

LETTER

The structure and organisation of an Amazonian bird community remains little changed after nearly four decades in Manu National Park

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Abstract

Documenting patterns of spatiotemporal change in hyper-diverse communities remains a challenge for tropical ecology yet is increasingly urgent as some long-term studies have shown major declines in bird communities in undisturbed sites. In 1982, Terborgh et al. quantified the structure and organisation of the bird community in a 97-ha. plot in southeastern Peru. We revisited the same plot in 2018 using the same methodologies as the original study to evaluate community-wide changes. Contrary to longitudinal studies of other neotropical bird communities (Tiputini, Manaus, and Panama), we found little change in community structure and organisation, with increases in 5, decreases in 2 and no change in 7 foraging guilds. This apparent stability suggests that large forest reserves such as the Manu National Park, possibly due to regional topographical influences on precipitation, still provide the conditions for establishing refugia from at least some of the effects of global change on bird communities.

KEYWORDS

Amazonia, bird census, bird communities, community stability, tropical long-term community similarity, undisturbed forest

INTRODUCTION

Declines of remote Amazonian bird communities have recently attracted attention due to the potential impacts of global change in the most extensively intact forest landscape on earth (Blake & Loiselle, 2015; Stouffer et al., 2020). However, our understanding of these trends in Amazonian bird communities comes from two studies: one based on two replicated large scale plots (Blake & Loiselle, 2015), and one based on networks of modern and historical sites (Stouffer et al., 2020). Blake and Loiselle (2015) reported declines over 8 years from a remote lowland rainforest in Tiputini, Ecuador, potentially explained by region-wide precipitation patterns, although they hypothesise that changes may be explained by a series of strong La Niña events. Stouffer et al. (2020) reported declines of terrestrial insectivores over >35 years in an isolated study site, near Manaus, Brazil. Recently, Pollock et al., 2022, showed steep declines in most species evaluated in a primary forest in Panama. Furthermore, 88% of declining species experienced a 50% or more decrease in abundance across 44 years. To broaden inference of trends across regions and species, we re-evaluated the entire bird community at a site in southeastern Peru over a 36-year interval and conducted a quantitative comparison of our results with those from Tiputini and Panama (Blake & Loiselle, 2015; Pollock et al., 2022). Our results contrast with previous findings and highlight the need for long term surveys to assess whether global change drives widespread species declines in the lowland tropics.

Studies of ecological communities in remote locales that are absent of other large-scale human impacts present an opportunity to evaluate how global change affects biodiversity. Several long-term studies of Neotropical tree communities have made theoretical and empirical advances in understanding long-term community dynamics (Katabuchi et al., 2017; Swenson et al., 2012, 2020). In animal studies, several authors have documented long-term community change in the tropics—albeit for subsets of communities (Blake & Loiselle, 2015; Brawn et al., 2017; Pollock et al., 2022; Stouffer et al., 2020). A major impediment to studying changes in tropical bird communities is deriving precise population estimates for most species in the community; suites of species require different sampling techniques across different spatial scales, complicating accurate abundance estimation (Robinson et al., 2018) and making establishment of baselines for comparisons difficult.

Terborgh et al. (1990) undertook what became a seminal censusing effort and fully described for the first time, the structure and organisation of the entire bird community present in a 97-ha plot of intact and mature Amazonian floodplain forest at Cocha Cashu Biological Station (Silman et al., 2003). At the time, the study was monumental: the scientific community had barely learned to identify many bird species in South America, let alone how to quantify their abundances. Terborgh et al's (1990) study was a major milestone for

neotropical community ecology, inspiring a generation of neotropical community ecologists and ornithologists. By July 2022, this study had been cited 456 times (Web of Science, 20 Jul 2022), which include studies from which we have gained great insight about the ecology and conservation of neotropical fauna.

Here, after 36 years, we re-censused the 97-ha plot at Cocha Cashu originally surveyed by Terborgh et al. (1990), using their methodologies, to evaluate changes to a remote Amazonian bird community that remains virtually untouched by human activities since the late 1800s. As in the original study, our approach allowed us to estimate population size for the entire bird community, providing a window into changes in community structure and organisation. The focus here is to document patterns of change in a hyperdiverse community over time. This large-scale observational comparative study is a first step to propose hypotheses regarding the role of fluctuating resources and biotic interactions such as competition and mutualism that may explain the patterns we recorded. We also stress the importance of combining new analytical techniques with traditional census methods to generate more consistent long-term datasets for tropical bird communities.

MATERIALS AND METHODS

We re-censused the avian community in a 97-ha mature forest floodplain plot located at Cocha Cashu Biological Station (CCBC), in Manu National Park in southeastern Peru, following methodologies of the 1982 census (Terborgh et al., 1990). We replicated all the original census methods to derive comparable estimates of abundance for most species found on the plot. Estimating abundances for an entire hyper-diverse bird community requires a massive effort that includes a large team of people for over 3 months at the site using the different census techniques outlined in (Terborgh et al., 1990) to estimate the abundance of birds with divergent ecologies. Such effort logistically has precluded regular periodic censuses. Over the course of the 2018 and 2019 field seasons, 17 different individuals (including two of the original census authors) contributed to data collection using census approaches outlined below. In addition, we re-digitised original territory maps of each species (requiring ~320 h). Below we describe the methods in detail. The scientific names of birds follow the latest taxonomy from the South American Classification Committee.

Field sampling

Spot-mapping

We spot-mapped nearly every morning from August 10th to November 8th, 2018 by estimating distance

and direction to all birds detected perpendicular to the nearest trail markers found at 25 m intervals along all trails. Whenever possible, we recorded positions of counter-singing territorial neighbours, which we used as boundary indicators for delimiting territorial boundaries. Each day, routes were randomised, and observers rotated their starting and ending positions on each route to provide even coverage of the plot. Most routes started pre-dawn and ended two to 3 h later. Routes were also conducted after dusk to census nocturnal species. Opportunistic detections at other parts of the day were also noted and observed. Over the 2018 field season, we logged 18,430 spot-map registrations of 224 species on the plot. These observations were digitised and corrected for observer sampling error (see Supplementary Information; [Figure S1](#)) and used for several methods of comparison.

After correcting for distance, we wrote a graphically interactive R program to detect and plot all counter-calling events that automatically produced individual species maps. These maps were inspected independently by AEM, SKR and JT to determine the number of territories within the plot. Natural history knowledge of each species, particularly, the number of individuals per territory/group, resulted in density estimates within the 97-ha plot, following the methodology used in Terborgh et al. (1990).

Mist-netting

We replicated mist-net sampling effort from the original study. We captured and banded birds as part of a standardised mist-netting regime, while also target-netting understory mixed-species flocks throughout the plot. We conducted standardised netting in seven locations on six trails, with lines of 18 mist-nets (12×3.2 m, 36 mm mesh) along 250–350 m of trail in each location, and operated nets from dawn to dusk on three consecutive days when weather allowed, as in Terborgh et al. (1990). During standardised netting we captured 360 different individuals of 79 species, and these were used to estimate abundances for army ant followers, hummingbirds, and manakins in the genus *Pipra*, following methods described in Terborgh et al. (1990). When target-netting understory mixed-species flocks, we operated nets in conjunction with playback from dawn until either we captured a significant portion of individuals in the flock, or until bird activity slowed between the hours of 09:30 and 11:00. Target mist-netting was avoided near any standardised mist-netting lanes. Core flock species and some additional species strongly associated with flocks (e.g., *Isleria hauxwelli*, *Myrmoborus myotherinus*) were colour-banded to facilitate following and mapping flock territories. We did not have appropriate bands for hummingbirds, and we did not clip rectrices due

to the high number of species that incorporate the tail in courtship displays. However, we photographed the right wing, tail, and body of all captured individuals, and with recent advances in individual identification through use of digital photography (Nelson & Pyle, 2013; Pyle & Sullivan, 2010), we feel that a combination of age, sex, measurements and moult pattern allowed us to identify all individual captured hummingbirds while accounting for recaptures.

Colonial birds

One observer (GB) surveyed the entire study plot for active nesting colonies of icterids and counted active nests. The number of individuals of each species was pro-rated on the plot after taking into consideration foraging ecology and natural history observations (Robinson, 1985a, 1985b; Robinson & Terborgh, 1995).

Monospecific flocks

Group sizes for parrots were counted from a canoe in the oxbow lake and from the bank of the Manu River, primarily at dusk as groups flew to roosting sites. Group sizes were averaged by species and combined with spot-mapping locations along the trail system to estimate number of individuals per species on the plot. As per the original study, we derived average encounter rates of birds perched on the plot per species per census route. We subsequently used these encounter rates and multiplied by the average group size per species by the fraction of the plot covered by each census route to derive density estimates of each parrot species on the plot.

Visual counts

Many species associate in permanent mixed-species flocks in both understory and canopy. By identifying individual flocks and censusing each, direct counts were made of each of the permanent flock species. Individual flocks were identified by colour-banded individuals and by mapping flock roosting sites. We mapped flock territories by following flocks daily between 9 September–6 November 2018, and 6 July–29 September 2019, starting at sunrise (Martínez & Gomez, 2013), and estimated the number of individuals in each flock, for a total of 446 h of flock-following.

Data analysis

From 379 species found during the two censuses combined, we included 275 species in our analyses ([Table S1](#)).

Abundance was set to 0 individuals per 100 ha for 40 species with no detections in 2018 but with abundance estimates in 1982. Furthermore, abundance was set to 0 for 35 species with no detections or reported with a + sign in Terborgh et al., 1990 but with an abundance estimate in 2018. One hundred and four species did not have abundance estimates in either of the two time periods. These species were recorded at the Cocha Cashu station during incidental observations rather than during the formal census methods.

Comparison of abundances between 1982 and 2018

To compare abundances between two time periods, we used four approaches. First, we used a simple randomisation test to compare community structure between the two time periods using both Shannon diversity and Bray–Curtis indices (Solow, 1993). For the Shannon diversity index, we calculated a test statistic δ consisting of the difference in the index between the two time periods. Since the Bray–Curtis is already a measure of difference, we used the raw Bray–Curtis as the test statistic. We compared the observed delta and Bray–Curtis indices against a null distribution of test statistics computed by constructing 2000 random communities for each time period. For each iteration, we calculated δ and Bray–Curtis index using the two randomly generated communities in that step. Random communities were generated by sampling the observed number of individuals in each time period from a multinomial distribution. Consequently, the random communities had the same number of individuals observed in 1982 and 2018 and had similar species richness and diversity (Supplementary materials). The probabilities for the multinomial distribution were defined as the proportion of individuals of each species in the sample. The proportion of individuals in the sample was computed by summing each species' abundance and dividing it by the total number of individuals across the two time periods. Failing to observe a value of δ within reasonable boundaries of this distribution (e.g., at a 0.05 alpha level) leads to a rejection of the null hypothesis that observed differences in community structure are due to random sampling. While Shannon diversity measures richness and evenness in the community, Bray–Curtis measures community turnover, and both are important metrics of community structure. The difference in Shannon diversity index was computed by subtracting the observed index in 2018 from the value of the index in 1982. If communities have not changed between time periods, we expected that the difference in Shannon index between the two time periods and Bray–Curtis index were close to 0. Finally, we computed a standardised effect size for each metric by subtracting from the observed index, the mean of the null distribution and dividing it by its standard deviation. If community diversity indices differed more than expected

by chance, then standardised effect sizes would be larger than 1.96 or smaller than -1.96 respectively.

Second, to compare abundance between the time periods, we used a generalised linear model (GLM) assuming a binomial distribution in which counts in 2018 were assumed to be successes of a binomial trial and counts in 1982 as failures. A probability of success of 0.5 would indicate species abundance has not changed over time, while a probability of success larger than 0.5 would indicate an increase. To determine if the entire community had changed, we first constructed a GLM with intercept only. To investigate how particular subsets of the community have changed, we constructed three independent models with intercepts: one with body mass, a second one with sociality and a third one with ecological guilds/foraging strata as independent variables. Sociality consisted of three levels: non-social, Canopy flocking species and Understory flocking species. We divided species according to three foraging strata levels, Terrestrial, Understory and Arboreal and to six ecological guilds Insectivores, Frugivores, Granivores, Omnivores, Nectarivores and Raptors (Blake & Loiselle, 2015; Pollock et al., 2022). Finally, we built two additional models one including only River edge species and the other including only Bamboo specialists. Although we fitted multiple models, we were not interested in performing model selection. Our objective was to investigate how the entire community and how particular subsets of the community had changed, our parameter of interest is the probability of the binomial distribution for the community as a whole and for each subset and whether it was significantly different from 0.5. To account for potential phylogenetic dependence, we compared phylogenetic and non-phylogenetic GLMs using BIC in package 'phyr' in R. We repeated this procedure for 1000 phylogenetic trees from [BirdTree.org](https://birdtree.org) and report the mean and the 2.5% and 97.5% quantiles difference in BIC between the non-phylogenetic and phylogenetically corrected models.

Spatially explicit comparison of abundances

We additionally compared local spatial distributions computing Kernel Density Estimates (KDEs, 25×25 m grid cell size), using raw detection points from spot maps (Calenge, 2006). To conduct Kernel Density Estimation (KDE) and analytical comparisons of geo-referenced observations, we manually digitalised and geo-referenced maps for 247 species produced in the original study and compared distributions of 111 species with >10 observations in both time periods. To quantitatively compare the distributions in 1982 and 2018, we computed Pearson's correlation coefficients of individual species abundances in grid cells (25×25 m size) using the Raster package (Hijmans, 2020) for both community diversity and single species. Since KDE is based on individual detections, KDE is a more objective metric to compare distributions of birds in the plot. Since the level of inference is not territories individual territories extending out of the plot do not affect KDE comparisons.

First, we compared community alpha diversity between the time periods, by multiplying the density in each pixel by estimated abundance to obtain an expected abundance per pixel. We then computed diversity in each of the 25×25 m grid cells using Hill numbers of order 1 (Hill 1973), which corresponds to computing the natural exponent of the Shannon-Diversity Index (also known as effective number of species; Jost 2006), analogous to Terborgh et al. (1990). Second, we compared KDEs for each of the 111 species separately. We computed the mean and median of the 111 single species correlation coefficients, and compared them to a null distribution constructed using a randomisation test (Supporting Information; Manly, 2006). This randomisation test indicates that spatial patterns in abundances of individual species at one time period are on average more similar to the spatial patterns in abundances of the same species at another time period than to the spatial patterns in abundances of a different species. Finally, to explore if particular ecological subsets of the community have changed in their spatial distribution, we repeated the randomisation test described above using only non-social, canopy flocking and understory flocking species, river edge and bamboo specialists, species in different ecological guilds and for different foraging strata. If the ecological processes driving community composition have not changed over the years, we would expect high spatial consistency (correlation) in the abundance of the community and in the different ecological guilds across time.

We also used a multi-model approach to determine if body mass, foraging strata, guild, sociality and abundance explained single species' spatial distribution similarity between time periods using generalised least squares (gls) accounting for phylogenetic non independence, assuming a Brownian motion model evolution (Paradis & Schliep, 2019). We fitted the data with all possible combinations of independent variables using the MuMIn package (Barton, 2018) with the Bayesian Information Criterion (BIC) as the model rank statistic. To propagate uncertainty in phylogenetic estimation, we repeated the model selection procedure using 100 randomly sampled trees from ones used in previous analyses. We report proportion of times each candidate model is deemed as best using a delta BIC of at least 3 points (Taper & Ponciano, 2016).

Comparison to other neotropical sites

Finally, abundance changes in Cocha Cashu were directly compared with those reported by two other long-term studies with comparable design (i.e., Pollock et al., 2022 in Panama and Blake & Loiselle, 2015 in Tiputini, Ecuador). Although data in Stouffer et al 2021 evaluates changes in species abundances across several decades their study design was not amenable to computing annualised proportional changes as in Blake & Loiselle, 2015 and Pollock et al., 2022. For Panama, we obtained the slopes β associated with year of the species-specific generalised linear models from

Pollock et al.'s (2022) supplementary information. We then estimated the slope associated with year of the relationship between abundance and year using the same models described in Pollock et al. (2022) accounting for zero inflation and overdispersion (see their model equations in their Methods section) for the Tiputini and Cocha Cashu data. Capture data for Ecuador was available in the Supplement 5 of Blake & Loiselle, 2015. In this case, GLMs were built using number of captures as the dependent variable and year and site as fixed effects and log mist net hours as an offset parameter. "Site" corresponded to captures in either Harpia or Puma plot for which birds were sampled. Unfortunately, low capture numbers of many species in Ecuador limited species-specific estimates. Consequently, GLMs were constructed using pooled data for all species together and by foraging guild for comparison with Pollock et al., 2022 results. Fortunately, this limitation was shared with Cocha Cashu data, allowing us to do the same type of pooling. For Cocha Cashu, we estimated the slope of the regression in abundance across all species using species abundance in 1982 and 2018 as dependent variable and year as independent variable. We were unable to compute β estimates for guilds in Panama since Pollock et al. (2022) do not report the raw capture data per species as in Blake and Loiselle (2015). Confidence intervals of β for Tiputini and Cocha Cashu were calculated using profile likelihood as implemented in R. Following Pollock et al., 2022, we derived total proportional change in abundance as $e^{t\beta} - 1$ for $t = 36$ (2018–1982) which represents the change in abundance from the beginning of the censuses. This formula allowed us to standardise total proportional change in time across all studies using $t = 36$ (i.e., the time between both census at Cocha Cashu) with the caveat that for Ecuador, using this time span assumes that the trend continues as estimated using data from 2001 through 2014. Although total proportional change for Cocha Cashu and Tiputini is derived by pooling abundance of species in each guild and in the entire community, these estimates are comparable to the distribution of the species-specific total proportional change reported for Panama. Estimates are comparable since the distribution of proportional changes per species also provides information about average tendencies of guilds across time. We interpreted patterns in proportional changes as significant if the confidence intervals of the regression's slope did not overlap zero. For Panama, we interpreted significant patterns for a guild when the 2.5 or 95% quantiles of the distribution of proportional changes did not overlap with zero.

RESULTS

Comparison of abundances between 1982 and 2018

The difference in Shannon diversity indices between time periods was not significantly different from its null expectation (Shannon 1982 = 5.03; Shannon 2018 = 5.02; SES.

shannon = 0.92, $p = 0.37$), but turnover showed higher dissimilarity than expected (Observed Bray-Curtis = 0.33; SES.Bray Curtis = 14.9, $p < 0.0001$). When the intercept only model (single abundance change parameter) was fitted for all species, the estimated change in abundance was not significantly different from zero. Accordingly, the probability of success of the binomial model was not significantly different from 0.5 ($p = 0.54$ 95% CI = 0.48–0.6). Independent body mass and guild analyses showed that larger and non-social species, river-edge specialists, insectivores, arboreal frugivores and raptors, have increased (Figure 1). Contrastingly, canopy flocks, bamboo specialists and understory and arboreal granivores have decreased (Figure 1). Finally, neither understory flocks, terrestrial or understory frugivores, terrestrial granivores, nor omnivores and nectarivores have changed (Figure 1).

Temporal consistency in spatial distributions

The distributions of point detections of individual species were relatively consistent over time. The community's alpha diversity was highly correlated between time periods (Rho = 0.6; Figure 2). Spatial patterns of abundance (across 25×25 m grid cells) of individual species in 1982 were on average significantly more correlated with those of the same species in 2018 than with those from a randomly selected species and year (not including the focal species; Figure 3). Mean correlation coefficient of spatial distribution across time periods among all species was ~ 0.40 and the median was 0.48 (Figure S2, $p < 0.0001$ for both the mean and the median). Only species' abundance explained temporal variation in species' KDEs correlation coefficients (KDEs correlation coefficient = 0.24 (95% CI = 0.14 – 0.35) + 0.014 (95% CI = 0.006 – 0.02) * Abundance). A null model (intercept, abundance and no phylogenetic correlation structure) was >4 BIC points better than any other model tested, even after propagating phylogeny estimation uncertainty.

Comparison to other neotropical sites

The trends of estimated proportional change in 36 years in Cocha Cashu were different from changes in Panama and/or Tiputini in eight out of ten ecological guilds (Figure 4). In contrast Panama trends were similar to those in Tiputini in seven of ten comparisons. In five of the guilds for Cocha Cashu, estimates of proportional change show increases, whereas in Panama and/or Tiputini, most guilds show decreases. Only Terrestrial Frugivores and Aquatic species showed no change in the three sites (Figure 4).

DISCUSSION

Over a period of 36 years, our results indicated few changes to the bird community with respect to point

alpha diversity or species abundances (Figures 1 and 2). Species evenness was relatively similar between time periods (little change in Shannon-Diversity indices), however we found significant community turn-over which is likely driven by increases in insectivores and decreases in granivores and canopy flocks. These increases in abundances are also reflected in the spatial visualisation of point diversity (Figure 2). Our findings contrast with other long-term studies of Neotropical bird communities that have reported large changes in community composition (Blake & Loiselle, 2015; Brawn et al., 2017; Robinson et al., 2000; Stouffer et al., 2020). We found high similarity or slight increases in the insectivore community, excepting canopy flocks. Our direct comparison between Cocha Cashu and other similar sites in the Neotropics show that overall changes in abundance are smaller at Cocha Cashu. Given extensive documentation of the sensitivity to change of insectivores (Powell et al., 2015), it is surprising that a group showing declines in other undisturbed (Blake & Loiselle, 2015; Stouffer et al., 2020) and fragmented forest sites (Bregman et al., 2014; Powell et al., 2015) shows little variation at Cocha Cashu (Figure 4).

In spite of community similarity, we identified significant declines in foraging guilds such as understory and arboreal granivores (Figure S2b), and bamboo specialists. These declines may be explained by different mechanisms. For example, many of these granivores (e.g., parrots) cue in on patchy and ephemeral resources. Thus, we speculate that decreases may be driven by stochastic fluctuations in local resources. Parrots often respond to seasonal changes in fruiting activity on scales larger than the plot. Alternatively, large variability in terrestrial and arboreal granivore abundance (i.e., *Odontophorus stellularis* and Parrots) may be due to inadequate sampling of group sizes. Also, some ground dwelling granivores showing large scale fluctuations may be susceptible to nest predation by white-lipped peccaries although this species was absent during both the 1982 and 2018 census periods (Terborgh et al., 1990). Decreases in some bamboo specialists are consistent with the disappearance of bamboo from the plot after a flowering event circa 2001.

A curious contrast appears in the apparent differences between understory and canopy flock stability. While understory species abundance and flock territories have remained almost unchanged, canopy flocks have drastically declined in the plot (Figures 2 and 4). Previous research has documented the unique interdependence of these permanent associations, suggesting that assemblages of species in these flocks would experience similar trajectories of growth or decline (Munn & Terborgh, 1979). One explanation for these differences is that our study's spatial scale is too small to capture natural territory size and habitat use variability of canopy flocks: point counts conducted over a larger spatial scale (but including the plot) revealed a higher abundance of canopy flocking species

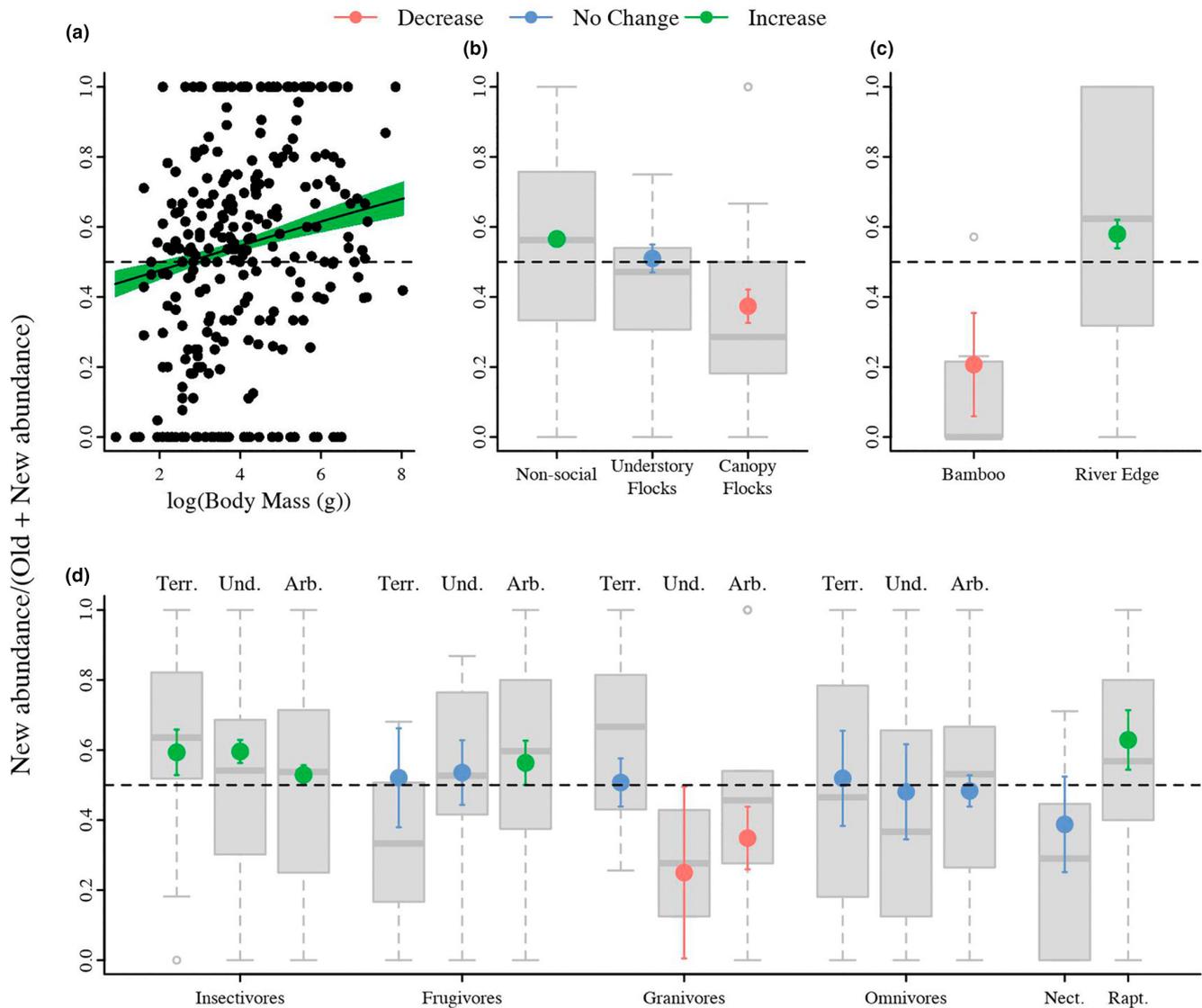


FIGURE 1 Results of the binomial generalised linear model assuming abundance in 2018 as successes and those in 1982 as failures for: (a) body mass, (b) sociality, (c) habitat specialists, (d) ecological foraging guild. Significant changes are shown based on the overlap of the 95% confidence interval of the estimate of the probability of success shown in orange, blue or green. Solid black points and grey boxplots show the raw data computed as the observed new abundance divided by the sum of the old and new abundances. Terr. = terrestrial, Und. = understory and Arb. = arboreal.

(unpublished data). Alternatively, as more fruits are found in the canopy, shifts in phenology and the dependent arthropod assemblage therein, may decrease and have greater effects on the abundance of omnivores, frugivores and insectivores common to canopy flocks. The extent to which canopy birds are affected by changes in canopy tree fruiting phenology at local levels at Cocha Cashu is unknown. Future work evaluating changes in territory size, habitat use, and forest phenology would help us understand potential drivers of change in canopy species.

Studies in other lowland Neotropical sites showed marked changes to abundances of specific groups (Figure 3). Blake and Loiselle (2015) report long term declines for multiple guilds of understory species over

~8-year period from Tiputini. Our new analyses of those data also point to a significant decline in all insectivores and nectarivores through time in that site (Figure 3). Absent anthropogenic impacts, changing regional precipitation events are one of the plausible explanations. Consistent with results of Blake and Loiselle (2015), declines in several species over 20 years were reported from a forest plot in Panama (Brawn et al., 2017). The Panama site has also experienced little direct human impact but has undergone species declines related to prolonged seasons of low precipitation (Brawn et al., 2017). The same research team has used long-term mist-net data for a larger group of species and found consistent declines in capture rates across most bird species (Pollock et al., 2022). Our comparison shows similar trends for almost every

1982 Census

2018 Census

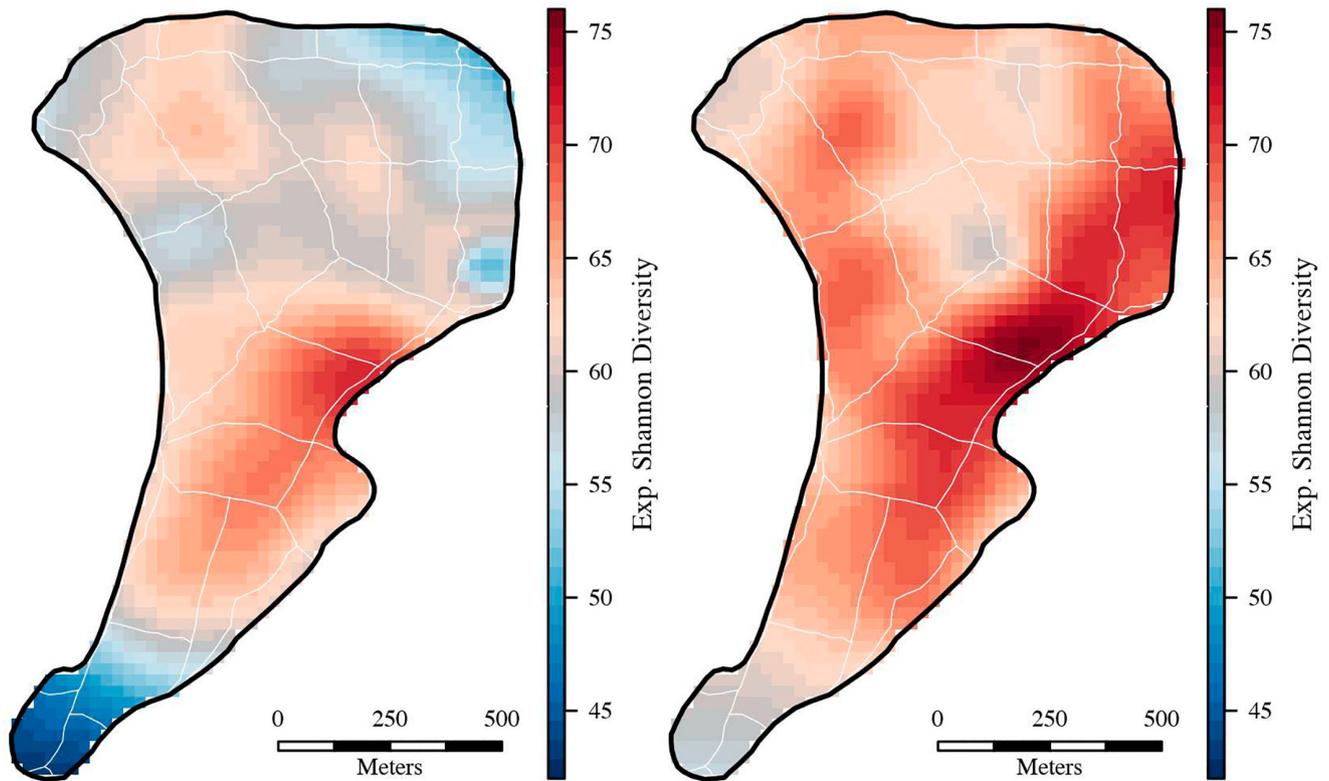


FIGURE 2 Community structure in 1982 vs 2018. Hotspots of alpha diversity within the plot in 1982 and 2018 based on a 25×25 m grid. Each map presents the exponential of the Shannon diversity index (i.e. effective number of species sensu Jost 2006) for each grid cell computed using each species' expected abundance. This plot is analogous to (Terborgh et al., 1990) point alpha diversity based on superimposed distributions for all species, using the same diversity scale in both time periods.

guild in Tiputini and Panama, and that both show steep declines in insectivores (Figure 3). Finally in Central Brazil, terrestrial insectivores have also steadily declined from undisturbed forests, driving the shift of the community from a historical baseline (Stouffer et al., 2020).

Cocha Cashu shows little change (and even increases in some guilds; Figures 2 and 3) compared to other remote tierra-firme forest plots. Changes in communities in Panama, Tiputini and Central Brazil have been attributed to changes in long term precipitation patterns. However, data on long-term regional precipitation patterns at Cocha Cashu do not show strong consistent changes (Figure S3; Aybar et al., 2020). Given observed bird community declines in other Neotropical sites, bird communities experiencing little to no change, such as those in Cocha Cashu, may serve as biodiversity refugia in the face of such global change (Guisan et al., 2013; Morelli et al., 2020; Trew & Maclean, 2021).

While mechanisms for lack of change in Cocha Cashu are unknown, one of the major differences between Cocha Cashu and the other sites is that it is a mature flood plain forest while the others are tierra firme forests. While declines in other sites (all tierra firme forests) have been attributed to drier precipitation patterns, floodplain forests receive seasonal recharge of the water

table independent of precipitation patterns. Thus, periodic inundation of the floodplain may also provide buffer to potential drought conditions. However, aspects of periodicity of flooding and how they are affected by larger climate patterns remains to be studied (Correa et al., 2022). Based on the results reported in Panama, Tiputini and Manaus, changes in rainfall patterns in other sites may be correlated with the decrease in insectivore birds. Since insects are particularly sensitive to changes in humidity and temperature it is possible that in Cocha Cashu microenvironmental conditions are less impacted due to its flood plain nature which guarantees humid conditions year-round and hence more stability. Thus, while in the other sites bird populations are indirectly influenced by climate change on insect resources, it is possible that due to its floodplain nature, insect abundance and diversity have not changed much in Cocha Cashu. The lack of change in insect abundance due to higher stability in humidity may also be true if Cocha Cashu has a more stable precipitation regime compared to other neotropical sites irrespective of its flooding nature.

Elucidating the mechanisms behind the changes or the maintenance of community abundance patterns requires examining long-term abundance data. Our

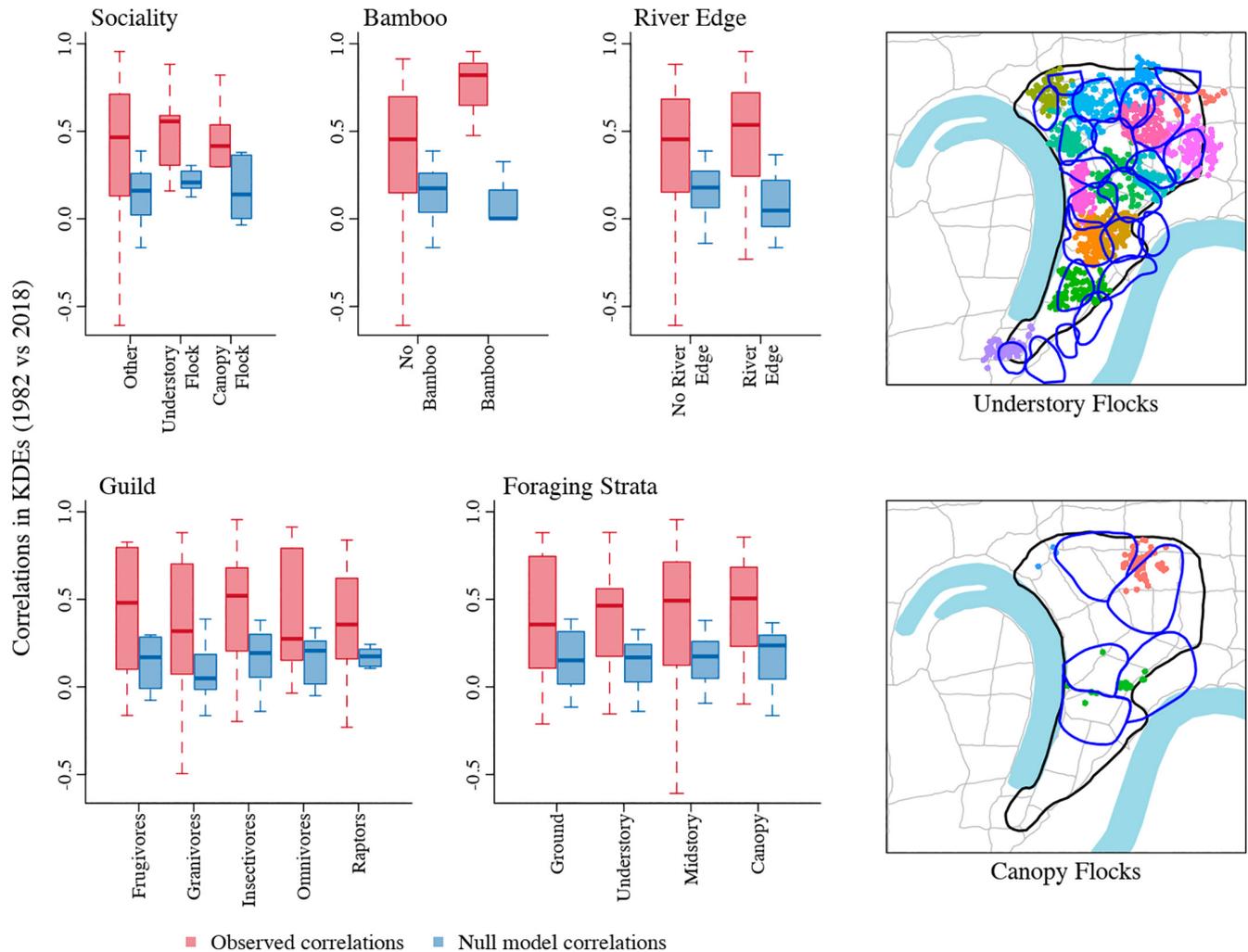


FIGURE 3 Comparison of spatial patterns of abundance (across 25×25 m grid cells) of individual species in 1982 and 2018 following partitioning along different ecological axes: Foraging guild, foraging strata, sociality, and habitat specialisation: Bamboo/No bamboo and river-edge/No river-edge. The rightmost panels with maps compare the distribution of understory and canopy flock territories from 1982 (blue polygons) with those from 2018 (coloured points). The 2018 coloured points correspond to 6965 direct observations of geo-referenced flock activity.

study focused on a snapshot of ecological process in two time periods, thus we cannot evaluate random year-to-year variation on resilience per-se. Small changes found in abundance and territory distribution allow us to speculate that this community is composed of species with low population variability and thus rather stable (*sensu* ecological theory) (Ives & Carpenter, 2007; MacArthur, 1955). Long-term temporal population variability has been demonstrated for specific components of insectivorous bird communities in several locations. Loiseau and Blake (1992) suggested that community dynamics of Neotropical bird communities are likely guild-dependent, with insectivores showing much less population variability over time compared to frugivores. Our data show some level of constancy across a far larger percentage of the community irrespective of guild or functional traits.

Given that stochasticity is an inherent process of any natural system (Dennis et al., 2006; Ferguson &

Ponciano, 2015) separating the effects of this process from deterministic processes is a necessary approach to evaluating community change moving forward. Studies of community resilience and stability, both theoretically and empirically have traditionally focused on communities with few species. The need for long-term time series data on hyper diverse communities cannot be overstated, from an empirical standpoint and to parameterise models of community stability where species richness is high. In addition, evaluating forest structural changes will be critical in understanding whether the Cocha Cashu bird community is (1) resilient to local or regional environmental change, or (2) whether changes to the forest are so small that they translate into small effects on the bird community. These scenarios would underscore different aspects of community stability that maintain community equilibrium (Ives et al., 2003; Ives & Carpenter, 2007). Understanding the likelihood of these scenarios is critical for understanding community-wide resilience to

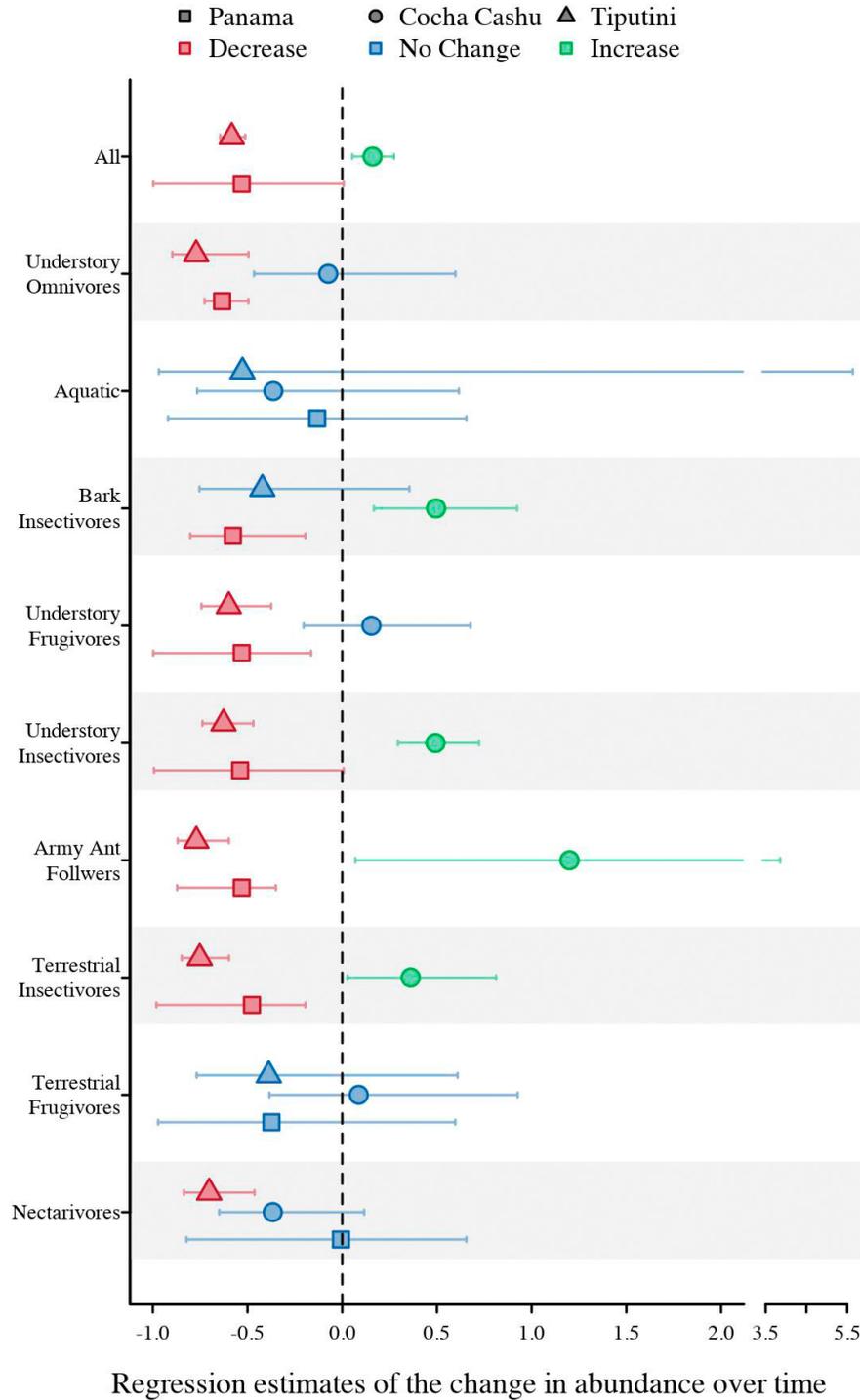


FIGURE 4 Comparison of the regression estimates of the change in abundance over time for species in Cocha Cashu (points), Panama (squares) and Tiputini (triangles). For Cocha Cashu and Tiputini, we show the estimates of the slope and 95% confidence interval of the relationship between abundance and time for all individuals pooled together and for all individuals in each guild. For Panama, we show the median, 2.5% and 97.5% quantiles of the distribution of the slope for all species and species in each guild as reported in Pollock et al., 2022.

natural environmental dynamics and to decouple the effects of local from regional scale processes, including those linked to climate change.

While our study compares only two points in time, new analytical approaches may streamline diverse arrays of sampling techniques currently used and allow for efficient long-term sampling of neotropical bird

communities (Gomez et al., 2018; Toms et al., 2006). Point count techniques typically yield largely unreliable density estimates of rare species in hyper-diverse bird communities (Robinson et al., 2018), yet the development of large families of statistical models allows for fine-tuned analyses incorporating point counts with other behavioural field observations (Gomez et al., 2018;

Sauer & Link, 2002; Yamaura et al., 2012). Combining geo-referencing of the movement and territory occupancy in obligatory understory flocking species with the spot-mapped territories, we calibrated density estimates obtained from additional point counts that we conducted in the same year, yielding a high degree of accuracy among the two techniques (unpublished data). We suggest that using supplementary visual group size data to estimate group means for monospecific flocking species, normally excluded from point count estimates, would permit a larger percentage of the community to be tracked with point counts. These combined methodologies, together with increased availability of inexpensive data loggers, and acoustic monitoring, allows for more efficient and financially feasible sampling (Burton et al., 2015; Shonfield & Bayne, 2017). For future fieldwork efforts here and elsewhere, we advocate a more intimate design of field and statistical sampling techniques in situ by inter-disciplinary teams. In that sense, the field sampling error calibration we devised for each observer represents a positive first step towards a robust estimation of multiple sources of uncertainty.

Patterns of little change seem to be a peculiarity of our sampling study compared to similar studies (Figure 3). The region of Madre de Dios within which Manu National Park is situated faces ever-mounting pressure from extractive industries and road construction to increase commerce between Brazil and Peru. Given the current focus on determining and predicting refugia in the face of future global change, our results suggest that the consequences of development around such sites should be an important consideration among regional stakeholders.

AUTHOR CONTRIBUTIONS

A.E.M., S.K.R., and T.V. conceived the study. J.W.T., S.K.R., and A.E.M. designed the study. All authors performed census methods in the field. A.E.M., J.M.P., and J.P.G. conceived the field experiments, carried out the statistical analyses, and wrote the paper. All authors contributed to interpretation of results. All authors helped to edit the manuscript.

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DATA AVAILABILITY STATEMENT

The data supporting the results have been archived in Dryad: <https://doi.org/10.5061/dryad.lrn8pk0z9>.

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SUPPORTING INFORMATION

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