**Predators have limited effects on plant-herbivore interaction networks in early secondary succession in a tropical rainforest.**

Piotr Szefer, Kenneth Molem, Austin Sau, Martina Vasutova & Vojtech Novotny

**Abstract**

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

Here we examine the impact of predators on ecological succession using replicated experimental exclusion of predators from 5 x 5 m plots with early successional vegetation in lowland tropical forest gaps in Papua New Guinea. We assess the strength of the top-down effects of vertebrate predators (birds and bats) on insect herbivores and arthropod predators.

Top predators had no effect on abundance of herbivores or arthropod predators, but they decreased biomass of both groups. The top predators also did not impact species richness of either herbivores or arthropod predators.. Interestingly, the enemy free space we experimentally created was thus not utilized by herbivores or arthropod predators. There was also no negative correlation between individual arthropod orders within or between trophic levels that would indicate competition among herbivores or arthropod predators, or intra-guild predation by top 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 initial secondary succession. Nevertheless, strength of indirect effect of top predators on plants were negatively correlated with increased proportion of AP in the community. There was no difference in response to the exclusion of top predators between generalist and specialist herbivores. Top predators 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 predator exclusion.

In summary, our results suggest that in early successional forest gaps the overall effects of vertebrate top predators (birds and bats) as well as intermediate arthropod predators (spiders and insects) on arthropod herbivores are weak..

**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 forests (Schnitzer and Carson 2001, Gripenberg et al. 2014, Fischer et al. 2016). After the removal of the existing vegetation by disturbance this process allows light-demanding species to establish themselves under otherwise impenetrable canopy. The initial stages of succession have long-term consequences for the 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) and leads to the distinct life-history syndrome of pioneer species considered optimum for such competition, as it maximizes growth rate in high light conditions, even at the expense of anti-herbivore defences (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 plant community assembly process in primary forests (Bagchi et al. 2014). Despite a generally stronger herbivory pressure found in regenerating tropical forest gaps (Piper et al. 2018) its impact is assumed to be muted by mechanisms of herbivory compensation. Specifically, plants with acquisitive species traits tend to compensate strongly for herbivore damage instead of investing into structural defenses at the expense of their growth (Strauss and Agrawal 1999, Turner 2001).

Bats and birds can effectively limit the abundance of tropical arthropods (Kalka et al. 2008, Morrison and Lindell 2012, Sam et al. 2015). However, top-down effects of vertebrate 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 be always the case in natural plant communities (Bael et al. 2003, Vidal and Murphy 2018, Harrison and Banks-Leite 2020). Correlation patterns between herbivore abundance and various plant community characteristics Arthropod communities in late successional forests appear to be shaped mainly by vegetation (Whitfeld et al. 2012, Mottl et al. 2020). This bottom-up control should 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 that the top vertebrate predators had surprisingly weak cascading effect on vegetation (Szefer et al. 2020). The strength of top-down control of plants by herbivores was found to be highly site-specific and difficult to predict accurately by climatic conditions, productivity or plant growth forms (Jia et al. 2018). The complex natural histories of both predators and herbivores within food-webs might be important in modulating plant responses. It is unclear why we observe weaker top-down and cascading effects at the initial stages of succession where assembly processes are more dynamic and plant natural enemies should be more relevant especially when trophic cascades on younger plants are expected to be stronger (Boege and Marquis 2006).

By focusing on top-down effect on herbivore abundance we might miss an important effect of body size shifts in response to predation (Gruner 2004). Studies from temperate regions report strong top-down effects only on herbivore abundance (Vidal and Murphy 2018) despite biomass being more indicative measure of a the impact on plants (Rossberg 2013). It is also known that prey size is important for vertebrate predators and that predation can change the size structure of the 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).

Strength of a top-down trophic cascade depends on the 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). 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 the temperate climatic zone (Privet and Petillon 2018). However, at least in tropical monoculture, IGP by vertebrate predators 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 vertebrate predators on intermediate arthropod predators and herbivores can be also be positively correlated (Mooney et al. 2010). The specific circumstances under which IGP attenuates or amplified top-down effects on herbivores remains 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 herbivores to predation can also affect top-down cascade strength (Carson and Root 1999). Key factors known to mediate predator-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 herbivores might be better at avoiding generalist predators . This utilization of the enemy free space (EFS) by herbivores 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, generalists tend to reduce network modularity (Ximenes Pinho et al. 2017, Robinson and Strauss 2020). However, EFS may not be available for many tropical predator-prey interactions (Novotny et al. 1999). 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). This potentially limits our abilities to detect EFS and mute cascading effects of primary predators on plants as well. Under food limitation population sizes of generalist herbivores is 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 plant species 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 paper we evaluate the strength of top-down effects of key vertebrate predators on insect herbivore and arthropod predator communities on early successional vegetation in tropical forest gaps, using experimental vertebrate predator exclusion from replicated plots. This analysis should also explain 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 the compensation by compositional , or due to intra-guild predation, or compensation by plants for increased herbivory.

I do not like this entire paragraph – you use the results to “predict” what should happen without much logical or empirical base for it, plus the logic is often hard to understand. I suggest to delete it all and use the simple logical prediction as above..

Specifically, we predict a presence of top-down effects on herbivores, with stronger effects on abundance than on biomass, caused by shifts in prey body size. We expect that these effects will not cascade down onto plants because of disproportionate predation on intermediate arthropod predators resulting in reduced pressure on herbivores and/or compensation for arthropod community size. Moreover we expect higher sensitivity of generalist herbivores to predation compared to specialists resulting in higher community specialization effect and increased modularity of plant-herbivore interaction networks under predator pressure.

**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. 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). We discuss 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. Specifically to prevent re-sprouting while at the same time minimizing any disturbance of the seed bank and soil conditions (Chazdon 2014). This study is a part of a larger experiment focused on evaluating the role of biotic factors in secondary forest succession (Szefer et al. 2020). For this study, two out of six 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 the effects of the surrounding forest edge on micro-climatic conditions within the plots.

The control and exclosure plots were randomly assigned within each block according to a randomized design. 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 wind dispersed and larger seeds to fall 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 attempted to reduce also the abundance of predatory ants, as key invertebrate predators were reduced by poisonous tuna baits (permethrin 0.5%) exposed in monthly intervals in enclosed traps. This way, the baits were accessible to ants but not to flying insects. This method was proved to be efficient and provided a 91.2% average decrease in ant abundance from secondary forest (Klimes et al. 2011). Despite proper execution of the eradication protocol, we were not able to reduce the abundance of epigeic ants. However, during insect collection we only encounter few individuals of small sized, non-predatory canopy ants, suggesting that the aggressive and mobile predaotey ants were most likely absent in our plots. Th 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 in order to account for the possible effect of fencing in exclosure plots.

Regeneration was allowed to proceed undisturbed for 12 months,. After that time, the complete above-ground vegetation from all the plots was destructively sampled. In each plot, all plants 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 size of individual leaves (Schneider, Rasband, & Eliceiri 2012). 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 was used to calculate water content. We used SLA 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 arthropod 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 guilds, 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 body length of up to 20 individuals per species and used it to estimate species biomass (dry weight) with the help ofbiomass equations (Ganihar 1997 for Homoptera, Wardhaugh 2013 for other orders) .Coleoptera and Heteroptera were considered herbivores since predatory species were almost absent from our samples.

*Statistical analyses*

All analyses were performed in the R statistical software (R Core Team 2020). Diet breath was measured by the normalized Paired Difference Index (PDI) (Poisot et al. 2011) . Predator 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 descriptor value form control over exclosure plot within the same experimental block. We evaluated diet shifts of species by Bray-Curtis dissimilarity index of their diets (inferred from the plants they were sampled from) in control vs exclosure plots. The plant-herbivore interaction networks in each plot were characterized by connectance, generality, nestedness and vulnerability using the *bipartite* R package (Dormann et al. 2008) andmodularity using DIRTLPAwb+ algorithm (Beckett 2016). We compared characteristics of arthropod communities using mixed effect models with block treated as a random effect. Abundance was modeled using negative binomial distribution, biomass using Gaussian distribution with a logit link function, and richness (number of species) using the quasi-Poisson distribution. For the diversity (Shannon index) we assumed normal error distribution. In case of modularity, PDI and diet shift we used beta distribution with logit link function, and random effect of block using the *glmmTMB* package (Brooks et al. 2017). Medians were used for size distributions of herbivore individuals and species were compared using Mann-Whitney’s test.

The effect of excluded predators was evaluated for herbivores and for arthropod predators (AP, spiders and insects except ants). We performed separate partial RDA (pRDA) analyses using their species composition with forward selection procedure to test for any important covariates that could affect community composition independently of the exclosure treatment. These variables can be then partialed out leaving only direct effect of exclosure on arthropod community. More specifically, for we performed pRDA, with effects of the exclosure and site partitioned out. We used the following variables: AP abundance, richness, and diversity as well as main axes of plant community pPCA (plant community variation, with the effect of the treatment partialed out). If any of these turned out to be significant we would then condition its effect in the final pRDA (conditioned on site and any significant variable from the forward selection procedure).

**Results**

We collected 5955 arthropod individuals (~73.8 g of dry mass) from the six control and six treatment plots (total 300 m2 area), sampled from 753.5 kg of plant biomass and 633.2 m2 of foliage. They belonged to seven dominant orders of herbivorous (Coleoptera, Heteroptera, Homoptera, Lepidoptera, Orthoptera) and AP (Aranea, Mantodea) guilds,. Coleoptera was the most abundant order (**Fig. S1**) but Orthoptera had the highest biomass (**Fig. S2**).

Predators significantly decreased biomass of both herbivores (T = -2.160, P = 0.031) and AP (T = -2.055, P = 0.040), and marginally significantly increased herbivore diversity (the inverse Simpson’s index), (T = 2.263, P = 0.073). The abundance and species richness of herbivores and APs were not affected (Fig.1). Density of AP showed a tendency to decrease due to predation but this effect was not significant. Predators had no effect on community characteristics (abundance, richness, inverse Simpson’s index, diversity and biomass, **Fig. S3**) of any individual arthropod order. Instead, we found that the abundance of arthropods was strongly correlated with plant biomass and that the presence of predators did not significantly modify this relationship for any individual arthropod order (**Fig. S4**).

Predators caused a shift towards smaller individuals in Orthoptera, Homoptera, Coleoptera and Araneae, and larger individuals in Mantodea and Lepidoptera (**Fig. S5**, Tab S1). Only in Aranea species sizes were reduced by predators. Size shifts, although significant overall, was observed only for certain orders on certain plant species (Tab S2,S3) and sites (Tab. S4,S5). In case of Orthoptera and Homoptera larger species tend to experience weaker top-down effects (**Fig. S6**).

We found a marginally significant (P = xxx) positive correlation between the indirect effect of predators on plant and their direct effect on herbivore abundance (Fig. 2, A). Similar pattern was found for direct effects on herbivores and AP (Fig. 2, B). The former relationship gained significance when we analysed individual insect orders (Fig. 2, C). The effect of predators on individual herbivore orders was also positively correlated with the effects on intermediate predatory taxa: spiders and mantids (P = xxx, Fig. 2, D). Qualitatively similar patterns were found for arthropod biomass (**Fig. S7**) with an exception of Mantodea, where the significance vanished in the order level analysis. The control as well as exclosure plots showed no or positive pair-wise correlations of abundance between individual arthropod orders across the six study blocks (Fig. S8). The effect size (LRR) of predator exclosure also impacted individual herbivore and AP orders similarly so that the pairwise correlations of effects between Aranea, Orthoptera, Heteroptera and Coleoptera were all positive and significant, while there were no significant correlations involving Lepidoptera, Homoptera or Mantodea (Fig. 3). Pattern of abundance and biomass correlation between all orders changed qualitatively between control and exclosure plots.

Plant community had no effect on arthropod community composition. Independently treatment did not predict the community composition of herbivore and AP communities (permutation test: F = 1.093, P = 0.442). Moreover, variance related to the site and residual variation were both high and amounted to 50% and 40.1% respectively.

On five common plant species, the host specificity of their herbivores was not correlated with the effect of predators on their abundance. When examining common herbivore species across all their hosts, there was also no relationships between host specialization and predator effects except in Homoptera where more specialized species showed an increasingly negative response to predators (**Fig. S9**). The species present in both control and exposure plots were on average less specialized than the species present in only one of the plots in three out of five herbivore orders (Fig S10, A). There was no consistent change in the diet breadth (change in PDI values) in response to predation within any herbivore order (**Fig. S11**). Individually, however, species with higher diet breadth were more willing to shift their diet (**Fig. S12**).

There was no interaction between specialization and plant quality in predicting individual herbivore species responses to predation (**Fig. S13**). However, the magnitude of herbivore response to predation exclosure was positively correlated with the leaf water content used as a proxy for the leaf quality, so that the abundance of herbivores increased after the exclusion of predators more on the plant species with high water content leaves (**Fig. S14**).

Plant-herbivore network structure was robust to the impact of predators. There was no response to predator exclusion in connectance, generality, vulnerability, nestedness and DPI specialization of the network, only modularity increased after the exclusion of predators (Z = 2.143, P = 0.032, Fig. 4).

Ratio of AP to herbivore abundance remained constant between control and exclosure plots (**Fig. S15**). Strength of indirect effect of predators on plants was decreasing with increasing ratio of AP to herbivore abundance (**Fig. S16, A**). This relationship was not observed for the communities on different plant species (**Fig. S18, B**)..

**Discussion**

In early stage of tropical forest gap regeneration the focal; predators only weakly impacted the arthropod communities. Against our expectations top-predators did not reduce herbivore or AP abundance. For arthropod – vertebrate predator systems it has previously been shown that strong bird predation pressure reduces the abundance of both herbivores and AP 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 the large-scale experiments (Bommarco and Banks 2003). However, as noted by (Mooney et al. 2010), negative effect of predators on their prey abundance can be compensated by a continuous influx of allochthonous herbivores from surrounding primary forest matrix. This can be plausible in the view of intense insect traffic in the rainforests. For instance, a Malaise trap set up in the primary forest understory at the Wanang study site for one year collected ~50 individual insects flying through m2 area per 24 hours (aproximately xxx insects per day per one m2) . In our parallel experiment we found that insects were able to re-colonize vegetation plots sprayed weekly with insecticide within days. Moreover, the number of arthropods showed a nearly perfect linear relationship with plant biomass, suggesting that the community assembly may be driven by plant biomass.

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. Further, 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 be able to fill niches of the more vulnerable prey. However, we did not detect any significant shifts in the AP to herbivore ratios, or in the herbivore community composition. Moreover, we found only positive or no correlation between the magnitude of predator effect (i.e., the change in the abundance of prey when the predators are present, compared to when they are excluded) on AP and herbivores, suggesting no compensation by AP for the excluded predators. Further, there was no negative correlation between the abundance of AP and herbivores, overall as well as 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 at least to exclude strong competition and/or top-down control. Similar correlation patterns between arthropod predators and herbivores have been reported recently 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 specialists should be evident under strong predatory pressure (Mooney et al. 2012, Singer et al. 2014, Bosc et al. 2018). However, specialists 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 (ref)...

In the light of the lack of general predator effect on the abundance, community composition and a limited effect on arthropod biomass, the most plausible explanation is a low predatory pressure in forest gaps. We also did not find any support for predators induced change in herbivore diet, that would allow generalists to avoid predation. Again, this general lack of a strong predator avoidance behaviour could be indicative of a weak predatory pressure (Belgrad and Griffen 2016). Both herbivorous and predaceous arthropods tracked changes in plant biomass instead of showing a significant response to exclosure. At least for Orthoptera, Heteroptera and Coleoptera this close correlation is suggestive of a 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 as such vulnerable to herbivory (Morante‐Filho et al. 2016). While the primary forest vegetation may be defended by secondary metabolites and poor nutrition quality, secondary forest vegetation may limit herbivore numbers more in line with its biomass.

Interestingly, in many cases we observed that removal of predators resulted in inflated variation in arthropod community characteristics. This might be related to the results of our previous analysis, where we concluded that predators have an ability to decrease randomness during plant community assembly. This suggests that both vegetation and arthropod community associated with it will show hight sensitivity to the initial conditions in the absence of predators. Limited role of top predators in gap succession is further supported by a recent findings from tropical forest in Brazil where similar limited top down effect of vertebrate predator removal on arthropod abundance and no indirect effect on plants was found in the forest edge (Harrison and Banks-Leite 2020). This lack of a predator effect was attributed to deterioration of vertebrate insectivore community near the forest edge. It is worth noting that community composition reported there was similar to the one found in our experiment, with a dominant role of Coleoptera, Heteroptera, Lepidoptera, and Orthoptera. Similar reduced foraging by insectivores might be true for forest gaps as these may pose barriers for 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.

Arthropod community showed some limited directional response to the exclosure including biomass increase, diversity and network modularity reduction, size shifts towards larger species of Aranea, and shifts in individual sizes in majority of arthropod orders. Despite no effect on abundance we found that top-predators removal resulted in higher herbivore and AP biomass. Moreover, we found shifts in species size distributions for Aranea, possibly released from primary predator pressure. Nevertheless, in food webs without top predators it was more probable to find larger individuals in nearly all arthropod orders. For a generalist predator individual size distributions probably matters more than species size distributions. Under abundance limit enforced by high quality plant biomass we should see compensating effect of herbivore body size/mass shifts within the community (Ritchie and Johnson 2009) as birds are known to prey on lager herbivores (Singer et al. 2017). This preference of top predators can explain increase in biomass coupled with a lack of the effect on abundance of herbivores and AP.

Additional effects of predators can be seen in the specialization pattern of putative interaction networks between plants and herbivores. Markedly, we did not detect any effect of predator exclusion on the interaction network structure, except for changes modularity. We however noted larger than expected variability in the exclosure plots for the generality and nestedness values, compared to the controls., Against our expectations, modularity decreased in the presence of predators with no effect on specialization or any other network descriptor. This effect was independent of the general network specialization. This might be caused by orthopterans and hemipterans extending their diet in response to predation. The trends of increased specialization and vulnerability in response to predation that would support this idea were however not significant, possibly because of a small sample size. This suggests that in tropical forest gaps extensive EFS is unlikely, as was previously shown to be also the case for *Ficus* species in Papua New Guinea (Novotny et al. 1999). It is puzzling why would the least specialized herbivore species increase in abundance in the presence of predators. It is possible that by decreasing their density through utilization of broader host plants generalists 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, similarly to a recent study (Robinson and Strauss 2020) diet modification by generalists, and not changes in community composition, generates a community response to biotic and abiotic factors and be responsible for the network stability. However, this pattern in modularity might be also caused by increased colonization of exclosure plots by species having narrow diet breadth as in our experiments. Under these circumstances predator effect on herbivores could remain independent of specialization as we can only calculate LRR for species that were present in both control and exclosure plots. This might be plausible since unexpectedly the presence of predators was associated with increased diversity of herbivores (the effect was marginally significant). However, we found no difference in abundance of species that were lost or gained in plots with predators.

Our results also confirm the important role of predators in shaping herbivore diversity (Zhang et al. 2018) and is in accordance with predicted weaker top down effects in diverse communities (Maas et al. 2016). However, it is difficult to explain this observation. Diversity maintenance through density-dependent action of predators would require high specialization of vertebrate predators in forest gaps, which is unlikely. We would expect that more versatile generalist predators would forage in such dynamically changing and unpredictable habitat. However, at least for generalist 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 limited effect of predator effects are impacted by forest type (Krishnadas et al. 2018).Increased sample size would also definitely 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 in the course of initial secondary succession.

Interestingly, despite no evident intraguild predation higher ratio of AP to herbivores translated onto weaker cascading effects on plants. This supports a prediction of food web theory that effects of vertebrate insectivores on herbivores and plants should attenuate trophic cascades in the presence of AP (Holt and Polis 1997, Daugherty et al. 2007). In opposition to the established general pattern (Mooney et al. 2010) lower AP/herbivore ratio were coupled with strong positive cascading effects, which resulted in negative slope of AP/herbivore ratio vs LRR of plants. Plausible explanations are that birds might either prefer to feed on AP, or that increased abundance of AP suppress herbivore insects. However, direct LRR of 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. Overcompensation of herbivore damage by plants might be important in explaining strong positive responses of plant community to predation. Higher abundance of herbivores, causing significantly more damage to plants, would trigger compensatory plant growth at the community level. Other explanation of the observed patterns could be related to additional detrital energy channels. In early successional gaps detrital communities might be an important component of a food web as predicted by the apparent trophic cascade hypothesis (Ward et al. 2015, Liu et al. 2016). With rising productivity top predators are able to derive significant fraction of their diet 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). This additional subsidies might increase the abundance of AP even when they still under control by vertebrate predators or by inter-guild competition and territoriality (Welti et al. 2020). Subsidies for both AP and top predators thus can explain 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.

**References**

Abdala‐Roberts, L., A. Puentes, D. L. Finke, R. J. Marquis, M. Montserrat, E. H. Poelman, S. Rasmann, A. Sentis, N. M. van Dam, G. Wimp, K. Mooney, and C. Björkman. 2019. Tri-trophic interactions: bridging species, communities and ecosystems. Ecology Letters 22:2151–2167.

Arihafa, A., and A. L. Mack. 2013. Treefall Gap Dynamics in a Tropical Rain Forest in Papua New Guinea. Pacific Science 67:47–58.

Augustyn, W. J., B. Anderson, and A. G. Ellis. 2016. Experimental evidence for fundamental, and not realized, niche partitioning in a plant–herbivore community interaction network. Journal of Animal Ecology 85:994–1003.

Bael, S. A. V., J. D. Brawn, and S. K. Robinson. 2003. Birds defend trees from herbivores in a Neotropical forest canopy. Proceedings of the National Academy of Sciences 100:8304–8307.

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506:85–88.

Barbier, M., and M. Loreau. 2019. Pyramids and cascades: a synthesis of food chain functioning and stability. Ecology Letters 22:405–419.

Beckett, S. J. 2016. Improved community detection in weighted bipartite networks. Royal Society Open Science 3.

Belgrad, B. A., and B. D. Griffen. 2016. Predator–prey interactions mediated by prey personality and predator hunting mode. Proceedings of the Royal Society B: Biological Sciences 283:20160408.

Boege, K., and R. J. Marquis. 2006. Plant quality and predation risk mediated by plant ontogeny: consequences for herbivores and plants. Oikos 115:559–572.

Bommarco, R., and J. E. Banks. 2003. Scale as Modifier in Vegetation Diversity Experiments: Effects on Herbivores and Predators. Oikos 102:440–448.

Bosc, C., F. Roets, C. Hui, and A. Pauw. 2018. Interactions among predators and plant specificity protect herbivores from top predators. Ecology 99:1602–1609.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.

Calcagno, V., C. Sun, O. J. Schmitz, and M. Loreau. 2011. Keystone Predation and Plant Species Coexistence: The Role of Carnivore Hunting Mode. The American Naturalist 177:E1–E13.

Carson, W. P., and R. B. Root. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. Oecologia 121:260–272.

Chazdon, R. L. 2014. Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation. Illustrated edition. University of Chicago Press, Chicago.

Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380.

Daugherty, M. P., J. P. Harmon, and C. J. Briggs. 2007. Trophic supplements to intraguild predation. Oikos 116:662–677.

Detmer, T. M., J. H. McCutchan, and W. M. Lewis. 2017. Predator driven changes in prey size distribution stabilize secondary production in lacustrine food webs. Limnology and Oceanography 62:592–605.

Dormann, C., B. Gruber, and J. Fründ. 2008. Introducing the bipartite Package: Analysing Ecological Networks. R News 8.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thébault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology Letters 10:522–538.

Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecology Letters 8:1299–1306.

Fischer, R., F. Bohn, M. Dantas de Paula, C. Dislich, J. Groeneveld, A. G. Gutiérrez, M. Kazmierczak, N. Knapp, S. Lehmann, S. Paulick, S. Pütz, E. Rödig, F. Taubert, P. Köhler, and A. Huth. 2016. Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests. Ecological Modelling 326:124–133.

Ganihar, S. R. 1997. Biomass estimates of terrestrial arthropods based on body length. Journal of Biosciences 22:219–224.

Gripenberg, S., R. Bagchi, R. E. Gallery, R. P. Freckleton, L. Narayan, and O. T. Lewis. 2014. Testing for enemy-mediated density-dependence in the mortality of seedlings: field experiments with five Neotropical tree species. Oikos 123:185–193.

Gruner, D. S. 2004. Attenuation of Top-down and Bottom-up Forces in a Complex Terrestrial Community. Ecology 85:3010–3022.

Harris, S. H., U. G. Kormann, T. D. Stokely, J. Verschuyl, A. J. Kroll, and M. G. Betts. 2020. Do birds help trees grow? An experimental study of the effects of land-use intensification on avian trophic cascades. Ecology 101:e03018.

Harrison, M. L. K., and C. Banks-Leite. 2020. Edge effects on trophic cascades in tropical rainforests. Conservation Biology: The Journal of the Society for Conservation Biology 34:977–987.

Holt, R. D., and G. A. Polis. 1997. A Theoretical Framework for Intraguild Predation. The American Naturalist 149:745–764.

Jia, S., X. Wang, Z. Yuan, F. Lin, J. Ye, Z. Hao, and M. S. Luskin. 2018. Global signal of top-down control of terrestrial plant communities by herbivores. Proceedings of the National Academy of Sciences 115:6237–6242.

Kagata, H., and T. Ohgushi. 2006. Bottom-up trophic cascades and material transfer in terrestrial food webs. Ecological Research 21:26–34.

Kalka, M. B., A. R. Smith, and E. K. V. Kalko. 2008. Bats Limit Arthropods and Herbivory in a Tropical Forest. Science 320:71–71.

Karp, D. S., and G. C. Daily. 2014. Cascading effects of insectivorous birds and bats in tropical coffee plantations. Ecology 95:1065–1074.

Klimes, P., M. Janda, S. Ibalim, J. Kua, and V. Novotny. 2011. Experimental suppression of ants foraging on rainforest vegetation in New Guinea: testing methods for a whole-forest manipulation of insect communities. Ecological Entomology 36:94–103.

Krishnadas, M., R. Bagchi, S. Sridhara, and L. S. Comita. 2018. Weaker plant-enemy interactions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. Nature Communications 9:4523.

Kurten, E. L. 2013. Cascading effects of contemporaneous defaunation on tropical forest communities. Biological Conservation 163:22–32.

Letourneau, D. K., L. A. Dyer, and G. V. C. 2004. Indirect Effects of a Top Predator on a Rain Forest Understory Plant Community. Ecology 85:2144–2152.

Liu, S., J. E. Behm, J. Chen, S. Fu, X. He, J. Hu, D. Schaefer, J. Gan, and X. Yang. 2016. Functional redundancy dampens the trophic cascade effect of a web-building spider in a tropical forest floor. Soil Biology and Biochemistry 98:22–29.

Maas, B., D. S. Karp, S. Bumrungsri, K. Darras, D. Gonthier, J. C.-C. Huang, C. A. Lindell, J. J. Maine, L. Mestre, N. L. Michel, E. B. Morrison, I. Perfecto, S. M. Philpott, Ç. H. Şekercioğlu, R. M. Silva, P. J. Taylor, T. Tscharntke, S. A. V. Bael, C. J. Whelan, and K. Williams‐Guillén. 2016. Bird and bat predation services in tropical forests and agroforestry landscapes. Biological Reviews 91:1081–1101.

Mooney, K. A., D. S. Gruner, N. A. Barber, S. A. Van Bael, S. M. Philpott, and R. Greenberg. 2010. Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. Proceedings of the National Academy of Sciences of the United States of America 107:7335–7340.

Mooney, K. A., R. T. Pratt, and M. S. Singer. 2012. The Tri-Trophic Interactions Hypothesis: Interactive Effects of Host Plant Quality, Diet Breadth and Natural Enemies on Herbivores. PLOS ONE 7:e34403.

Morante‐Filho, J. C., V. Arroyo‐Rodríguez, M. Lohbeck, T. Tscharntke, and D. Faria. 2016. Tropical forest loss and its multitrophic effects on insect herbivory. Ecology 97:3315–3325.

Morrison, E. B., and C. A. Lindell. 2012. Birds and bats reduce insect biomass and leaf damage in tropical forest restoration sites. Ecological Applications: A Publication of the Ecological Society of America 22:1526–1534.

Mottl, O., P. Fibich, P. Klimes, M. Volf, R. Tropek, K. Anderson‐Teixeira, J. Auga, T. Blair, P. Butterill, G. Carscallen, E. Gonzalez‐Akre, A. Goodman, O. Kaman, G. P. A. Lamarre, M. Libra, M. E. Losada, M. Manumbor, S. E. Miller, K. Molem, G. Nichols, N. S. Plowman, C. Redmond, C. L. Seifert, J. Vrana, G. D. Weiblen, and V. Novotny. 2020. Spatial covariance of herbivorous and predatory guilds of forest canopy arthropods along a latitudinal gradient. Ecology Letters 23:1499–1510.

Murphy, S. M., D. Lewis, and G. M. Wimp. 2020. Predator population size structure alters consumption of prey from epigeic and grazing food webs. Oecologia 192:791–799.

Novotny, V., Y. Basset, J. Auga, W. Boen, C. Dal, P. Drozd, M. Kasbal, B. Isua, R. Kutil, and M. Manumbor. 1999. Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time. Australian Journal of Ecology 24:477–483.

Novotny, V., S. E. Miller, J. Leps, Y. Basset, D. Bito, M. Janda, J. Hulcr, K. Damas, and G. D. Weiblen. 2004. No tree an island: the plant–caterpillar food web of a secondary rain forest in New Guinea. Ecology Letters 7:1090–1100.

Oliveira, J. B. B. S., M. L. Faria, M. A. Z. Borges, M. Fagundes, and W. S. de Araújo. 2020. Comparing the plant–herbivore network topology of different insect guilds in Neotropical savannas. Ecological Entomology 45:406–415.

Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell, M. L. Pace, J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Perkins, M. J., R. Inger, S. Bearhop, and D. Sanders. 2018. Multichannel feeding by spider functional groups is driven by feeding strategies and resource availability. Oikos 127:23–33.

Petschenka, G., and A. A. Agrawal. 2016. How herbivores coopt plant defenses: natural selection, specialization, and sequestration. Current Opinion in Insect Science 14:17–24.

Pfisterer, A. B., M. Diemer, and B. Schmid. 2003. Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. Oecologia 135:234–241.

Piper, F. I., S. H. Altmann, and C. H. Lusk. 2018. Global patterns of insect herbivory in gap and understorey environments, and their implications for woody plant carbon storage. Oikos 127:483–496.

Poisot, T., G. Lepennetier, E. Martinez, J. Ramsayer, and M. E. Hochberg. 2011. Resource availability affects the structure of a natural bacteria–bacteriophage community. Biology Letters 7:201–204.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

Privet, K., and J. Petillon. 2018. Differences in tropical vs. temperate diversity in arthropod predators provide insights into causes of latitudinal gradients of species diversity. bioRxiv:283499.

Pujoni, D. G. F., P. M. Maia-Barbosa, F. A. R. Barbosa, C. R. Fragoso Jr., and E. H. van Nes. 2016. Effects of food web complexity on top-down control in tropical lakes. Ecological Modelling 320:358–365.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Recalde, F. C., C. P. B. Breviglieri, and G. Q. Romero. 2020. Allochthonous aquatic subsidies alleviate predation pressure in terrestrial ecosystems. Ecology 101:e03074.

Redmond, C. M., J. Auga, B. Gewa, S. T. Segar, S. E. Miller, K. Molem, G. D. Weiblen, P. T. Butterill, G. Maiyah, A. S. C. Hood, M. Volf, L. R. Jorge, Y. Basset, and V. Novotný. 2019. High specialization and limited structural change in plant-herbivore networks along a successional chronosequence in tropical montane forest. Ecography 42:162–172.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Robertson, O. J., and J. Q. Radford. 2009. Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecology 34:435–446.

Robinson, M. L., and S. Y. Strauss. 2020. Generalists are more specialized in low-resource habitats, increasing stability of ecological network structure. Proceedings of the National Academy of Sciences 117:2043–2048.

Rodgers, G. M., B. Downing, and L. J. Morrell. 2015. Prey body size mediates the predation risk associated with being “odd.” Behavioral Ecology 26:242–246.

Rogers, H., J. H. R. Lambers, R. Miller, and J. J. Tewksbury. 2012. ‘Natural experiment’ Demonstrates Top-Down Control of Spiders by Birds on a Landscape Level. PLOS ONE 7:e43446.

Rossberg, A. G. 2013. Food Webs and Biodiversity: Foundations, Models, Data. John Wiley & Sons.

Sam, K., B. Koane, and V. Novotny. 2015. Herbivore damage increases avian and ant predation of caterpillars on trees along a complete elevational forest gradient in Papua New Guinea. Ecography 38:293–300.

Schmitz, O. 2017. Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. F1000Research 6.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. The American Naturalist 155:141–153.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters 7:153–163.

Schnitzer, S. A., and W. P. Carson. 2001. Treefall Gaps and the Maintenance of Species Diversity in a Tropical Forest. Ecology 82:913–919.

Singer, M. S., R. E. Clark, I. H. Lichter‐Marck, E. R. Johnson, and K. A. Mooney. 2017. Predatory birds and ants partition caterpillar prey by body size and diet breadth. Journal of Animal Ecology 86:1363–1371.

Singer, M. S., I. H. Lichter-Marck, T. E. Farkas, E. Aaron, K. D. Whitney, and K. A. Mooney. 2014. Herbivore diet breadth mediates the cascading effects of carnivores in food webs. Proceedings of the National Academy of Sciences of the United States of America 111:9521–9526.

Stewart, A. B., and M. R. Dudash. 2018. Foraging strategies of generalist and specialist Old World nectar bats in response to temporally variable floral resources. Biotropica 50:98–105.

Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. Trends in Ecology & Evolution 14:179–185.

Szefer, P., K. Molem, A. Sau, and V. Novotny. 2020. Impact of pathogenic fungi, herbivores and predators on secondary succession of tropical rainforest vegetation. Journal of Ecology 108:1978–1988.

Turner, I. M. 2001. The Ecology of Trees in the Tropical Rain Forest. Cambridge University Press, Cambridge.

Van Bael, S. A., S. M. Philpott, R. Greenberg, P. Bichier, N. A. Barber, K. A. Mooney, and D. S. Gruner. 2008. Birds as predators in tropical agroforestry systems. Ecology 89:928–934.

Velázquez, E., and T. Wiegand. 2020. Competition for light and persistence of rare light-demanding species within tree-fall gaps in a moist tropical forest. Ecology 101:e03034.

Vidal, M. C., and S. M. Murphy. 2018. Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. Ecology Letters 21:138–150.

Ward, C. L., K. S. McCann, and N. Rooney. 2015. HSS revisited: multi-channel processes mediate trophic control across a productivity gradient. Ecology Letters 18:1190–1197.

Wardhaugh, C. W. 2013. Estimation of biomass from body length and width for tropical rainforest canopy invertebrates. Australian Journal of Entomology 52:291–298.

Welti, E. A. R., R. M. Prather, N. J. Sanders, K. M. de Beurs, and M. Kaspari. 2020. Bottom-up when it is not top-down: Predators and plants control biomass of grassland arthropods. Journal of Animal Ecology 89:1286–1294.

Whitfeld, T. J. S., V. Novotny, S. E. Miller, J. Hrcek, P. Klimes, and G. D. Weiblen. 2012. Predicting tropical insect herbivore abundance from host plant traits and phylogeny. Ecology 93:S211–S222.

Wise, D. H., W. E. Snyder, P. Tuntibunpakul, and J. Halaj. 1999. Spiders in Decomposition Food Webs of Agroecosystems: Theory and Evidence. The Journal of Arachnology 27:363–370.

Wray, A. K., M. Z. Peery, M. A. Jusino, J. M. Kochanski, M. T. Banik, J. M. Palmer, D. L. Lindner, and C. Gratton. 2021. Predator preferences shape the diets of arthropodivorous bats more than quantitative local prey abundance. Molecular Ecology 30:855–873.

Ximenes Pinho, B., W. Dáttilo, and I. R. Leal. 2017. Structural breakdown of specialized plant-herbivore interaction networks in tropical forest edges. Global Ecology and Conservation 12:1–8.

Zhang, J., H. Qian, M. Girardello, V. Pellissier, S. E. Nielsen, and J.-C. Svenning. 2018. Trophic interactions among vertebrate guilds and plants shape global patterns in species diversity. Proceedings of the Royal Society B: Biological Sciences 285:20180949.