RESEARCH ARTICLE

Tree diversity effects through a temporal lens: Implications for the abundance, diversity and stability of foraging birds

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Abstract

1. Tree diversity exerts a strong influence on consumer communities, but most work has involved single time point measurements over short time periods. However, describing temporal variation associated with diversity effects over longer time periods is necessary to fully understand the consequences of tree diversity for ecological function.

2. We conducted a year-long study in an experimental system in southern Mexico assessing the effects of tree diversity on the abundance and diversity of foraging birds. To this end, we recorded bird visitation patterns for 32 tree plots (21 × 21 m; 12 tree species monocultures, 20 four-species polycultures) every 45 days (n = 8 surveys) and for each plot estimated bird abundance, richness, functional diversity (FD) and phylogenetic diversity (PD). In each case, we reported temporal (intra-annual) variation in the magnitude of tree diversity effects, and calculated the temporal stability of these bird responses.

3. Across surveys, tree diversity noticeably affected bird responses, demonstrated by significantly higher abundance (43%), richness (32%), PD (25%) and FD (25%) of birds visiting polyculture plots compared to monoculture plots, as well as a distinct species composition between plot types. We also found some degree of intra-annual variation in tree diversity effects on these response variables, ranging from surveys for which the diversity effect was not significant to surveys where a significant 80% increase (e.g. for bird FD and PD) was observed in polyculture relative to monoculture plots. Notably, tree diversity increased the stability of all bird responses, with polycultures having a greater stability abundance (18%), richness (38%), PD (32%), and FD (35%) of birds visiting tree species polycultures compared to monocultures.

4. These results show that tree diversity not only increases bird visitation to plots, but also stabilizes bird habitat usage over time in ways that could implicate insurance-related mechanisms. Such findings are highly relevant for understanding the long-term effects of plant diversity on vertebrates and the persistence of bird-related ecosystem functions. More work is needed to unveil the ecological mechanisms underlying temporal variation in vertebrate responses to tree diversity and their consequences for community structure and function.

 | **1**

1 | INTRODUCTION

Plant species diversity can shape ecosystem functions such as primary productivity and resilience to abiotic stressors (Cardinale et al., 2011; Hector, Bazeley-White, Loreau, Otway, & Schmid, 2002; Hooper et al., 2005; Tilman, Reich, Knops, Wedin, & Mielke, 2001), as well as have strong effects on the abundance, composition and diversity of associated fauna (Cardinale et al., 2006; Moreira, Abdala-Roberts, Rasmann, Castagneyrol, & Mooney, 2016). Our understanding of such effects stems mainly from experimental studies manipulating herbaceous plant diversity (e.g. grasslands; Haddad et al., 2009; Scherber et al., 2010), and, to a lesser extent, tree species diversity (reviewed by Grossman et al., 2018). Although the number of manipulative studies testing for tree diversity effects has increased in recent years, research in arboreal communities still lags behind the bulk of work in herbaceous systems. This is a crucial consideration since over a third of the Earth's land surface is covered by forests (FAO, 2012), and tree species account for most of the biomass in forested ecosystems (Grossman et al., 2018). Furthermore, another important research bias has been that most studies have focused on plant diversity effects on invertebrates, whereas work involving vertebrates is much more limited (but see Cook-Patton, LaForgia, & Parker, 2014; Muiruri, Milligan, Morath, & Koricheva, 2015; Muiruri, Rainio, & Koricheva, 2016; Nell, Abdala-Roberts, Parra-Tabla, & Mooney, 2018). Accordingly, filling current gaps in research on vertebrate responses to tree diversity is crucial if we are to achieve a full understanding of the effects of plant diversity in terrestrial ecosystems.

A robust understanding of biodiversity effects, particularly for plant communities with long-lived species, necessarily requires a perspective that accounts for temporal variation. On the one hand, documenting temporal variation in long-term studies has allowed to identify fluctuations in biodiversity effects such as, for example, gradual increases in the strength of plant species positive interactions that increase primary productivity (e.g. Hector et al., 2002; Tilman et al., 2001) and other types of temporal (e.g. cyclic) changes in ecosystem functions related to shifts in plant species composition, diversity, or seasonal changes in abiotic factors affecting species' phenologies (e.g. Forrest & Miller-Rushing, 2010). On the other hand, long-term studies have also shown that, as result of interspecific variation in resource use and acquisition over time (negative-covariance effect; Tilman, 1999), more diverse plant communities exhibit increased temporal stability in ecosystem functions (Hector et al., 2010; Tilman, Reich, & Knops, 2006) with this leading to greater resilience to disturbances and environmental unpredictability (Insurance Hypothesis; Hector et al., 2010; Yachi & Loreau, 1999). In turn, these stabilizing effects on plant communities are predicted to have extended consequences for associated fauna (Haddad, Crutsinger, Gross, Haarstad, &

Tilman, 2011; Proulx et al., 2010), as consumer species and functional groups track temporal changes in resource availability differently depending on traits such as mobility, reproductive phenology and tolerance to biotic (e.g. predation) or abiotic stressors (Mittelbach, 2012; Morin, 2011). A few experimental studies have shown that the mechanisms that enhance plant community stability account for effects on consumer stability (e.g. Borer, Seabloom, Tilman, & Novotny, 2012; Haddad et al., 2011; Jiang & Pu, 2009; Proulx et al., 2010). In addition, others have found that increased consumer stability may also arise through processes occurring within consumer communities independently of plant-based stability mechanisms (Jiang & Pu, 2009; Proulx et al., 2010). However, to the best of our knowledge there are no experimental studies on temporal variation in plant diversity effects on vertebrates, a severe limitation in biodiversity research that prevents a full understanding of the links between plant diversity, consumer community structure, and ecosystem resilience.

Birds represent a taxomically and functionally diverse group of vertebrates that occur in most ecosystem types and contribute to key ecological functions such as pollination, seed dispersal and insect herbivore control (Sekercioglu, 2006; Van Bael et al., 2008; Whelan, Wenny, & Marquis, 2008). There have been a number of observational (i.e. correlational) studies addressing associations between bird community structure and plant community features, such as for example: plant diversity (e.g. Ihuma, Chima, & Chapman, 2011; Kissling, Rahbek, & Böhning-Gaese, 2007; Laiolo, 2002), sucessional stage (e.g. Almazán-Núñez, Arizmendi, Eguiarte, & Corcuera., 2015; Smith, Salgado Ortiz, & Robertson, 2001), and vegetation structure and physiognomy (e.g. Azpiroz & Blake, 2016; Fleishman et al., 2003). These studies have found positive associations between bird diversity and plant diversity and other variables associated with plant-based habitat complexity, presumably due to an increase in the number of available niches and granted that bird species generally exhibit marked differences in habitat requirements and foraging habits (Cramer & Willig, 2005; Holmes & Recher, 1986; MacArthur & MacArthur, 1961). In addition, some of this research (e.g. successional studies) has had clear implications for understanding how plant community variables and bird communities relate to each other over time (e.g. Hovick, Elmore, Fuhlendorf, Engle, & Hamilton, 2015; Karp, Ziv, Zook, Ehrlich, & Daily, 2011; Loiselle & Blake, 1991). However, experimental studies involving tree diversity and bird responses to such manipulations are lacking (but see Nell et al., 2018), and to our knowledge there are no experimental tests of temporal variation associated with tree diversity effects on bird communities. This is of central importance given that temporal variation is inherent to bird communities due to their high mobility (including migration) and ability to track resources in time and space (Johnson & Sherry, 2001; Loiselle & Blake, 1991; Malizia, 2001; Salgado Ortiz, Marra, & Robertson, 2009), particularly in tropical tree communities

which harbour a large amount of resources and habitats for birds and are characterized by a high diversity of plants and birds (Karr, 1976; Nell et al., 2018; Sekercioglu, 2012). Importantly, by harnessing a temporal perspective one can also gain insight into the effects of tree diversity on bird community stability (i.e. temporal consistency in abundance or diversity), a key challenge for understanding the extent to which reductions in tree diversity affect ecosystem function through temporal changes in bird community structure and foraging patterns.

The present study sought to evaluate the effects of tree diversity on local-scale patterns of bird visitation and foraging activity by measuring multiple variables associated with bird habitat use (e.g. reflecting differences in feeding, courtship, territoriality, etc.) in a tropical tree diversity experiment in southern Mexico (Yucatan). In addition, we further describe temporal changes in the bird community and in bird responses to tree diversity over a 1-year period. We previously documented the effects of tree diversity on descriptors of bird foraging behaviour and habitat use in this system, and its consequences on top-down control of insects by birds (Nell et al., 2018). While that study was restricted to a 1-month period during the rainy season, here we aim to build on this work by documenting temporal changes in these descriptors of bird habitat use over 1 year. Specifically, we evaluated the following: (a) Is there an overall effect of tree diversity on community-level variables describing bird habitat use, namely abundance, diversity (taxonomic, functional and phylogenetic) and composition of visiting birds; (b) Is there temporal variation in tree diversity effects on these bird responses? (c) Does tree diversity increase the temporal stability in these bird responses? Given previous evidence for causal links between insectivorous birds and predation rates (Nell et al., 2018), this study has important implications for the conservation of bird communities and the maintenance of bird-related ecosystem services such as regulation of insect populations.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was conducted at the UADY Tree Diversity Experiment, a large-scale system established at the Sitio Experimental Uxmal (20°24′44″N, 89°45′13″W), which is owned by INIFAP (Instituto Nacional de Investigaciones Forestales, Agricolas y Pecuarias) and located 70 km southwest of Merida (Yucatan, Mexico). The system was planted in December 2011, covers 7.2 ha, and is composed of 74, 21 × 21 m plots, each with a planting density of 64 individuals per plot (3 m between rows), and a distance of 6 m between plots (see Figure S1; Abdala-Roberts et al., 2015). We planted six tropical tree species native to the Yucatan Peninsula, namely: *Swietenia macrophylla* King (Melliaceae), *Enterolobium cyclocarpum* Jacq. (Leguminoseae), *Tabebuia rosea* Bertol. (Bignoniaceae), *Ceiba pentandra* L. (Malvaceae), *Piscidia piscipula* L. (Fabaceae), and *Cordia dodecandra* A. DC (Boraginaceae). Most of these species naturally co-occur in tropical forests of the Yucatan Peninsula, and were selected because they exhibit substantial differences in attributes such as growth rate and leafing phenology which are expected to increase

ecological complementarity (Abdala-Roberts et al., 2015). Plots were classified as monocultures containing one tree species or polycultures with random combinations of four out of the six species. At the time this study was conducted, mean tree height ranged from 4 to 12 m depending on the species. All species were planted in equal densities in polycultures. The features of this experimental system differ in several ways relative to natural tropical forests of the region, such as constant distances among neighbouring trees, substantially lower tree diversity and stem density (i.e. in polycultures), and a more simplified understory (Abdala-Roberts et al., 2015; Nell et al., 2018). At the same time, the simplified nature of the experimental system make ecological dynamics and processes underlying tree diversity effects more tractable while keeping constant other confounding factors.

2.2 | Sampling protocol

We conducted eight visual surveys of bird species visiting the experimental plots, and all the data were recorded at the plot level. Surveys took place roughly every 45 days from February 2017 to January 2018 (i.e. the plantation was 6 years old at the start of this study). We selected 32 out of the total 74 plots in the system (Figure S1), and these same plots were resampled over the course of the study, specifically: 12 monocultures (*n* = 2 plots/species) and 20 polycultures (14 unique combinations of four out of the six species). Each survey spanned a 6-day period during which all plots were visited three times in different days, with each visit consisting of a 20-min observation period. All bird observations were conducted between 6.00 and 9.30 hr and the order in which plots were visited was randomized both within and across surveys. During each plot visit, we visually documented bird species and abundance, considering only cases where individuals were perched or foraging on trees in the plot (Nell et al., 2018). When observing a given plot, we did not consider cases where the same individual revisited the plot to avoid overestimating bird counts. It is still likely, however, that the same individual visited multiple plots during a given census day. Accordingly, bird responses should be taken as descriptors of foraging activity or habitat use (Nell et al., 2018), rather than as estimates of actual bird abundance and richness associated to experimental plots. This contrasts with previous studies involving responses by smaller-bodied and less-mobile invertebrate consumers (e.g. arthropods; Haddad et al., 2009; Scherber et al., 2010) for which effects on actual abundance and diversity of consumers can be inferred.

2.3 | Statistical analyses

2.3.1 | Descriptors of bird visitation

We calculated plot-level bird abundance, richness, phylogenetic diversity (PD), and functional diversity (FD) by computing cumulative values across surveys for each plot. The latter two represent estimates of overall phylogenetic and functional richness of visiting birds per plot. Estimates of PD were obtained

from the sum of all branches of phylogenetic trees based on the bird species found in each (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011), whereas FD was obtained from the sum of all branches of dendograms of functional traits of the bird species recorded on each plot (Petchey & Gaston, 2002). The bird traits used to estimate FD represent attributes associated with diet and foraging behaviour obtained from a global dataset (Wilman et al., 2014), namely: body weight, main type of diet (vertebrate prey, invertebrate prey, fruit, nectar, seeds or omnivore), percentage of the diet by type (vertebrate, invertebrate, fruit, nectar, seeds or other plant-based diet) and relative amount of time spent foraging in different forest strata (gound, understory, mid-canopy, canopy and aerial). We also included the migratory status of each species in Mexico (i.e. resident or migrant) based on Berlanga et al. (2017) and Chesser et al. (2019). The functional dendrogram was based upon pairwise Gower's distances calculated from trait values, in which numeric traits were rescaled to a mean of 0 and standard deviation of 1, and UPGMA clustering was applied. In the case of PD, branch lengths of phylogenetic trees were deducted from a 95% consensus tree with mean branch lengths. Trees were obtained from 200 calibrated phylogenies (Hackett-backbone) obtained from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Values of PD and FD were calculated using the APE, PHYTOOLS, PICANTE, and CLUSTER packages in R version 3.4.4 (R Studio Team, 2016). We also compared trait composition between migrant and resident bird species by using a permutational analysis of variance (PERMANOVA) based on 10,000 permutations. In this test, Gower's pairwise dissimilarity was calculated using all aforementioned traits except migratory status, with traits scaled to a mean of 0 and standard deviation of 1. Subsequently, the relationships between trait composition and migratory status were assessed by relating each individual trait to the multivariate trait space fit by non-metric multidimensional scaling analysis (NMDS; Cox & Cox, 1994).

2.3.2 | Tree diversity effects on descriptors of bird visitation

We tested for an effect of tree diversity on each bird response using aggregated data across surveys for each plot by using log-response ratios (LRRs), calculated as the natural logarithm of the mean value in polyculture over the weighted mean value in monoculture (Cardinale et al., 2006; Hedges, Gurevitch, & Curtis, 1999). For each LRR, we calculated a 95% CI following Hedges et al. (1999), and a LRR was considered statistically significant when the CI did not bracket zero (Koricheva, Gurevitch, & Mengersen, 2013). This approach has two advantages. First, it allowed us to control for differences in tree species relative frequencies (and thus, indirectly, effects of species composition) between monoculture and polyculture by weighting monoculture values by the frequency of occurrence of each tree species in polyculture (Nell et al., 2018).

Specifically, the monoculture mean was obtained by summing the products of the mean value of each species in monoculture by the proportion of individuals represented by each species across all polyculture plots (i.e. species's relative frequency across all mixtures). Second, the use of LRRs provides a unitless, standardized measure of the diversity effect that can be compared consistently across all bird responses (Cardinale et al., 2006). To account for an effect of abundance on bird diversity measures (richness, FD and PD), we also calculated LRRs at the plot-level after using individual-based rarefaction. The diversity of each plot was estimated at a sample size of 100 birds using the INEXT and INEXTPD packages in R (Hsieh & Chao, 2016). In addition, for each bird response, we also tested for transgressive overyielding (Cardinale et al., 2006) by comparing the mean value across all polycultures with the mean value of the monoculture with the highest value for that response. This tested whether observed diversity effects were over and above the influence of dominant species shaping bird community descriptors.

Parallel to assessing the effects of tree diversity on bird responses using LRRs, we also ran Bayesian mixed models with a Markov chain Monte Carlo sampler using the MCMCGLMM package for R (Hadfield, 2010). For each response variable, we ran a model that included tree diversity as a fixed effect, plot as a random effect, and a multimembership random term for tree composition with constant variance structure. The multimembership term defined the tree species in each plot weighted by their relative abundance (1 in monoculture or 0.25 per tree species in polyculture). By using this multimembership term, these models account for shared tree species among plots in estimating tree diversity effects and are able to evaluate tree species effects on the bird responses. All models were run for 400,000 iterations with a burn in period of 20,000 iterations, a thinning parameter of 100, and using parameter expanded priors to improve model convergence (Hadfield, 2010). To assess model convergence we visually examined the autocorrelation in posterior distibutions, and ensured the effective sample size was in excess of 1,000 for all model parameters. For fixed effects, we report GLMM fit in terms of the posterior mean, 95% credible intervals, MCMC p-values, and the effective sample size of each term. In addition, the individual random effects for tree composition were used to assess whether any tree species had positive or negative effects on the response variable. Model parameters were deemed statistically significant when the 95% credible intervals did not overlap zero. The MCMCglmm models were run for bird abundance and diversity (richness, FD and PD), as well as using rarefied richness and diversity estimates based on a reference sample size of 100 individuals using individual-based rarefaction in the INEXT and INEXTPD packages in R (Chao et al., 2014; Hsieh & Chao, 2016; Hsieh, Ma, & Chao, 2019), to account for underlying variation in bird abundance. Bird abundance and unrarefied species richness were modelled using a Poisson distribution for count data, while FD, PD and all rarefied variables fit a Gaussian distribution.

To test for an effect of tree diversity on bird species composition and its variability, we ran a permutational analysis of variance (PERMANOVA) and permutational analysis of multivariate dispersions (PERMDISP) respectively, using aggregated data at the plot-level. The PERMANOVA and PERMDISP are complementary to one another in that both use multivariate dissimilarities to test for differences between groups and their results inform the interpretation of the other. A PERMANOVA tests for differences in group centroids (between group variation, 'location' effect) in multivariate space and the PERMDISP compares the average distance of each data point from the group centroid (within-group variation, 'dispersion' effect) among groups (Anderson, 2006; Anderson, Ellingsen, & McArdle, 2006). In this way, PERMDISP can be used to infer consistency in community composition using a measure of multivariate beta diversity and PERMANOVA provides a test for differences in the average group composition. Both analyses were based on 10,000 permutations of a Bray-Curtis dissimilarity matrix using the VEGAN package in R (R Studio Team, 2016).

2.3.3 | Temporal variation in tree diversity effects and stability in bird visitation

We calculated bird responses by survey for each plot using values summed across visits within each survey. To describe the temporal variation in tree diversity effects, for each survey we calculated plot-level LRRs and 95% CIs following the above procedure. We calculated effect sizes using all bird species, as well as by species' primary diet source (fruit, invertebrates, nectar, plants and omnivores) and migratory status (Wilman et al., 2014). In parallel fashion, we also tested for temporal variation in diversity effects on bird foraging visitation by running linear models in the MCMCGLMM package. These included the effects of tree diversity treatment survey, and a diversity by survey interaction on each bird response variable using the same priors and procedures as the models with aggregated data across surveys previously described. To evaluate whether the effect of tree diversity varied by survey we used joint tests to obtain and test interaction contrasts for the main effects of tree diversity and month, and within-month contrasts for the tree diversity effect (e.g. whether monocultures and polycultures differed each month).

Finally, we computed the temporal stability in bird responses for each plot by dividing the mean value across surveys for a given bird response by the standard deviation across surveys for that response (i.e. inverse of the coefficient of variation; Haddad et al., 2011; Pimm, 1991; Tilman et al., 2006). For each bird response, we then calculated LRRs and 95% CIs (as above) by dividing the mean stability value across all polyculture plots by the weighted mean stability across monocultures. In addition, we also ran MCMC linear models (see above) testing for a diversity effect on the stability of each bird response.

All statistical analyses described above are summarized in Figure S2.

3 | RESULTS

3.1 | Descriptors of bird foraging and habitat use

We recorded 84 bird species across the sampled plots and surveys, belonging to seven orders, 19 families and 53 genera (Table S1). The best represented families were Tyrannidae and Parulidae with 16 and 13 species respectively. Of the total species, 73% were resident (61 species) and 27% were migrant (23 species), and with respect to trophic specialization, 60% of the species had a primarily invertebrate-based diet (50 species), 19% were omnivorous (16 species), 7% frugivorous (6 species), 7% nectarivorous (6 species), and 7% granivorous (6 species; Table S1). In addition, migrant birds differed from resident species with respect to the studied traits (PERMANOVA; $p = 0.003$): compared to residents, migrants tended to have a smaller body size ($R^2 = 0.61$, $p = 0.001$), were biased towards invertebrate ($R^2 = 0.16$, $p = 0.003$), and nectar-based diets ($R^2 = 0.35$, $p = 0.001$), and spend less time foraging on the ground ($R^2 = 0.72$, $p = 0.001$).

3.2 | Tree diversity effects on descriptors of bird foraging and habitat use

Of the total 84 bird species, 22 were observed exclusively in polyculture plots whereas only three species were unique to monocultures. Rarefaction analyses indicated that our surveys captured >80% of the species predicted for both monoculture and polyculture plots (Chao 1 and Jacknife 1 estimators). Estimated species richness in polycultures (81 species) was greater than extrapolated richness in monocultures (70.38 ± 5.56 species [estimator, *SE*]; Figure S3). Similarly, FD and PD in polycultures exceeded estimates based on monocultures after controlling for sampling effort (Figure S3).

The analysis of tree diversity effect sizes indicated significant positive effects of diversity on all bird responses. Namely, polycultures exhibited, on average, a 43% greater bird abundance (LRR ± 95% CI = 0.36 ± 0.12), 32% greater richness (0.27 ± 0.07), 25% greater PD (0.22 ± 0.05), and 25% greater FD (0.22 ± 0.05) than monocultures (Figure 1). In addition, for all bird responses the mean value across polycultures did not exceed (and in some cases was lower than) the mean value of the species in monoculture with the highest bird abundance (*E. cyclocarpum*, *C. pentandra* and *C. dodecandra*) and diversity (*E. cyclocarpum*), indicating no transgressive overyielding (Figure 2). Follow-up mixed models controlling for tree species composition similarly indicated a significant effect of tree diversity on bird abundance, richness, FD and PD (Table S2), as well as variation in tree species effects on bird abundance (significant and strongest for *E. cyclocarpum*, *C. pentandra* and *C. dodecandra*), but no significant effect of any individual tree species on bird richness or diversity (Figure S4a). In addition, estimates of LRRs and mixed models for rarefied bird richness, FD and PD similarly showed significant tree diversity effects (Table S2; Figure S5), though for FD the diversity LRR was substantially reduced and the tree diversity effect was non-significant in the mixed model (Table S2; Figure S5).

The permutation tests indicated a significant effect of tree diversity on bird community composition (PERMANOVA pseudo-$F_{1,30}$ = 1.74, p = 0.029) and multivariate dispersion (PERMDISP; $F_{1,30}$ = 21.5, p < 0.0001) in which there was less within-group variation in bird species composition among polyculture plots compared to monocultures (Figure S6).
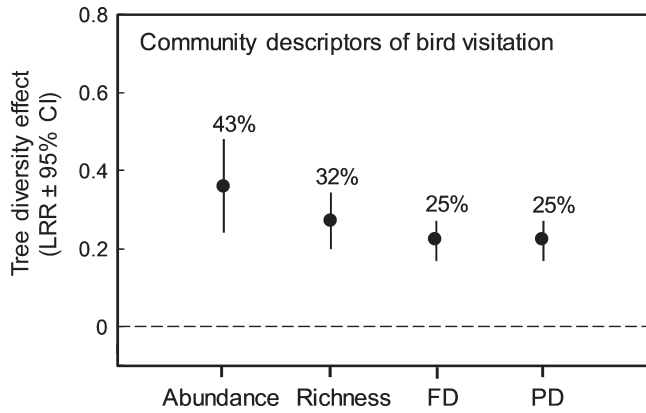

FIGURE 1 Effect of tree species diversity on descriptors of bird visitation to experimental plots in a tree diversity experiment, namely: bird abundance, species richness, functional diversity (FD), and phylogenetic diversity (PD). Diversity effects were estimated as log-response ratios (LRRs), see Section 2. Error bars are 95% confidence intervals around each ratio

3.3 | Temporal variation in tree diversity effects on community descriptors of bird visitation

We observed variation across sureys in our estimates of visiting bird abundance and diversity (Figure 3a–d). Mean bird abundance, species richness, and diversity per plot were highest at the end of the dry season (April–May) and initial period of the rainy season (July), and lowest during the winter months despite the influx of migrants (November–January) (Figure 3a–d). Likewise, we also observed shifts across surveys in the relative abundance and species richness of bird feeding guilds (Figure S7). Follow-up linear regression models correcting for error autocorrelation (i.e. non-independence) among surveys (Milhøj, 2013) indicated that variation across surveys in bird abundance and richness was significantly positively associated with temporal variation in temperature (t ≥ 2.59, p ≤ 0.04) and also tended to be positively correlated (albeit not significantly) with precipitation (t ≥ 1.74, p ≤ 0.14).

Notably, tree diversity had a significant positive effect on temporal stability of all bird responses. Polycultures exhibited, on average, an 18% greater stability in abundance (LRR = 0.16 ± 0.09), 38% greater stability in richness (LRR = 0.31 ± 0.10), 32% greater stability in PD (LRR = 0.28 ± 0.11)and 35% greater stability in FD (LRR = 0.30 ± 0.09) relative to monocultures (Figure 4). Similarly, results from GLMMs were generally consistent with these results indicating a significant and marginally significant positive effects of
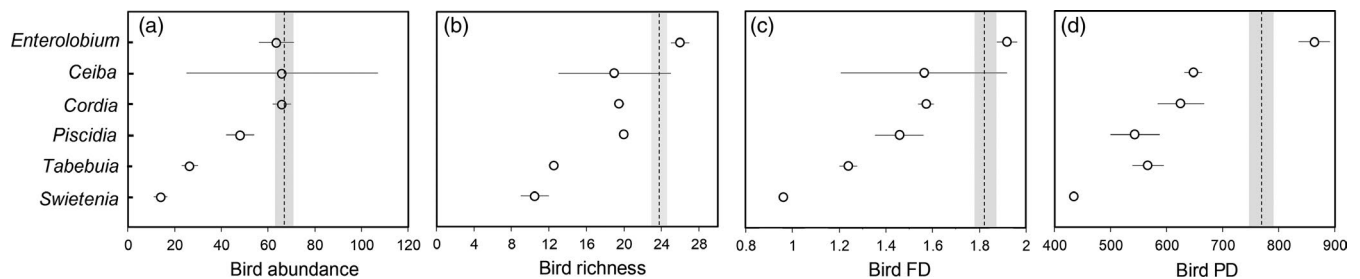

FIGURE 2 Mean values (±SE) of (a) bird abundance, (b) species richness, (c) functional diversity (FD), and (d) phylogenetic diversity (PD) for each tree species in monoculture. The vertical dotted line is the mean value across all tree species polyculture plots (shaded area is the SE)
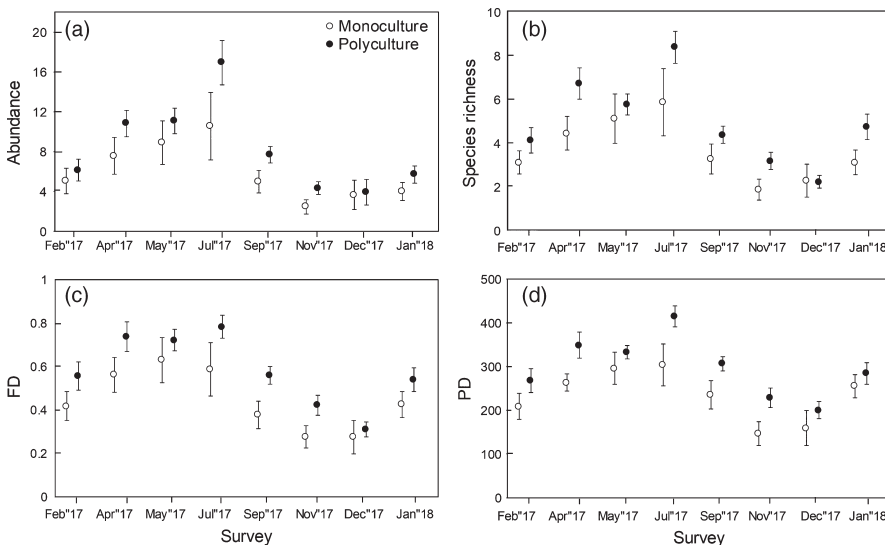

FIGURE 3 Temporal variation in descriptors of bird visitation to experimental plots, namely: (a) bird abundance, (b) species richness, (c) functional diversity (FD), and (d) phylogenetic diversity (PD) associated with the experimental plots. Values are plot-level means and SEs, shown separately for tree species monoculture and polyculture plots

diversity on stability of bird richness and FD respectively (but not on stability in bird abundance or PD; Table S2).

The tree diversity effect sizes varied across surveys for all bird responses (among-survey variance in LRRs = 0.029; Figure 5), as well as by migratory status and bird diet (Figures S8 and S9 respectively). For bird abundance, effect sizes ranged from polycultures having an 11% (December LRR = 0.11 ± 0.37) to an 80% (November
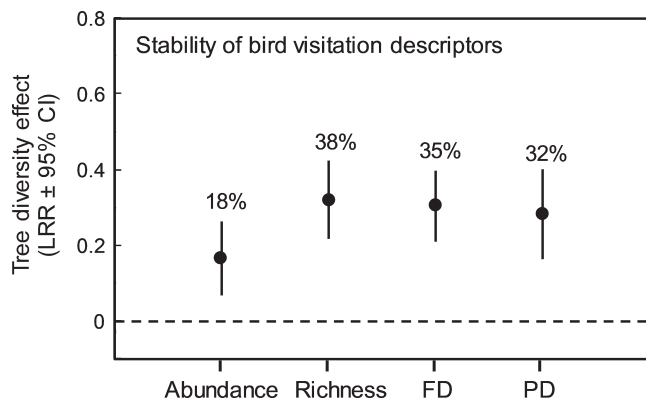
LRR = 0.58 ± 0.22) greater mean value than monocultures (Figure 5a). Similarly, effect sizes for bird richness ranged from polycultures having 0.5% (LRR = 0.005 ± 0.26) to 76% (LRR = 0.56 ± 0.20) greater mean value than monocultures (Figure 5b). In addition, effect sizes for FD ranged from polycultures having a 13% greater to a 54% greater mean value than monocultures depending on the survey (Figure 5c), whereas those for PD ranged from polycultures having 8% to 58% greater mean value than monocultures (Figure 5d). It is important to note that there was also substantial variation within surveys (i.e. among plots) and CIs were largely overlapping. Results from the mixed models indicated significant diversity and survey effects on all responses, and contrasts comparing diversity levels in similarly indicated variation among surveys in diversity effects, with some but not all surveys exhibiting significant differences between monoculture and polyculture (Table S3). Such changes in significance across surveys were usually consistent with changes in the magnitude of LRRs. These models also indicated variation in tree species effects on bird abundance and diversity (significant and strongest for *E. cyclocarpum*, *C. pentandra* and *C. dodecandra*; Figure S4b). Finally, additional inspection indicated that the mean value in polyculture was not greater than that of the species in monoculture with the highest value for any of the surveys or bird community responses (i.e. no transgressive overyielding; Figure 6). However, the identity of the species with the highest mean value in monoculture changed across surveys (Figure 6), indicating marked
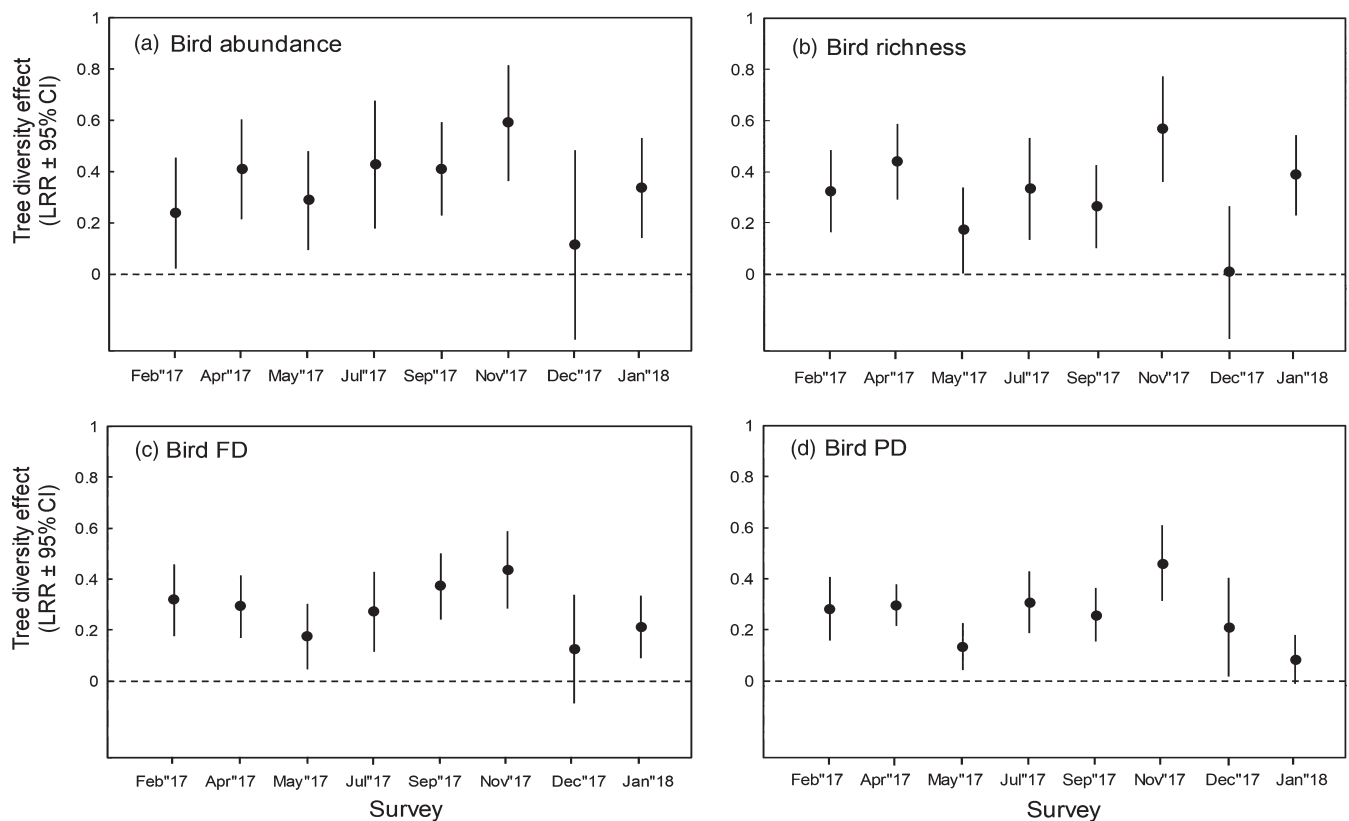

FIGURE 4 Effect of tree species diversity on the temporal stability of bird abundance, species richness, functional diversity (FD), and phylogenetic diversity (PD), where stability is the mean across surveys over the standard deviation across surveys for each bird response. Diversity effects were estimated as log-response ratios (LRRs) and error bars are 95% confidence intervals

FIGURE 5 Temporal variation in tree diversity effects on descriptors of bird visitation, namely: (a) bird abundance, (b) species richness, (c) functional diversity (FD), and (d) phylogenetic diversity (PD). Diversity effects are estimated as log-response ratios (LRRs), and error bars are 95% confidence intervals
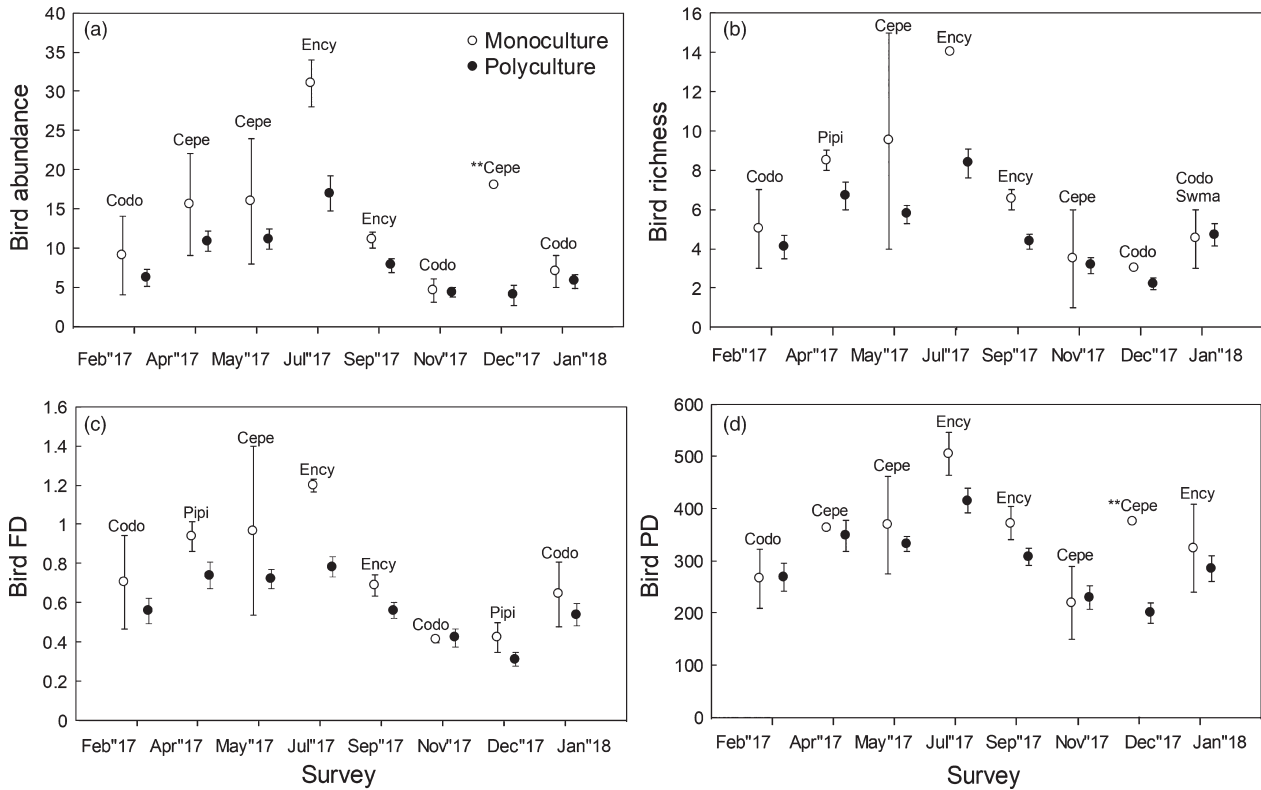
FIGURE 6 Mean (±*SE*) values of bird (a) abundance, (b) richness, (c) functional diversity (FD), and (d) phylogenetic diversity (PD) for the tree species with the highest mean in monoculture and the overall mean across tree polyculture plots, shown for each survey. An abbreviation of the name of species with the highest mean value in monoculture for each survey is provided: 'Codo' (*Cordia dodecandra*), 'Cepe' (*Ceiba pentandra*), 'Ency' (*Enterolobium cyclocarpum*), 'Pipi' (*Piscidia piscipula*), 'Swma' (*Swietenia macrophylla*), and 'Taro' (*Tabebuia rosea*). For one survey there were two tree species with virtually the same monoculture value and we thus show both species names. In most cases, however, the species with the highest monoculture value had a mean value clearly higher than the other species (indicated by slight or no overlap in error bars). **Monoculture with no replication (*n* = 1 plot)

temporal changes in the identity of tree species with the strongest bird effects.

Results from all the statistical analyses performed in the study are summarized in Table S4.

4 | DISCUSSION

4.1 | Overview

Tree species diversity drove substantial increases in descriptors of bird visitation to experimental plots, namely abundance and diversity, and also influenced species composition. In addition, we found that the strength of tree diversity effects on these bird responses varied across surveys, possibly responding to seasonal (or other type of periodic) changes in bird behaviour and abiotic (e.g. weather) conditions. Furthermore, tree diversity also decreased temporal variability in bird responses, with polycultures exhibiting greater stability in bird abundance and diversity compared to monocultures. Together, these findings have important implications for understanding how bird communities respond to local-scale changes in tree diversity and the stabilizing effects of tree diversity on bird foraging and habitat use.

4.2 | Effect of tree diversity on bird visitation

Studies experimentally testing for plant diversity effects on vertebrate community structure and foraging behaviour are scarce (but see Nell et al., 2018). Most work with birds has involved observational studies correlating vegetation features (physiognomical complexity, availability of food resources; e.g. Chen et al., 1999; Kissling et al., 2007; Malizia, 2001; Yahya et al., 2017) with bird behaviour, abundance and diversity (reviewed by Castagneyrol & Jactel, 2012; Maas et al., 2016; Sekercioglu, 2012). To the best of our knowledge, only three studies to date have provided unambiguous tests of causal links between tree diversity and bird foraging and community structure by experimentally manipulating tree diversity (Muiruri et al., 2015; Nell et al., 2018; Yang, He, Zhang, Bruelheide, & Schuldt, 2018). In one of such studies, Muiruri et al. (2016) found positive effects of tree diversity on foraging intensity by insectivorous birds in a temperate system, but did not ascribe these patterns to changes in bird community structure. Similarly, in a previous study at the UADY diversity experiment, we found positive effects of tree diversity on descriptors of insectivorous bird foraging activity, and the diversity of this subset foraging birds was in turn found to be associated with heightened

predation rates by insectivorous birds (Nell et al., 2018). Our present work builds on these findings by testing for effects across all trophic guilds of visiting birds and provides compelling evidence for tree diversity effects on small-scale patterns of bird habitat use and its temporal variability.

Tree polyculture plots likely offer more favorable biotic or abiotic conditions which enhance bird visitation. In addition, tree diversity effects on bird richness and (phylogenetic) diversity persisted (but did weaken, e.g. LRRs, see Figure S5) after accounting for bird abundance, indicating that increases in bird abundance alone cannot explain higher bird diversity in polycultures. However, and in contrast to our previous work (Nell et al., 2018), we found no evidence of transgressive overyielding as the polyculture mean values for bird abundance, richness, and diversity (both PD and FD) did not exceed those of the species monoculture with the higest value in each of these cases. In this sense, *E. cyclocarpum* monocultures, followed by those of *C. pentandra* and *C. dodecandra*, exhibited the highest richness and diversity of visiting birds, suggesting that these tree species were the largest contributors to tree diversity effects on bird recruitment. Having said this, results from the GLMMs showed significant tree diversity effects on bird richness and diversity after accounting for tree species effects, indicating that although these tree species have a strong influence on bird visitation, the effect of tree diversity is greater than can be explained by species identity effects alone.

4.3 | Temporal variation in tree diversity effects on bird visitation

There was substantial variation in bird visitation to the experimental plots over the sampling period. Bird abundance and diversity tended to increase at the end of the dry season (April, May) and peaked during the first third of the rainy season (e.g. July), a pattern that was possibly associated with changes in behaviour during the reproductive season of resident species (e.g. mate search and nest construction; Gill, 1990) which increased bird visitation to the experimental plots. In contrast, bird abundance and diversity were lowest during the winter months (December–January) and the first half of the dry season (February–March), likely explained by lower resource availability (e.g. seeds, insects) and less favourable weather conditions (e.g. high temperatures) affecting bird activity levels (and possibly also population sizes). It is also important to note that we recorded a greater number of migratory species during the winter months, as this is the time of year when North American migratory birds arrive to the Yucatan Peninsula (Cortés-Ramírez, Gordillo, & Navarro, 2012; Deppe & Rotenb, 2005; Guerrero, 2002). However, bird abundance and diversity in experimental plots were usually low during these winter months, indicating that changes in bird visitation were driven predominantly by resident species and that the influx of migratory species did not offset this temporal trend.

Crucially, our analyses showed that tree diversity had a stabilizing effect on bird visitation expressed over time. To our knowledge,

this is the first study to test for and find an effect of plant diversity on the stability of vertebrate consumers. In contrast, past studies have focused on stability in plant diversity-productivity relationships (e.g. Cottingham, Brown, & Lennon, 2001; Hector et al., 2010; Lehman & Tilman, 2000; Tilman et al., 2006) and stability in invertebrate communities (e.g. Borer et al., 2012; Haddad et al., 2011; Proulx et al., 2010). Our findings should, however, be taken as a measure of stability in foraging activity or habitat use (Nell et al., 2018), rather than as estimates of stability in actual bird abundance and richness as in studies with arthropods (Haddad et al., 2009; Scherber et al., 2010). Regardless, some of the same mechanisms invoked in those studies can be used to explain bird responses in our work. For example, polycultures may exhibit reduced temporal fluctuations in biotic or abiotic variables, which in turn stabilized bird visitation in tree species mixtures. A mechanism for this could be asynchrony in tree species leafing phenologies which contributes to a more sustained reduction in abiotic stress (e.g. lower maximum temperatures due to shading) throughout the year, as well as greater temporal consistency in resource availability (e.g. invertebrate prey associated to foliage for insectivorous birds). In support of this, the identity of the tree species in monoculture with the highest abundance and diversity of visiting birds varied across surveys and polycultures attracted birds more consistently throughout the study, tracking closely the highest monoculture in most surveys. Thus, it appears that variation among tree species in leafing phenology or some other traits important for birds favours consistently high bird visitation to polycultures throughout the year, a stability-promoting mechanism that is in line with the Insurance Hypothesis (Hector et al., 2010; Yachi & Loreau, 1999). Likewise, other mechanisms emanating within bird communities (independently of plant community-based ones) could relate to increased asynchrony of bird species responses in polycultures producing a stabilizing effect on bird visitation, including a negative covariance effect (Tilman, 1999), a portfolio effect (Doak et al., 1998), or response diversity (Karp et al., 2011). Whatever the mechanism(s) driving the stabilizing effect of tree diversity on bird behaviour and habitat use, we expect these effects to strengthen over time. Moreover, in light of our previous results in this system showing that increased diversity of insectivorous birds was related to higher predation rates (Nell et al., 2018), our present findings imply increased stability and long-term persistence of pest regulation in more diverse natural as well as planted tree communities used in forestry or reforestation.

Results also indicated changes in the strength of tree diversity effects (LRRs) on bird visitation throughout the study. Such temporal variation in the tree diversity effect appeared not to be associated with fluctuations in bird species richness or weather conditions. Notably, the strongest diversity effect on bird diversity was observed at the start of the winter season (November) when bird numbers were lowest, whereas the following survey had a similar bird abundance and diversity but exhibited the weakest effect size. In addition, intermediate effect sizes were scattered throughout the dry (April) and rainy seasons (July and September), whereas the end of the dry season/start of rainy season (May) tended to exhibit

weak effect sizes but had the highest bird abundance, FD, and PD. It is, however, possible that temporal changes in diversity effects were related to changes in bird species composition as observed in previous studies correlating temporal (e.g. seasonal) changes in bird species composition and vegetation characteristics (e.g. Deppe & Rotenb, 2005; Johnson, Sherry, Strong, & Medori, 2005; Malizia, 2001). At the same time, it is important to keep in mind that there was also substantial within-survey variation and LRR confidence intervals overlapped for most surveys, thus calling for moderation in interpreting the observed patterns of temporal variation in diversity effects.

The influx of migratory bird species to the Yucatan Peninsula during the winter months (October to February) is likely an important factor shaping the associations between tree diversity and bird visitation. Migrants were absent or at low abundance from April to September, which is also when resident bird abundance and species richness was highest, and it is during this time that we observed consistent positive effects of tree diversity on bird visitation. In contrast, the tree diversity effect tended to be more variable during the winter months when migratories were present. These patterns, combined with the fact that residents and migrants appeared to respond differently to tree diversity (see Figure S8), suggests trait- and niche-related differences associated with migratory status which shape bird foraging choices and habitat use within and among plots. For example, migratory species might be more generalist in their feeding habits or habitat requirements than residents (Greenberg, 1995; Levey, 1994) and respond less strongly to changes in tree diversity, thus explaining weaker effect sizes for several winter surveys. Interestingly, however, the November (winter) survey exhibited the highest effect sizes whereas the following survey had a similar abundance and richness of migrant species but exhibited the weakest effect size throughout the study. In fact, the November survey exhibited a strong positive effect size for migrants but no effect on residents, whereas the following survey exhibited a weak effect on migrants (and residents; Figure S8). This instead suggests that migrants responded more strongly to diversity than residents and dictated the diversity effect during the November survey, making it difficult to draw conclusions about the influence of migratory species on overall bird responses. In addition, temporal changes in bird guild composition and differential responses to tree diversity among guilds (Figures S7 and S9) could have also dictated temporal variation in bird habitat use and the outcome of diversity effects. Finally, we cannot discount the possibility that seasonal changes in weather conditions affected bird movement and foraging behaviour (Crick, 2004; Walther, Chen, Lin, & Sun, 2017), independently of (or in addition to) changes in species composition.

4.4 | Study design considerations

Results should be interpreted in light of several important features of our experimental design. First, the plot size used (21 m × 21 m) is considerably small considering bird movement and therefore results reflect bird responses to small-scale changes in tree diversity and species composition (i.e. microhabitat-level responses; Naugle, Higgins, Nusser, & Johnson, 1999). In this sense, previous studies have reported scale-dependent bird responses to habitat features (e.g. Naugle et al., 1999; Thompson & McGarigal, 2002) and a recent experimental study highlighted the importance of scale in testing for tree diversity effects on bird visitation (Muiruri et al., 2016). Thus, further tests of tree diversity effects at multiple spatial scales are warranted. Second, close proximity among plots could influence tree diversity effects on bird visitation due to spill-over among neighbouring plots. However, this would presumably weaken tree diversity effects and the fact these were detectable (and strong) in any case suggests that our results provide an underestimate. In addition, that our experiment was conducted at a small spatial scale within a homogeneous landscape helped to control for other factors varying at broader spatial scales (e.g. bird species composition, climatic conditions). Future experimental work measuring local-scale bird (or other vertebrate taxa) responses to tree diversity should consider design features that address the effects of spatial scale (e.g. by including several plot sizes) and plot proximity (by testing different levels of spatial aggregation) within the same landscape or ecosystem type, as well as ultimately replicate these efforts across community types to increase inference.

5 | CONCLUSIONS

This study provides novel evidence of plant diversity effects on the stability of measures associated with bird (and more generally, vertebrate) foraging activity and habitat use. We found no indication that tree diversity affected birds via non-additive dynamics (i.e. transgressive overyielding), but rather suggest an important role of dominant tree species in driving bird visitation to diverse tree plots. At the same time, tree diversity effects persisted after accounting for tree species effects (from the linear mixed models), suggesting that dominant tree species did not fully account for bird visitation patterns to experimental plots. In addition, diversity effects on bird diversity persisted after controlling for bird abundance showing that observed increases in bird diversity were not entirely driven by bird abundance. Importantly, in asessing temporal variation we show that tree diversity stabilizes bird visitation over time, implying insurance-related mechanisms. This affirmation is supported by the fact that the identity of tree species in monoculture with the highest bird numbers varied throughout the year, whereas polycultures generally exhibited similar values to the most dominant species in monoculture. This finding is key for understanding the long-term effects of plant diversity on vertebrates and the persistence of ecosystem functions. At the same time, our findings also emphasize that tree diversity effects on bird communities are inherently variable through time and call for future efforts to unveil the biotic and abiotic drivers of temporal variation in consumer responses to tree diversity.

AUTHORS' CONTRIBUTIONS

L.A.-R., Y.M.-U., C.S.N. and V.P.-T. conceived the ideas and designed the methodology; Y.M.-U. collected the data; L.A.-R., Y.M.-U., C.S.N. and J.N. analysed the data; Y.M.-U. and L.A.-R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pzgmsbch5 (Abdala-Roberts, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.