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Effects of topical tree diversity and prey spatial distribution on predation by birds and arthropods

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Abstract

Tree diversity exerts strong controls on predator–prey interactions, generally boosting predation pressure and thus pest control. One of the reasons for this outcome is that carnivores are better able to respond to changes in prey location or availability with increasing plant diversity. To address this, we manipulated prey vertical location within the canopy on mahogany trees planted in monoculture and polyculture plots in a tree diversity experiment using plasticine caterpillars. We conducted three surveys of predation, estimated as the daily proportion of models attacked per tree ($n = 288$ trees and 3456 caterpillars). We found no effect of tree diversity on attack by birds or arthropods. There was, however, an effect of prey vertical location, with higher bird and arthropod predation rates in the mid-canopy vs. low canopy. There were no interactions between diversity and prey location, suggesting diversity did not affect predator responses to prey availability along the canopy. Finally, bird predation correlated negatively with arthropod predation, but only in polyculture, suggesting diversity influenced bird–arthropod interactions. These findings call for work assessing the mechanisms behind tree diversity effects on predator responses to prey availability to better understand of how plant community heterogeneity shapes top-down control.

Introduction

Plant diversity has strong effects on species interactions and ecosystems (Cardinale et al. 2011; Tilman et al. 2014; Moreira et al. 2016). Notably, studies have shown that plant diversity frequently boosts the abundance and diversity of predators, and this in turn predicted to favor increased predation pressure (reviewed by Moreira et al. 2016). Such effects take place via predator niche partitioning, as well as behavioral changes in herbivores and predators resulting in heightened predation (Philpott et al. 2009; Straub et al. 2014; Gontijo et al. 2015). This prediction, known as the Enemies Hypothesis (Root 1973), has been mainly studied in grassland communities (e.g., Haddad et al. 2009; Scherber et al. 2010) and agroecosystems (reviewed by Russell 1989; Letourneau et al. 2011), whereas systematic tests in forest communities have lagged behind historically but are now gaining more attention (see Staab and Schuldt 2020).

The spatial distribution of prey is a key determinant of predation rates (Basset et al. 2003; Ulyshen 2011). In particular, prey abundance can strongly vary vertically along tree canopies (hereafter prey vertical distribution) as a result of changes in microclimatic conditions and predation risk (reviewed by Basset et al. 2003). In turn, such variability in prey location has been shown to influence predator abundance and distribution, resulting in gradients in predation rates within forest canopies (Loiselle and Farji-Brener 2002; Aikens et al. 2013; Šigut et al. 2018). For example, some observational studies have found higher predation rates in the canopy than in the understory (e.g., birds, ants), possibly linked to stronger trophic interactions associated with increased productivity across trophic levels (Loiselle and Farji-Brener 2002) or due to greater predator diversity (and niche complementarity) from increased availability of refuges (Langellotto and Denno 2004). To date, however, and despite previous empirical and theoretical work addressing parasitoid or predator responses to prey availability under a spatial context (reviewed by Walde and Murdoch 1988; Pareja et al. 2008), manipulative studies assessing effects of

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prey vertical distribution on predation remain scarce, particularly under natural settings (but see above).

Experimental studies testing for both tree diversity and prey vertical distribution effects on predation are also similarly lacking. Such joint tests are especially important given that tree diversity shapes canopy biotic and abiotic features which affect both prey and predators. For example, a greater number of vegetation strata or greater canopy architectural complexity with increasing diversity can result in changes in prey vertical distribution within the canopy (Aikens et al 2013) as well as predator diversity and behavior (Langellotto and Denno 2004; Šipoš and Kindlmann 2013). This could lead to contrasting predator responses to variation in vertical distribution of prey across levels of tree diversity either due to pre-established predator search patterns or changes in predator complementarity determining predation rates. In addressing these joint and potentially interactive effects, studies looking at effects on different predator groups (e.g., vertebrate and invertebrate) would be especially useful to infer the role of predator traits or life histories in shaping variation in predation pressure (e.g., Yang et al. 2018), as well as to assess potential predator interactions such as intra-guild predation determining overall top-down pressure and pest control (e.g., Finke and Denno 2003; Nell and Mooney 2019).

The goal of this study was to experimentally test for effects of tree diversity and vertical distribution of prey on predation rates by different types of predators. We additionally tested correlations between predator groups, namely birds and arthropods, to test whether predator interactions influenced responses to tree diversity and prey vertical distribution. To this end, we manipulated prey vertical distribution on big-leaf mahogany, *Swietenia macrophylla*, trees planted in monocultures and polycultures at a long-term tree diversity experiment in Yucatan (Mexico). We placed plasticine caterpillars at two canopy heights (2.5 vs. 5 m aboveground) on mahogany trees and documented predation rates by insectivorous birds and predatory arthropods. Previous studies in this system have found that polycultures exhibit a higher abundance and diversity of predatory arthropods (e.g., Abdala-Roberts et al. 2015; Esquivel-Gómez et al. 2017), as well as higher diversity and predation rates by birds (Nell et al. 2018; May-Uc et al. 2020). We build on these findings by testing for tree diversity and prey vertical distribution effects to better understand how these bottom-up factors shape predation pressure. We predicted (i) predation rates would be higher in polyculture, (ii) predation would increase higher in the canopy, and (iii) the presence of non-additive effects between these factors whereby tree diversity will weaken the effect of prey vertical distribution due to a more even (and therefore complete) exploitation of prey across the canopy, hence equalizing differences across heights. Additionally, we expected a negative correlation

between bird and arthropod attack rates due to interference or intra-guild predation (i.e., birds feeding on arthropods), and that such association would be strongest at high diversity where bird foraging is expected to be more intense. Overall, results from the present study can inform management strategies seeking to enhance ecological services provided by predators in natural and managed forests.

Materials and methods

Study system

The study was conducted at the UADY Tree Diversity Experiment (https://treedivnet.ugent.be/ExpUADY.html), a large-scale system located at the Sitio Experimental Uxmal (20° 24′ 44″ N, 89° 45′ 13″ W) of INIFAP (Instituto Nacional de Investigaciones Forestales, Agricolas y Pecuarias), 70 km southwest of Merida, Yucatan (Mexico). The system was established in December 2011, covers an extension of 7.2 ha, and includes 74 21×21 m plots, each with a planting density of 64 trees per plot (3 m between plants), and a distance of 6 m between plots (Abdala-Roberts et al. 2015). We planted six species of tropical trees, namely, *Swietenia macrophylla* King (Meliaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae), *Tabebuia rosea* (Bertol.) Bertero ex A.DC. (Bignoniaceae), *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), and *Cordia dodecandra* A.DC. (Boraginaceae), all of which are native to the Yucatan Peninsula. Plots were classified as monocultures (i.e., one tree species) or polycultures composed of random combinations of four out of the six species. Big-leaf mahogany (*S. macrophylla*), the focal tree species, is a long-lived tree distributed from southern Mexico to Bolivia (Pennington and Sarukhán 2005), and recent work in this system found that attack rates on plasticine caterpillars are higher in polyculture than monoculture for this species (Nell et al. 2018).

Experimental design

To test for diversity and prey vertical distribution effects on predation rates by insectivorous birds and predatory arthropods, we used green plasticine models to mimic caterpillars (Lewis Newplast, UK), a broadly used approach for assessing predation pressure (e.g., Muiruri et al. 2016; Roslin et al. 2017; Nell et al. 2018; Zvereva et al. 2019). We previously used these plasticine models in the study system to assess bird predation rates (Nell et al. 2018). We randomly selected 12 monoculture and 12 polyculture plots, and for each one selected 12 mahogany trees, avoiding individuals on plot edges (total $n = 288$ trees). We randomly assigned half of the experimental trees per plot to one of two levels of prey

vertical distribution, representing low canopy and mid-canopy. The lower canopy was defined as the first layer branches encountered (2–2.5 m) and the middle canopy as the layers of branches at the midpoint of total tree foliage (4.5–5 m). These heights were chosen based on the vertical distribution of mahogany canopy heights in the system and based on previous work assessing biologically relevant predation rates on mahogany at the site (Nell et al. 2018). In addition, at these two heights we placed either two or four models as part of an assessment of effects of prey density on predation. However, this effect was non-significant in all cases and therefore removed from analyses. The resulting experiment was a fully crossed factorial design between tree diversity and prey vertical distribution. Within each tree, models were distributed in different branches and separated by at least 1 m. We conducted three surveys from mid-November to mid-December 2020. The first and third surveys consisted in recording attack after 48 h of placing the models, whereas the second survey involved two rounds of 48 h each (models were re-set after the first round, replacing lost or attacked models). As a result, throughout the study each plot and plant was sampled over four 48-h periods, for a total of 3456 models (i.e., caterpillar/days). We standardized our measure of predation by expressing attack rates as the proportion of attacked caterpillars per 24 h for each tree, separately for bird and arthropods. Attacks by each group can be easily identified based on the types of marks left on the models (see Low et al. 2014) as well as prior experience working with model caterpillars in the system (Nell et al. 2018). The number of cases for which attack could not be determined, such as when models were lost, was negligible and were removed from the analyses (less than 2% of models placed).

Statistical analyses

We ran generalized linear mixed models (GLMMs) testing for effects of tree diversity (2 levels, fixed), prey distribution (2 levels, fixed), and their interaction on the proportion of attacked models per tree, separately for birds and arthropods. In both cases, we used a betabinomial error and logit link function as the data were overdispersed (Harrison 2014, 2015). Models included plot and survey as random effects to control for spatial heterogeneity and temporal variation in attack rates, respectively. We also separately tested for effects on bird predation during the third (last) survey, as this is by far when most bird attacks occurred (see "Results" section).

In addition, we ran a GLMM to test for effects of bird predation, diversity, prey distribution, and two-way interactions between bird predation and diversity and prey distribution on arthropod predation to evaluate whether there was a correlation between bird and arthropod attack (i.e., negative interactions between predator groups) and if any such correlation differed on tree diversity or prey distribution. This model also controlled for plot as a random effect. We included bird predation as a predictor of arthropod attack (rather than the reverse) since birds feed on arthropods and usually have stronger effects than arthropod on birds (although not the case in our system, some invertebrate predators such as ants can negatively affect birds in some cases; e.g., Philpott et al. 2005). We ran this model using means across trees for each level of prey distribution within each plot (i.e., two values per plot) and pooling data across surveys to reduce the number of zeros and more robustly test the correlation between bird and arthropod predation. In this case, we used a binomial distribution and logit link as the betabinomial model did not converge. We did not test for an interaction between height and diversity as our goal here was to exclusively test for interactions between main factors and bird predation. The height by diversity interaction was the focus of the initial models (see above) which were intended to be equivalent to compare effects on bird and arthropod predation.

In all cases, we report model (back-transformed) least-square means and standard errors as descriptive statistics. Analyses were conducted in R v. 4.2.1 (R Core Team 2022), using package glmmTMB and the glmmTMB function (Brooks et al. 2017). To visuaize results from the model testing for an association between bird and arthropod predation, we calculated the fixed effects, random effect, and residual contributions to each observed data point using the fitted model (i.e., estimated Y values) and then subtracted the plot effect for each observation using the broom package in R ver. 1.0.0 (Robinson 2014). This provided model predicted values after accounting for the random effect.

Results

We analyzed a total of 3389 caterpillar models across the three surveys, and found that 355 (10.47%) were attacked, of which 202 (57%) were due to arthropods and 153 (43%) due to birds. Pooling data across surveys, the mean proportion of models attacked was 0.104 ± 0.018, and mean values by predator group were 0.059 ± 0.012 for arthropods and 0.045 ± 0.014 for birds. In addition, we observed marked variation across surveys. For the first survey we placed 855 models, of which 76 (8.8%) were attacked, 64 (84%) by arthropods and 12 (16%) by birds. Mean attack rate was 0.088 ± 0.032, with arthropods exhibiting a mean value of 0.074 ± 0.03 and 0.014 ± 0.011 for birds. For the second survey, we placed 1706 models (858 in the first round and 848 in the second), of which 156 (9.14%) were attacked, 110 (71%) by arthropods and 46 (29%) by birds. The mean attack rate was 0.091 ± 0.022, with arthropods having a mean value of 0.064 ± 0.018 and birds of 0.026 ± 0.013. Lastly, for the third survey we observed a substantial increase in attack rate

driven by birds; we placed a total of 838 models, of which 123 were attacked (14%), 95 (77%) by birds and 28 (23%) by arthropods. The mean attack rate was 0.146 ± 0.047, whereby the mean value for birds was 0.113 ± 0.045 and for arthropods of 0.033 ± 0.018.

Results from the GLMMs indicated no effect of tree diversity on the proportion of attacked models by either birds (monoculture: 0.039 ± 0.021; polyculture: 0.025 ± 0.014) or arthropods (monoculture: 0.044 ± 0.010; polyculture: 0.058 ± 0.012) (Table 1; Fig. 1A). On the other hand, we found a significant effect of prey vertical distribution on predation by arthropods but not birds (Table 1), with a 1.6-fold higher mean value of arthropod predation in the mid-canopy (0.065 ± 0.013) relative to low (0.039 ± 0.009) canopy

(Fig. 1B). There was no significant interaction between tree diversity and vertical distribution for either predator group (Table 1). A follow-up analysis of bird predation during the third survey did, however, show a significant effect of height ($\chi^2 = 4.172$, $P = 0.041$; Table S1, Supplementary Information), where the mean proportion of attacked models was 1.8-fold greater for the mid-canopy (0.076 ± 0.030) compared to the low canopy (0.042 ± 0.018) (Fig. 2). Finally, the GLMM testing for predator interactions indicated a significant bird predation by diversity interaction on arthropod predation (Table S2, Supplementary Information), whereby bird predation significantly negatively correlated with arthropod predation in polyculture (arthropod predation $= 0.085 - 0.540 \times$ bird predation; $R^2 = 0.522$, $P < 0.001$),

Table 1 Results from general linear mixed models testing for effects of tree diversity, prey vertical distribution, and their interaction on attack rates (proportion of attacked caterpillar models in 24 h) by predatory arthropods and insectivorous birds on mahogany (*Swietenia macrophylla*) trees

Effect	Arthropod predation			Bird predation		
	χ^2	df	P	χ^2	df	P
Diversity (DI)	1.146	1	0.284	1.542	1	0.214
Prey distribution (PD)	10.288	1	**0.001**	1.005	1	0.316
DI×PD	1.136	1	0.286	0.052	1	0.819

Models also included the effect of plot and survey (random factors, statistics not shown). Statistics shown are Wald χ^2-values, numerator degrees of freedom (df), and P values. Significant ($P < 0.05$) effects are in bold
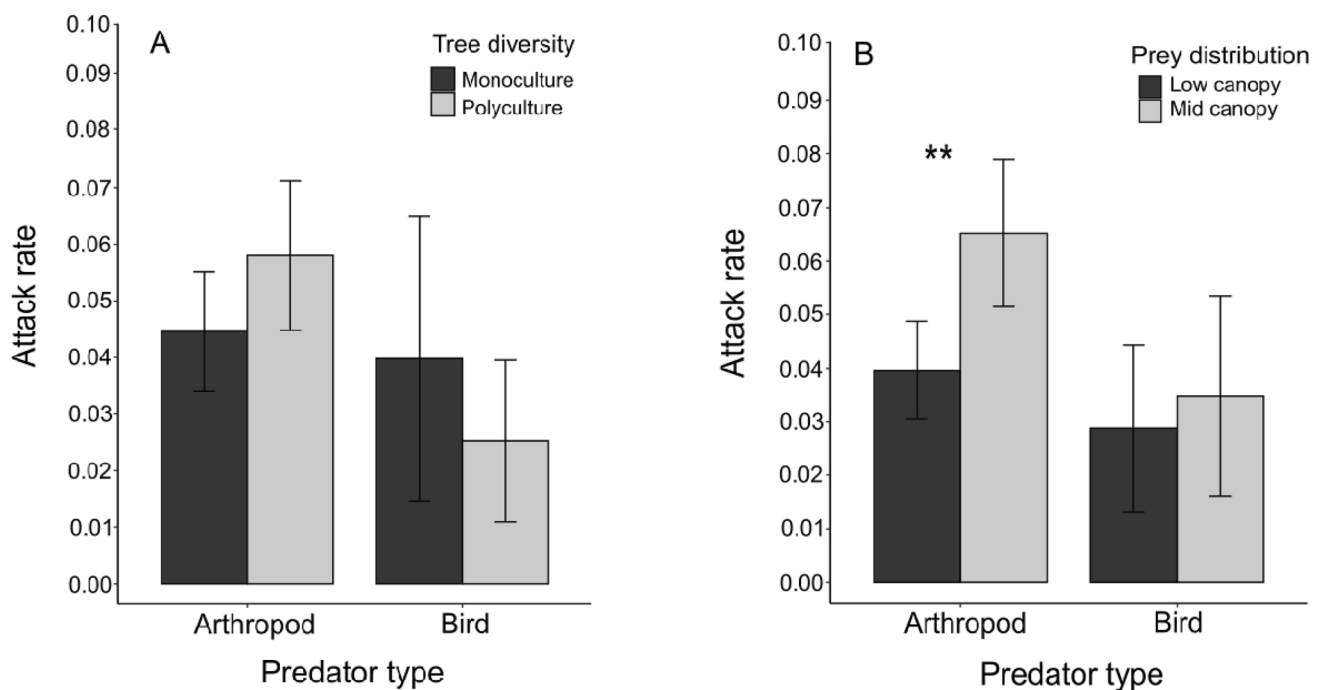
Fig. 1 Effects of tree diversity (panel **A**) and prey vertical distribution (**B**) on attack rates (proportion of attacked caterpillar models in 24 h) by predatory arthropods and insectivorous birds on mahogany (*Swietenia macrophylla*) trees. Shown are model least-square means and standard errors. **$P < 0.05$
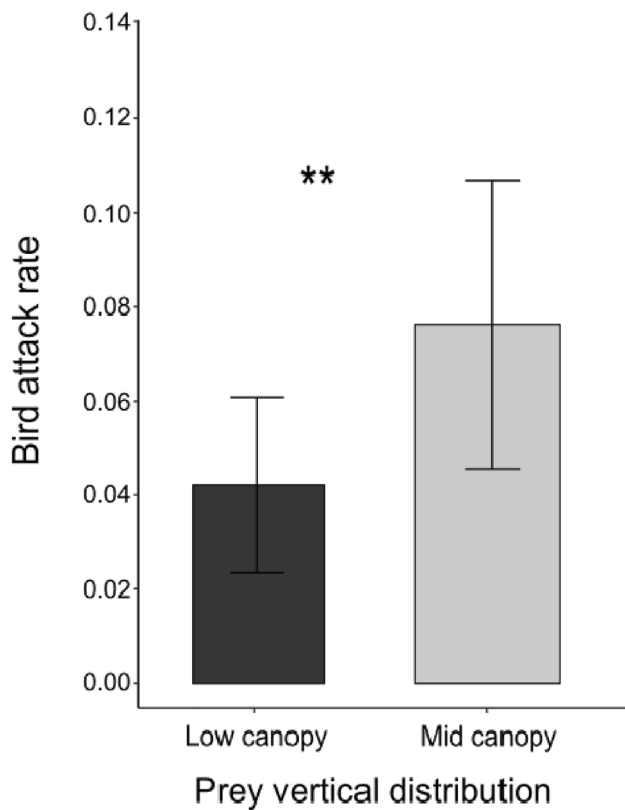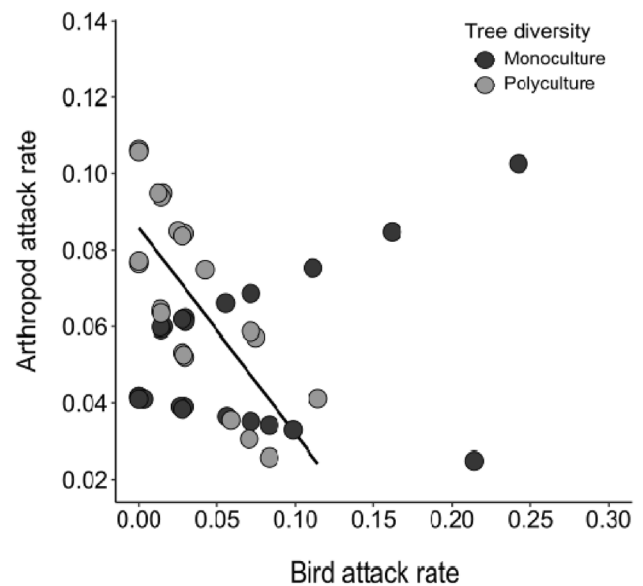
Fig. 2 Effects of prey vertical distribution on the attack rate (proportion of attacked models in 24 h) by insectivorous birds on mahogany (*Swietenia macrophylla*) trees during the third survey. Shown are model least-square means and standard errors. **$P < 0.05$

Fig. 3 Relationship between bird predation and arthropod predation (proportion of attacked caterpillar models in 24 h). Shown are predicted relationships and standard errors using fitted values from a generalized linear mixed model after controlling for the effect of plot (see "Statistical analyses" section). Values are means across trees of each level of prey vertical distribution, pooling data across surveys. Bird predation significantly negatively predicted arthropod predation in tree polycultures ($0.085 - 0.540 \times$ bird predation; $R^2 = 0.522$, $P < 0.001$), whereas in monoculture there was no significant correlation ($0.047 + 0.098 \times$ bird predation; $R^2 = 0.119$, $P = 0.098$)

whereas in monoculture attack rates did not correlate significantly (arthropod predation $= 0.047 + 0.098 \times$ bird predation; $R^2 = 0.119$, $P = 0.098$) (Fig. 3).

Discussion

Overall, attack rates were lower compared to previous work in this system (on average, 10 vs. 20% in Nell et al. 2018). Arthropod attack rates were higher than bird attack rates, also contrasting with previous work at this site by Nell et al. (2018) who found that plasticine caterpillars were attacked mainly by birds (vs. arthropods) during summer surveys (July 2015), as well as with previous work in other tropical and temperate systems (e.g., Van Bael et al. 2003; Philpott et al. 2009). Contrary to expectations, we found no effect of tree diversity on either bird or arthropod predation, which is also inconsistent with the previous findings in this system (Nell et al. 2018). However, we found a significant effect of prey vertical distribution in the canopy, where the prediction of increased attack rates higher in the canopy was supported for both birds and arthropods. In addition, this difference in

predation was not contingent on tree diversity. Finally, there was a negative correlation between bird and arthropod predation but only in polycultures suggesting that tree diversity promotes negative interactions between predator groups.

Effect of tree diversity on predation

We found no evidence that tree diversity influenced predation rates by either arthropods or birds, which is unsupportive of the Enemies Hypothesis (Root 1973; Russell 1989), in this case for an arboreal community (see studies in: Staab and Schuldt 2020). This finding also runs counter to previous work in the study system reporting a positive effect of tree diversity on bird predation rates on model caterpillars across all tree species, including mahogany (albeit with a moderate increase for this species; Nell et al. 2018). While a similar methodology and sampling design were used in both studies, one important difference is the time of year the studies were performed. Nell et al. (2018) was conducted during the summer (July), whereas our work took place during the winter months (November and December) when temperatures are lower and weather conditions are more variable. Accordingly, recent work in this system found that bird abundance and diversity during were lower in the winter months and highest during the spring and summer (May-Uc et al. 2020),

and this also included marked seasonal changes in bird composition (e.g., presence of migratory species with more generalist eating habits during winter months). This temporal variation in the bird community and foraging behavior can result in concomitant changes in predation rates. For example, previous studies have reported temporal changes in predation rates by both vertebrate (birds, reptiles) and invertebrate (arthropods) (Lister and Aguayo 1992; Molleman et al. 2016; Ferreira and Faria 2021) resulting in strong variation in top-down pressure on herbivore populations. Interestingly, one of the few studies comparing predation by vertebrates vs. invertebrates across a plant diversity gradient found that predation by arthropods increased while predation by birds decreased with increasing tree diversity (Yang et al. 2018). While our findings suggest that bird and arthropod were consistently irresponsive to tree diversity, biases in predation pressure toward specific tree species deserve more attention, including dominance effects (e.g., Vehviläinen et al. 2008; Schuldt and Scherer-Lorenzen 2014). Further work replicating our study across multiple tree species is needed to address the mechanisms behind potential diversity effects on multiple predator groups (e.g., selection vs. complementarity effects among tree species; Nell et al. 2018), as well as multiple surveys within each season to adequately correlate temporal changes in predation pressure to variation in predator community structure. Both aspects are being addressed by ongoing work in this system.

It is important to also note that tree diversity effects on predators are not always positive, and that our non-significant findings are in line with other studies which have not found effects of tree diversity on predation rates (see Staab and Schuldt 2020; Stemmelen et al. 2021). One possible explanation for these findings are negative interactions between predator groups, including foraging interference (e.g., Philpott et al. 2005) or consumptive effects (e.g., intraguild predation; Finke and Denno 2003; Cuny et al. 2021). Accordingly, we found a negative correlation between bird and arthropod predation but only in tree polycultures, suggestive of negative effects of birds on predatory arthropods (e.g., via consumption), possibly mediated by greater abundance or richness of birds in polyculture (Nell et al. 2018), which could dampen tree diversity effects on predation by arthropods (Philpott et al. 2004; Gunnarsson 2007; Mooney et al. 2010). Experimental manipulations of bird predation (exclosures) to test for bird–arthropod interactions are needed to formally test this possibility.

Effect of prey vertical distribution on predation

Results indicated that attack rates by predatory arthropods were significantly higher at the mid-canopy relative to low canopy, consistent with the expected vertical gradient in predation pressure. This pattern has been attributed to higher

structural complexity of the canopy at greater heights which increases the availability of refuges or suitable microhabitats for arthropod predators (Basset et al. 2003; Riihimäki et al. 2006). For example, Loiselle and Farji-Brener (2002) found that predation on caterpillars, mainly by ants, was higher in the canopy compared to the understory in a tropical forest in Peru. However, other studies have found different patterns. Aikens et al. (2013) instead found higher predation rates by arthropods in the understory, followed by the lower canopy, upper canopy, and finally mid-canopy which had the lowest level of predation. It is important to view observed vertical gradients in predation in light of variation in community structure and traits of different predator groups. For example, the degree of mobility can influence how readily predators respond to increases in prey availability at higher strata, and canopy complexity may increase the availability of refuges but also reduce foraging efficiency by making it more difficult for some predator taxa to locate their prey (Riihimäki et al. 2006; Šipoš and Kindlmann 2013).

In the case of birds, while no effect of prey vertical location was found across surveys, a closer look at the third survey, which is by far when the highest number of bird attacks occurred, indicated a significant (1.8-fold) increase in bird predation at the mid-canopy relative to low canopy. While previous studies have found that some bird species show a foraging preference for lower strata (Robinson and Holmes 1984; Aikens et al. 2013), possibly because reduced physical complexity and foliage density facilitate prey detection, others have found, in line with our findings, higher bird predation pressure at higher canopy strata (reviewed by Van Bael et al. 2008). Namely, Van Bael et al. (2003) found greater arthropod abundance, and, concomitantly, bird predation in the canopy than in the understory in an agroforestry system in Panama, possibly due to greater canopy productivity (Basset et al. 2003; Ulyshen 2011). Likewise, microhabitats (e.g., for roosting) could be more favorable in mid-strata to higher strata for some bird species, which preferentially forage in these sites (Bereczki et al. 2014).

Interactive effects of tree diversity and prey vertical distribution

There was no detectable interaction between tree diversity and prey vertical distribution on predation rates by either birds or arthropods, meaning that predation responses to prey distribution remained unchanged across levels of tree diversity. In the case of arthropods, we speculate that negative interactions with birds (see above) could have also limited the detection of these non-additive effects. For instance, an observational study by Sobek et al. (2009) reported a greater abundance and diversity of parasitic wasps in the canopy than in the understory and that this difference increased with tree diversity. Nonetheless, while parasitism

rates were correspondingly higher in the canopy, the magnitude of difference in parasitism across forest strata was not contingent on plant diversity in such study, suggesting non-additive effects were not present. Studies testing for non-additive effects between tree diversity and prey spatial distribution are needed, particularly those involving experimental approaches to achieve a mechanistic understanding of variation in top-down control with changing tree diversity.

Conclusions

Overall, our findings indicate consistent effects of prey vertical distribution in predation by birds and arthropods and suggest negative interactions between groups contingent on tree diversity, but are unsupportive of diversity and interactive effects between factors (non-significant tree diversity × prey distribution) on predation rates. These findings point to relevant avenues of future research, including experimental manipulations of bird predation to test for predator interactions and their effects on herbivore populations and herbivory. In addition, studies are needed which address temporal changes in predator community structure and behavior to explain variation in predation pressure. By better understanding the sources of variation in tree diversity effects on predation, we can design more effective management strategies for enhancing pest regulation in both managed and natural forests.

Declarations

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