**Predators have limited effects on plant-herbivore interaction network in early succession in tropical forest gaps**

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**Abstract**

Succession in canopy gaps is driving tropical forest dynamics. Conventional wisdom points to plant competition as the key driving force of initial secondary succession. However, the relative roles of plants racing for resources versus top-down control of vegetation by herbivores, in turn impacted by predators, remain poorly understood.

Here we examine the impact of birds, bats and ants on ecological succession using replicated experimental exclusion of these focal predators from 5 x 5 m plots from early successional vegetation in lowland tropical forest gaps in Papua New Guinea to assess the strength of their top-down effects on insect herbivores and arthropod predators.

Focal predators had no effect on abundance of herbivores or arthropod predators, but they decreased biomass and density of both groups. They also did not impact species richness of either herbivores or arthropod predators. The experimentally created enemy free space was thus not utilized by herbivores or arthropod predators. There was also no negative correlation between the strength and direction of the focal predators effect on individual arthropod orders within or between trophic levels that would indicate competition among herbivores or arthropod predators, or intra-guild predation by focal predators. Instead, herbivore and arthropod predator abundance and biomass correlated strongly with the plant biomass. This suggests bottom-up or abiotic control of arthropod communities during secondary succession. There was no difference in response to the focal predators exclusion between generalist and specialist herbivores. Birds, bats and ants had no effect on the structure of plant-herbivore interaction network characterized by connectance, generality, vulnerability, nestedness and specialization. Only the network modularity increased in response to the predator exclusion.

In summary, our results suggest that in early successional forest gaps the overall effects of insectivorous birds, bats, ants, and intermediate arthropod predators (spiders and insects) on arthropod herbivores are weak and that herbivores are mainly bottom-up controlled by plants.

**Key words:** tri-trophic interactions, plant-arthropod herbivore networks, intermediate predation, succession, interaction networks, top-down effects, cascading effects, tropical secondary forest.

**Introduction**

Secondary succession in forest gaps plays an important role in sustaining hyper-diversity of tropical forest (Schnitzer and Carson 2001, Gripenberg et al. 2014, Fischer et al. 2016). After removal of coexisting vegetation by disturbance this process allows some light-demanding species to establish themselves under the otherwise impenetrable canopy, and these initial stages of succession have long-term consequences for forest structure and diversity. Competitive interactions among plants are generally assumed to be the key force that structures early successional vegetation (Velázquez and Wiegand 2020). These interactions lead to the distinct life-history syndrome of pioneer species, as it maximizes growth rate in high light conditions, even at the expense of anti-herbivore defenses (Turner 2001). This might be a reason why top-down effects of herbivores and their predators on plants have rarely been considered in studies of vegetation dynamics during regeneration (Fischer et al. 2016). In contrast, herbivorous insects and pathogenic fungi were shown to strongly affect community assembly process in primary forests (Bagchi et al. 2014). Despite generally stronger herbivore pressure found in regenerating tropical forest gaps (Piper et al. 2018) its impact is assumed to be muted by mechanisms of plants compensation for herbivory. Specifically plants with acquisitive species traits tend to increase their growth rate in response to herbivore damage instead of investing into structural defenses at the expense of their growth (Strauss and Agrawal 1999, Turner 2001).

Insectivorous birds, bats and ants can effectively limit the abundance of tropical arthropods (Kalka et al. 2008, Morrison and Lindell 2012, Sam et al. 2015, Wills et al. 2019). However, top-down effects of focal predators in tropics can be highly variable (Maas et al. 2016). While in tropical agro-ecosystems top-down and cascading effects seem to be strong, prevalent, and predictable, this may not always be the case in natural plant communities (Bael et al. 2003, Vidal and Murphy 2018, Harrison and Banks-Leite 2020). Positive correlations between herbivore abundance and food quality (e.g. foliar nitrogen) and availability (e.g. leaf biomass) suggest that arthropod communities in late successional forests are shaped mainly by vegetation (Whitfeld et al. 2012, Mottl et al. 2020). This bottom-up control should in turn result in weakened top-down cascades. This observation seems to be consistent with some theoretical expectations e.g., that higher productivity would result in stronger bottom-up control of herbivores by vegetation (Kagata and Ohgushi 2006, Mooney et al. 2010). However, we have recently shown that in early successional tropical forest gaps herbivorous insects do shape plant community composition, but focal predators had surprisingly weak cascading effect on vegetation (Szefer et al. 2020). In fact, the strength of top-down control of plants by herbivores was found to be highly site specific (Jia et al. 2018) and the complex natural histories of predators and herbivores within food-webs might be important in modulating plant responses.

By focusing solely on top-down effects of predators on arthropod herbivore abundance we might miss an important effect of their body size shifts in response to predation (Gruner 2004). Studies from temperate region report strong top-down effects only on herbivore abundance (Vidal and Murphy 2018) even though biomass in general is more indicative measure of population size (Rossberg 2013). It is also known that prey size is important in predator-prey interactions and that predation can change the size structure of prey communities (Rodgers et al. 2015, Detmer et al. 2017). However, simultaneous evaluation of how predators affect herbivore abundance and biomass are surprisingly rare (Gruner 2004, Harris et al. 2020), particularly for arthropod predators (Maas et al. 2016).

The strength of a top-down trophic cascade depends on food web structure (Daugherty et al. 2007, Pujoni et al. 2016). Specifically intra-guild predation (IGP) is hypothesized to weaken any top-down cascading effect (Polis and Holt 1992, Finke and Denno 2005). A significant role of arthropod predators in tropical food webs can be seen from a recent comparative analysis that showed up to 82 times higher diversity of arthropod predators in the tropics than in temperate zones (Privet and Petillon 2018). However, at least in tropical mono-cultures, IGP by birds and bats seems to impact arthropod predators with its effects cascading onto plants (Karp and Daily 2014). In natural arthropod communities vertebrate, predators may feed preferentially on spiders (Rogers et al. 2012). This can produce a negative correlation between herbivores and their arthropod predators (Bosc et al. 2018, Recalde et al. 2020). However, top-down effects of focal predators on intermediate arthropod predators and herbivores can be also positively correlated (Mooney et al. 2010). Therefore, specific circumstances under which IGP attenuates or amplifies top-down effects on herbivores remain unclear, particularly in diverse tropical forests where studies reporting top-down and/or cascading effects on plant community composition are scarce (Bael et al. 2003, Letourneau et al. 2004, Kurten 2013, Harrison and Banks-Leite 2020).

Species-specific responses of arthropod herbivores to predation can also affect top-down cascade strength (Carson and Root 1999). Key factors known to mediate predator-arthropod prey interactions are specialization, ability to switch between resources (or habitats), and feeding mode of herbivores (Pace et al. 1999, Duffy et al. 2007, Van Bael et al. 2008, Singer et al. 2014, Maas et al. 2016, Schmitz 2017). Specialist arthropod herbivores might be better at avoiding generalist predators, which leads to utilization of the enemy free space (EFS) by herbivores and should weaken any top-down cascade (Schmitz et al. 2000, Petschenka and Agrawal 2016). In plant-herbivore interaction networks exposed to predation, the EFS promoting herbivore specialization can increase network modularity (Augustyn et al. 2016, Oliveira et al. 2020). In contrast, increased proportion of generalist herbivores tends to reduce this measure of network clustering (Ximenes Pinho et al. 2017, Robinson and Strauss 2020). Plant-herbivore interaction networks were shown to be equally specialized in both primary and secondary tropical forests (Novotny et al. 2004, Redmond et al. 2019) and EFS simply may not be available for many tropical predator-prey interactions (Novotny et al. 1999).

When food is limited, population sizes of generalist herbivores are predicted to be strongly reduced by their predators according to the tri-trophic interaction hypothesis (Mooney et al. 2012). However, relative strength of bottom-up and top-down forces on herbivores seems to be similar irrespective of diet breadth in complex natural communities (Vidal and Murphy 2018). It is possible that predatory pressure can force some herbivores to shift their diet instead of reducing the number of utilized plants and mitigate negative effect of natural enemies on their abundance (Calcagno et al. 2011, Schmitz 2017). Moreover, in species-rich plant communities generalist herbivores should be more flexible in their diet choice (Pfisterer et al. 2003).

In this study we evaluate the strength of top-down effects of insectivorous vertebrate predators (birds and bats) and predatory ants on insect herbivore and arthropod predator communities on early successional vegetation in tropical forest gaps, using experimental predator exclusion from replicated plots. This analysis should also explain the weak cascading effects of predator removal on plants that we previously found in this habitat (Szefer et al. 2020). The lack of effects can be due to compensation by other herbivorous orders, specialist herbivores replacing generalists, or due to intraguild predation on arthropod predators, or compensation by plants for increased herbivory.

**Materials and methods**

*Study sites and experimental design*

The experiment was conducted in the primary tropical rainforest surrounding Wanang village (145°5′32″E, 5°14′26″S) located in the Wanang Conservation Area, Papua New Guinea. The study was conducted in abandoned food gardens created during slash-and-burn subsistence agriculture. Old gardens create an artificial canopy gap usually larger than the average size of gaps created naturally (Arihafa and Mack 2013). This study is a part of a larger experiment focused on evaluating the role of biotic factors in secondary forest succession and we discussed the advantages of using abandoned gardens for studying secondary successional in our previous paper (Szefer et al. 2020). Within a radius of 3 km from the village, we selected six experimental gardens (blocks) 3-5 years old, each covering an area of approximately 400 m2, separated by a minimal distance of 200 m. At each garden we initiated regeneration by clearing all aboveground vegetation. We removed (without tillage) all the rocks, dead wood, and visible tree stumps and roots from the top 30 cm of soil to obtain approximately 95% bare soil coverage of each plot. These procedures were aimed to standardize, as far as possible, the initial conditions for succession. Specifically, to prevent re-sprouting while at the same time minimizing any disturbance of the seed bank and soil conditions (Chazdon 2014). For this study, two 5x5 m experimental plots were established within six blocks (12 experimental plots in total). Individual plots were separated by at least 1 m distance. We cleared 3 m wide margins around each (approximately rectangular) block to minimize any effects of the surrounding forest edge on micro-climatic conditions within the plots.

Control and exclosure plots were randomly assigned within each of the block following a completely randomized design. In the exclosure plots we used a transparent fishing net (1.5-2.0 cm mesh size) to protect vegetation from foraging birds and bats. Mesh size was chosen so that it would allow for any flying herbivores as well as wind dispersed and larger seeds to freely pass through the netting. Additionally, every week all litter-fall potentially containing seeds and insects was collected from the top of the exclosure and randomly placed inside the experimental plot. We used poisonous tuna baits (permethrin 0.5%) exposed in monthly intervals in enclosed traps to reduce the abundance of the predatory ants. This way, the baits were accessible to ants but not to flying insects. This method was previously efficient and provided a 91.2% average decrease in ant abundance from secondary forest (Klimes et al. 2011). Exclosure plots were originally surrounded by a plastic fence to prevent ants from re-colonizing the plot. A 50 cm high, dummy plastic fence was built around the control plots with a 10 cm gap left open on the ground level to account for possible effect of fencing in the exclosure plots.

Regeneration was allowed to proceed undisturbed for 12 months. After that time, all above-ground vegetation from all plots was destructively sampled. In each plot, all woody plant species equal or above one cm DBH were sorted and identified to species and their leaves and stems were weighed separately with 1 g accuracy. Leaf area was calculated by randomly sampling leaves from the pool of all leaves for each species at a given plot until 50x50 cm area (“leaf frame”) was filled. The frame was then photographed and processed using ImageJ software, measuring the area of individual leaves (Schneider et al. 2012, Volf et al. 2019). Leaf frame samples were then oven dried and weighed. The SLA (in cm2/g) was calculated as a ratio of leaf area to its dry mass. The difference between wet and dry mass of the leaves was used to calculate their water content. We used SLA and water content as an approximation of leaf quality for herbivores (Cornelissen et al. 2003, Barbier and Loreau 2019).

Before harvesting, individual plants were covered with insect-net and all arthropods were sampled using knock-down insecticide (MORTEIN®, active ingredients: allethrin [2.09 g/kg] and resmethrin [0.39 g/kg]). The arthropods were preserved in 70% ethanol and assigned to trophic guilds (herbivore or arthropod predator), Orders, and morpho-species (further referred to as species). We constructed putative interaction networks, based on the presence of these arthropods on individual plants in each plot. This allowed us to evaluate the diets (or habitat use) of all species in our experiment. We measured the body length of up to 20 individuals per arthropod species and used it to estimate individual species biomass (dry weight) with the help of biomass equations ((Ganihar 1997) for Homoptera and (Wardhaugh 2013) for other orders). Coleoptera and Heteroptera were considered herbivores since predatory species were almost absent from our samples. Arthropod density was calculated as the number of individuals per square meter of the leaf area, estimated for woody plant individuals by multiplying their leaf weight (in g) and SLA values (in cm2/g).

*Statistical analyses*

All analyses were performed in R statistical software (version 3.6.1; R Core Team 2019). Code for the analyses is available on github: <https://bit.ly/3diklxk>. Diet breadth was measured by the normalized Paired Differences Index (PDI; Poisot et al. 2011). The focal predators’ direct effect on arthropods and indirect effects on plants were evaluated using log-response ratios (LRR), which was calculated as a natural logarithm of a ratio of some focal descriptor value evaluated at the control and the exclosure plot within the same experimental block. Diet shifts of herbivorous arthropod species were estimated by calculating Bray-Curtis dissimilarity index of their food plant composition (inferred from the plants they were collected from) in control vs predator exclosure plots. The plant-herbivore interaction network in each plot was characterized by connectance, generality, nestedness, and vulnerability calculated using the *bipartite* R package (Dormann et al. 2008). Modularity for each network was evaluated using DIRTLPAwb+ algorithm (Beckett 2016). The distribution of interactions was measured by the evenness of the degree distribution of plants.

Statistical significance of the effect of focal predator removal was evaluated using linear and generalized linear models. Each model was tested for the significance of the random effect by comparison of their AIC values and visual evaluation of the model’s ability to predict the empirical data. If two nested models were not significantly different or predictions differed from the observed values, we used the simplest model that reproduced well the empirical data points. Removal of the random effect does not affect the evaluation of individual contrasts between treatment averages but only reduces their standard error estimation (Dixon 2016). Models used for each analysis are specified in detail in Table S1. Size distributions of herbivore individuals were compared using non-parametric Mann-Whitney’s test.

We performed partial PCA analysis (conditioned on the experimental block) on the woody plant community composition from 12 experimental plots to obtain main axes of variation in vegetation. We further performed partial RDA (pRDA) analysis using block and first four of the PC axes (~91% of the total variation in plant community composition) as conditional variables. This allowed to test for the effect of focal predators on herbivore and arthropod predator community (AP, spiders and insects except ants) independently of the change in vegetation caused by the cascading effects of birds and bats on plants.

**Results**

We collected 5955 arthropod individuals (~73.8 g of dry mass) from the six control and six exclosure plots (total 300 m2 area), sampled from 753.5 kg of plant biomass and approximate 633.2 m2 of foliage. We found 417 species from seven dominant orders of herbivorous (305 species) and AP (112 species) guilds. For herbivores these were Coleoptera (80 species), Heteroptera (64 species), Homoptera (19 species), Lepidoptera (68 species), and Orthoptera (74 species). For AP we found 99 species of Aranea and 13 species of Mantodea. Coleoptera was the most abundant order but Orthoptera had the highest biomass. Aranea, Orthoptera and Coleoptera had the highest species richness (Fig. S1).

Focal predators significantly decreased biomass of both herbivores (T = 2.160, P = 0.031, Table S1, S2) and AP (T = 2.055, P = 0.040), significantly reduced density of herbivores (T = 2.743, P = 0.006) and marginally significantly density of AP (T = 1.179, P = 0.073), and marginally significantly increased herbivore community diversity (T = 2.263, P = 0.073). The abundance and species richness of herbivores and AP were not affected (Fig. 1). For any individual arthropod order focal predators had no effect on any of the community characteristics (abundance, richness, diversity, density and biomass, Fig. S2) Instead, we found that the abundance of arthropods was strongly correlated with plant biomass and that the presence of birds, bats, and ants did not significantly modify this relationships for any individual arthropod order (Fig. S3). There was a negative correlation between herbivore damage and SLA. However, removal of focal predators did not affect leaf damage, SLA (Fig. S4) and total leaf area (Fig. S5).

Focal predators caused a shift towards smaller individuals in Orthoptera, Homoptera, Coleoptera and Araneae, and larger individuals in Mantodea and Lepidoptera (Fig. S6, Table S3). Size shifts, although significant overall, were observed only for certain orders on certain plant species (Tab. S4) and experimental blocks (Table S5). In case of Orthoptera and Homoptera larger species experienced stronger top-down effects (Fig. S7).

We found a marginally significant (T = 2.407, P = 0.074) positive correlation between the indirect effect of predators on plant and their direct effect on herbivore abundance (Fig. 2A). A similar pattern was found for direct effects on herbivores and AP (Fig. 2B). The former relationship gained significance when we analyzed individual insect orders (Fig. 2C). The effect of predators on individual herbivore orders was also positively correlated with the effects on intermediate predatory taxa: spiders and mantids (Fig. 2D). Qualitatively similar patterns were found for arthropod biomass (Fig. S8) with the exception of Mantodea, where the significance vanished in the Order-level analysis. The control and the exclosure plots showed no or positive pair-wise correlations of abundance and biomass between individual arthropod orders across the six study blocks (Fig. S9). Focal predators impacted individual herbivore and AP orders similarly so that the pairwise correlations of the predator effects (LRR) between Aranea, Orthoptera, Heteroptera, and Coleoptera were all positive and significant (Fig. 3).

In the pRDA analysis the effect of focal predators did not change the community composition of herbivore and AP communities (permutation test: F = 0.775, P = 0.519, Fig. S10).

On five common plant species, the host specificity of herbivores was not correlated with the effect of predators on their abundance (Fig. S11). When examining common herbivore species across all their hosts, there was also no relationship between host specialization and the effect of birds and bats except in Homoptera where more specialized species showed an increasingly negative response to the predators. Herbivore species present in both control and exclosure plots were on average less specialized than the species present in only one of the plots in three out of five herbivore orders (Fig S12A). There was no consistent change in the diet breadth in response to predation within any herbivore order (Fig. S13). Individually, however, species with higher diet breadth were more willing to shift their diet (Fig. S14).

There was no interaction between specialization and plant quality in predicting individual herbivore species responses to predation (Fig. S15). However, the magnitude of these responses was positively correlated with the leaf water content used as a proxy for the leaf quality, so that the abundance of herbivores decreased after the exclusion of predators more on the plant species with high water content leaves (Fig. S16).

Plant – herbivore network structure was robust to the impact of focal predators. There was no response to their exclusion in connectance, generality, nestedness, and PDI specialization of the network. Only modularity increased (Z = 2.143, P = 0.032, Fig. 4) and vulnerability marginally significantly decreased (T = -1.791, P = 0.073) in the exclosure plots. Evenness of the plant degree distribution did not respond to the exclosure (Fig. S17).

The AP:herbivore abundance ratio remained constant between control and exclosure plots (Fig. S18). Strength of indirect effect of predators on plants decreased with an increasing ratio of AP to herbivore abundance (Fig. S19). This relationship was not observed for arthropod communities on individual plant species (Fig. S20).

**Discussion**

In the early stage of tropical forest gap regeneration birds and bats weakly impacted the arthropod communities. For arthropod – vertebrate predator systems it has previously been shown that strong bird predation pressure reduces the abundance of both herbivores and APs simultaneously (Mooney et al. 2010). This is not the case here. At the same time, exclosure studies on small scales are more likely to report stronger effects of predators than large-scale experiments (Bommarco and Banks 2003). However, as noted by Mooney et al. (2010), a negative effect of predators on their prey abundance can be compensated by a continuous influx of allochthonous herbivores from surrounding primary forest matrix. This is plausible with respect to the intense insect traffic in the rainforest. For instance, Malaise traps set up in the primary forest understory at the Wanang study site for one year collected ~88 individuals flying through one m2 area per 24 hours (~ 3500 individuals daily crossing the side area of our plot approximated by a cuboid with average 2 m height throughout the one-year period; Ratnasingham and Hebert 2007). In our parallel experiment we found that insects were able to rapidly (within a few days) re-colonize vegetation plots sprayed weekly with a broad-spectrum insecticide. Moreover, the number of arthropods showed nearly perfect linear relationship with plant biomass, suggesting that the community assembly process may be driven by vegetation.

Further, the lack of top-down and cascading effects may be also due to compensation within the arthropod community, particularly an increase in the AP to herbivore ratio. Moreover, the herbivore community can also respond to changes in predation pressure. Some herbivores are less vulnerable to predation, either because they are of smaller size or they can use EFS, and could fill niches of the more vulnerable prey (Jeschke and Tollrian 2000, Green and Côté 2014). However, we did not detect any significant shift in the AP to herbivore ratios, or in herbivore community composition. Moreover, we found only positive or no correlation between the magnitude of the predator effect (LRR) between any of the AP and herbivore orders, which suggests no compensation by AP for the excluded predators. Furthermore, there was no negative correlation between the abundance of AP and herbivores, overall or for individual orders. Likewise, individual orders were not negatively correlated within the same trophic level. While this cannot be considered a hard evidence for a bottom-up regulation of herbivores it allows us to exclude strong competition and/or top-down control. Similar correlation patterns between arthropod predators and herbivores have been recently reported from the canopies of both tropical and temperate forests (Mottl et al. 2020), as well as for herbivores in lowland PNG forests (Novotny et al. 2012).

Compensation by specialized prey should be evident under strong predatory pressure (Mooney et al. 2012, Singer et al. 2014, Bosc et al. 2018). However, specialist herbivores did not perform better than generalists in our study system. The only exception was Homoptera, where higher predation impact was associated with a less specialized community, contrary to the theoretical expectations of better performance of specialists under predation (Bernays et al. 2004, Mooney et al. 2012).

Considering generalist predators had little effect on abundance and community composition, and a limited effect on arthropod biomass and density, the most plausible explanation is low predatory pressure in forest gaps (Tvardíková 2010, Tvardikova and Novotny 2012). Moreover, focal predators did not induce any change in herbivore diets which could be a mechanism allowing generalists to escape predation. Again, this general lack of strong predator avoidance behaviour could be indicative of weak predatory pressure (Belgrad and Griffen 2016). Both herbivorous and predacious arthropods tracked changes in plant biomass instead of showing a significant response to exclosure. At least for Orthoptera, Heteroptera, and Coleoptera this close correlation (relatively high R2 values) is suggestive of bottom-up control by plant biomass (Welti et al. 2020). Strong positive correlation of arthropod abundance with plant biomass conforms to the general characterization of pioneer plants as poorly defended and thus vulnerable to herbivory (Morante‐Filho et al. 2016). While primary forest vegetation may be defended by secondary metabolites and poor nutrition quality, secondary forest vegetation may limit herbivore numbers more in the line with its biomass.

Overall higher SLA values (lower density of the leaf tissue per unit area) were correlated with lower leaf damage which could be a sign of plant compensation for herbivory (Schuldt et al. 2017). However, SLA and herbivory damage of individual plant species was not affected by focal predator removal and we could not confirm that plants were actively responding to increased herbivory pressure with increasing producing larger and thinner leaves (Reese et al. 2016).

Despite no data on activity of birds and bats from our experimental blocks, our results found limited top-down effect of focal predator removal on arthropod abundance and no indirect effect on plants in the forest edge, corroborating the findings of a recent study from tropical forest in Brazil (Harrison and Banks-Leite 2020). Their study attributed lack of predator effect to deterioration of vertebrate insectivore community. Notably, we found that our arthropod herbivore community composition was similar to their study, with Coleoptera, Heteroptera, Lepidoptera, and Orthoptera dominating the community. Similar reduced foraging by insectivores might be true for forest gaps as these may simply be avoided by some birds (Robertson and Radford 2009). In conclusion, our results suggest that during early succession of tropical forest gaps the effects of birds and bats are limited and herbivores and AP respond mainly to changes in vegetation quantity.

In our study arthropod community showed some limited directional response to experimental exclosure, including biomass increase, diversity and network modularity reduction, and shifts towards larger individual sizes in the majority of arthropod orders, except for Mantodea and Lepidoptera. Because birds (relative to bats and ants) prefer to prey on lager herbivores (Singer et al. 2017), shifts in size structure of herbivores in response to predation are expected (Ritchie and Johnson 2009). Under the herbivore abundance limit enforced by plant biomass this preference of top predators can explain the increase in biomass coupled with a lack of the effect on abundance of herbivores and AP.

Markedly, we did not detect any effect of bird and bat exclusion on the interaction network structure, except for changes in modularity and vulnerability (average number of herbivores per plant species). Against our expectations, modularity and vulnerability deceased in the presence of focal predators with no effect on specialization, generality, connectance, or nestedness. This might be caused by herbivores shifting diets to focus more on their preferred host plant in response to the absence of focal predator pressure. However, the distribution of interactions between herbivores and plants did not respond to removal of predators. Nevertheless, increased clustering (modularity) and reduced vulnerability of the networks suggests that in tropical forest gaps extensive EFS is unlikely, as was previously shown for *Ficus* species in Papua New Guinea (Novotny et al. 1999). It is puzzling why the least specialized herbivore species would increase in abundance in the presence of predators. It is possible that generalist herbivores – by decreasing their density through utilization of broader host plant range – are able to avoid density dependent predation (Abdala‐Roberts et al. 2019). This could be supported by our findings that generalists were more flexible in their diet choice. Thus, similar to a recent study by Robinson and Strauss (2020), diet modification by generalists, and not changes in community composition, generates a community response to biotic and abiotic factors and is responsible for network stability. However, this pattern in modularity might also be caused by increased colonization of exclosure plots by species having narrow diet breadth as in our experiments. Under these circumstances predator effect (LRR) on herbivores could remain independent of specialization as we can only calculate LRR for species that are present in both control and exclosure plots. This might be plausible since, unexpectedly, the presence of focal predators was associated with increased diversity of herbivores (the effect was marginally significant). However, we found no difference in the abundance of species that were lost or gained in plots with predators.

Our results also confirm the important role of insectivorous birds and bats in shaping herbivore diversity (Zhang et al. 2018) and are in accordance with predicted weaker top-down effects in diverse communities (Maas et al. 2016). However, it is difficult to explain this observation. We would expect that versatile generalist predators would forage in such dynamically changing and unpredictable habitat and focus their predation efforts on prey form their diet range that is most abundant at the time (Sih 1984, Terraube et al. 2011). However, at least for generalist insectivorous bats, foraging appears to be density independent (Wray et al. 2021). Our understanding of this system would benefit from direct comparisons between forest interior and gaps to test whether the limited effects of predators are impacted by forest type (Krishnadas et al. 2018). Increased sample size would also improve our ability to detect more subtle changes in herbivore communities and overcome the problem of high local variation in plant and herbivore community composition during initial secondary succession.

Interestingly, despite no evident intraguild predation, the higher AP:herbivore abundance ratio translated onto weaker cascading effects on plants. This supports a prediction of food web theory suggesting that the effects of focal predators on herbivores and plants should attenuate trophic cascades in the presence of AP (Holt and Polis 1997, Daugherty et al. 2007). In our study, lower relative abundance of APs were coupled with positive and negative strong cascading effects of predators on plants. However, there was no clear positive correlation as we would expect from the literature (Mooney et al. 2010). Plausible explanations are that birds and bats might either prefer to feed on AP, or that increased abundance of AP suppress herbivore insects. However, direct effects of predators on AP were positively correlated with those of herbivores (for both abundance and biomass) which suggest that AP and herbivores are both positively affected by their resources. Compensation for herbivore damage by plants might be important in explaining strong positive responses of plant community to predation. Higher biomass of herbivores, causing significantly more damage to plants, would trigger compensatory plant growth at the community level. Larger bodied arthropod herbivores can also induce this type of response. Despite overall presence of plant compensation in our experiment exclosure did not increase damage and woody plant SLA. Other explanation of the observed patterns could be related to additional energy channels for intermediate AP (mostly spiders) as predicted by the apparent trophic cascade hypothesis (Ward et al. 2015, Liu et al. 2016). With rising productivity, intermediate AP may derive significant fraction of their diet not from herbivores but from an increasingly productive bottom-up controlled detrital channels. Spiders are known to cause top-down and cascading effects on detritivores and decomposition rates (Wise et al. 1999, Perkins et al. 2018, Murphy et al. 2020). These additional subsidies might increase the abundance of AP even when they still under control by their predators or by inter-guild competition and territoriality (Welti et al. 2020). Subsidies for AP thus can be related to the lack of effect on herbivores and no cascading effect on plant. Nevertheless, there is still a need for more systematic studies of tropical systems involving epigeic and soil herbivores and detritivore communities.

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**Figure 1.** Mean (points) and 95% bootstrapped CIs (whiskers) of the invertebrate herbivores (H) and arthropod predator (AP) community indices (A – no. of individuals, B – biomass in grams, D – inverse Simpson diversity, R – number of species, Dens – density [individuals/m2 of the leaf area]) in the control (C) and exclosure (Ex) plots. Grey points indicate empirical values for six experimental blocks, and dashed lines connect plots within blocks. Red color indicates significance at the α = 0.05, and yellow at the α = 0.1.

**Figure 2.** Relationships of predator (birds, bats and ants) effects on biomass between different trophic levels in individual plots: A – herbivores vs plants; B – herbivores vs arthropod predators (AP); C) herbivore orders vs plants, and D) AP divided into orders vs herbivores. Predator effects were evaluated using log response ratios (LRR): the logarithm of the ratio between the biomass at the control and predator exclosure treatment within the same experimental block. Positive/negative values of the LRR indicate increase/decrease in biomass of a given trophic level in the presence of predators. Solid line represents significance at the α = 0.05 level and dashed line at the α = 0.1 level. 95% CIs also plotted for significant relationships.

**Figure 3**. Pairwise Pearson correlations of the effects of birds, bats and ants on arthropod abundance between studied orders, Predator effects were evaluated using log response ratios (LRR): the logarithm of the ratio between the abundance at the control and predator exclosure treatment, within the same experimental block: LEPI – Lepidoptera; MANT – Mantodea; ORTH – Orthoptera; HETE – Heteroptera; COLE – Coleoptera; ARAN – Aarneae; HOMO – Homoptera. Significance is indicated with asterisks: P < 0.001 (\*\*\*); P < 0.01 (\*\*); p < 0.05 (\*).

**Figure 4**. Mean (points) and 95% bootstrapped CIs (whiskers) for plant-herbivore network descriptors in control (C) and exclosure (Ex) plots. Grey dots represent empirical data. Dashed lines connect control and predator exclosure treatment plots within the same experimental block. Significance (α = 0.05) is indicated with the red colour.







