**Limited effects of predators on plant-herbivore interaction network in early tropical secondary forest.**

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**Abstract**

Succession in canopy gaps is an important part of tropical forest dynamics. Conditions under which natural enemies cause top-down and cascading effects in these habitats are not yet fully understood. In regenerating tropical forest, however, studies of inter-trophic level dynamics are still largely missing.

Here we present results of a replicated exclosure experiment from an early successional vegetation in lowland tropical forest gaps in Papua New Guinea. We assessed strength of the top-down effects of primary predators (birds and bats) on insect herbivores and arthropod predators (AP). Further we evaluated whether changes in community composition, individual species specialization, and shifts in body size contributed to previously observed limited cascading effect on vegetation.

Primary predators had no effect on abundance, but decreased arthropod biomass and increased herbivore diversity. There was a weak indication of intra-guild predation on AP, however, it did not contribute to releasing herbivores from predation. There was no negative correlation between the effect of primary predators on population size of any guild nor arthropod order, which suggests bottom-up or abiotic control of arthropod communities. Instead, herbivore and AP abundance and biomass correlated strongly with the plant biomass. Nevertheless, cascading effects on plant biomass were alleviated by increased proportion of AP in the community. Surprisingly generalist performed as good as specialist under predatory pressure, but we found evidence for their higher flexibility in diet choice. Utilization of enemy free space was unlikely. Surprisingly, however, modularity decreased in response to predatory pressure possibly due to extending generalist diet breadth in order to avoid predation. There was no effect on other network indices.

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 flexibile diets of generalist herbivores may have an important consequences for food-web and network stability. Further studies are needed to evaluate whether effects of primary predators are truly small or there might be some additional compensation mechanism in place.

**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 (Fischer et al., 2016; Gripenberg et al., 2014; Schnitzer and Carson, 2001). After disturbance this competitive replacement process allows light-demanding species to establish themselves in otherwise impenetrable canopy and has a long-term consequences for the forest structure and diversity. Even today competitive interactions among plants are assumed to be the key force that structures early successional vegetation structure (Velázquez and Wiegand, 2020). 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, for primary forest herbivorous insects and pathogenic fungi were shown to strongly affect community assembly process (Bagchi et al., 2014). Despite a generally stronger herbivory pressure found in regenerating tropical forest gaps (Piper et al., 2018) impact of natural enemies is assumed to be muted by acquisitive character of plant species traits (Strauss and Agrawal, 1999; Turner, 2001).

Bats, birds and ants as primary predators effectively limit abundance of tropical arthropods and respond to and reduce leaf damage (Kalka et al., 2008; Morrison and Lindell, 2012; Sam et al., 2015). However, top-down effects of key predators in tropics are found to be highly variable (Maas et al., 2016). While in tropical agro-ecosystems these seem to be strong and prevalent, univesality of top-down and cascading effects in natural plant communities is debatable (Bael et al., 2003; Harrison and Banks-Leite, 2020; Vidal and Murphy, 2018). Correlation patterns between herbivore abundance and various plant community characteristics suggest that arthropod communities in late successional forest are shaped mainly by vegetation (Mottl et al., 2020; Whitfeld et al., 2012). This bottom-up control should result in weak top-down cascades. Recently it was shown that herbivorous insects shape community composition, but predators had surprisingly weak cascading effect on vegetation in early succesional tropical forest gaps (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). It is unclear whether the same is true for the initial stages where assembly processes are more dynamic and plant natural enemies might be more relevant especially when trophic cascades are expected to be stronger on younger plants (Boege and Marquis, 2006). 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) and complex natural histories of both predators and herbivores within food-webs might be important.

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 stronger top-down effects 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 can change the size structure of their prey (Detmer et al., 2017; Rodgers et al., 2015). However, simultaneous evaluations 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 a food web structure (Daugherty et al., 2007; Pujoni et al., 2016) and the presence of intra-guild predation (IGP) is hypothesized to weaken any top-down cascading effect (Finke and Denno, 2005; Polis and Holt, 1992). 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 cascading effects (Karp and Daily, 2014). In natural arthropod communities primary predators may feed preferentially on spiders (Rogers et al., 2012), which should result in a negative correlation between herbivores and their arthropod 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 and we need more studies to evaluate its effect in diverse tropical forest. Yet studies reporting top-down and/or cascading effects on plant community composition from tropics are scarce (Bael et al., 2003; Harrison and Banks-Leite, 2020; Kurten, 2013; Letourneau et al., 2004).

Individual herbivore responses 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 (guild identity) (Duffy et al., 2007; Maas et al., 2016; Pace et al., 1999; Schmitz, 2017; Singer et al., 2014; Van Bael et al., 2008). Due to hypothesized superior physiological and behavioral adaptations specialist might be able to avoid generalist predators irrelevant of the plant quality on which they feed. This utilization of the enemy free space (EFS) by herbivores should weaken any top-down cascade (Petschenka and Agrawal, 2016; Schmitz et al., 2000). In plant-herbivore interaction networks, the presence of EFS, and its niche reducing effect on herbivorous insects can be evaluated by increase in network modularity in response to predation (Augustyn et al., 2016; Oliveira et al., 2020), whereas presence of generalists tend to reduce this measure of network clustering (Robinson and Strauss, 2020; Ximenes Pinho et al., 2017). However, EFH has not been yet confirmed to be universal for tropical predator-prey interactions (Novotny et al., 1999). In both primary and secondary tropical forests plant-herbivore interaction networks were shown to be highly specialized (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 size of generalists is predicted to be strongly reduced by their predators as predicted the tri-trophic interaction hypothesis (TTI) (Mooney et al., 2012). However, in complex communities relative strength of bottom-up vs top-down forces on herbivores seems be of a similar magnitude irrespective of their diet breadth (Vidal and Murphy, 2018). It is possible that predatory pressure can force some herbivores to shift their diet 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 will respond in reduced feeding if its own habitat domain (habitat specialization) is narrow, or it will prefer to shift habitat if its mobile and have a broad habitat domain (Schmitz et al., 2004). This flexibility in habitat choice can possibly translate into wider diet breadth as it is the case for example for predators (Stewart and Dudash, 2018).

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 previously found weak cascading effects of predator removal on plants. 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. However, we expect that these effects will not casacde 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 biomass. 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 compaensating mechanism that would prevent top-down effects of predators to cascade domwn onto plants.

**Materials and methods**

*Study sites*

The experiment was conducted in the tropical rainforest surrounding Wanang village (145°5′32″E, 5°14′26″S) located in the Wanang Conservation Area in the Ramu River basin, Madang Province, Papua New Guinea. The climate in the region is humid, with a mild dry season from July to September. Annual rainfall averages ~3500 mm and the mean annual temperature is 26°C (McAlpine, Keig, & Falls 1983). The study was conducted in abandoned food gardens created during slash-and-burn subsistence agriculture within the primary forest matrix. Old gardens can be considered a promising model system for manipulating biotic factors during succession. They are created by clearing patches of primary (and sometimes secondary) forest, usually larger than the average size of a canopy gap (Arihafa and Mack, 2013). After clearance, felled trees are burned to fertilize the soil, gardens are planted with mixed crops, and after a few harvests (typically after three years) they are abandoned and left for spontaneous forest regeneration. Old gardens have open canopies and mostly undisturbed seed banks from the surrounding forest, which is required for initiation of secondary growth. The lack of tillage and the lack of pesticide or fertilizer use during cultivation make soil properties and microbial biomass practically indistinguishable from those in naturally created forest gaps (Kukla et al., 2019). Usually the structure of regenerating forests resembles that of the nearby natural forest tree gaps (Richards, 1996), suggesting a natural course of regeneration. Besides increased nutrient availability, gardens should not differ from primary forest gaps in soil conditions and seed bank composition (Kukla et al., 2019). In particular, variation in seed rain is expected to be small among gardens enclosed within the primary forest matrix, which should allow for a natural course of regeneration (Chazdon, 2003; 2014). Abandoned food gardens in a primary rainforest matrix thus represent an excellent study system for experimentation with secondary succession, enabling a high degree of control over the initial soil and environmental conditions among replicated experimental sites.

*Experimental design*

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. To ensure unified conditions for the initial succession within each block, we cleared all aboveground vegetation and removed all the rocks and dead wood so that bare soil covered ≥95% of each plot. We also removed, without tillage, all visible stumps, and tree roots from the top 30 cm of soil to prevent re-sprouting. These preparations were expected to have little effect on the seed bank and soil conditions (Chazdon, 2014). We randomly assigned plots to control and exclosure.

Within each of the six blocks, two 5x5 m experimental plots were established, resulting in 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.

We used a transparent fishing net (1.5-2.0 cm mesh size) to protect vegetation from foraging birds and bats. Abundance of 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). The plot was additionally surrounded by a plastic fence to prevent ants from re-colonizing the plot. 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. In order to account for the possible effect of fencing in exclosure plots a 50 cm high dummy plastic fence with a 10 cm gap was build around the control plots. A control plot and exclosure plot were randomly assigned within each block according to a randomized design and regeneration was allowed to proceed undisturbed for 12 months, with the minimal maintenance within the plots. After that time, the complete above-ground vegetation from all 36 plots was destructively sampled.

In each plot, all plant species were sorted and identified to species and weighed with 1 g accuracy. During sampling all the stems with diameter at breast height (DBH) ≥1 cm were counted to evaluate woody plant abundance. 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). Herbivory, defined as a proportion of leaf area loss due to insect feeding, was obtained by comparing leaf area measured to the total estimated area for intact leaves. Leaf frame samples were then oven dried and weighed, and leaf dry matter content (LDMC g dry mass /g wet mass) was recorded.

Individual woody plants were covered with insect-net and knocked-down with insecticite (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 morphospecies. From this data we constructed putative interaction networks, summarising arthrropod individuals collected from woody plants present in each plot. This allowed us to evaluate the diets (or habitat use) of all morpho-species in our experiment. We used body length to estimate individual morpho-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 morphospecies.

*Statistical analysis*

All analysis were performed in the R statistical software (R Core Team, 2020). For individul herbivore species and for a network specialization we evaluated the normalised Paired Difference Index (PDI) based on all sites sampled during our experiment (Poisot et al., 2011) to evaluate individuial morpho-species diet breadth. Predator direct effect on arthropods and indirect effects on plant were evaluated uisng log response ratios (LRR), which was a natural logarithm of a descriptor value form control over exclosure plot within the same experimental block. We evaluated diet switching abilities of species by calculating dissmilarity (Bray-Curtis) of their diets in control vs exclosure plots. We calculated connectance, generality, nestedness and vulnerability using networklevel function in 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 charactersititcs of arthropod communities using liner 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 Quasi-Poisson distribution. For the diversity (Shannon index) we assumed normal error distribution. In case of modularity and diet shift we used beta distribution with logit link function, and random effect of block using the *glmmTMB* package (Brooks et al., 2017).

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 perfomed 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 partialled out leaving only direct effect of exclosure on arthropod community. More specifically, for we performed pRDA, with effects of the exclosure and site partialled 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 partialled 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 6524 individuals (~100.005 g of dry mass) from seven dominant orders belonging to herbivorous (Coleoptera, Hemiptera, Homoptera, Lepidoptera, Orthoptera) and AP (Aranea, Mantodea) guild, from 753.5 kg of plant biomass and approximate 633.2 m2 of foliage. The most abundant orders belonged to Coleoptera (**Fig S15**) but Orthoptera had generally the highest biomass (**Fig S16**). Dominance structure: based on biomass and base on abundance (**Fig S13** and **Fig. S14**).

Predators decreased biomass and increased diversity of herbivores, but the latter effect was marginally significant (P = 0.052). Abundance and richness were not affected (**Fig.1**). We found no effect of predators on AP community. Additionally, no difference in descriptors was found for any order (**Fig S2**). We found that abundance of arthropods was strongly correlated with plant biomass and that exclosures did not significantly modify this relationship for any arthropod order **(Fig. S1)**.Species size distribution of Orthoptera and Araneae shifted towards larger species in the exclosure (**Fig. S3**). Size shift, however was not consistent between plant species nor sites (**Tab. S1**). i.e. arthropod orders did not respond consistently thorough plant species or sites. We found significant correlation between LRR of herbivores and AP, and marginally significant correlation between LRR of plants and herbivores (**Fig. 2**). However, when we performed regression analysis independently at the group level the latter relationship became significant. The order identity did not modify this relationships. Correspondingly, we found positive correlation between LRR for each AP order and herbivores. Qualitatively similar patterns were found for LRR based on arthropod biomass (**Fig. S4**) with an exception of Mantodea, where the significance vanished in the order level analysis. In pairwise comparisons we only found significant positive, or no correlation of the predator effects (LRR) between Aranea, Orthoptera, Hemiptera and Coleoptera (**Fig. 3**). There was no negative correlation between AP and herbivore population size (**Fig. S6**). Pattern of abundance and biomass correlation between all groups changed qualitatively between control and exclosure plots i.e. exclosure did not result in negative correlation.

There was no independent (controlled for the treatment and site) effect of the plant community variability (any of the PCA axes for plant community composition) nor AP community descriptors (biomass, abundance, richness, diversity) on herbivore community composition (**Tab. ???**). Abundance-based AP community was independently influenced by total herbivore abundance and the biomass-based community composition was not independently influenced by herbivore community nor plant composition. Partial RDA showed no effect of predators on herbivore nor AP community composition (both biomass- and abundance-based). However, we found high proportion of unconditioned as well as conditioned (site variation) variance (**Tab. X**). Based on pRDA coordinates both biomass and abundance of Coleoptera and Hemiptera were more often positively, and Lepidoptera negatively affected by top predators (**Fig. S8**). However, there was no general difference in LRR of individual species for any order (**Fig. S9**). In case of AP Mantodea abundance and biomass was negatively affected and the latter effect was marginally significant.

Only in case of Homoptera more specialized species showed an increasingly negative response to predators (**Fig. NS3**). Otherwise, specialization had no effect on the species’ performance and this lack of correlation prevailed across studied plant species. Among studied network descriptors only modularity decreased as a response to predator pressure (Z = 2.143, P = 0.032, **Fig. 4**). Species from Coleoptera, Orthoptera and Lepidoptera that 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, than those that stayed (**Figure XXX\_specialization and colonization).T**here was no interaction between specialization and predator effect for any herbivore group on any plant (**Fig. S10**). We also found that in case of Orthoptera and Homoptera larger species experienced weaker top-down effects **(Fig. S11)**. There was no consistent shift in diet (change in PDI values) in response to predation for any studied herbivore group (**Fig. S12**). Individually, however, species with higher diet breadth were also more willing to shift their diet (**Fig. NS5**). […] I also present correlations between descriptors Fig. S12 […].

Higher AP to herbivore ratio was related to lower cascading effects on plants (**Fig. S7**), i.e. the more AP relative to herbivores more LRR values of plants are near zero. However this relationship vanished at the individual species level.

**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 whenever strong effects on birds are present the abundance of both herbivores and AP is reduced 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 truly small and remain undetected due to a low sample size. We would, however, expect that the opposite is true as small scale experiments usually report stronger effects of predators (Bommarco and Banks, 2003). 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. Under strong predatory pressure constant influx of indivduals would require equal colonization success for all arthropod group and for the vertebrate predator effects to be density independent. Whether the second condition has previously been reported for bats (Wray et al., n.d.) equal colonization success seem to be less likely (Steyn et al., 2016) which suggest that the effect of predators are at most weak. We expected that the lack of top-down and cascading effects reported earlier for this system might be 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 either because of smaller size or utilization of EFS are less vulnerable to predation, 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 LRR of AP and herbivores and never significantly negative either between herbivores and AP nor 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 corrleation patterns have been reprorted recently from secondary tropical forest (Mottl et al., 2020). Compensation by specialists should be evident under strong predatry pressure (Bosc et al., 2018; Mooney et al., 2012; Singer et al., 2014) In contrasts to our expectations specialists did not perform better than generalists, with an exception of Homoptera. 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 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 a strong support for predators induced change in diet that would allow generalists to avoid predation. Again this general lack of a strong predator avoidance behaviour is indicative of a weak predatory pressure (Belgrad and Griffen, 2016). Instead of showing significant response to exclosure arthropods (both herbivorous and predaceous) tracked changes in plant biomass, although with variable strength. At least for Orthoptera, Hemiptera and Coleoptera this is suggestive of a bottom-up control by plant biomass (Welti et al., 2020). Strong positive correlation of arthropod abundance and biomass with plant biomass is in concert with a previous hypothesis, stating that disturbed forest will favour insect herbivory. Due to changes in vegetation a shift in bottom-up control mechanism through plant secondary metabolites to bottom-up controll through plant abundance may occur, which would lead to herbivore proliferation (Morante‐Filho et al., 2016). 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). It is worth noting that we also found similar community composition in our experiment with a dominant role of Coleoptera, Hemiptera, Lepidoptera, and Orthoptera. This lack of effect was attributed to deterioration of insectivore community near the forest edge. Similar reduced foraging might be true for forest gaps as these may pose barriers for some birds (Robertson and Radford, 2009). In conclusion, during early succession of tropical forest gaps the effects of birds, bats and ants 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 redution, and size shifts towards larger species of Orthoptera and Aranea. 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 and Orthoptera, possibly released from primary predator pressure. Under abundance limit enforced by an available 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 exclosures can bee seen in the specialization pattern of putative interaciton networks between plants and herbivores. 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 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 least specialize herbivores (or ones that utilize broader habitat ranges) increase in abundance in the presence of predators. It is possible that by decreasing abundance 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 mainly caused by increased colonization of exclosure plots by species having narrow diet breadth in exclosures as was shown in case of our experiments. This phenomenon would not be captured in our LRR and PDI analysis where we were only able to compare species that were present in both control and exclosure plots. This is possible because we unexpectedly also found that predators **increased diversity** of the herbivore guild (effect was marginally significant). Thus, our result confirm important role of predators in shaping herbivore diversity (Zhang et al., 2018) and is in accordance with predicted weaker top down effects diverse communities (Maas et al., 2016). However, it is difficult to explain this observation. Diversity maintanance throught density-dependent action of predators would require high specialization of predatory herbivores in forest gaps, which is unlikely. We would rather expect that more versatile generalist predators would forage in such dynamically changing and unpredictable habitat. However, as we mentioned earlier, at least for generalist bats foraging is density independent (Wray et al., n.d.). 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 meachanisms unstudied here. More thorough evaluation of top predator natural history and foraging behavior 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 truly result from a change in forest structure. 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.

Interestingly, despite no evident intraguild predation higher ratio of IAPs to herbivores still tranlated onto weaker cascading effects on plants. This supports predictions of food web theory that effects of vertebrate insectivores on herbivores and plants should attenuate trophic cascades in the presence of AP (Daugherty et al., 2007; Holt and Polis, 1997). In opposition to the established general patten (Mooney et al., 2010) we did not find negative cascading effects, and in our case lower AP/herbivore ratio resulted in strong positive cascading effects, which resulted in negative slope of AP/herbivore ration vs LRR of plants. Plausible explanations are that birds might either prefer to feed on IAP, or that increased abundance of IAP reduce herbivore insects. We believe that bird activity was lower in our experiment which leaves us with the second explanation, as we disccuss above. However, direct LRR of IAPs were positively correlated with those of herbivores (for both abundance and biomass) which suggest that IAPs and herbivores are both positively affected by their resources. 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. Other explanation might be related to additional detrital energy channels. In early successional gaps detrital communities might be an imortant component of a food web as predicted by the apparent trophic cascade hypothesis (Liu et al., 2016; Ward et al., 2015). With rising productivity top predators should 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 (Murphy et al., 2020; Perkins et al., 2018; Wise et al., 1999). 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.

Besides general caveats of any exclosure experiment (Maas et al., 2016) there are other possible mechanisms that could affected strength of top-down and cascading effect in our study. These were explored in more detail in *Supplementary discussion* in the Appendix.

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