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

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**Abstract**

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

Here we examine the impact of predators 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 assessed strength of the top-down effects of vertebrate predators (birds and bats) on insect herbivores and arthropod predators (AP).

Top predators had no effect on arthropod abundance nor species richness, but decreased their biomass and increased herbivore diversity. The enemy free space (EFS) was thus not utilized for increase in arthropod abundance. There was no negative correlation between any AP and herbivore orders that would be an indication of strong competition within the community or intra-guild predation by top predators. Instead, herbivore and AP abundance and biomass correlated strongly with the plant biomass. This suggests bottom-up or abiotic control of arthropod communities. 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 predators between generalist and specialist. However, flexibility in diet choice decreased with specialization of herbivores. Predators had little effect on the structure of interaction network. Surprisingly, however, modularity decreased in response to predatory pressure possibly due to diet breadth extension of generalist herbivores.

Our results suggest that in early successional forest gaps effects of top predators are weak. However, some responses of arthropod communities to top predator removal were observed which suggests that flexible diets of generalist herbivores determine food web structure in tropical forest gaps.

**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 tropical 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 disturbance this competitive replacement process allows light-demanding species to establish themselves under otherwise impenetrable canopy. The initial stages of succession have a long-term consequences for the forest structure and diversity. Competitive interactions among plants are assumed to be the key force that structures early successional vegetation structure (Velázquez and Wiegand 2020) and the distinct life-history syndrome of pioneer species is seen as an optimization for such competition, including maximized growth rate and low 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 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) the impact of natural enemies 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 cost of their growth rate (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 are found to be highly variable (Maas et al. 2016). While in tropical agro-ecosystems top-down and cascading effects seem to be strong and prevalent, their universality in natural plant communities is debatable (Bael et al. 2003, Vidal and Murphy 2018, Harrison and Banks-Leite 2020). Correlation patterns between herbivore abundance and various plant community characteristics 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 result in weakened top-down cascades. Recently it was shown that in early successional tropical forest gaps herbivorous insects shape plant community composition, but top predators had surprisingly weak cascading effect on vegetation (Szefer et al. 2020). 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). Unfortunately, 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). Therefore, 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 abundance we might miss an important effect of body size shifts in response to predation (Gruner 2004). Studies from temperate region usually report strong top-down effects only on herbivore abundance (Vidal and Murphy 2018) despite biomass being more indicative measure of a population size (Rossberg 2013). Especially when it is known that prey size is crucial for vertebrate predators and that predation can change the size structure of the prey (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). Especially studies of arthropod predators (AP) are scarce (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 the presence of 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 AP in the tropics than in temperate climatic zone (Privet and Petillon 2018). However, at least in tropical monoculture, IGP by vertebrate predators in arthropod-plant interaction seems to be characterised by stronger effects cascading onto plants (Karp and Daily 2014). In natural arthropod communities primary predators may feed preferentially on spiders (Rogers et al. 2012). This is expected to result in a negative correlation between herbivores and their arthropod predators in the presence of predators (Bosc et al. 2018, Recalde et al. 2020). Interestingly, however, it was shown that in plant-arthropod herbivore systems top-down effects on intermediate AP and herbivores tend to be positively correlated (Mooney et al. 2010). Therefore, specific circumstances under which IGP attenuates or amplified these effects is still unclear. To better understand relationship between the presence of IGP and strength of top-down effects we first need more studies from natural habitats from various bioms including diverse tropical forest. Yet studies reporting top-down and/or cascading effects on plant community composition from tropics 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 mechanism (Pace et al. 1999, Duffy et al. 2007, Van Bael et al. 2008, Singer et al. 2014, Maas et al. 2016, Schmitz 2017). Due to hypothesized superior physiological and behavioral adaptations specialist herbivores might be able to avoid generalist predators irrespective of the plant quality on which they feed. 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, the presence of EFS, and its specialization promoting effect in herbivorous insect communities can result in increase of the network modularity in response to predation (Augustyn et al. 2016, Oliveira et al. 2020). In contrast, presence of generalists tend to reduce this measure of network clustering (Ximenes Pinho et al. 2017, Robinson and Strauss 2020). However, EFS has not been yet confirmed to be universal for tropical predator-prey interactions (Novotny et al. 1999). Plant-herbivore interaction networks were shown to be highly 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 (TTI) (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 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). It was shown that prey with narrow habitat domain (habitat specialization) will respond with reduced feeding, or habitat shift if its mobile and have a broad habitat domain (Schmitz et al. 2004). This flexibility in habitat choice can possibly translate into a wider diet breadth as it is the case, for example, for predators (Stewart and Dudash 2018). However, this mechanism has not been explored in diverse natural communities, let alone in tropical forests.

In this paper we evaluate the strength of top-down effects of key vertebrate predators on insect herbivore and AP communities in a plot-based experiment in early successional large tropical forest gaps. We also explore reasons for a weak cascading effects of predator removal on plants previously found in this habitat. Specifically we predict a presence of top-down effects on herbivores, with stronger effects on abundance than on biomass, that could be caused by shifts in prey body size. However, we expect that these effects will not cascade down onto plants because of a disproportionate predation on AP and different herbivorous orders resulting in reduced pressure on herbivores and/or compensation for arthropod community size. Moreover we expect lower performance of generalist than specialists resulting in negative correlation between specialization and predator effect and reduced modularity of plant-herbivore interaction networks under predator pressure. This would provide additional compensating mechanism that would prevent top-down effects of predators to cascade down onto plants.

**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 previuos 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 prevented 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 fators in secondary forest succession (Szefer et al. 2020). For this stydy, 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 (on the ground) ants. However, during insect collection we only encounter few individuals of small sized, non-predatory canopy ants, suggesting that the ant eradication was successful, at least for aggressive and mobile dominants most likely to attend tuna baits. 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 build 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, with minimal maintenance within the plots. After that time, the complete above-ground vegetation from all the plots was destructively sampled. In each plot, all plant species were sorted and identified to species and leaf and stem 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 (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. Proportion of the difference between wet and dry mass to wet mass was recorded as the water content. We used and specific leaf area (SLA) as an approximation of leaf quality for herbivores (Cornelissen et al. 2003, Barbier and Loreau 2019).

Before cutting individual woody plants were covered with insect-net and knocked-down with insecticide (MORTEIN®, active ingredients: allethrin [2.09 g/kg] and resmethrin [0.39 g/kg]). All arthropods were then collected, preserved in 70% ethanol, and assigned to guilds, orders and morpho-species (further referred to as species). We constructed putative interaction networks, summarising arthropod individuals collected from woody plants present in each plot. This allowed us to evaluate the diets (or habitat use) of all species in our experiment. We used body length to estimate individual species biomass (dry weight). For majority of arthropod orders we used biomass equations of (Wardhaugh 2013) and in case of Homoptera of (Ganihar 1997). Length of each species was based on an average estimation of their length of a sample of maximum 20 individuals, or all individuals form a given species. Although, there are known species of Coleoptera and Heteroptera that are predatory our samples contained almost exclusively herbivorous species.

*Statistical analyses*

All analyses were performed in the R statistical software (R Core Team 2020). For individual herbivore species and for a network specialization we evaluated the normalized Paired Difference Index (PDI) based on all sites sampled during our experiment (Poisot et al. 2011) to evaluate individual species diet breadth. Predator direct effect on arthropods and indirect effects on plant were both 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 switching abilities (diet shifts) of species by calculating dissimilarity (Bray-Curtis index) of their diets in control vs exclosure plots. For the plant-herbivore interaction networks we calculated connectance, generality, nestedness and vulnerability using the *bipartite* R package (Dormann et al. 2008). To quantify modularity of plant-herbivore interactions for each plot (12 networks) we used 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 for size distributions of herbivore individuals and species were compared using Mann-Whitney’s test.

Effect of predators on herbivores might be an effect of their indirect effect on vegetation or their AP. To take that fact into consideration for both herbivores and AP we performed separate partial RDA (pRDA) analyses with forward selection procedure to test for any important covariates, that would 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. Using forward selection we fitted variables that might be important in shaping herbivore community structure independently of the top predators. We used: 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 individuals (~73.8 g of dry mass) from seven dominant orders belonging to herbivorous (Coleoptera, Heteroptera, Homoptera, Lepidoptera, Orthoptera) and AP (Aranea, Mantodea) guilds, from 753.5 kg of plant biomass and approximate 633.2 m2 of foliage. Generally 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 increased herbivore community diversity (the inverse Simpson’s index), but difference in the latter was only marginally significant (T = 2.263, P = 0.073). The abundance and species richness of herbivore and AP 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 relationships 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 marginally significant (P = xxx) positive correlation between the indirect effect of predators on plant and herbivore abundance (Fig. 2, A). Similar significant patter was found for 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. In pairwise comparisons we found significant positive correlation of the predator effects between Aranea, Orthoptera, Heteroptera and Coleoptera (Fig. 3). There was also no negative correlation between AP and herbivore community size (**Fig. S8**). Pattern of abundance and biomass correlation between all orders changed qualitatively between control and exclosure plots. However, in any case the effect of predators resulted in a shift from positive or no correlation to a negative one.

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.

Only in the case of Homoptera more specialized species showed an increasingly negative response to predators (**Fig. S9**). Otherwise, specialization had no effect on the species’ performance and this lack of correlation prevailed across studied plant species. For Coleoptera, Orthoptera and Lepidoptera species which were present in both exclosure and control plots had significantly lower specialization and species that were lost or gained in a plot were more specialized (Fig S10, A). The amount of individuals gained equated to those that were lost due to predators (Fig S10, B). There was no interaction between specialization and predator effect for any herbivore order on any of the studied woody plant. 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, herbivore responses to predation were positively correlated with the leaf water content (**Fig. S14**).

Network structure was robust to the predator pressure. Among studied characteristics of the networks structure only modularity consistently decreased due to predation (Z = 2.143, P = 0.032, Fig. 4).

Ratio of AP to herbivore community size remained constant between control and exclosure plots (**Fig. S15**). Strength of the predators indirect effect on plants was decreasing with the ratio of AP to herbivore community size (**Fig. S16, A**). This relation vanished at the individual plant species level (**Fig. S18, B**). For individual plant species higher AP to herbivore ratio was related to weaker cascading effects on plants (**Fig. S17, S18**), i.e. the more AP relative to herbivores then indirect effect of predators on plants are coming closer to zero. Hovewer, in the above analysis we observed more positive indirect effects of predators than we would expect.

**Discussion**

In early stage of tropical forest gap regeneration top-predators weakly impacted arthropod communities. Against our expectations top-predators did not reduce herbivore nor 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. It is not unlikely that in our experiment the top-down effects on arthropod abundance could be so small as to remain undetected. We would expect the opposite since exclosure studies more likely report stronger effects of predators on small than on large scale experiments (Bommarco and Banks 2003). However, as noted previously by (Mooney et al. 2010), detrimental 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 as Malaise traps set up in primary forest in Papua New Guinea reported high flux of insects (aproximately xxx insects per day per one m2) in the canopy and understorey. In our parallel experiment we found that insects were able to re-colonize vegetation plots sprayed weekly with insecticide within days. Moreover, community sizes showed nearly perfect linear relationship with plant biomass, suggesting that assembly process in this case may be follow rules similar to the law of mass action. We expected that the lack of top-down and cascading effects reported earlier for this system might have been also due to some type of compensation within the arthropod community, whether by different trophic guilds (AP and herbivores), orders, or specialists. Some herbivores which are less vulnerable to predation (either because of smaller size or utilization of EFS), should be able to easily fill niches emptied at the cost of more vulnerable prey. However, we did not detect any significant shift in the community composition, which excludes compensatory colonization by herbivores. Moreover, we found only positive or no correlation between predator effect on AP and herbivores and no significant negative correlation between any orders within and between each guild. While this cannot be considered to be a hard evidence for a bottom-up regulation it allows at least to exclude strong competition and/or top-down control. Similar correlation patterns have been reported recently from secondary tropical forest (Mottl et al. 2020). Compensation by specialists should be evident under strong predatory pressure (Mooney et al. 2012, Singer et al. 2014, Bosc et al. 2018). In contrasts to our expectations specialists did not perform better than generalists, with an exception of Homoptera. Surprisingly this relationship was in the opposite direction than predicted (negative instead of positive). Under specific circumstances i.e. high plant quality and specialization of tropical food webs, it would be consistent with predictions of the TTI. However, in the light of the lack of general predators effect on the abundance, community composition and limited effect on arthropod biomass, the most plausible explanation is simply 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 community size with plant biomass is in concert with a previous hypothesis, stating that disturbed forest will favour insect herbivory (Morante‐Filho et al. 2016). Due to changes in vegetation a shift in bottom-up control mechanism through plant secondary metabolites to bottom-up control through plant abundance may occur, which would lead to herbivore proliferation. Interestingly in many cases we observed that removal of predators would result 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 predators can be seen in the specialization pattern of putative interaction networks between plants and herbivores. First of all except for modularity we did not detect any difference in the interaction network structure, and in case of generality and nestedness larger than expected variability in the exclosure plots. Secondly, 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. There were some signals of increased specialization and vulnerability in response to predation that would support this idea. However, possibly because of small sample size we remained undetected. This might suggest that in tropical forest gaps EFS is unlikely, as it was previously shown to be doubtful for *Ficus* species in Papua New Guinea (Novotny et al. 1999). It is puzzling why would the least specialized herbivore species (or ones that utilize broader habitat ranges) 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 a 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 this circumstances predators 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 predators showed tendency to increase diversity of the herbivore guild (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 rather expect that more versatile generalist predators would forage in such dynamically changing and unpredictable habitat. As we mentioned earlier, at least for generalist bats foraging is density independent (Wray et al. 2021). Despite the presence of the above effects in our exclosure experiment, it is unclear whether they were caused by reduction in predator activity or other compensating mechanisms unstudied here. More thorough evaluation of top predator natural history and foraging behaviour in gaps is needed. Our understanding of this system would also benefit from direct comparisons between forest interior and gap comparisons to test whether limited effect of predator effects actually result from change in forest type (Krishnadas et al. 2018). Moreover, increase in sample size would definitely improve our abilities to detect more subtle changes in herbivore communities and overcome the problem of high local variation in plant and herbivore community composition. Despite some puzzling patterns emerging form our analyses, our results confirm important role of predators in shaping specialization and size structure of arthropods in plant - herbivore interaction networks.

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. It is also worth mentioning that in our experiment the significance of this relationship vanished when we looked at individual plant species. However, general pattern of stronger effects with lower proportion of IAP to herbivores prevailed. Plausible explanations are that birds might either prefer to feed on AP, or that increased abundance of AP suppress herbivore insects. We believe that bird activity was lower in our experiment which leaves us with the second explanation, as we discussed above. 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 community sizes 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.