mid canopy, and upper canopy of tropical forests (Clark et al. 2008, Sánchez-Azofeifa et al. 2009, Marvin et al. 2016, Rodríguez-Ronderos et al. 2016, Moorthy et al. 2018). Liana fruits, flowers, leaves, and stems are also valuable food resources to the animal community. Thus, lianas increase heterogeneity throughout the vertical profile of tropical forests, which can provide myriad habitat and food resources that maintain animal abundance and diversity (Yanoviak and Schnitzer 2013, Arroyo-Rodríguez et al. 2015, Lambert and Halsey 2015, Adams et al. 2017, Odell et al. 2019).

Indeed, there are indications that the structure and food resources provided by lianas may increase animal diversity. Liana tangles in the forest understory may provide habitat and protection for many animal species (Lambert et al. 2006). Lianas connect canopy trees together, increasing ecosystem complexity (*sensu* Hufaker 1958), which can maintain animal diversity (Yanoviak and Schnitzer 2013, Yanoviak 2015). For example, in central Panama, Adams et al. (2019) removed lianas from trees and found that ant diversity decreased significantly after liana removal. In the same experiment, the addition of climbing ropes between trees increased ant diversity to pre-liana-removal levels, indicating that connectivity among trees was an important structural addition by lianas. There are also many reports of the importance of lianas as a food source for animals, particularly primates (reviewed by Arroyo-Rodríguez et al. 2015) and especially during the dry season (Dunn et al. 2012). Lianas tend to be far more active during the dry season in terms of growth than co-occurring trees (Schnitzer 2005, 2018, Schnitzer and van der Heijden 2019), and thus lianas may be an important source of dry-season flower, fruit, and foliage for herbivorous animals. In addition, lianas appear to attract many generalist and specialist invertebrate herbivore species (Ødegaard 2000, Odell et al. 2019), which provide a rich food resource for predators. Therefore, lianas may maintain tropical forest animal diversity by increasing habitat heterogeneity across numerous niche axes.

Birds may be particularly sensitive to habitat heterogeneity (Tews et al. 2004), and bird communities may benefit from lianas in a variety of ways. Lianas provide fruit, nectar, and leaves that are used by many bird species (Michel et al. 2015b). Lianas also support many arthropod species that are likely consumed by insectivorous birds (Odell et al. 2019). Several species of rain-forest understory birds, notably insectivorous antwrens and flycatchers, specialize on arthropods in dead leaf clusters caught in liana tangles (Gradwohl and Greenberg 1980), and densities of these specialist birds correlate with occurrence of liana tangles in the forest understory (Michel et al. 2015a). Lianas provide

perching, lekking, and breeding sites, as well as nest materials and nesting sites for many bird species (Michel et al. 2015b). Indeed, in an observational study in a dry forest in the Guanacaste province of Costa Rica, Hilje et al. (2017) found that bird community diversity increased with increasing liana density.

By contrast, high habitat heterogeneity can possibly result in a decrease in bird abundance and diversity. Lianas suppress canopy tree fruit production (Kainer et al. 2014, García-León et al. 2018), thus reducing food availability for birds. The majority of neotropical tree species produce resource-dense fleshy fruits, whereas the majority of neotropical liana species produce wind-dispersed fruits, and thus lianas do not compensate for the reproductive output that they suppress in trees (García-León et al. 2018). Furthermore, lianas can provide a convenient path to bird nests for nonvolant predators, such as snakes, possums, and small mammals, which can predate bird eggs, nestlings, and even adults (Roper 1996, Koenig et al. 2007, Michel et al. 2015b).

Apart from recent experimental studies on ants (Adams et al. 2019), there are almost no *in situ* studies that experimentally reduce tropical forest complexity to study the effects on animal communities (Tews et al. 2004). We used a large-scale liana-removal experiment in central Panama to test whether habitat heterogeneity provided by lianas has a positive, negative, or neutral effect on the bird community. We monitored bird abundance and bird community diversity in a series of 16 80×80 m plots that contained both lianas and trees. We then cut all of the lianas in eight of the plots and conducted two additional bird surveys to determine the effects of lianas on bird abundance, diversity, and community composition. Because of the potentially large beneficial effects of lianas on birds, we predicted that greater habitat heterogeneity provided by lianas would have a net positive effect on birds, and that bird abundance and species diversity would be higher in more heterogeneous control plots where lianas were present. We also predicted that insectivorous birds, particularly understory insectivores, many of which forage primarily or exclusively in liana tangles, would have the most noticeable decreases in abundance, diversity, and community composition following liana removal.

METHODS

We conducted this study in a 60-yr old seasonal, semideciduous moist forest on Gigante Peninsula, in the Republic of Panama. The forest receives $\sim 2,600$ mm of rain per year, most of which falls from May until January each year (Schnitzer and van der Heijden 2019). In 2008, we established 16 80×80 m plots in continuous forest; plots were separated by at least 300 m (van der Heijden et al. 2015). Each plot was divided into nine 20×20 subplots, which were marked with a PVC tube at each corner, and a 10-m buffer zone that surrounded the subplots. In 2008, we tagged, mapped, measured the

diameter, and identified to species all trees and lianas ≥ 1 -cm diameter in the center 60×60 portion of each plot. In late April 2011, we cut all of the lianas near the soil surface in eight randomly selected plots, with the remaining eight plots serving as positive controls where lianas were present. We returned to the plots every 3–4 months in the year following the liana removal to prune any new stems that may have sprouted from the cut lianas. We also visited the control plots at this same frequency to avoid the influence of a researcher visitation effect (Cahill et al. 2001, Schnitzer et al. 2002).

We conducted two bird counts (censuses) before the liana cutting, during the wet season in August 2010, and during the dry season in early April 2011; and two post-cutting counts at the beginning of the wet season, in January 2012 and 2013, approximately 8 months and 20 months after the liana manipulation. For each census, we recorded all bird species encountered in the plots, excluding the species that were outside of the plots. We monitored the bird community using a modified line-transect method. At each plot the surveyor walked four linear transects running the length of the plot (60 m), each spaced 20 m apart (i.e., 0, 20, 40, and 60 m), to cover the plot area. We conducted transect surveys for 20 min at each plot, and each plot was visited one time per census. For each observation, the surveyor noted the number of birds, time of detection, distance to the bird(s), whether the bird(s) were on or off the plot, and the surveyor's location at the time of observation (within 10 m in both cardinal directions). A single surveyor conducted all censuses and the surveyor tracked the location and movement of individual birds to avoid double counting. All surveys were conducted on days with relatively calm winds and no rain between 07:00 to 09:30, when birds are most active. We identified and counted birds using visual confirmation or from their vocalizations (call, song, or drumming). Birds that were flying above the forest canopy (e.g., vultures) were not recorded. For each census, we recorded all bird species encountered within the 80×80 m plots, excluding birds located outside of the plots.

Data analyses

We assigned each bird species observed in liana control or removal plots to one of four dietary guilds based on Robinson (2001): frugivore, insectivore, nectarivore, and omnivore (Appendix S1: Table S1). We summed observations and calculated Shannon's diversity of all birds and by guild for each plot annually for each census. We collected auxiliary data (i.e., distance, time of first observation) to estimate density corrected for imperfect detection, and we had the minimum 60 observations necessary for distance estimation for eight species (Buckland et al. 2001). Rather than evaluate the effects of liana removal on only a few highly abundant species, we chose to use the observed (uncorrected) count as an index of abundance (hereafter "abundance") and to

assess the bird community response. Indices are often more strongly correlated with true density than detection-corrected estimates (Rigby 2016). Moreover, using uncorrected counts provides a conservative estimate of bird response to liana removal because denser vegetation in one treatment (e.g., control plots; Rodriguez-Ronderos et al. 2016) could result in lower detection probability and, consequently, higher density estimates.

We analyzed Shannon's diversity and abundance using generalized linear mixed models in R version 3.5.2 (R Development Core Team 2018). Plot-level diversity included zero values, and therefore was not suited to gamma or beta distributions. Therefore, we log-transformed diversity values and used Gaussian models in package *nlme* (Pinheiro et al. 2018). For count data, we fit generalized linear mixed models with Poisson (with and without zero inflation), negative binomial (1 and 2, with and without zero inflation), and Gaussian (using log-transformed count) distributions using package *glmmTMB* (Brooks et al. 2017). Model fit was compared using AIC (Appendix S1: Table S2) and explored further using quantile–quantile plots and plots of residual vs. fitted values. As the Gaussian model of log-transformed count best fit the data, we used *nlme*, as it enabled fitting of variance structures to account for heterogeneity in variance.

For both diversity and abundance models, treatment (control, removal), year (2010, 2011, 2012, 2013), guild, and their two- and three-way interactions were included as fixed effects and plot was included as a random effect in the model. We treated year as a categorical variable because of the predicted sharp change in responses post-treatment (2012 and 2013). We used AIC to evaluate the fit of variance structures accounting for heterogeneity in variances of treatment, year, and guild. The final models included variance structures for guild (abundance) and year (diversity; see Appendix S1: Table S2 for model selection data, and Appendix S1: Table S3 for model results). Fixed effects were evaluated using R package *emmeans* (Lenth 2019) using multivariate *t* (mvt) adjustments for multiple comparisons and were plotted using *ggplot2* (Wickham 2016).

We compared bird community composition between the liana-removal and control plots using a Jaccard's dissimilarity index and an analysis of similarities (ANO-SIM). We used nonmetric multidimensional scaling (NMDS) to identify clusters of species and sites post-liana removal. We removed one outlier site (plot 14) prior to conducting the 2012 NMDS analysis because it contained only a single species (keel-billed toucan), which was not observed at any other site that year. All compositional analyses were conducted and plotted using *vegan* (Oksanen et al. 2019).

RESULTS

For the two premanipulation surveys, bird abundance and diversity were nearly identical for all species and

guilds in the control and liana-removal plots (Fig. 1A–D). Eight months after liana removal, however, bird abundance was 78.4% lower ($\beta = -1.59 \pm 0.34$ SE, $P < 0.001$) and bird diversity was 77.4% lower ($\beta = -1.11 \pm 0.22$ SE, $P < 0.001$) compared to the controls (in 2012; Fig. 1E, F; Appendix S1: Table S3). Twenty months after liana removal (in 2013), both total bird abundance (40.0%, $\beta = -1.09 \pm 0.34$ SE, $P = 0.002$) and species diversity (51.7%, $\beta = -0.83 \pm 0.24$ SE, $P = 0.001$) remained significantly lower in the liana-removal plots compared to the control plots (Fig. 1G, H). Liana removal reduced insectivorous bird abundance and diversity in both post-liana-removal censuses (Fig. 1E–H). Insectivorous bird abundance and diversity were 91.8% ($\beta = -1.66 \pm 0.25$ SE, $P = 0.001$) and 89.5% ($\beta = -1.11 \pm 0.21$ SE, $P < 0.0001$) lower relative to control plots 8 months after liana removal, and 77.3% ($\beta = -1.17 \pm 0.25$ SE, $P = 0.02$) and 76.2% ($\beta = -0.83 \pm 0.22$ SE, $P = 0.02$) lower relative to control plots 20 months after liana removal. Liana removal did not significantly alter the abundance or diversity of nectarivores, frugivores, or omnivores ($P > 0.5$ for all comparisons; Fig. 1E–H; Appendix S1: Table S3). Bird abundance and diversity in control plots was highest in April 2011 (Fig. 1C, D), lowest in August 2010 (Fig. 1A, B), and moderate in January 2012 and 2013 (Fig. 1E–H).

Bird community composition was similar between control and liana-removal plots prior to treatment (2010: $R = 0.01$, $P = 0.38$; 2011: $R = -0.07$, $P = 0.74$); there was substantial overlap in multidimensional space (Fig. 2A, B) and dissimilarity indices were similar (Jaccard's index of dissimilarity 2010: 0.83 ± 0.01 SE; 2011: 0.80 ± 0.01 SE). Following the liana-removal treatment, however, bird community composition was significantly different between control and liana-removal plots (2012: $R = 0.49$, $P = 0.001$; Fig. 2C, D). The effect of liana removal on bird community composition was strongest in 2012, 8 months posttreatment, where birds grouped into clearly distinct clusters in multidimensional space (Fig. 2C) and the dissimilarity index was high (Jaccard's index of dissimilarity 2012: 0.96 ± 0.01 SE). Insectivorous birds were disproportionately associated with the control plots following liana removal: 16 of 21 species (76%) overlapped or were included within the boundaries of polygons delineating control plot space in NMDS. The other three bird groups had lower associations with the control plots: 67% of the frugivores, 60% of the nectarivores, and 60% of the omnivores (Fig. 2C). By 2013, the bird community in liana removal and control plots partially overlapped in multidimensional space (Fig. 2D), but the communities still differed significantly ($R = 0.24$, $P = 0.01$) and the dissimilarity index remained high (Jaccard's index of dissimilarity 2013: 0.94 ± 0.01 SE). Community differences between liana control and removal plots in 2012 and 2013 were driven by changes in removal-plot composition (Fig. 2). Removal-plot community composition significantly

differed between 2011 and 2012 ($R = 0.33$, $P = 0.001$) and between 2011 and 2013 ($R = 0.19$, $P = 0.03$). Conversely, although control-plot community composition differed somewhat between 2011 and 2012 ($R = 0.21$, $P = 0.04$), control plot community composition was similar in 2011 and 2013 ($R = -0.04$, $P = 0.67$).

DISCUSSION

Our findings support the spatial habitat heterogeneity hypothesis. High habitat heterogeneity from lianas had a clear positive influence on bird abundance and diversity. The steep declines in bird abundance and diversity after liana cutting were driven primarily by insectivorous birds, which constituted the vast majority of bird individuals and species recorded in the study. Our findings are consistent with most tests and meta-analyses of the habitat heterogeneity hypothesis, particularly for vertebrates (e.g., Tews et al. 2004, Stein et al. 2014). However, our study represents one of the few large-scale, in situ experimental manipulations in forests to evaluate the spatial habitat heterogeneity hypothesis.

Determining the effect of habitat heterogeneity and lianas on birds is important because birds play a variety of roles in tropical forest functioning. Birds control insect herbivores, which can defoliate and reduce plant vigor (Michel et al. 2015b, c, Whelan et al. 2016, Odell et al. 2019). Birds are also key pollinators and seed dispersers for many tropical plant species (Michel et al. 2015b, Anderson et al. 2016, Wenny et al. 2016). Furthermore, lianas are increasing in abundance relative to trees in many neotropical forests (Schnitzer and Bongers 2011, Schnitzer 2015), which may alter bird abundance, diversity, and species composition. Therefore, understanding the relationship between lianas and birds is important to understanding how tropical forests function now and how they may function in the future.

Bird abundance and diversity in the control plots changed relatively little during the study. The increased abundance between August 2010 and January 2011 was likely due to seasonal differences. Birds are most active and sing most frequently during January–April, prior to nesting, and vocalize less during August (Robinson et al. 2000). Yet since the 2011–2013 surveys all occurred during peak activity period of January–April, it is clear that the liana-removal manipulation was responsible for the abrupt change in avian abundance and diversity. Like most habitat manipulation experiments, plot sizes were small relative to the home ranges of most of the bird species that we encountered (Robinson 2010). Therefore, changes in bird density, diversity, and composition are likely an accurate reflection of the local changes in habitat use within the plots. Similarly, the small increases in bird abundance and diversity between 2012 and 2013 may reflect birds responding to tree leaf and stem production that was observed in liana-removal plots 1–2 yr following the treatment (Rodríguez-Ronderos et al.

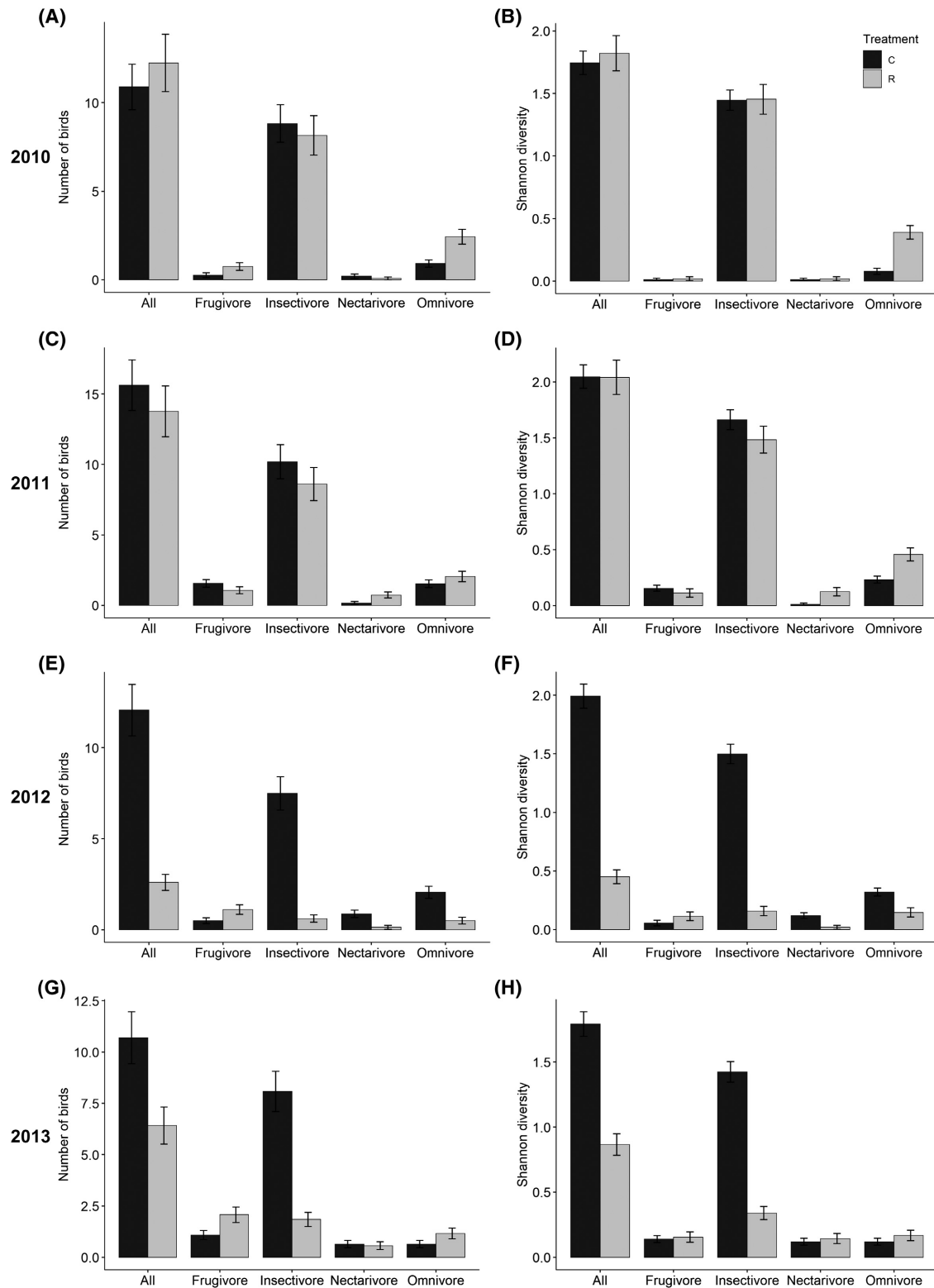


FIG. 1. Model-estimated mean number and Shannon's diversity of birds in liana-removal and control plots before liana removal in 2010 (A, B) and in 2011 (C, D), and after liana removal in 2012 (E, F) and 2013 (G, H) on Gigante Peninsula in central Panama. Responses are summarized by guilds, including all birds, frugivores, insectivores, nectarivores, and omnivores. Error bars represent 95% confidence intervals.

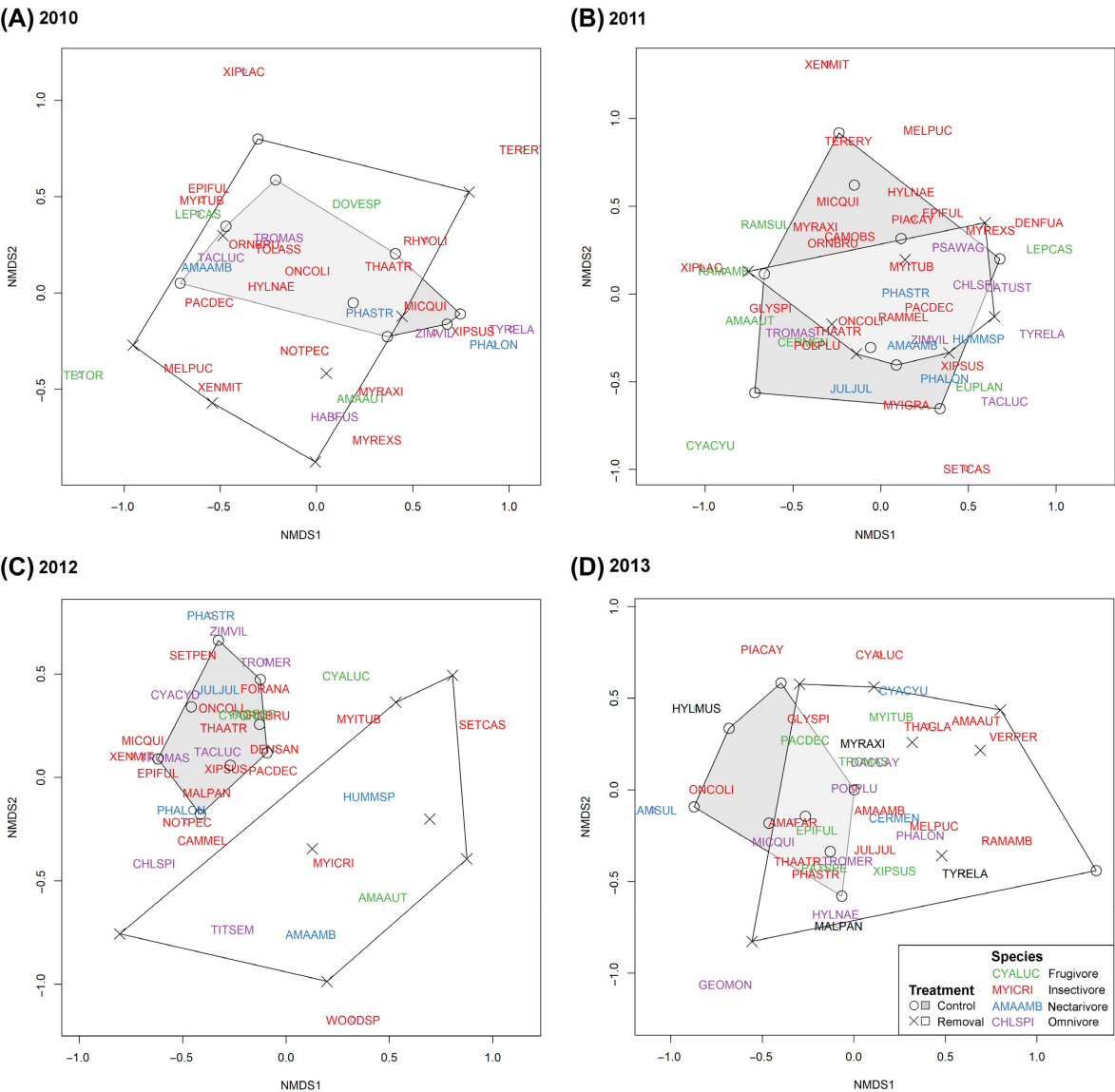


FIG. 2. Community composition of liana control (gray) and removal (white) plots before liana removal in 2010 (A) and 2011 (B), and after liana removal in 2012 (C) and 2013 (D) on Gigante Peninsula in central Panama. Bird species are color-coded by guilds: frugivores (green), insectivores (red), nectarivores (blue), and omnivores (purple). [Color figure can be viewed at wileyonlinelibrary.com]

2016), and the possible increase in arthropod resources accompanying that regrowth.

Bird community composition was essentially the same in the control and liana-removal plots prior to the liana removal; however, following habitat simplification via liana cutting, the bird communities in the liana removal and control plots were distinctly different (Fig. 2). The striking change in bird community composition in the liana-removal plots was driven disproportionately by the loss of insectivorous bird species. The few insectivorous birds that were associated with removal plots included species that sally from the forest canopy to catch insects in midair (e.g., great crested flycatcher [MYICRI] and

dusky-capped flycatcher [MYITUB]). Fewer liana stems in the understory may have enhanced the ability of flycatchers to fly, and thus to forage in the understory. Woodpeckers, such as the crimson-crested woodpecker (CAMMEL), were also strongly associated with the liana removal plots, possibly because the presence of decaying liana stems increased beetle and termite abundances, which provided a rich resource pulse.

Lianas may generally benefit insectivorous birds by increasing the abundance of arthropods (Ødegaard 2000, Yanoviak and Schnitzer 2013, Adams et al. 2019, Odell et al. 2019). Lianas add a complex array of stems to the forest understory, which provide food sources for

herbivorous insects (i.e., liana leaves and stems). Lianas also form dense tangles of stems that trap dead leaf clusters, which provide shelter and food for a wide range of arthropods. Neotropical insectivorous bird abundance and diversity are greater in forests with dense and heterogeneous understories (Banks-Leite and Cintra 2008, Castaño-Villa et al. 2014, 2019). More specifically, several species of understory insectivorous birds, such as the checker-throated stipplethroat and dot-winged antwren, have been observed foraging for arthropods primarily in dead leaf clusters (Gradwohl and Greenberg 1980). Recently, Michel et al. (2015a) showed that these two species, plus the ruddy-tailed flycatcher, preferentially foraged in areas with higher densities of liana tangles, and the densities of these bird species were positively correlated with liana tangle frequency across six sites in Panama, Costa Rica, and Nicaragua. These bird species travel in mixed flocks that rapidly deplete arthropod resources, and some (notably ruddy-tailed flycatcher; Sherry 1984) use high-energy pursuit and glean-ing foraging strategies, and as a result may benefit from the high arthropod densities found in the dense vegetation provided by liana tangles (Gradwohl and Greenberg 1980, Sherry 1984).

Many insect species specialize on liana species, which may further increase insect abundances and thus benefit insectivorous birds compared to liana-free areas (Janzen 1970, Wolda 1979, Odell et al. 2019). For example, in nearby, highly seasonal forest in central Panama, Ødegaard (2000) found that beetles specialized significantly more on liana species than on tree species, and that an average of 47 beetle species had a specialized relationship with each liana species. The ability of lianas to grow exceptionally well during the dry season in seasonal forests, when trees are less active (Schnitzer and van der Heijden 2019, van der Heijden et al. 2019), may provide important dry-season resources to herbivorous and stem-tapping insects. In an extensive review of the literature, Odell et al. (2019) reported that lianas appear to increase the abundance of multiple arthropod taxa in both neotropical forests as well as forests of Borneo and Australia. At least 149 species of insectivorous birds forage for arthropods that are associated with lianas (Michel et al. 2015b). Therefore, the presence of lianas, and the arthropods that they support, may explain why insectivorous bird abundance and diversity—and, therefore, total bird abundance and diversity—was high in the presence of lianas.

Lianas provide nesting sites and materials for many bird species, which also may explain the positive relationship between lianas and bird abundance and diversity. However, few insectivorous birds are known to nest in lianas or to use liana leaves or branches. Only 2 of the 41 species known to nest in or on lianas, or to use liana material in nests, are insectivores (Michel et al. 2015b). Similarly, no insectivorous birds use lianas for lekking, and only 10 species of insectivorous birds are known to benefit from reduced predation (Michel et al. 2015b). Therefore, lianas most likely increase bird abundance

and diversity by hosting a high density of arthropods, and thus providing a rich resource base for insectivorous birds, rather than providing safe nesting or lekking opportunities.

Bird abundance and diversity may have decreased following liana removal because of the influx of light into the understory; light penetration into the liana-removal plots increased by ~20% during the first year (Rodríguez-Ronderos et al. 2016; see also Sánchez-Azofeifa et al. 2009, Estrada-Villegas et al. 2020). Many understory birds are adapted to relatively dark microclimates and avoid brightly lit gaps or matrix habitats (Walther 2002, Moore et al. 2008, Pollock et al. 2015). Light avoidance is particularly pronounced in understory insectivorous birds, many of which have large eyes that allow them to detect and capture insects in the relatively dark forest understory (Stratford and Robinson 2005). Thus, the increase in understory light levels following liana removal may have contributed to the decrease in insectivorous birds following liana removal. Furthermore, the increase in tree vegetation between Years 1 and 2 post-liana removal and the accompanying decrease in understory light levels (Rodríguez-Ronderos et al. 2016) may explain why the liana-removal effect on bird abundance and diversity weakened 20 months following treatment.

We had expected to find an increase in frugivorous birds after removing lianas. Lianas in neotropical forests tend to produce relatively small and nutrient-poor wind-dispersed seeds, whereas trees produce far larger and more nutritious animal-dispersed fruits that should be preferred by frugivorous birds (Muller-Landau and Hardesty 2005). Lianas, however, significantly reduced tree flower and fruit production in the control plots compared to the liana-removal plots (García-León et al. 2018), and lianas themselves were not able to fully replace the quantity of lost tree flowers fruits with their own (van der Heijden et al. 2015). Indeed, frugivorous birds appeared to increase slightly (but not significantly) following liana cutting, which is consistent with greater tree fruit production following liana cutting in these plots (García-León et al. 2018). The lack of a significant difference in frugivorous bird abundance and diversity in the liana-removal and control plots may have been due, in part, to the relatively small sample sizes and thus low statistical power compared to the far more common insectivorous birds.

Because lianas increase habitat heterogeneity, determining the factors that influence liana abundance in tropical forests may be critical to predict bird abundance and diversity accurately, particularly for the diverse guild of insectivorous birds. Liana abundance tends to increase with decreasing rainfall and increasing seasonality in tropical forests, varying twofold across a gradient from relatively aseasonal wet forest to seasonal moist forest (Schnitzer 2005, DeWalt et al. 2015, Schnitzer 2018, Parolari et al. 2020). Liana abundance is also high in young, regenerating tropical forests (Barry et al. 2015), decreasing with forest age after 70–100 yr of

forest regeneration (DeWalt et al. 2000). Within mature forests, liana density and distribution are influenced by disturbance (Schnitzer 2018), and treefall gaps may explain local liana distribution (Dalling et al. 2012, Schnitzer et al. 2012, Ledo and Schnitzer 2014). Thus, if insectivorous birds are dependent on lianas, then insectivorous bird abundances should be high in seasonal and recently disturbed forests, as well in more disturbed areas of older forests.

Our findings support the spatial habitat heterogeneity hypothesis and suggest that the contribution of habitat heterogeneity by lianas regulates tropical bird abundance, diversity, and community composition. Insectivorous birds in particular were influenced by the presence of lianas, presumably because lianas increased arthropod abundance and diversity, which provided a rich resource base for insectivorous birds. The few insectivorous bird species that preferred the liana-free areas may be the exceptions that prove the rule and may be explained by their particularly foraging strategies. Determining the factors that influence liana abundance and diversity in tropical forests is important for a number of reasons (Schnitzer 2018); one important reason is that lianas strongly influence bird abundance and diversity.

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