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ORIGINAL RESEARCH

Temporal variation in tree diversity effects on birds and its implications for top-down control of insect herbivores in a tropical system

Carla Vázquez-González[1,2] · Edith Villa-Galaviz[3] · Martha Reyes-Hernández[3] · Biiniza Perez-Niño[3] · Teresa Quijano-Medina[3] · Víctor Parra-Tabla[3] · Kailen A. Mooney[1] · Luis Abdala-Roberts[3]

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Abstract

Tree diversity promotes predator abundance and diversity, but evidence linking these effects to increased predation pressure on herbivores remains limited. In addition, tree diversity effects on predators can vary temporally as a function of environmental variation, or due to contrasting responses by different predator types. In a multi-year study, we assessed temporal variation in tree diversity effects on bird community abundance, diversity, and predation rates as a whole and by functional group based on feeding guild (omnivores vs. insectivores) and migratory status (migrant vs. resident). To this end, we conducted bird point counts in tree monocultures and polycultures and assessed attacks on clay caterpillars four times over a 2-year period in a tree diversity experiment in Yucatan, Mexico. Tree diversity effects on the bird community varied across surveys, with positive effects on bird abundance and diversity in most but not all surveys. Tree diversity had stronger and more consistent effects on omnivorous and resident birds than on insectivorous and migratory species. Tree diversity effects on attack rates also varied temporally but patterns did not align with variation in bird abundance or diversity. Thus, while we found support for predicted increases in bird abundance, diversity, and predation pressure with tree diversity, these responses exhibited substantial variation over time and the former two were uncoupled from patterns of predation pressure, as well as contingent on bird functional traits. These results underscore the need for long-term studies measuring responses by different predator functional groups to better understand tree diversity effects on top-down control.

Keywords Natural enemies · Predation · Species diversity · Tri-trophic interaction · Tropical trees

Introduction

Plant diversity effects on species interactions and ecosystem function have been widely documented (Tilman et al. 2001; Cardinale et al. 2011; Hooper et al. 2005). Within this body of work, the “Enemies Hypothesis” poses that plant diversity promotes the abundance and diversity of natural enemies (i.e., predators and parasitoids), ultimately favouring top-down control of herbivores (Root 1973; Haddad et al. 2009; Letourneau et al. 2011). In the case of forests, however, a recent meta-analysis by Stemmelen et al. (2022) found support for predicted increases in natural enemy abundance and diversity with tree diversity but no overall effect of tree diversity on predation pressure. As such, these patterns challenge the generality of the Enemies Hypothesis in forests, underscoring the need for experimental studies assessing tree diversity effects on predation in order to robustly test

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Kailen A. Mooney and Luis Abdala-Roberts share the senior authorship.

✉ Luis Abdala-Roberts
Abdala.luis@yahoo.com

[1] Department of Ecology and Evolutionary Biology, University of California-Irvine, Irvine, CA 92697, USA

[2] Misión Biológica de Galicia (MBG-CSIC), Apartado de Correos 28, 36080 Pontevedra, Galicia, Spain

[3] Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Apartado Postal 4-116, Itzimná, 97000 Mérida, Yucatán, Mexico

predictions and reveal underlying mechanisms (see Staab and Schuldt 2020).

Most tree diversity studies have involved single time-point assessments and those involving repeated sampling time points are often conducted within the same season. Nevertheless, tree diversity effects on predators are expected to fluctuate within and among seasons due to changes in biotic (e.g., predator species composition, prey availability) or abiotic (e.g., climate) co-occuring factors (Piovia-Scott et al. 2017; Staab and Schuldt 2020). For instance, building on the Stress Gradient Hypothesis (Bertness and Callaway 1994), it has been proposed that tree diversity effects on ecosystem functioning (e.g., productivity) should be stronger under environmentally limiting conditions, via mechanisms such as increased plant–plant facilitation and amelioration of abiotic stress (Gessner and Hines 2012; Jucker and Coomes 2012; Forrester 2014; Schnabel et al. 2023). Expanding on this to higher trophic levels, tree diversity effects on predators should be more pronounced under environmentally limiting periods, when diverse tree stands can more greatly enhance favorable microhabitat conditions and buffer against abiotic and prey abundance variability. This, in turn, would result in greater predator attraction and residence times (Betts et al. 2018; McGinn et al. 2023), thus favoring enhanced top-down control. To date, however, long-term studies of tree diversity effects on predator communities and foraging behaviour are scarce but essential to understand variations in top-down control and its drivers.

Birds are functionally diverse predators exerting strong top-down effects on insects (Mooney et al. 2010; Maas et al. 2016; Whelan et al. 2008), and are also highly responsive to changes in tree diversity via its effects on habitat complexity or prey availability (Betancurt-Grisales et al., 2021; Castaño-Villa et al. 2014; Langellotto and Denno 2004). Yet, birds are underrepresented in tests of the Enemies Hypothesis compared with other predator groups, mainly arthropods (Stemmelen et al. 2022). Experimental tests conducted thus far have reported positive effects of tree diversity on bird abundance and diversity (Stemmelen et al. 2022; Staab and Schuldt 2020), and, in turn, higher predation rates by birds in some cases (Nell et al. 2018; Muiruri et al. 2016), but not in others (Yang et al. 2018; Interian-Aguiñaga et al. 2022). Such variation in tree diversity effects on predation could be explained by contrasting responses by different bird functional groups (May-Uc et al., 2020; Van Bael et al. 2008). For instance, highly generalist omnivorous species might benefit to a greater extent from more diverse food sources found in mixed stands and, therefore, show stronger responses to tree diversity compared to specialists (e.g., obligate insectivores) (Zhang et al. 2017; Staab and Schuldt 2020). Relatedly, migratory status may also be predictive of responses to tree diversity, as migratory species tend to exhibit more specialized (e.g., highly insectivorous) diets than generalists (May-Uc et al. 2020; Van Bael et al. 2008; Greenberg 1995), and would therefore show weaker responses to tree diversity. At the same time, migratory status is also a proxy for traits associated with responses to abiotic conditions. Species migrating to tropical regions, for example, have greater abiotic (e.g., temperature) tolerance or a broader abiotic niche than residents (Cohen et al. 2020), and therefore, may be less sensitive to environmental buffering resulting from increased tree diversity. Nuanced tests of tree diversity that account for responses by different bird feeding guilds or functional groups are needed to test these predictions.

To address these gaps, we conducted a two-year study on the effects of tree diversity on bird community metrics (i.e., bird abundance and phylogenetic and functional diversity) and predation rates in a large-scale tree diversity experiment in Yucatán, Mexico (https://treedivnet.ugent.be/ExpUADY.html). We conducted four surveys from 2018 to 2020, two during the summer season (favourable environmental conditions and higher productivity) and two in the cold fronts season (more limiting conditions and lower productivity). We aimed to: (i) assess temporal variation in tree diversity effects on bird community metrics as a whole and by bird functional group (feeding guild: omnivores vs. insectivores; migratory status: migrant vs. resident), as well as on bird attack rates, and (ii) test for linkages between bird community metrics and attack rates underlying tree diversity effects on predation. Following the Enemies Hypothesis, we anticipated positive effects of tree diversity on bird community metrics and on attack rates, where higher bird abundance or diversity would positively correlate with attack rates. Furthermore, following the Stress Gradient Hypothesis, we expected temporal variation in such responses, with stronger effects occurring under environmentally limiting conditions, i.e., in the cold fronts season. Finally, we predicted that tree diversity effects would vary by bird functional group, with stronger effects on omnivorous and resident birds.

Methods

Experimental design

We conducted this study at the UADY Tree Diversity Experiment (20.412222 N, −89.753611 W; Fig. S1), a long-term experiment located in Yucatan, Mexico. A total of 74 replicate forest plots (21 × 21 m each; 0.1 ha) were established in December 2011, covering 7.4 ha and randomly assigned as either polycultures of four tree species or monocultures from a pool of six species, namely: *Swietenia macrophylla* King (Meliaceae), *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae), *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae), *Piscidia* *piscipula* (L.) Sarg. (Fabaceae), and *Cordia dodecandra* A. DC. (Boraginaceae); all species are native to the region (for more details on the design see: Abdala-Roberts et al. 2015). Each plot had 64 trees with 3 m spacing between trees. The understory of the plots had very limited growth in the last 5 years due to canopy closure. For this study, we focused on a subset of 28 plots, comprising 12 monocultures (two plots for each of the six tree species) and 16 polycultures (Fig. S1). Although distance between plots was limited in relation to bird movement and this could result in "spill-over" effects among neighbouring plots, consistent with the scale and design used in other tree diversity experiments testing for effects on predators (Staab and Schuldt 2020; Stemmelen et al. 2022), by using a small spatial scale (relative to bird movement) we ensured that all plots were accessible to birds (i.e., no effect of predator dispersal limitation; Bommarco and Banks 2003), thus evaluating bird stand or patch selection while controlling for other factors varying at broader scales such as bird species composition or abiotic conditions.

Bird community

We performed four visual bird surveys in three consecutive calendar years (Table S1) in each of the 28 plots. Specifically, we conducted surveys in December 2018 and February 2020 which corresponded to the cold fronts (winter) season, as well as in August 2019 and October 2020 which corresponded with the more productive summer season (Table S1). Surveys were conducted following methods in Nell et al. (2018). Briefly, we performed 10-min point count surveys at peak bird activity (06.00 to 09.30 am on rain-free days) using 10 × 42 binoculars and field guides for identification. We recorded whether birds were perching or foraging within the focal plot and excluded individuals that were not actively using the plot (e.g. passing through or flying above canopy). During each survey, we visited each experimental plot on four separate days (randomized sampled plots within and across days) during a one-week period, totalling 40 min of observation per plot. We pooled data across observations days for each plot to obtain a single value per plot and survey to calculate bird community response metrics (see next) for statistical analyses. Since more than one plot was surveyed at the same time during a given visit (two or three observers), we spaced concurrent surveys by each observer by a minimum of 50 m and did not survey neighbouring plots consecutively.

For each survey, we computed three community metrics at the plot level: bird abundance (total number of individuals), bird functional trait diversity (FD), and bird phylogenetic diversity (PD) (see May-Uc et al., 2020; Nell et al. 2018). Then, we categorized bird species based on their migratory status according to Berlanga et al. (2015) and Chesser et al. (2018), and their feeding guild. We determined feeding guilds based on each species' primary diet component according to Wilman et al. (2014) (Table S2). Subsequently, we computed bird community metrics for both the whole bird community as well as separately for insectivores vs. omnivores (the main feeding guilds) and for migrant vs. resident. We computed FD and PD as the sum of all branches in a trait-based dendrogram and a phylogenetic tree, respectively. Briefly, we calculated FD based on available species-level traits (Wilman et al. 2014) known to be important for herbivore suppression, namely body mass, period of activity (diurnal vs. nocturnal) major diet type (vertebrate, invertebrate, fruit/nectar, plant/seed, omnivore), proportion of diet by type, and relative time foraging in forest strata (ground, understory, mid-canopy, canopy, aerial). We log-transformed body mass to reduce the influence of a few uncommon and larger-bodied species. We scaled all functional traits to mean 1 and standard deviation 1, and weighted them equally to calculate Gower's pairwise dissimilarity among species (Gower 1971). Then, we applied a hierarchical clustering analysis to construct a trait-based dendrogram that represents the functional similarity among species. In the case of PD, we used a 95% consensus tree containing average branch lengths from 200 time-calibrated phylogenies of the Hackett-backbone, pruned to the species observed (Hackett et al. 2008; Jetz et al. 2012).

Attack rates by birds

During each bird survey, we assessed predation by birds using artificial clay caterpillars at the plot level following Nell et al. (2018). Briefly, we placed two model caterpillars made of light green plasticine clay (Lewis Newplast TM, fabrication place) on two opposing branches for each of 12 trees per plot (resulting in 24 caterpillars per plot equally distributed among three trees per species in polycultures) using superglue (Loctite TM) to adhere them to the upper side of the leaves or branches. Caterpillars were placed between on branches ranging from 2 to 4 m above ground level and we avoided trees located on the perimeter of the plot. Models were 25-mm long and mimicked generalist caterpillars found at the experimental site Nell et al. (2018). We assessed predation marks made by birds twice at 48-h intervals, replacing models that were attacked or lost without any predation marks in between to maintain a constant model density per plot. We calculated plot-level attack rates as the average proportion of caterpillar models attacked per 48 h period. Cases where the fate of the model was uncertain were rare ($n = 67$; 4.05% of models) and thus we excluded them from attack rates calculations.

Tree diversity effect sizes

For each bird community metric (abundance, FD, and PD) we computed tree diversity effect sizes as log-response ratios (LRR) separately for each survey. LRRs provide a unitless, standardized measure of the diversity effect that can be compared consistently across all bird community metrics and surveys (Cardinale et al. 2006). Effect sizes were calculated as the natural log of the ratio between observed and expected bird communities for each polyculture, where the expected value was the weighted mean of monoculture values for each tree species in that specific polyculture, thus controlling for tree species relative abundances in polycultures (Nell et al. 2018). LRR were considered significant when the 95% CI did not overlap zero. A positive effect of tree diversity indicates that polycultures exceeded predicted values under an additive scenario based on tree species monoculture values. In addition to analyses performed for the entire bird community, we computed LRR by survey separately for insectivores vs. omnivores as well as for migratory vs. resident species. In the same way, we computed survey LRRs for attack rates on plasticine caterpillars. As a complementary approach, we also ran generalized linear mixed models (GLMMs) testing for tree diversity effects on bird community metrics and attack rates using the using the *glmer* function from the *lmerTest* package in R version 4.3.1 (Kuznetsova et al. 2017). Models included tree diversity, survey, and their interaction all as fixed effects, and plot as a random factor to control for resampling of the same plots across surveys. Bird functional and phylogenetic diversity were normally distributed whereas for bird abundance and attack rates we used a poison and binomial distribution with a log-link function, respectively. We additionally performed post-hoc mean contrast using the *lsmeans* function from the *lsmeans* package in R (Lenth 2016) to test differences between monocultures and polycultures for each survey. Results from these models, namely tree diversity effects, were largely consistent with those using LRRs (see supplementary material: Table S3; Figs. S2, S3, S4). Therefore, for simplification purposes, in the results section, we focus on LRR analyses based on the above-mentioned advantages of this approach.

Finally, we tested associations between bird community metrics (as predictors) and attack rates, and whether such associations differed among surveys. To do so, we ran GLMMs with a binomial distribution and log-link function using the *glmer* function in R. In each model we included a different bird community metric as a predictor, the survey, and their interaction as fixed effects, as well as plot as a random effect. To visualize the relationships between attack rates and each predictor, we present bivariate plots separately for each survey.

Results

Temporal variation in the bird community

We recorded a total of 70 bird species across surveys, of which we focus on 67 bird species that feed (partly or entirely) on insects (i.e., three species did not feed on insects and are hereafter excluded) (Table S3). Within this subsample, insectivorous ($>50\%$ invertebrate-based diet) and omnivorous (multiple diet components, including invertebrates, each $<50\%$) birds accounted for $>80\%$ of the bird community (58.21% and 22.39% of the recorded species, respectively). In addition, 14.93% species were nectarivore/frugivorous ($>50\%$ diet is nectar or fruits), 2.99% carnivorous ($>50\%$ vertebrates), and 1.49% as granivorous ($>50\%$ seeds) (Fig. S5a). With respect to migratory status, we found that 72% of the species were resident species and 28% were migratory (Fig. S5b).

We found temporal variation in both the abundance and diversity of birds (Fig. 1). Specifically, there was a 1.56-fold change in bird abundance across surveys, and a 1.37-fold and a 1.44-fold change in bird FD and PD, respectively (Fig. 1b, c). Bird abundance and diversity did not consistently differ between summer and cold front surveys (Fig. 1). We also found temporal variation in the relative abundance of different feeding guilds, with a 2.13-fold and a 1.99-fold change in the frequency of insectivore and omnivore species, respectively (Fig. S5a). Likewise, regarding bird migratory status, there was a 1.20-fold and an 8.22-fold change in the frequency of resident and migratory birds, respectively (Fig. S5b).

Temporal variation in tree diversity effects on the bird community

Tree diversity had significant positive effects on bird community metrics in several surveys, although there was considerable variation across surveys and metrics in the magnitude and significance of these effects (Fig. 2). The diversity effect on bird abundance was significant in only one survey (October 2020; 67% increase in polycultures relative to monoculture) (Fig. 2a), whereas on FD, it was significant in two surveys (February: 31% increase; October 2020: 34% increase; Fig. 2b), and on PD in three surveys (December 2018: 33.5%; February 2020: 31.4%; and October 2020: 47.7%; Fig. 2c). Additionally, analyses by feeding guild and migratory status revealed that diversity effects were stronger and more often significant for omnivores than for insectivores (Fig. 3), as well as for resident than migratory species (with a negative effect observed in one case for the latter) (Fig. 4).

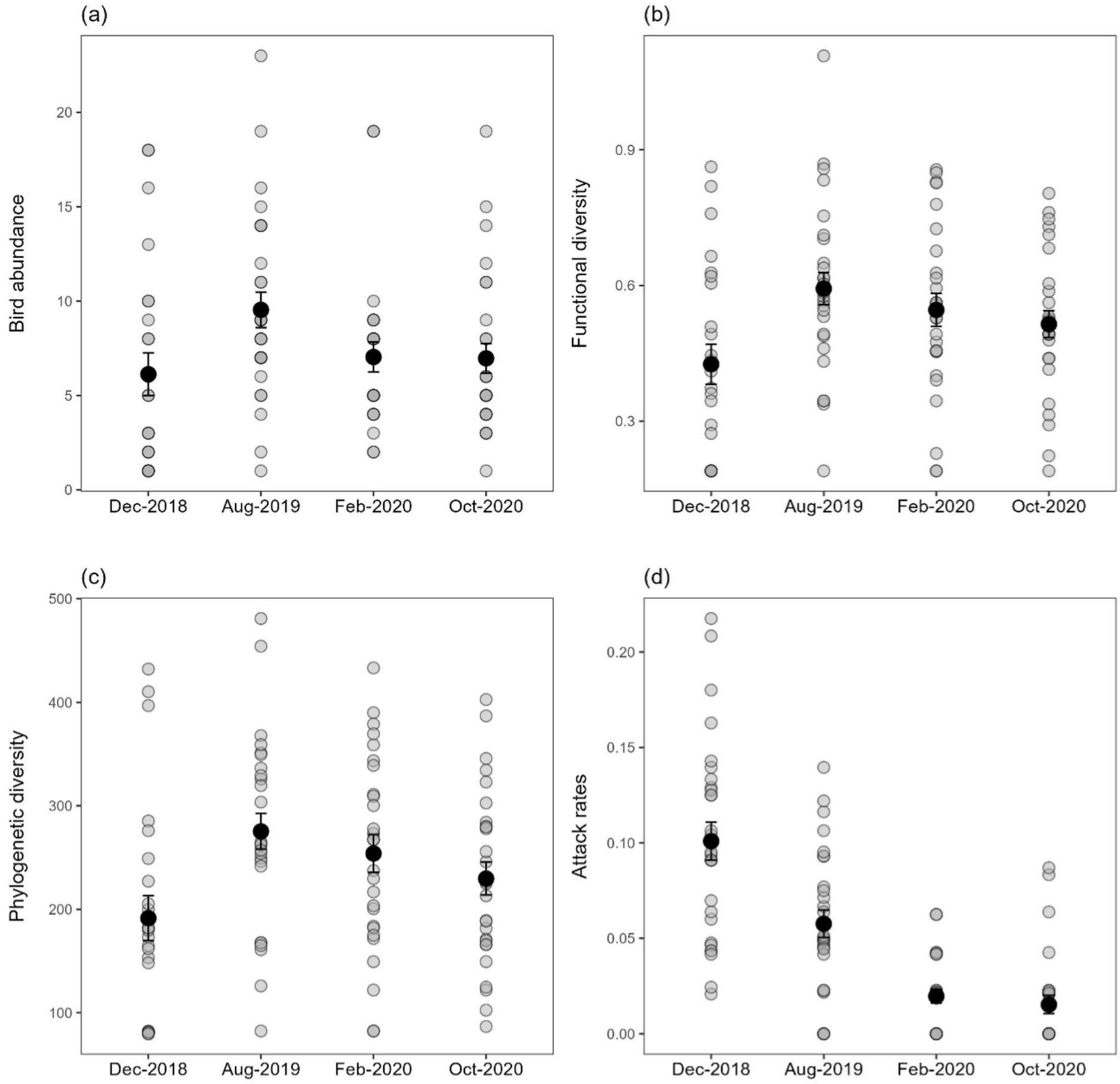

Fig. 1 Temporal variation in bird community metrics, namely: **a** bird abundance, **b** functional diversity, and **c** phylogenetic diversity, as well as on **d** attack rates by birds on clay caterpillars. Grey circles in the background represent values at the tree plot level. Circles in the front represent means (±SE) for each survey (December 2018, August 2019, February 2020, and October 2020)

Temporal variation in tree diversity effects on attack rates by birds

The overall rate of caterpillars attacked per 48 h was 0.05 ± 0.005 (mean ± SE), with the highest value observed in December 2018 and the lowest in October 2020 (Fig. 1d). We found positive effects of tree diversity on attack rates, but also substantial variation across surveys. Specifically, we found a significant effect on attack rates in two of the four surveys (December 2018 and October 2020), for which the attack rate was, on average, 20.55% and 1203.3% higher in polycultures than monocultures, respectively (Fig. 5).

We found no detectable associations between bird community metrics (abundance or diversity) and attack rates (no significant predictor effects in GLMMs; Table S4), and this was consistent across years (no significant predictor by survey interactions on GLMMs; Table S4), for the overall bird community (Table S4, Fig. S6) as well as when analysed separately by feeding guild (Table S4, Fig. S7) and migratory status (Table S4, Fig. S8).

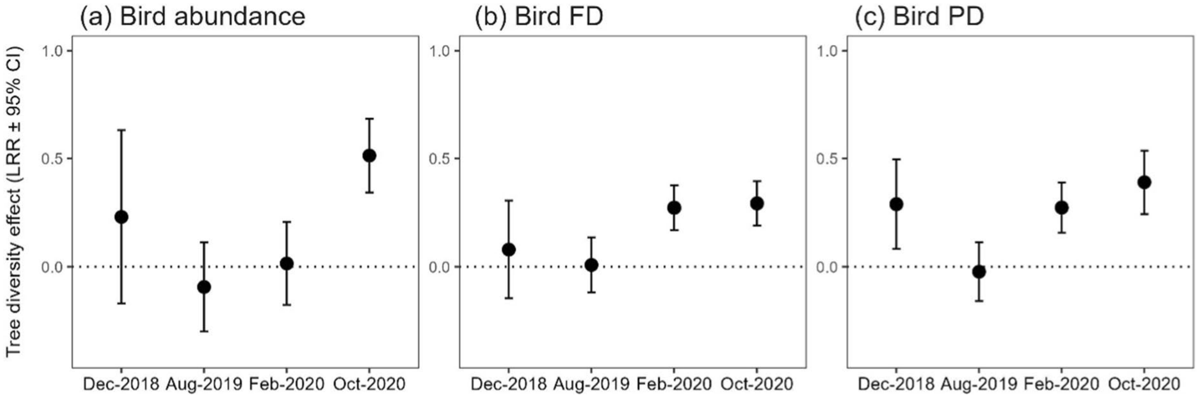

Fig. 2 Variation across surveys in tree diversity effect sizes on bird community metrics represented as Log- Response Ratios (LRRs) for each variable (±95% CI; $N=16$), computed separately for each survey (December 2018, August 2019, February 2020, and October 2020)

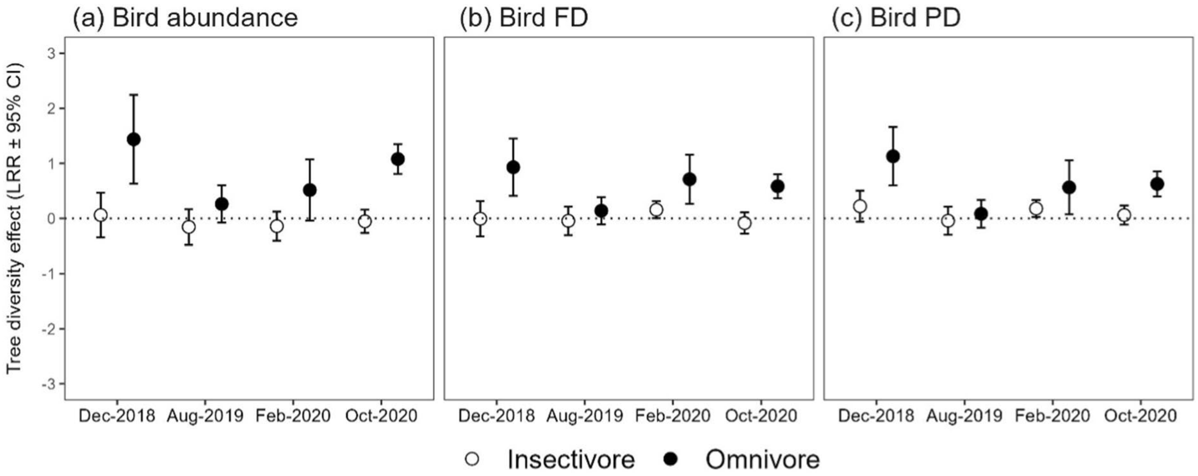

Fig. 3 Variation across surveys in tree diversity effect sizes on bird community metrics represented as Log- Response Ratios (LRRs) for each variable (±95% CI; $N=16$), computed separately for insectivorous (open circles) and omnivorous (filled circles) birds in each survey (December 2018, August 2019, February 2020, and October 2020)

Discussion

As expected, bird abundance and diversity were generally higher in tree mixtures than in monocultures. However, patterns were marked by substantial variation in the strength of responses across surveys, including cases where no significant effect was observed for any bird community metric (August 2019). Furthermore, temporal variation did not follow the anticipated pattern of stronger effects of tree diversity in the cold front seasons, and responses varied considerably among surveys conducted in the same season. Following predictions, however, tree diversity effects were stronger and more consistent for specialist insectivorous and resident species. Finally, we also observed positive effects of tree diversity on attack rates but only in two surveys—one conducted during the summer and another in the winter (i.e., also inconsistent with expected stronger effects in the cold fronts season), and thus seemingly unrelated to temporal variation in tree diversity effects on bird abundance and diversity. Consistently, we did not find significant associations between attack rates and bird abundance or diversity.

Tree diversity effects on the bird community vary temporally

Our results align with a recent meta-analysis that reported positive effects of tree diversity on natural enemies (Stemmelen et al. 2022) and are also consistent with previous experimental research (including our previous work at the UADY system) showing positive effects on bird abundance

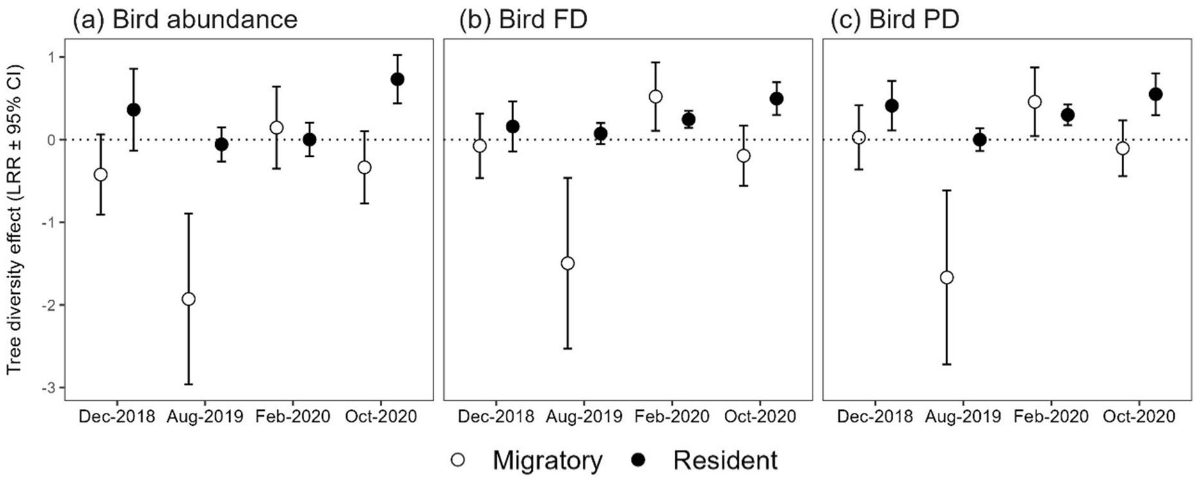

Fig. 4 Variation across surveys in tree diversity effect sizes on bird community metrics represented as Log- Response Ratios (LRRs) for each variable (±95% CI; $N = 16$), computed separately for migratory (open circles) and resident (filled circles) in each survey (December 2018, August 2019, February 2020, and October 2020)

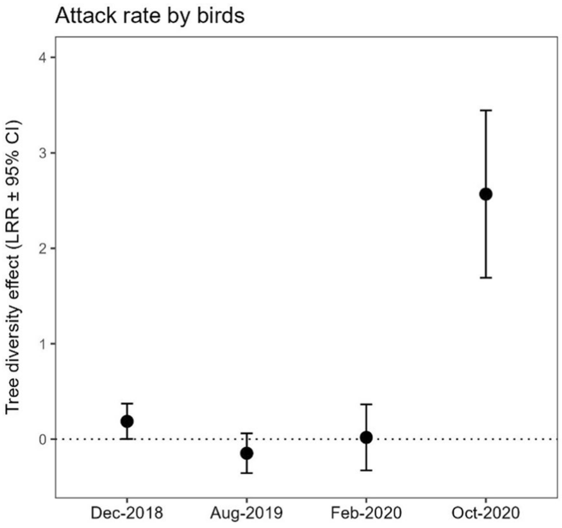

Fig. 5 Variation across surveys in tree diversity effect sizes on attack rates by birds on clay caterpillars represented as Log- Response Ratios (LRRs ± 95% CI; $N = 16$), shown separately for each survey (December 2018, August 2019, February 2020, and October 2020)

and diversity (Nell et al. 2018; Ampoorter et al. 2020, May-Uc et al. 2020). Nevertheless, tree diversity effects were highly variable over time, suggesting these bottom-up controls on the bird community are dynamic. Specifically, tree diversity effects did not exhibit clear seasonal patterns, i.e., consistently stronger during winter surveys, and we also observed substantial variation even between surveys conducted in the same season. Our earlier work in this system similarly revealed among-season variation in tree diversity effects on bird abundance and diversity, seemingly unrelated to abiotic conditions (May-Uc et al. 2020). In that study, there was also substantial within-season variation in tree diversity effects, possibly in response to factors fluctuating at a finer scale, such as weekly or monthly variation in weather, bird foraging behaviour, or prey abundance. Collectively, these findings indicate that a more detailed examination of variation in biotic and abiotic factors within seasons across multiple years is necessary to gain insight into factors underlying diversity effects on tri-trophic interactions at different temporal scales.

Tree diversity effects are contingent on bird functional traits

We predicted that dietary generalist birds would show stronger responses to plant diversity than specialists, given the greater variety of food sources available in mixed stands (Haddad et al. 2009; Zhang et al. 2017). This might also involve an insurance effect, where polycultures have a higher likelihood of containing suitable food types for generalist birds. In line with expectations, omnivores showed stronger and more consistent responses to tree diversity compared to insectivores, with the latter showing non-significant responses in most cases. These patterns align with a prior study showing that omnivorous birds were more affected than insectivores by changes in plant species composition in urban parks (Huang et al. 2015). However, other studies, mainly observational, have found similar effects of tree diversity on different bird feeding guilds (Jankowski et al. 2013) and in at least one case stronger positive effects on specialist insectivores than on omnivores (Harvey et al. 2006). These mixed patterns may be explained by differences in species composition within guilds influencing the degree of specialization and resulting responses to habitat features. More detailed assessments of behavioral responses by different bird functional groups can contribute to a better understanding of patterns within systems and potentially explain variation among systems, ideally involving manipulations of tree diversity.

Results also indicated that tree diversity had stronger and more consistent effects on resident than migratory birds. In most cases, effects on migratory species were non-significant, aligning with our hypothesis and with previous research in this study system that also reported weaker or inconsistent responses by this bird group (May-Uc et al. 2020). Migratory status strongly overlapped with dietary specialization, as 84% of migratory species recorded during the study were insectivores, while residents included a more balanced mix of insectivorous (47.92%) and omnivorous (27%) species. Notably, for one survey, we observed a negative effect of tree diversity on migratory bird abundance and diversity in August 2019. This suggests that, in certain cases, migrants preferentially forage in monospecific stands, possibly due to higher availability of specific food types (e.g., outbreaks of specialist herbivores). At the same time, it is important to note that positive effects of tree diversity on migratory species were previously found in this study system (May-Uc et al. 2020), emphasizing that conclusions about migratory bird responses are not straightforward and not necessarily only dictated by dietary specialization. Other traits such as higher foraging behavioural plasticity (Greenberg 1995) and differences in abiotic tolerance (Both et al. 2010; Cohen et al. 2020), could explain responses of migratory vs. resident species. Overall, these findings call for investigations on dietary specialization, foraging behaviour, and abiotic niche-related traits for migratory and resident birds. Insights gained from this can be highly relevant for both managed (e.g., restored) and natural forests (Van Bael et al. 2008), particularly in regions such as the Neotropics where the influx of North American migrants strongly influences local ecosystems, especially tropical forests.

Tree diversity effects on predation pressure by birds

In line with a previous study in this system by Nell et al. (2018), we observed higher attack rates by birds on clay caterpillars in tree polycultures relative to monocultures for two surveys, one in winter (December 2018) and another in late summer (October 2020). These results align with the Enemies Hypothesis, suggesting that plant diversity enhances predation pressure (Root 1973). However, they also indicate that these effects are not universal but rather dynamic and context-dependent. Consistent with these findings, a recent meta-analysis reported inconsistent and an overall non-significant effect of tree diversity on predation (Stemmelen et al. 2022), including at least one study reporting negative effects of tree diversity on attack rates by birds (Yang et al. 2018). The overall patterns across studies, including ours, challenge the generality of this prediction in forests and underscore the need for more nuanced evaluations that incorporate temporal variation.

Temporal patterns in tree diversity effects on bird attack rates were expected to mirror those on bird abundance and diversity. However, we found no support for this expectation, as surveys in which tree diversity positively affected bird abundance and diversity did not consistently show higher attack rates. Accordingly, we did not observe significant associations between bird community metrics and attack rates for any of the surveys (Table S4). This finding is inconsistent with results reported by Nell et al. (2018) in the same study system, who found that bird diversity mediated the tree diversity effect on bird attack rates during 2015 summer surveys conducted in the early to mid-summer. Several arguments can be given to explain these contrasting results. Firstly, bird foraging activity is highly density-dependent and contingent on prey abundance (Singer et al. 2012; Molleman et al. 2016; Zvereva and Kozlov 2022). Therefore, we would anticipate associations between bird abundance or diversity and attack rates to be stronger during periods of high prey availability, as this is when birds would be foraging more intensely (Molleman et al. 2016). Accordingly, early in the rainy season (July), Nell et al. (2018) reported bird abundance one to three times greater (depending on the survey used for comparison) and attack rates four to 26 times greater than our study. Unfortunately, we could not conduct surveys during the early summer, preventing a more robust comparison across studies. Secondly, due to logistic constraints, model caterpillars were placed at a similar height compared to earlier work (2–4 m above ground), but habitat features likely changed to some extent due to tree growth. Compared to earlier work, increased tree height and self-thinning would have resulted in assessments of predation in a lower portion of the canopy relative to Nell et al., characterized by lower architectural complexity and increased shade which would lead to lower predation rates. Thirdly, specific bird species might contribute disproportionately to predation rates (see Muiruri et al. 2016), such that temporal fluctuations in the abundance of these species, rather than in the bird community or its subsets (e.g., guilds), dictate predation patterns. Future work including bird species-specific surveys of foraging activity and behaviour, including direct observations of predation attempts, is needed to test this. Finally, we also speculate that if specialist insectivorous birds accounted for a larger portion of predation rates compared to previous work, then the fact that these species were less responsive to tree diversity effects (see above) could have weakened overall associations between bird community metrics and attack rates. However, the consistency of non-significant associations across surveys and bird functional groups (assessed separately for omnivores vs. insectivores), calls into question this explanation.

Final remarks

Our assessment of bird responses within a large-scale experimental system revealed that tree diversity effects on bird abundance and diversity vary over time and are contingent on the feeding guild and migratory status. Positive effects of tree diversity on bird abundance and diversity did not consistently translate into increased attack rates by birds across surveys. This suggests a potential decoupling of effects on bird communities and predation pressure. Alternatively, the lack of associations could be due to methodological considerations or low overall predation pressure, potential explanations which require further investigation. Together, our results indicate that tree diversity-mediated top-down control of insect herbivores by predators is highly variable and contingent on bird functional traits, calling for the development of a more nuanced theory of plant diversity effects on predators that accounts for temporal dynamics in predation and corresponding longitudinal studies to identify biotic and abiotic factors underpinning temporal variation in tree diversity effects on birds and other predator groups.

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Author contribution statement Formulated the idea of the manuscript and designed the experiment: LAR. Performed the experiment: MRH, EVG, BPN, TQM. Analysed the data: CVG. Wrote the first draft of the manuscript: CVG. Contributed critically to the writing: LAR and KAM. All co-authors contributed with editions to previous versions of the manuscript and all authors gave final approval for publication and agree to be held accountable for the work performed therein.

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Data availability All data generated or analysed during this study will be included in the supplementary information files and/or stored in a public repository.

Declarations

Conflict of interest The authors report no conflicts of interest in this work and have nothing to disclose.

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