



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

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Abstract:	Conventional wisdom points to plant competition as the key driving force of initial secondary succession. However, the relative roles of plants racing for resources versus top-down control of vegetation by herbivores, in turn impacted by predators, remain poorly understood. Here we examine the impact of birds, bats and ants on ecological succession using replicated experimental exclusion of these focal predators from 5 x 5 m plots from early successional vegetation in lowland tropical forest gaps in Papua New Guinea to assess the strength of their top-down effects on insect herbivores and arthropod predators. Focal predators had no effect on abundance of herbivores or arthropod predators, but they decreased biomass and density of both groups. They

	<p>also did not impact species richness of either herbivores or arthropod predators. There was no negative correlation between the strength and direction of the focal predators effect on individual arthropod orders within or between trophic levels that would indicate competition among herbivores or arthropod predators, or intra-guild predation by focal predators. Instead, herbivore and arthropod predator abundance and biomass correlated strongly with the plant biomass. There was no difference in response to the focal predators exclusion between generalist and specialist herbivores. Birds, bats and ants had no effect on the structure of plant-herbivore interaction network characterized by connectance, generality, vulnerability, nestedness and specialization. Only the network modularity increased in response to the predator exclusion.</p> <p>In summary, our results suggest that in early successional forest gaps the overall effects of insectivorous birds, bats, ants, and intermediate arthropod predators (spiders and insects) on arthropod herbivores are weak and that herbivores are mainly bottom-up controlled by plants.</p>

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

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11    **Abstract**

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33

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

## 36 Introduction

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

52       Insectivorous birds, bats and ants can effectively limit the abundance of tropical  
53 arthropods (Kalka et al. 2008, Morrison and Lindell 2012, Sam et al. 2015, Wills et al. 2019).  
54 However, top-down effects of focal predators in tropics can be highly variable (Maas et al.  
55 2016). While in tropical agro-ecosystems top-down and cascading effects seem to be strong,  
56 prevalent, and predictable, this may not always be the case in natural plant communities (Bael et  
57 al. 2003, Vidal and Murphy 2018, Harrison and Banks-Leite 2020). Positive correlations  
58 between herbivore abundance and food quality (e.g. foliar nitrogen) and availability (e.g. leaf  
59 biomass) suggest that arthropod communities in late successional forests are shaped mainly by  
60 vegetation (Whitfeld et al. 2012, Mottl et al. 2020). This bottom-up control should in turn result

in weakened top-down cascades. This observation seems to be consistent with some theoretical expectations e.g., that higher productivity would result in stronger bottom-up control of herbivores by vegetation (Kagata and Ohgushi 2006, Mooney et al. 2010). However, we have recently shown that in early successional tropical forest gaps herbivorous insects do shape plant community composition, but focal predators had surprisingly weak cascading effect on vegetation (Szefer et al. 2020). In fact, the strength of top-down control of plants by herbivores was found to be highly site specific (Jia et al. 2018) and the complex natural histories of predators and herbivores within food-webs might be important in modulating plant responses.

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

The strength of a top-down trophic cascade depends on food web structure (Daugherty et al. 2007, Pujoni et al. 2016). Specifically intra-guild predation (IGP) is hypothesized to weaken any top-down cascading effect (Polis and Holt 1992, Finke and Denno 2005). A significant role of arthropod predators in tropical food webs can be seen from a recent comparative analysis that showed up to 82 times higher diversity of arthropod predators in the tropics than in temperate zones (Privet and Petillon 2018). However, at least in tropical mono-cultures, IGP by birds and bats seems to impact arthropod predators with its effects cascading onto plants (Karp and Daily 2014). In natural arthropod communities vertebrate, predators may feed preferentially on spiders (Rogers et al. 2012). This can produce a negative correlation between herbivores and their arthropod predators (Bosc et al. 2018). However, top-down effects of focal predators on

intermediate arthropod predators and herbivores can be also positively correlated (Mooney et al. 2010). Therefore, specific circumstances under which IGP attenuates or amplifies top-down effects on herbivores remain unclear, particularly in diverse tropical forests where studies reporting top-down and/or cascading effects on plant community composition are scarce (Bael et al. 2003, Letourneau et al. 2004, Kurten 2013, Harrison and Banks-Leite 2020).

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

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

abundance (Calcagno et al. 2011, Schmitz 2017). Moreover, in species-rich plant communities generalist herbivores should be more flexible in their diet choice (Pfisterer et al. 2003).

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

**Materials and methods**

*Study sites and experimental design*

The experiment was conducted in the primary tropical rainforest surrounding Wanang village (145°5'32"E, 5°14'26"S) located in the Wanang Conservation Area, Papua New Guinea. The study was conducted in abandoned food gardens created during slash-and-burn subsistence agriculture. Old gardens create an artificial canopy gap usually larger than the average size of gaps created naturally (Arihafa and Mack 2013). This study is a part of a larger experiment focused on evaluating the role of biotic factors in secondary forest succession and we discussed the advantages of using abandoned gardens for studying secondary successional in our previous paper (Szefer et al. 2020). Within a radius of 3 km from the village, we selected six experimental gardens (blocks) 3-5 years old, each covering an area of approximately 400 m<sup>2</sup>, separated by a minimal distance of 200 m. At each garden we initiated regeneration by clearing all aboveground vegetation. We removed (without tillage) all the rocks, dead wood, and visible tree stumps and roots from the top 30 cm of soil to obtain approximately 95% bare soil coverage of each plot. These procedures were aimed to standardize, as far as possible, the initial conditions for succession. Specifically, to prevent re-sprouting while at the same time minimizing any



disturbance of the seed bank and soil conditions (Chazdon 2014). For this study, two 5x5 m experimental plots were established within six blocks (12 experimental plots in total). Individual plots were separated by at least 1 m distance. We cleared 3 m wide margins around each (approximately rectangular) block to minimize any effects of the surrounding forest edge on micro-climatic conditions within the plots.

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

Regeneration was allowed to proceed undisturbed for 12 months. After that time, all above-ground vegetation from all plots was destructively sampled. In each plot, all woody plant species equal or above one cm DBH were sorted and identified to species and their leaves and stems were weighed separately with 1 g accuracy. Leaf area was calculated by randomly sampling leaves from the pool of all leaves for each species at a given plot until 50x50 cm area ("leaf frame") was filled. The frame was then photographed and processed using ImageJ software, measuring the area of individual leaves (Schneider et al. 2012). Leaf frame samples

were then oven dried and weighed. The SLA (in  $\text{cm}^2/\text{g}$ ) was calculated as a ratio of leaf area to its dry mass. The difference between wet and dry mass of the leaves was used to calculate their water content. We used SLA and water content as an approximation of leaf quality for herbivores (Cornelissen et al. 2003, Barbier and Loreau 2019).

Before harvesting, individual plants were covered with insect-net and all arthropods were sampled using knock-down insecticide (MORTEIN®, active ingredients: allethrin [2.09 g/kg] and resmethrin [0.39 g/kg]). The arthropods were preserved in 70% ethanol and assigned to trophic guilds (herbivore or arthropod predator), Orders, and morpho-species (further referred to as species). We constructed putative interaction networks, based on the presence of these arthropods on individual plants in each plot. This allowed us to evaluate the diets (or habitat use) of all species in our experiment. We measured the body length of up to 20 individuals per arthropod species and used it to estimate individual species biomass (dry weight) with the help of biomass equations ((Ganihar 1997) for Homoptera and (Wardhaugh 2013) for other orders). Coleoptera and Heteroptera were considered herbivores since predatory species were almost absent from our samples. Arthropod density was calculated as the number of individuals per square meter of the leaf area, estimated for woody plant individuals by multiplying their leaf weight (in g) and SLA values (in  $\text{cm}^2/\text{g}$ ).

*Statistical analyses*

All analyses were performed in R statistical software (version 3.6.1; R Core Team 2019). Code for the analyses is available on github: <https://bit.ly/3diklxx>. Diet breadth was measured by the normalized Paired Differences Index (PDI; Poisot et al. 2011). The focal predators' direct effect on arthropods and indirect effects on plants were evaluated using log-response ratios (LRR), which was calculated as a natural logarithm of a ratio of some focal descriptor value evaluated at the control and the exclosure plot within the same experimental block. Diet shifts of

herbivorous arthropod species were estimated by calculating Bray-Curtis dissimilarity index of their food plant composition (inferred from the plants they were collected from) in control vs predator exclosure plots. The plant-herbivore interaction network in each plot was characterized by connectance, generality, nestedness, and vulnerability calculated using the *bipartite* R package (Dormann et al. 2008). Modularity for each network was evaluated using DIRTLPAbw+ algorithm (Beckett 2016). The distribution of interactions was measured by the evenness of the degree distribution of plants.

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

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

## Results

We collected 5955 arthropod individuals ( $\sim 73.8$  g of dry mass) from the six control and six exclosure plots (total 300 m<sup>2</sup> area), sampled from 753.5 kg of plant biomass and approximate 633.2 m<sup>2</sup> of foliage. We found 417 species from seven dominant orders of herbivorous (305 species) and AP (112 species) guilds. Coleoptera was the most abundant order but Orthoptera had the highest biomass. Aranea, Orthoptera and Coleoptera had the highest species richness (Fig. S1).

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

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

We found a marginally significant ( $T = 2.407$ ,  $P = 0.074$ ) positive correlation between the indirect effect of predators on plant and their direct effect on herbivore abundance (Fig. 2A). A similar pattern was found for direct effects on herbivores and AP (Fig. 2B). The former

relationship gained significance when we analyzed individual insect orders (Fig. 2C). The effect of predators on individual herbivore orders was also positively correlated with the effects on intermediate predatory taxa: spiders and mantids (Fig. 2D). Qualitatively similar patterns were found for arthropod biomass (Fig. S8) with the exception of Mantodea, where the significance vanished in the Order-level analysis. The control and the exclosure plots showed no or positive pair-wise correlations of abundance and biomass between individual arthropod orders across the six study blocks (Fig. S9). Focal predators impacted individual herbivore and AP orders similarly so that the pairwise correlations of the predator effects (LRR) between Aranea, Orthoptera, Heteroptera, and Coleoptera were all positive and significant (Fig. S10).

In the pRDA analysis the effect of focal predators did not change the community composition of herbivore and AP communities (permutation test:  $F = 0.775$ ,  $P = 0.519$ , Fig. S11).

On five common plant species, the host specificity of herbivores was not correlated with the effect of predators on their abundance (Fig. S12). When examining common herbivore species across all their hosts, there was also no relationship between host specialization and the effect of predators except in Homoptera, where more specialized species showed an increasingly negative response to the predators. Herbivore species present in both control and exclosure plots were on average less specialized than the species present in only one of the plots in three out of five herbivore orders (Fig S13A). There was no consistent change in the diet breadth in response to predation within any herbivore order (Fig. S14). Individually, however, species with higher diet breadth were more willing to shift their diet (Fig. S15).

There was no interaction between specialization and plant quality in predicting individual herbivore species responses to predation (Fig. S16). However, the magnitude of these responses was positively correlated with the leaf water content used as a proxy for the leaf quality, so that

the abundance of herbivores decreased after the exclusion of predators more on the plant species with high water content leaves (Fig. S17).

Plant – herbivore network structure was robust to the impact of focal predators. There was no response to their exclusion in connectance, generality, nestedness, and PDI specialization of the network. Only modularity increased ( $Z = 2.143$ ,  $P = 0.032$ , Fig. 3) and vulnerability marginally significantly decreased ( $T = -1.791$ ,  $P = 0.073$ ) in the exclosure plots. Evenness of the plant degree distribution did not respond to the exclosure (Fig. S18).

The AP:herbivore abundance ratio remained constant between control and exclosure plots (Fig. S19). Strength of indirect effect of predators on plants decreased with an increasing ratio of AP to herbivore abundance (Fig. S20). This relationship was not observed for arthropod communities on individual plant species (Fig. S21).

## Discussion

In the early stage of tropical forest gap regeneration birds and bats and ants weakly impacted the arthropod communities. For arthropod – predator systems it has previously been shown that strong bird predation pressure reduces the abundance of both herbivores and APs simultaneously (Mooney et al. 2010). This is not the case here. At the same time, exclosure studies on small scales are more likely to report stronger effects of predators than large-scale experiments (Bommarco and Banks 2003). However, as noted by Mooney et al. (2010), a negative effect of predators on their prey abundance can be compensated by a continuous influx of allochthonous herbivores from surrounding primary forest matrix. This is plausible with respect to the intense insect traffic in the rainforest. For instance, Malaise traps set up in the primary forest understory at the Wanang study site for one year collected ~88 individuals flying through one m<sup>2</sup> area per 24 hours (~ 3500 individuals daily crossing the side area of our plot approximated by a cuboid with average 2 m height throughout the one-year period; Ratnasingham and Hebert 2007). In our

parallel experiment we found that insects were able to rapidly (within a few days) re-colonize vegetation plots sprayed weekly with a broad-spectrum insecticide. Moreover, the number of arthropods showed nearly perfect linear relationship with plant biomass, suggesting that the community assembly process may be driven by vegetation.

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

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

309           Considering generalist predators had little effect on abundance and community  
310 composition, and a limited effect on arthropod biomass and density, the most plausible  
311 explanation is low predatory pressure in forest gaps (Tvardíková 2010, Tvardikova and Novotny  
312 2012). Moreover, focal predators did not induce any change in herbivore diets which could be a  
313 mechanism allowing generalists to escape predation. Again, this general lack of strong predator  
314 avoidance behaviour could be indicative of weak predatory pressure (Belgrad and Griffen 2016).  
315 Both herbivorous and predacious arthropods tracked changes in plant biomass instead of  
316 showing a significant response to exclosure. At least for Orthoptera, Heteroptera, and Coleoptera  
317 this close correlation (relatively high  $R^2$  values) is suggestive of bottom-up control by plant  
318 biomass (Welti et al. 2020). Strong positive correlation of arthropod abundance with plant  
319 biomass conforms to the general characterization of pioneer plants as poorly defended and thus  
320 vulnerable to herbivory (Morante-Filho et al. 2016).

321           Overall higher SLA values (lower density of the leaf tissue per unit area) were correlated  
322 with lower leaf damage which could be a sign of plant compensation for herbivory (Schuldt et al.  
323 2017). However, SLA and herbivory damage of individual plant species was not affected by  
324 focal predator removal and we could not confirm that plants were actively responding to  
325 increased herbivory pressure with increasing producing larger and thinner leaves (Reese et al.  
326 2016).

327           Our results found limited top-down effect of focal predator removal on arthropod  
328 abundance and no indirect effect on plants in the forest edge, corroborating the findings of a  
329 recent study from tropical forest in Brazil (Harrison and Banks-Leite 2020). Their study  
330 attributed lack of predator effect to deterioration of vertebrate insectivore community. Notably,  
331 we found that our arthropod herbivore community composition was similar to their study, with  
332 Coleoptera, Heteroptera, Lepidoptera, and Orthoptera dominating the community. Similar  
333 reduced foraging by insectivores might be true for forest gaps as these may simply be avoided by



some birds (Robertson and Radford 2009). In conclusion, our results suggest that during early succession of tropical forest gaps the effects of birds and bats are limited and herbivores and AP respond mainly to changes in vegetation quantity.

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

Markedly, we did not detect any effect of bird, bat and ant exclusion on the interaction network structure, except for changes in modularity and vulnerability (average number of herbivores per plant species). Against our expectations, modularity and vulnerability decreased in the presence of focal predators with no effect on specialization, generality, connectance, or nestedness. Increased clustering (modularity) and reduced vulnerability of the networks suggests that in tropical forest gaps extensive EFS is unlikely, as was previously shown for *Ficus* species in Papua New Guinea (Novotny et al. 1999). It is puzzling why the least specialized herbivore species would increase in abundance in the presence of predators. It is possible that generalist herbivores – by decreasing their density through utilization of broader host plant range – are able to avoid density dependent predation (Abdala-Roberts et al. 2019). This could be supported by our findings that generalists were more flexible in their diet choice. Thus, similar to a recent study by Robinson and Strauss (2020), diet modification by generalists, and not changes in community composition, generates a community response to biotic and abiotic factors and is responsible for network stability. However, this pattern in modularity might also be caused by

359 increased colonization of exclosure plots by species having narrow diet breadth as in our  
360 experiments. Under these circumstances predator effect (LRR) on herbivores could remain  
361 independent of specialization as we can only calculate LRR for species that are present in both  
362 control and exclosure plots. This might be plausible since, unexpectedly, the presence of focal  
363 predators was associated with increased diversity of herbivores (the effect was marginally  
364 significant). However, we found no difference in the abundance of species that were lost or  
365 gained in plots with predators.

366         Our results also confirm the important role of insectivorous birds and bats in shaping  
367 herbivore diversity (Zhang et al. 2018) and are in accordance with predicted weaker top-down  
368 effects in diverse communities (Maas et al. 2016). We would expect that versatile generalist  
369 predators would forage in such dynamically changing and unpredictable habitat and focus their  
370 predation efforts on prey form their diet range that is most abundant at the time (Terraube et al.  
371 2011). However, at least for generalist insectivorous bats, foraging appears to be density  
372 independent (Wray et al. 2021). Our understanding of this system would benefit from direct  
373 comparisons between forest interior and gaps to test whether the limited effects of predators are  
374 impacted by forest type (Krishnadas et al. 2018). Increased sample size would also improve our  
375 ability to detect more subtle changes in herbivore communities and overcome the problem of  
376 high local variation in plant and herbivore community composition during initial secondary  
377 succession.

378         Interestingly, despite no evident intraguild predation, the higher AP:herbivore abundance  
379 ratio translated onto weaker cascading effects on plants. This supports a prediction of food web  
380 theory suggesting that the effects of focal predators on herbivores and plants should attenuate  
381 trophic cascades in the presence of AP (Holt and Polis 1997, Daugherty et al. 2007). In our  
382 study, lower relative abundance of APs were coupled with positive and negative strong  
383 cascading effects of predators on plants. However, there was no clear positive correlation as we

would expect from the literature (Mooney et al. 2010). Plausible explanations are that birds and bats might either prefer to feed on AP, or that increased abundance of AP suppress herbivore insects. However, direct effects of predators on AP were positively correlated with those of herbivores (for both abundance and biomass) which suggest that AP and herbivores are both positively affected by their resources. Compensation for herbivore damage by plants might be important in explaining strong positive responses of plant community to predation. Higher biomass of herbivores, causing significantly more damage to plants, would trigger compensatory plant growth at the community level. Larger bodied arthropod herbivores can also induce this type of response. Despite overall presence of plant compensation in our experiment exclosure did not increase damage and woody plant SLA. Other explanation of the observed patterns could be related to additional energy channels for intermediate AP (mostly spiders) as predicted by the apparent trophic cascade hypothesis (Ward et al. 2015, Liu et al. 2016). With rising productivity, intermediate AP may derive significant fraction of their diet not from herbivores but from an increasingly productive bottom-up controlled detrital channels. Spiders are known to cause top-down and cascading effects on detritivores and decomposition rates (Perkins et al. 2018). These additional subsidies might increase the abundance of AP even when they still under control by their predators or by inter-guild competition and territoriality (Welti et al. 2020). Nevertheless, there is still a need for more systematic studies of tropical systems involving epigeic and soil herbivores and detritivore communities.

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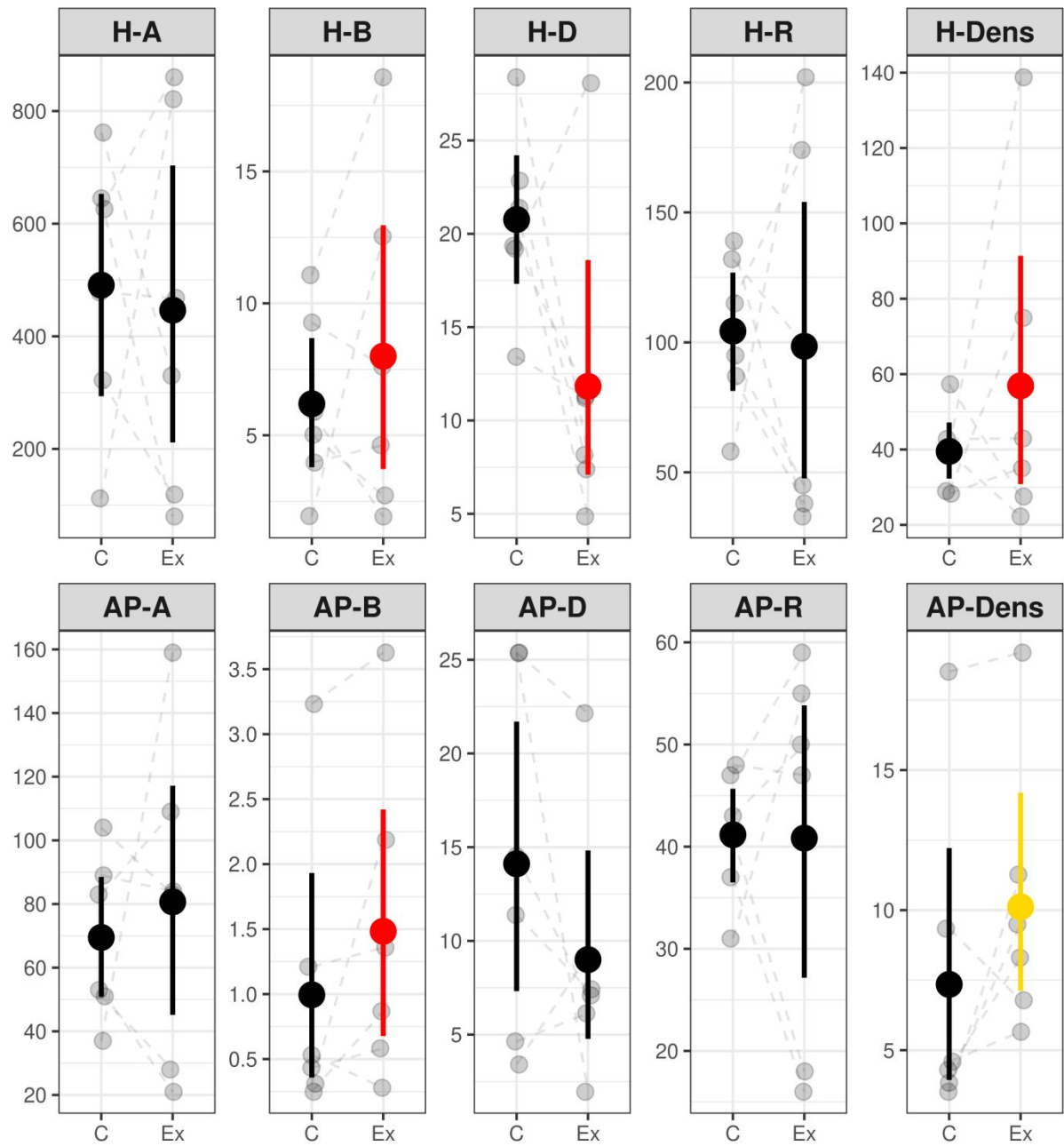
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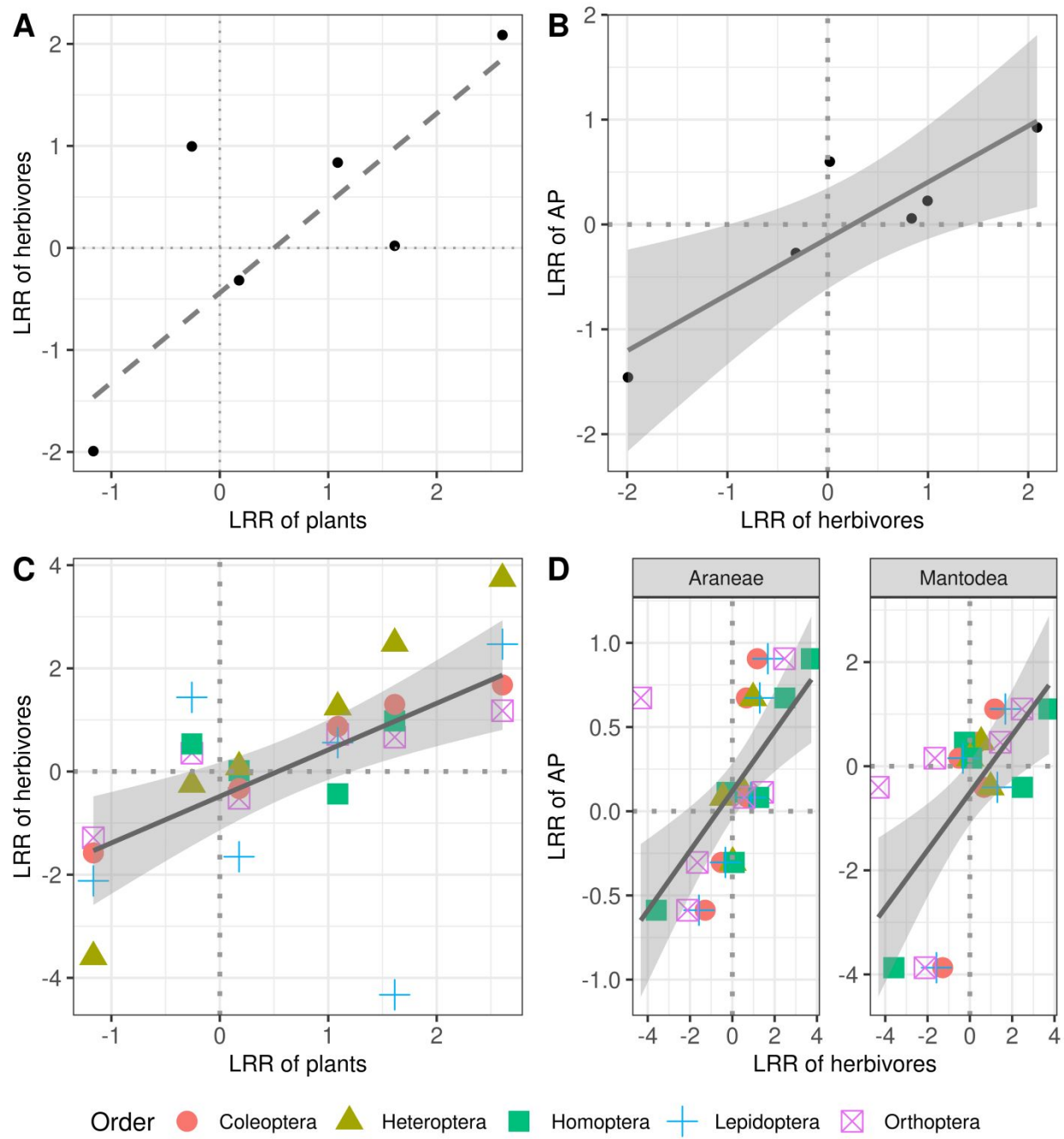
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**Figure 1.** Mean (points) and 95% bootstrapped CIs (whiskers) of the invertebrate herbivores (H) and arthropod predator (AP) community indices (A – no. of individuals, B – biomass in grams, D – inverse Simpson diversity, R – number of species, Dens – density [individuals/m<sup>2</sup> of the leaf area]) in the control (C) and enclosure (Ex) plots. Grey points indicate empirical values for six experimental blocks, and dashed lines connect plots within blocks. Red color indicates significance at the  $\alpha = 0.05$ , and yellow at the  $\alpha = 0.1$ .

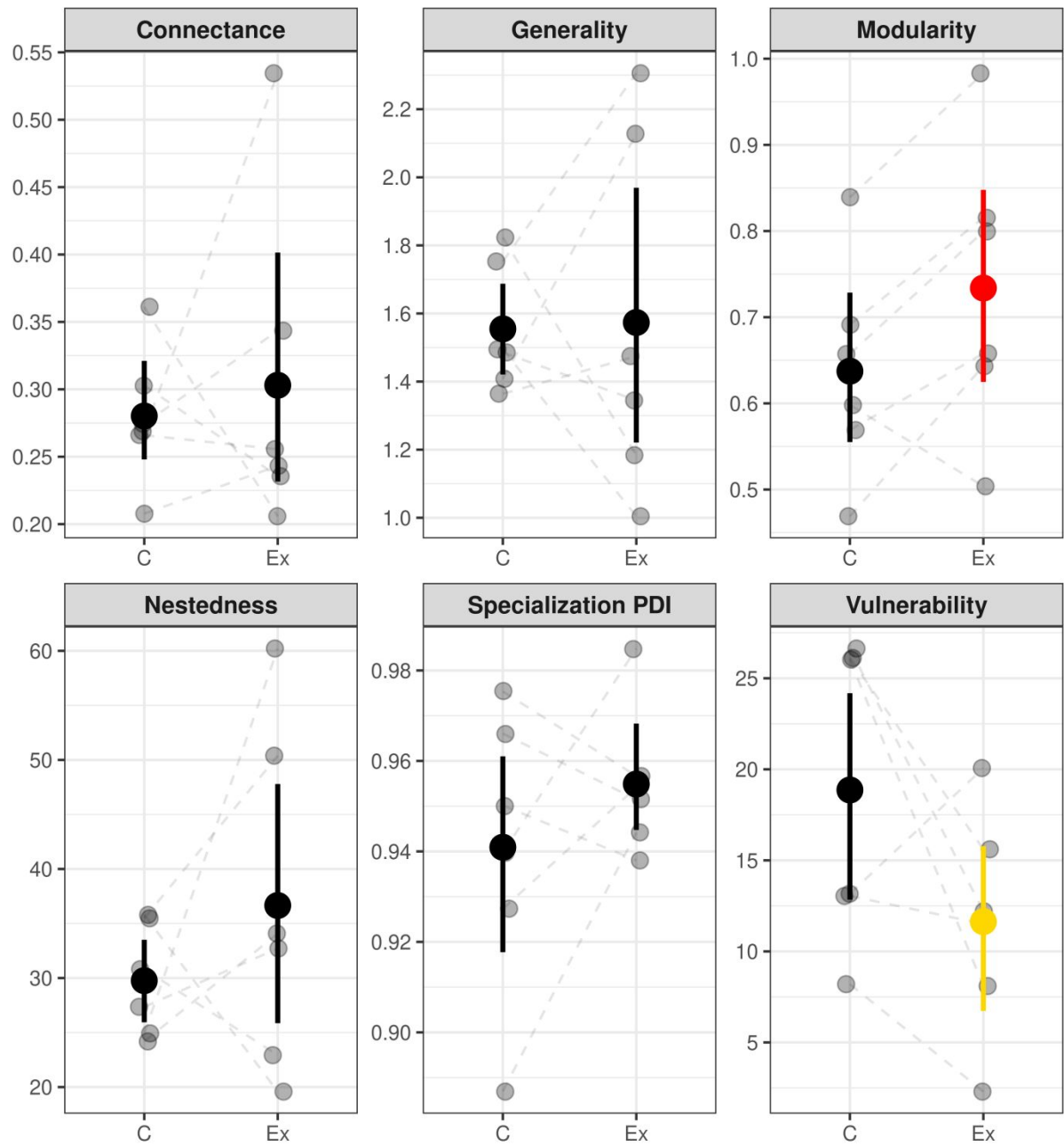
**Figure 2.** Relationships of predator (birds, bats and ants) effects on biomass between different trophic levels in individual plots: A – herbivores vs plants; B – herbivores vs arthropod predators (AP); C) herbivore orders vs plants, and D) AP divided into orders vs herbivores. Predator effects were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

**Figure 3.** Plant-herbivore network descriptors in control (C) and enclosure (Ex) plots. Mean (points) and 95% bootstrapped CIs (whiskers) are plotted. Grey dots represent empirical data. Dashed lines connect control and predator enclosure treatment plots within the same experimental block. Significance ( $\alpha = 0.05$ ) is indicated with the red colour.





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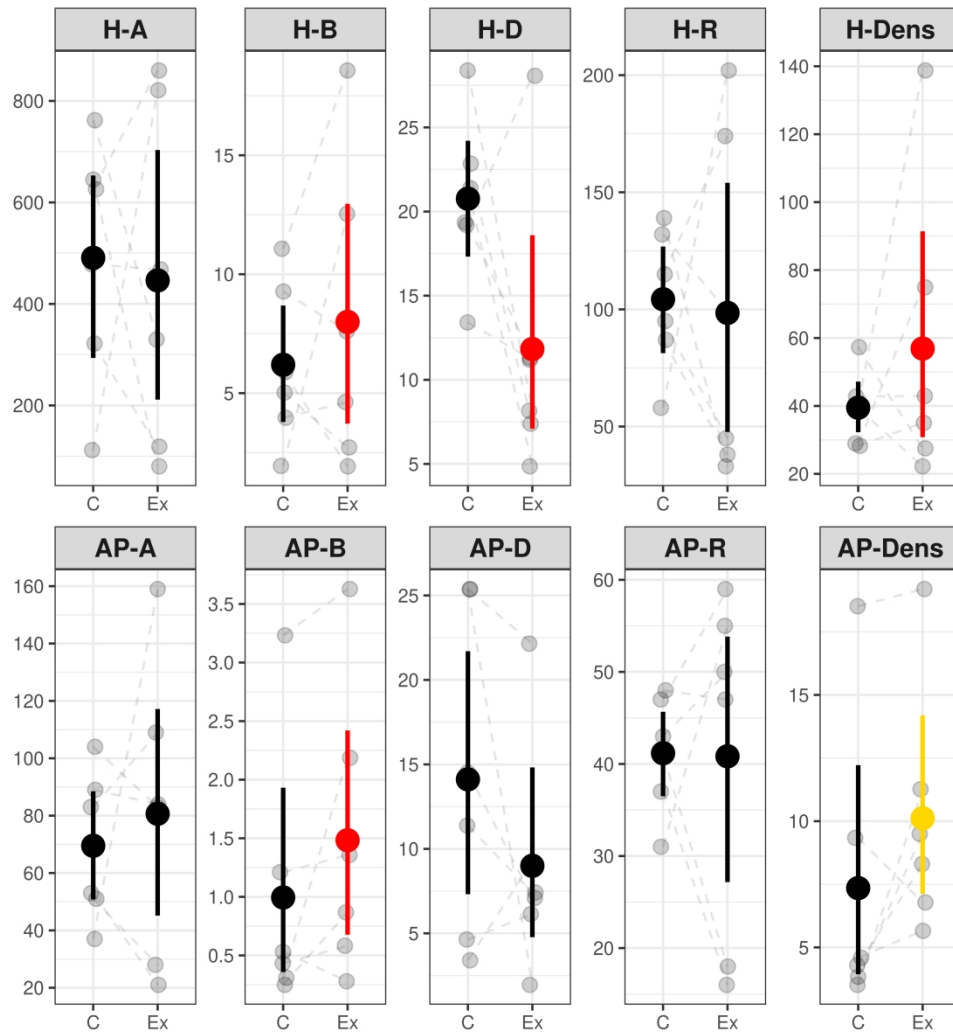


Figure 1. Mean and 95% bootstrapped CIs of the invertebrate herbivores (H) and arthropod predator (AP) community indices (A – no. of individuals, B – biomass in grams, D – inverse Simpson diversity, R – number of species, Dens – density [individuals/m<sup>2</sup> of the leaf area]) in the control (C) and exclusion (Ex) plots. Grey points indicate empirical values for six experimental blocks, and dashed lines connect plots within blocks. Red color indicates significance at the  $\alpha = 0.05$ , and yellow at the  $\alpha = 0.1$ .

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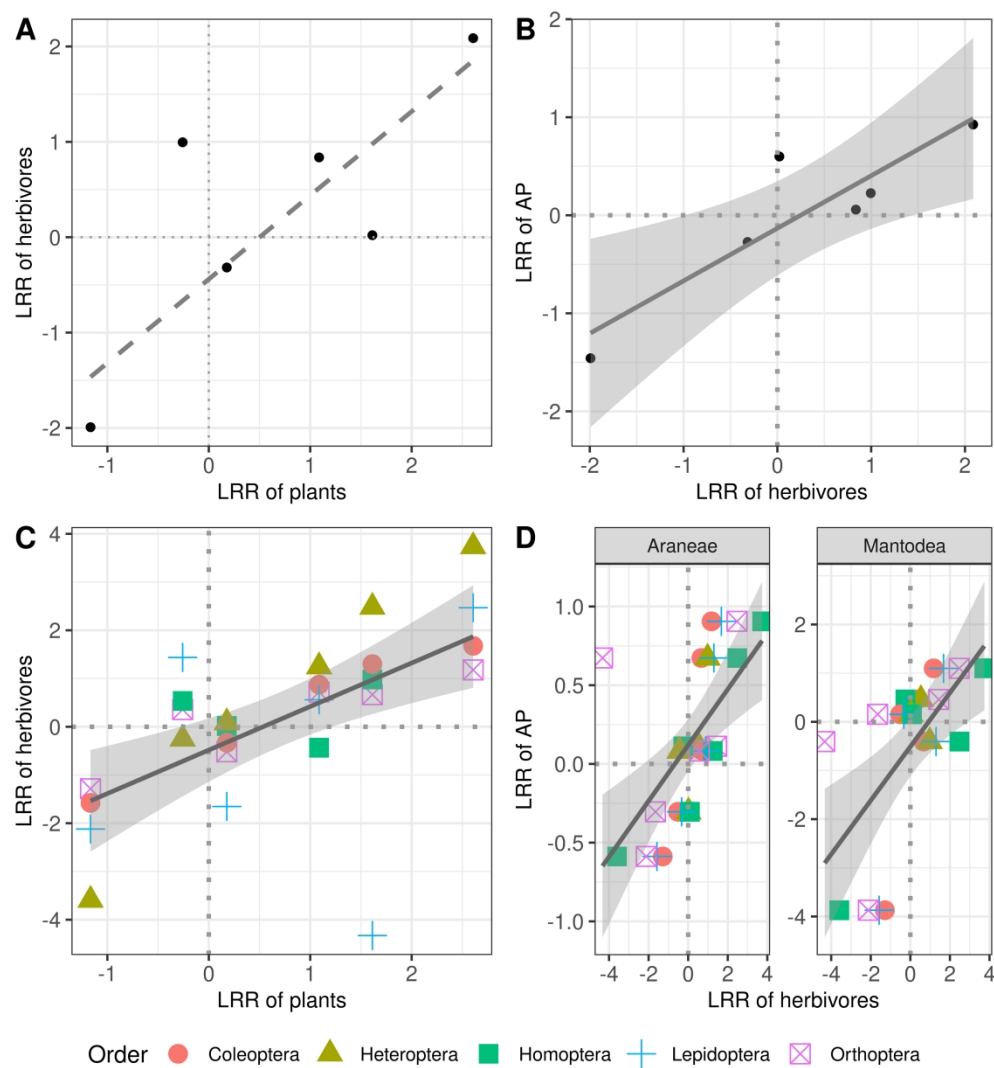


Figure 2. Relationships for predator effects on biomass (LRR – log response ratio) between different trophic levels in individual plots: A – herbivores vs plants; B – herbivores vs arthropod predators (AP); C) herbivore orders vs plants, and D) AP divided into orders vs herbivores. Solid line represents significance at the  $\alpha = 0.05$  level and dashed line at the  $\alpha = 0.1$  level. 95% CIs also plotted for significant relationships.

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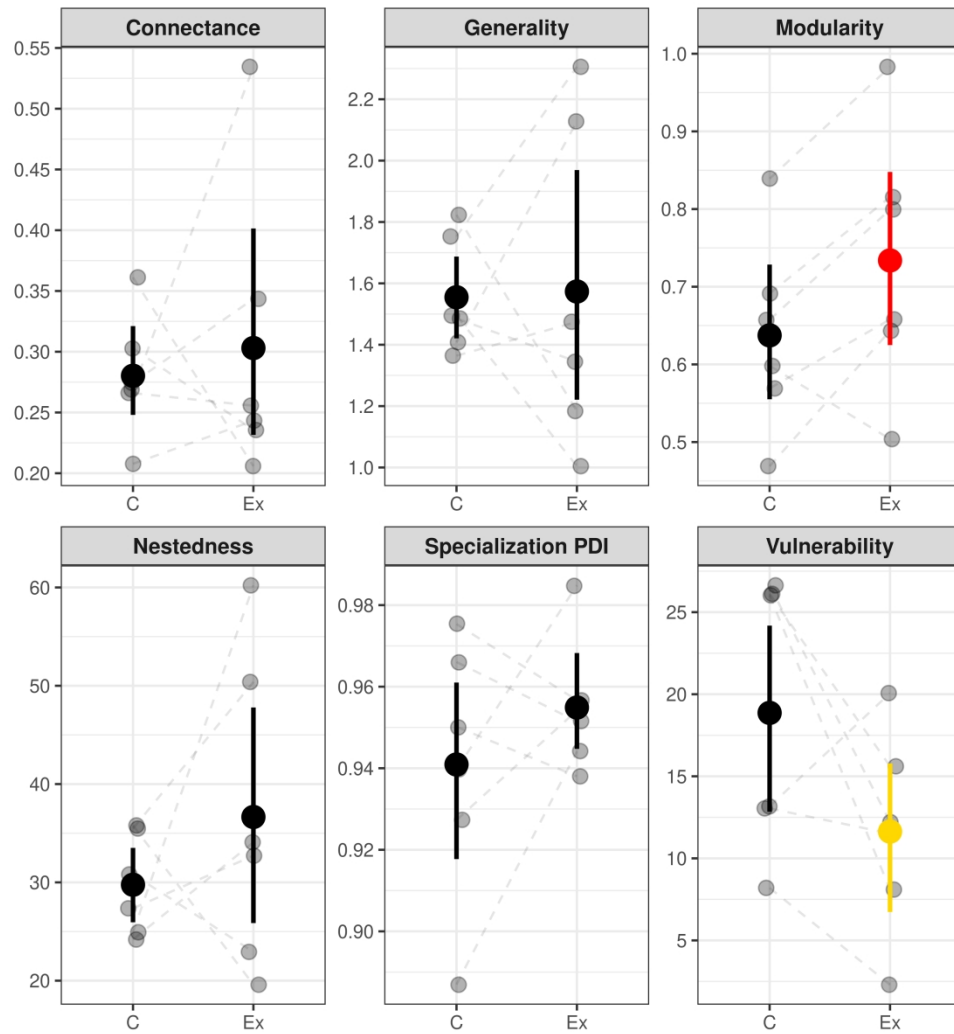
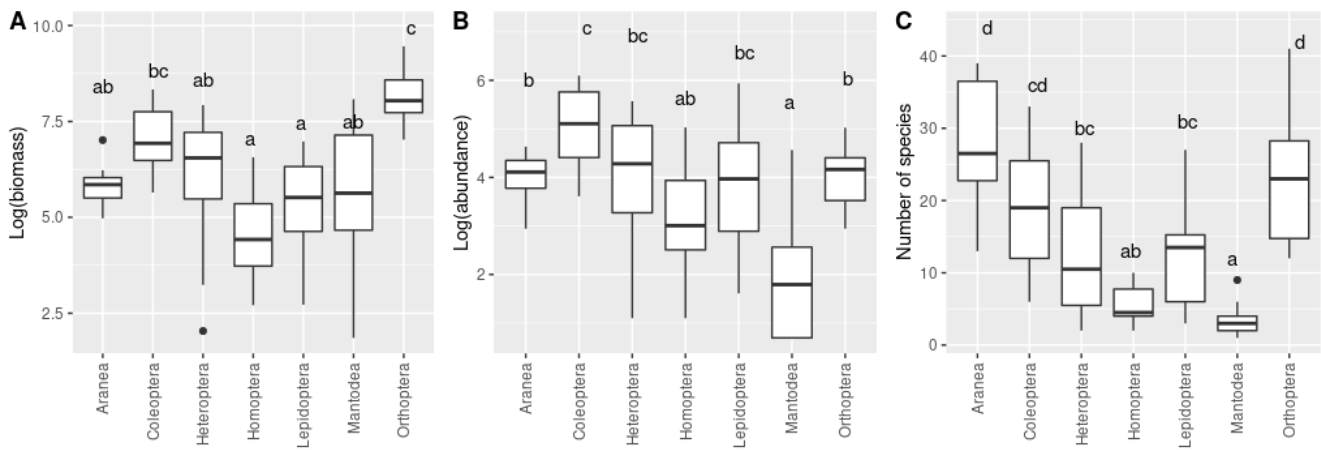


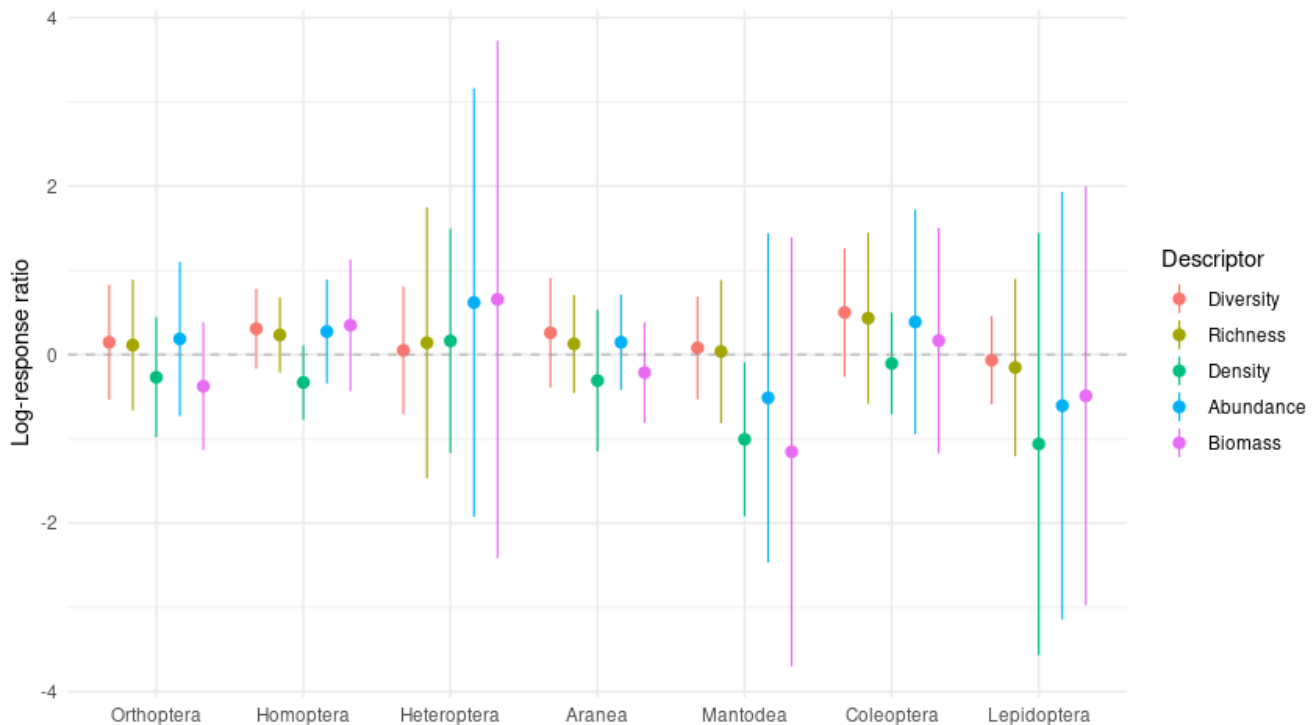
Figure 3. Plant-herbivore network descriptors in control (C) and exclusion (Ex) plots. Mean (points) and 95% bootstrapped CIs (whiskers) are plotted. Grey dots represent empirical data. Dashed lines connect control and predator exclusion treatment plots within the same experimental block. Significance ( $\alpha = 0.05$ ) is indicated with the red color.

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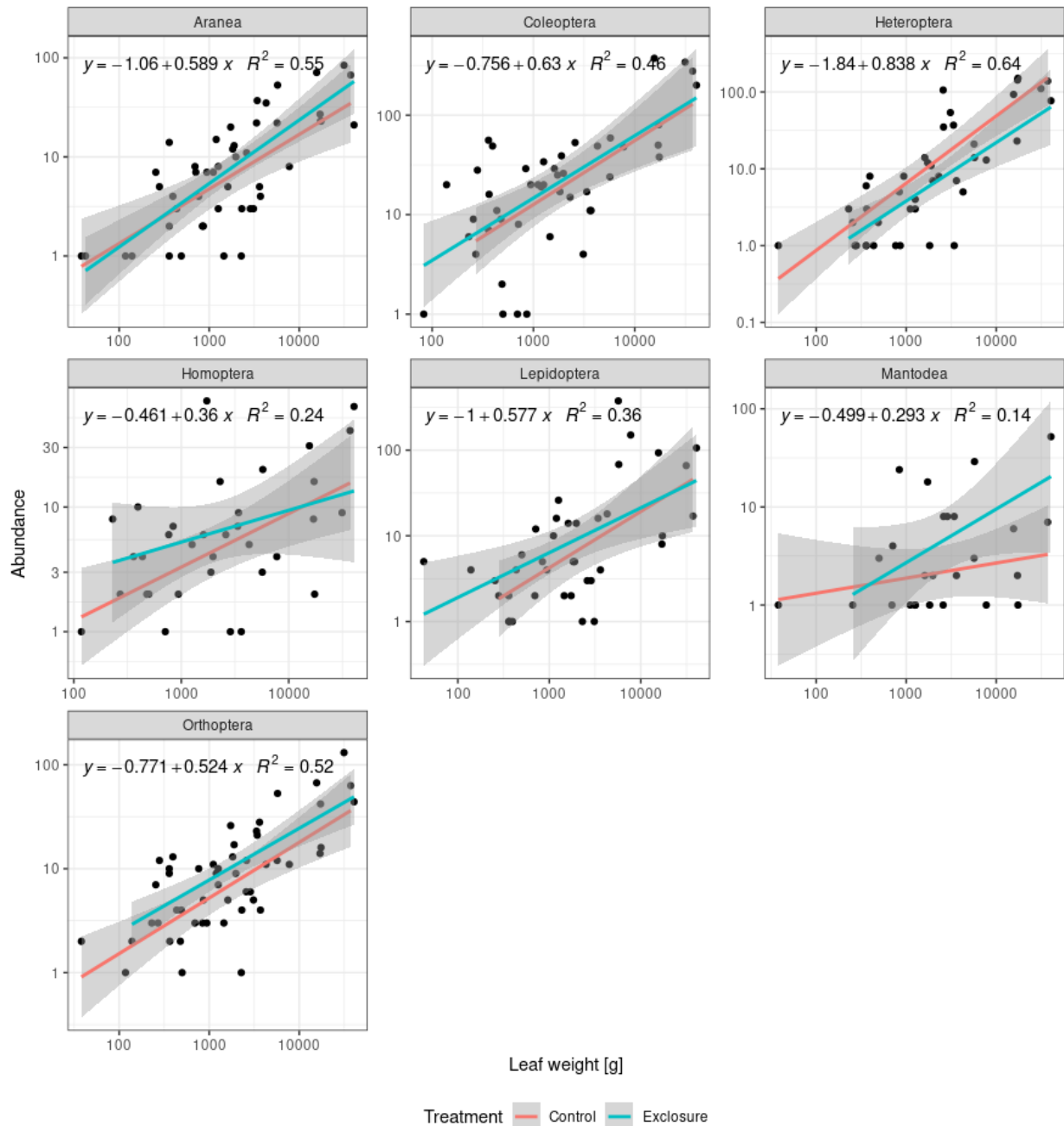


**Figure S1.** Characteristics of arthropod orders collected in exclosures and control plots: biomass (A), abundance (B), and number of species (C). Different Latin letters indicate groups for which differences in mean values were statistically significant at the  $\alpha = 0.05$  level (pairwise comparisons with the Tukey's correction for multiplicity).

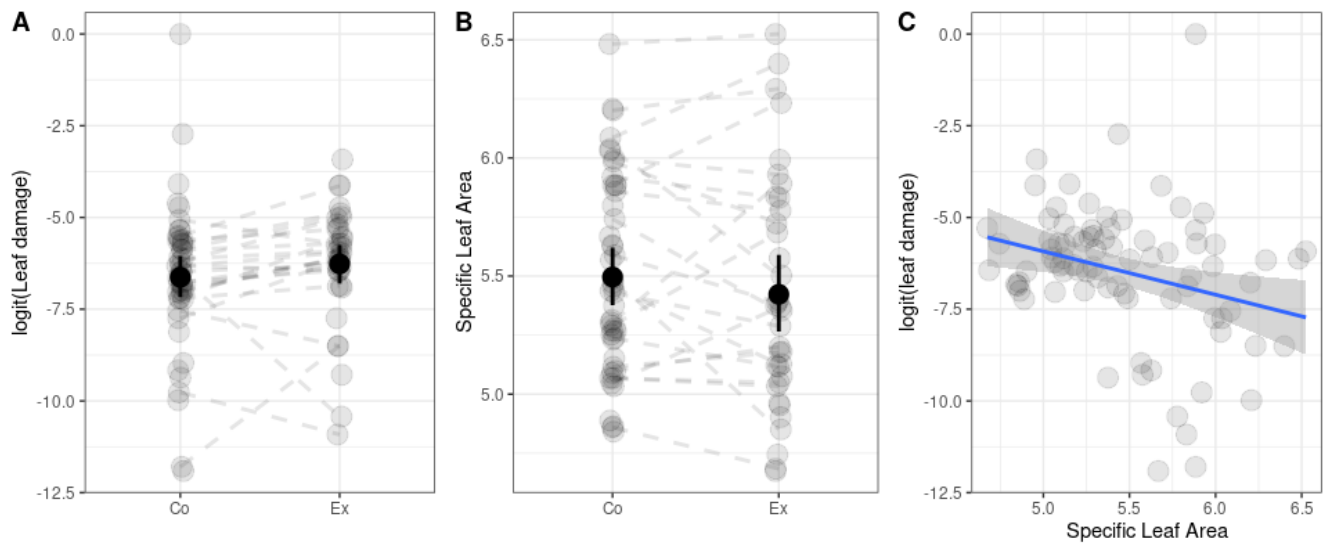


**Figure S2.** Predator effects on various community descriptors for individual insect orders. Predator effect were measured using the log-response ratio (LRR), which is a natural logarithm of a ratio of descriptor value from the control to the exclosure within a given experimental block.

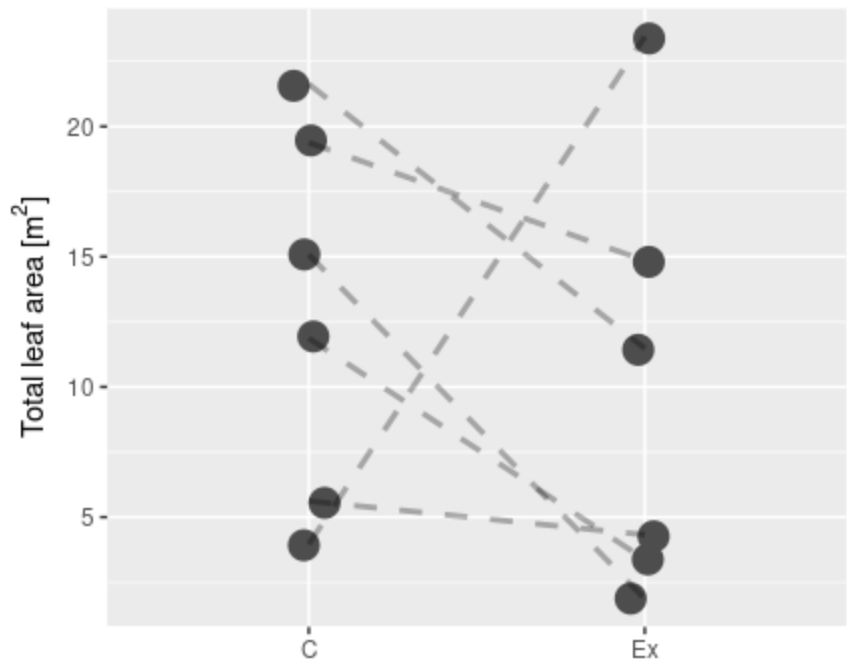
Negative/zero/positive value of the LRR indicate negative/no/positive effect of predators on a given descriptor. Mean and 95% bootstrapped confidence intervals for the log-response ratios are presented. No predator effect was different from zero (dashed line) for any descriptor within any arthropod Order. Diversity was measured with the inverse Simpson index, and density as a number of arthropod individuals per one square meter of foliage.



**Figure S3.** Linear relationship between leaf weight and the abundance of studied arthropod orders in exclosure (blue line) and control (red line) plots. Black points represent individual plant species from experimental plots. Vertical and horizontal axis are in logarithmic scales. For each Order presented r-square values and equations are for the the overall regression model because there was no significant interaction between the treatments.

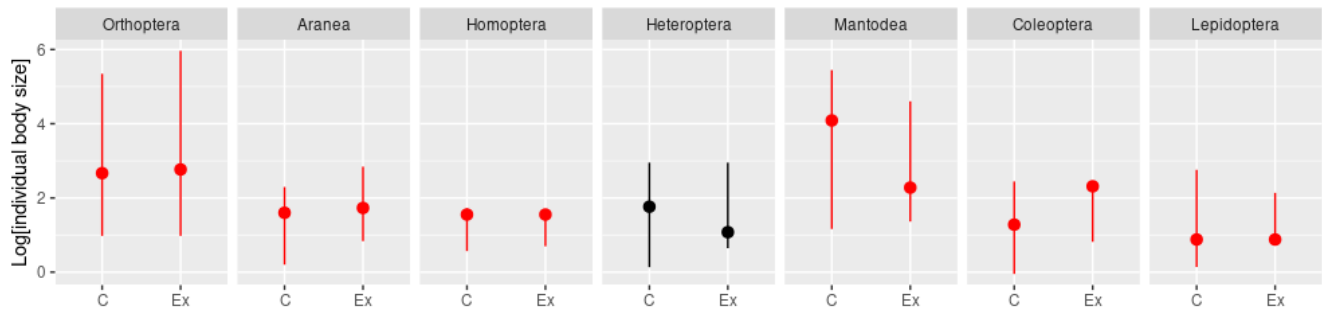


**Figure S4.** Comparison of (A) leaf damage and (B) specific leaf area between woody plant individuals from control (Co) and predator exclusion (Ex) plots, and correlation (C) between specific leaf area and the leaf damage. Leaf damage was measured as a logit percentage of leaf area lost due to herbivore feeding. Specific leaf area was evaluated as area of a leaf per one gram of its mass. Black points and whiskers on panels (A) and (B) represent mean values and 95% CIs respectively. Grey points represent individual plant species at each experimental block. Dashed lines (if present) connect plant species within the same block but at different treatment plots. Solid line on the panel (C) indicates significant correlation ( $T = -2.475$ ,  $P = 0.015$ ) evaluated using a linear mixed-effect model with plant species and block as random effects. Details of the statistical models can be found in Tables S1 and S2.



**Figure S5.** Total leaf area (in m<sup>2</sup>) of all woody plants in control (C) and predator exclusion plots (Ex). Points indicate total area for individual experimental plots. Lines connect values from different treatments within an experimental block. Linear mixed effect models with a random effect of block showed no difference in the total area between control and predator exclusion plots.





**Figure S6.** Distribution of body length (in cm) of individual arthropods in control (C) and enclosure plots (Ex). Dots represent log-transformed median values, whiskers 5th and 95th percentiles of studied insect Orders in control (C) and enclosure (Ex) plots. Red color indicates significant differences of the medians between the treatments evaluated using the non-parametric Mann-Whitney test.

**Table S1.** Specifications of all statistical models used in our analyses of 12 experimental (six control and six predator exclosure) plots grouped in six blocks. Explanations of indices and links to individual figures in the text and supplement are given in the *Description* column. The *Response* column indicates the distribution and parameters used by a model. The *Variance* column shows formula used to calculate variance of a descriptor, and linear predictors are defined in the *Mean* column. Random structure, if used, is defined in the last column.

Model	Description	Response	Variance	Mean	Random structure
<b>Arthropod community characteristics</b>					
M.1	Fig. 1, H-A, AP-A. Abundance of herbivores or arthropod predators in control and exclosure plots modeled as the negative binomial distribution.	$Abu \sim NB(\mu, k)$	$var(Abu) = \mu + \frac{\mu^2}{k} = \mu + \alpha \times \mu^2$	$\log(\mu) \sim \alpha + \beta \times Exclosure$	-
M.2	Fig. 1, H-B, AP-B. Biomass of herbivores or arthropod predators in control and exclosure plots within an <i>i</i> -th block.	$Bio_i \sim N(\mu_i, \sigma_{residual}^2)$	$var(Bio_i) = \sigma_{residual}^2$	$\log(\mu_{ij}) \sim \alpha + \beta \times Exclosure + Block_i$	$Block_i \sim N(0, \sigma_{block}^2)$
M.3	Fig. 1, H-R, AP-R. Number of species of herbivores or AP in control and exclosure plots modeled with the Poisson	$Rich \sim Poisson(\mu)$	$var(Rich) = \theta \mu$	$\log(\mu) \sim \alpha + \beta \times Exclosure$	-

	distribution.				
M.4	Fig. 1, H-D, AP-D. Diversity (inverse Simpson's index) of herbivores or AP in control and exclosure plots.	$Diversity \sim N(\mu, \sigma_{residual}^2)$	$var(Diversity) = \sigma_{residual}^2$	$\mu \sim \alpha + \beta \times Exclosure$	-
M.5	Fig. 1, H-Dens, AP-Dens. Density of herbivores or AP in control and exclosure plots within at $i$ -th block .	$Dens_i \sim N(\mu_i, \sigma_{residual}^2)$	$var(Dens_i) = \sigma_{residual}^2$	$\log(\mu_i) \sim \alpha + \beta \times Exclosure + Block_i$	$Block_i \sim N(0, \sigma_{block}^2)$
<b>Network descriptors</b>					
M6	Fig. 4. Connectance modeled using the Beta distribution.	$Conn \sim Beta(\pi)$	$var(Conn) = \frac{\pi \times (1 - \pi)}{1 + \theta}$	$logit(\pi) \sim \alpha + \beta \times Exclosure$	-
M.6	Fig. 4. Generality modeled using the truncated normal distribution.	$Gen \sim TN(\mu, \sigma^2, 0)$	$var(Gen) = \sigma_{residual}^2 \left[ 1 - \delta \left( \frac{a - \mu}{\sigma_{residual}} \right) \right]$ $\delta(\alpha) = \lambda(\alpha) [\lambda(\alpha) - \alpha]$ $\lambda(\alpha) = \phi(\alpha) / [1 - \phi(\alpha)]$	$\mu \sim \alpha + \beta \times Exclosure$	-
M.7	Fig. 4. Modularity modelled using the Beta distribution. $Mod_i$ indicates value of modularity at the $i$ -th block.	$Mod_i \sim Beta(\pi_i)$	$var(Mod_i) = \frac{\pi_i \times (1 - \pi_i)}{1 + \theta}$	$logit(\pi_i) \sim \alpha + \beta \times Exclosure + Block_i$	$Block_i \sim N(0, \sigma_{block}^2)$
M.8	Fig. 4. Nestedness	$Nestedness \sim N(\mu, \sigma_{residual}^2)$	$var(Nestedness) = \sigma_{residual}^2$	$\mu \sim \alpha + \beta \times Exclosure$	-
M.9	Fig. 4. Specialization modelled	$PDI_i \sim Beta(\pi_i)$	$var(PDI_{ij}) = \frac{\pi_{ij} \times (1 - \pi_{ij})}{1 + \theta}$	$logit(\pi_i) \sim \alpha + \beta \times Exclosure + Block_i$	$Block_i \sim N(0, \sigma_{block}^2)$

	using the Beta distribution. $PDI_i$ indicates value of specialization (paired difference index) at the $i$ -th block.				
M.10	Fig. 4. Vulnerability, modeled with the truncated binomial distribution.	$Vul \sim TN(\mu, \sigma_{residual}^2   0)$	$var(Vul) = \sigma_{residual}^2 \left[ 1 - \delta \left( \frac{a - \mu}{\sigma_{residual}} \right) \right]$ $\delta(x) = \lambda(\alpha) [\lambda(\alpha) - \alpha]$ $\lambda(\alpha) = \phi(\alpha) / [1 - \phi(\alpha)]$	$\mu \sim \alpha + \beta \times Enclosure$	-
Supplementary analyses					
MS.1	Fig. S1A. Biomass of an $j$ -th arthropod Order at $i$ -th block	$Bio_{ij} \sim N(\mu_{ij}, \sigma^2)$	$var(Bio_{ij}) = \sigma^2$	$\log(\mu_{ij}) \sim \alpha + \beta \times Order_j + Block_i$	$Block_i \sim N(0, \sigma_{block}^2)$
MS.2	Fig. S1B,C. Abundance and richness modeled using the negative binomial distribution. $X_{ij}$ is a descriptor value of an $j$ -th arthropod Order at $i$ -th block	$X_{ij} \sim NB(\mu_{ij}, k)$	$var(X_{ij}) = \mu_{ij} + \frac{\mu_{ij}^2}{k} = \mu_{ij} + \alpha \times \mu_{ij}^2$	$\log(\mu_{ij}) \sim \alpha + \beta \times Order_j + Block_i$	$Block_i \sim N(0, \sigma_{block}^2)$
MS.3	Fig. S12. Log-response ratio (logged ratio of control to enclosure value) of community descriptors for individual arthropod orders	$LRR \sim N(\mu, \sigma^2)$	$var(LRR) = \sigma^2$	$\mu \sim 0$	-
MS.4	Fig. S3. Plant biomass and	$\log(Abund_{ij}) \sim N(\mu_{ij}, \sigma^2)$	$var[\log(Abund_{ij})] = \sigma^2$	$\mu_{ij} \sim \alpha + \beta \times \log(LeafWeight_{ij})$	-

	herbivores abundance relationship. Abund <sub>ij</sub> indicates abundance of <i>i</i> -th plant species at the <i>j</i> -th plot				
MS.5.1	Fig. S4 A,C. Leaf damage at different treatments: <i>j</i> -th observation on <i>k</i> -th plant.	$\text{logit}(\text{Damage}_{jk}) \sim N(\mu_{ij}, \sigma^2)$	$\text{var}[\text{logit}(\text{Damage}_{jk})] = \sigma^2$	$\log(\mu_{jk}) \sim \alpha + \beta \times \text{SLA}_{jk} + \text{Plant}_k$	$\text{Plant}_k \sim N(0, \sigma_{\text{plant}}^2)$
MS.5.2	Fig. S4B. SLA values at control and exclosure plots. SLA <sub>ij</sub> indicates observation for the <i>i</i> -th block and <i>j</i> -th plant.	$\text{SLA}_{ij} \sim N(\mu_{ij}, \sigma^2)$	$\text{var}(\text{SLA}_{ij}) = \sigma^2$	$\mu_{ij} \sim \alpha + \beta \times \text{Exclosure} + \text{Block}_i + \text{Plant}_j$	$\text{Block}_i \sim N(0, \sigma_{\text{block}}^2)$ $\text{Plant}_j \sim N(0, \sigma_{\text{plant}}^2)$
MS.6	Fig S5. Leaf area (in m <sup>2</sup> ) for <i>i</i> -th block.	$\text{Area}_i \sim N(\mu_i, \sigma^2)$	$\text{var}(\text{Area}_i) = \sigma^2$	$\mu_i \sim \alpha + \beta \times \text{Exclosure} + \text{Block}_i$	$\text{Block}_i \sim N(0, \sigma_{\text{block}}^2)$
MS.7	Fig. S7. Herbivore species performance (measured as log-ratio of the abundance from the control to the predator exclosure plots) in relation to body size. LRR <sub>ij</sub> indicate <i>i</i> -th order and <i>j</i> -th herbivore species.	$\text{LRR}_{ij} \sim N(\mu_{ij}, \sigma^2)$	$\text{var}(\text{LRR}_{ij}) = \sigma^2$	$\mu_{ij} \sim \alpha + \beta_1 \times \log(\text{Length}_{ij}) + \beta_2 \times \text{Order}_j + \beta_3 \times \log(\text{Length}_{ij}) \times \text{Order}_j$	-
MS.8	Fig. S11. Response variable is	$\text{LRR}_{ij} \sim N(\mu_{ij}, \sigma^2)$	$\text{var}(\text{LRR}_{ij}) = \sigma^2$	A) $\mu_{ij} \sim \alpha + \beta \times \text{PDI}_{ij} + \beta_2 \times \text{Tree}_j$	$\text{Block}_i \sim N(0, \sigma_{\text{block}}^2)$

	weighted by cumulative abundance of each species.			$+\beta_3\times PDI_{ij}\times Tree_j+Block_i$ $B) \mu_{ij}\sim \alpha\beta\times PDI_{ij}+\beta_2\times Order_j$ $+\beta_3\times PDI_{ij}\times Order_j+Block_i$	
MS.9	Fig S12A. Specialization modeled with the Beta distribution. $PDI_{ijk}$ indicates specialization value from the $i$ -th group, $j$ -th order, and $k$ -th block	$PDI_{ijk}\sim Beta(\pi_{ijk})$	$var(PDI_{ijk})=\frac{\pi_{ij}\times(1-\pi_{ij})}{1+\theta}$	$logit(\pi_{ijk})\sim \alpha+\beta_1Group_i+\beta_2\times Order_j$ $+\beta_3\times Order_j\times Group_i+Block_k$	$Block_k\sim N(0,\sigma_{block}^2)$
MS.10	Figure S12B. Abundance modeled with the negative binomial distribution. $Abu_{ijk}$ indicates abundance of the $i$ -th group, $j$ -th order, and $k$ -th block	$Abu_{ijk}\sim NB(\mu,k)$	$var(Abu_{ijk})=\mu+\frac{\mu^2}{k}=\mu+\alpha\times\mu^2$	$\log(\mu_{ijk})\sim \alpha+\beta_1Group_i+\beta_2\times Order_j$ $+\beta_3\times Order_j\times Group_i+Block_k$	$Block_k\sim N(0,\sigma_{block}^2)$
MS.11	Figure S13. Testing whether log response ratios (log-ratio of the specialization from the control to the predator exclosure plots) are different from zero. $lrrPDI_i$ indicate log-respons ratio of specialization at $i$ -th block.	$lrrPDI_i\sim N(\mu_i,\sigma^2)$	$var(lrrPDI_i)=\sigma^2$	$\mu_i\sim 0+\beta\times Exclosure+Block_i$	$Block_i\sim N(0,\sigma_{block}^2)$

MS.12	Fig. 14. Case-weighted (ln[herbivore species abundance]) beta regression of diet shift dependence on specialization of $j$ -th herbivore species at $i$ -th block.	$BCdiss_{ij} \sim \text{Beta}(\pi_{ij})$	$\text{var}(BCdiss_{ij}) = \frac{\pi_{ij} \times (1 - \pi_{ij})}{1 + \theta}$	$\text{logit}(\pi_{ij}) \sim PDI_j + \text{Block}_i$	$\text{Block}_i \sim N(0, \sigma_{block}^2)$
MS.13	Figure S15. Mean LRR value for $k$ -th quality category, $j$ -th herbivore species at $i$ -th block.	$LRR_{ijk} \sim N(\mu_{ijk}, \sigma^2)$	$\text{var}(LRR_{ijk}) = \sigma^2$	$\mu_{ijk} \sim \alpha + \beta_1 \times \text{Quality}_k + \beta_2 \times PDI_{jk} + \beta_3 \times \text{Quality}_k \times PDI_{jk} + \text{Block}_i$	$\text{Block}_i \sim N(0, \sigma_{block}^2)$
MS.14	<b>Figure S16.</b> Water content effect on LRR of $j$ -th herbivore on $k$ -th plant at $i$ -th block. Model selection that showed lack of interaction with herbivore Orders	$LRR_{ijk} \sim N(\mu_{ijk}, \sigma^2)$	$\text{var}(LRR_{ijk}) = \sigma^2$	$\mu_{ijk} \sim \alpha + \beta \times \text{WaterContent}_{jk} + \text{Block}_i$	$\text{Block}_i \sim N(0, \sigma_{block}^2)$
MS.15	<b>Figure S17:</b> Evenness of the degree distribution at $i$ -th experimental block.  <b>Figure S18:</b> Trophic community composition at $i$ -th experimental block.	$X_i \sim \text{Beta}(\pi_i)$	$\text{var}(X_i) = \frac{\pi_i \times (1 - \pi_i)}{1 + \theta}$	$\text{logit}(\pi_i) \sim \alpha + \beta \times \text{Exclosure} + \text{Block}_i$	$\text{Block}_i \sim N(0, \sigma_{block}^2)$

	<p><b>Figure S19:</b> Trophic community composition (ratio of AP to herbivores) and distribution of interactions (evenness of plant degree distribution) in response to exclosure at <i>i</i>-th experimental block.</p>				
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**Table S2.** Estimates, standard errors, test statistics, and p-values for the parameter of selected statistical models defined for our experimental data of 12 experimental plots (six control and six predator exclosure plots) grouped within six blocks. Model names refer to the model equations in the Table S.1.

<i>Model</i>	<i>Parameter</i>	<i>Estimate</i>	<i>Std. Error</i>	<i>Statistic</i>	<i>P-value</i>
M1. H-A	$\alpha$	6.196	0.278	T = 22.294	<0.001
	$\beta$	-0.095	0.393	T = -0.242	0.809
	k	2.1673	0.832		
M.1 AP-A	$\alpha$	4.241	0.214	T = 19.809	<0.001
	$\beta$	0.149	0.302	T = 0.493	0.622
	k	3.836	1.600		
M.2 H	$\alpha$	8.481	0.264	T = 32.120	< 0.001
	$\beta$	0.402	0.186	T = 2.160	<b>0.031</b>
	$\sigma_{\text{block}}$	1248.0			
	$\sigma_{\text{residual}}$	2316.0			
M.2 AP	$\alpha$	6.693	0.313	T = 21.399	< 0.001
	$\beta$	0.275	0.134	T = 2.055	<b>0.040</b>
	$\sigma_{\text{block}}$	260.9			
	$\sigma_{\text{residual}}$	352.6			
M.3 Richness Herbivore	$\alpha$	4.648	0.226	T = 20.536	<0.001
	$\beta$	-0.057	0.325	T = -0.177	0.867
	$\theta$	32.064			
M.3 Richness AP	$\alpha$	3.718	0.141	T = 26.440	<0.001
	$\beta$	-0.008	0.199	T = -0.041	0.968
	$\theta$	4.883			
M.4 Herbivores (inverse Simpson's index)	$\alpha$	20.763	2.791	T = 7.438	<0.001
	$\beta$	-8.935	3.948	T = -2.263	<b>0.047</b>
	$\sigma_{\text{residual}}$	6.837			
M.4 AP (inverse Simpson's index)	$\alpha$	14.114	3.422	T = 4.124	0.003
	$\beta$	-5.116	4.840	T = -1.057	0.315
	$\sigma_{\text{residual}}$	8.382			

M.5 Density herbivores	$\alpha$	3.367	0.272	T = 12.385	<0.001
	$\beta$	0.6351	0.232	T = 2.743	<b>0.006</b>
	$\sigma_{\text{block}}$	7.286			
	$\sigma_{\text{residual}}$	16.745			
M.5 Density AP	$\alpha$	1.973	0.184	T = 10.711	<0.001
	$\beta$	0.214	0.120	T = 1.179	<b>0.073</b>
	$\sigma_{\text{block}}$	0.689			
	$\sigma_{\text{residual}}$	2.077			
<b>Network Descriptors</b>					
M.6 Connectance	$\alpha$	-0.920	0.159	Z = -5.771	<0.001
	$\beta$	0.078	0.223	Z = 0.348	0.728
	$\theta$	30.93	12.46	Z = 2.482	0.013
M.7 Generality	$\alpha$	1.555	0.147	T = 10.565	<0.001
	$\beta$	0.019	0.208	T = 0.090	0.928
	$\sigma_{\text{residual}}$	0.360			
M.8 Modularity	$\alpha$	0.620	0.327	Z = 1.893	0.058
	$\beta$	0.533	0.249	Z = 2.143	<b>0.032</b>
	$\sigma_{\text{block}}$	0.451			
	$\sigma_{\text{residual}}$	0.671			
	$\theta$	26.6			
M.9 Nestedness	$\alpha$	29.790	4.803	T = 6.202	<0.001
	$\beta$	6.862	6.792	T = 1.010	0.336
	$\sigma_{\text{residual}}$	11.765			
M.10 Specialization	$\alpha$	2.780	0.183	15.316	<0.001
	$\beta$	0.024	0.254	0.931	0.352
	$\sigma_{\text{block}}$	0.023			
	$\sigma_{\text{residual}}$	0.153			
	$\theta$	102			
M.11 Vulnerability	$\alpha$	18.775	2.9722	T = 6.317	<0.001
	$\beta$	-8.156	4.554	T = -1.791	<b>0.073</b>
	$\sigma_{\text{residual}}$	7.144			
<b>Selected Supplementary Analyses</b>					
MS.5.1 Best model	$\alpha$	0.763	2.862	T = 0.267	0.790
	$\beta$	-1.307	0.526	T = -2.486	<b>0.015</b>
	$\sigma_{\text{plant}}$	1.508			
	$\sigma_{\text{residual}}$	1.288			
MS.5.2 SLA	$\alpha$	5.382	0.094	T = 56.943	<0.001

	$\beta$	<i>-0.044</i>	<i>0.060</i>	<i>T = -0.737</i>	<i>0.464</i>
	$\sigma_{block}$	<i>0.280</i>			
	$\sigma_{plant}$	<i>0.156</i>			
	$\sigma_{residual}$	<i>0.243</i>			

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**Table S3.** Arthropod individual body lengths analysed with the Mann-Whitney’s tests for comparisons of in control and predator exclosure plots. Abbreviations: NC – number of individuals in the control, NEx - number of individuals in the exclosure plots. HL – Hodges-Lehman centrality estimator (median of the differences between individuals from control and exclosure), ns – not significant. ‘Direction’ indicates how median changes from predator exclosure (no focal predators: birds, bats and ants) to the control plots (predators present).

Order	NC	NEx	HL	P	Direction
Orthoptera	422	369	-2.77E+00	<0.001	decrease
Homoptera	135	252	-3.10E-05	0.019	decrease
Heteroptera	785	362	-7.27E-05	0.208	ns
Aranea	362	351	-8.88E-01	<0.001	decrease
Mantodea	55	133	1.47E+01	0.006	increase
Coleoptera	1214	993	-1.36E+00	<0.001	decrease
Lepidoptera	389	702	1.10E-05	0.016	increase

**Table S4.** Arthropod individual body lengths at individual plant species analysed with the the Mann-Whitney's tests. Abbreviations: NC – number of individuals in the control, NEx - number of individuals in the exclosure plots. HL – Hodges-Lehman centrality estimator (median of the differences between individuals from control and exclosure), ns – not significant. 'Direction' indicates how median changes from predator exclosure (no focal predators: birds, bats and ants) to the control plots (predators present).

Order	Plant	NC	NEx	HL	P	Direction
Orthoptera	Pipturus argenteus	84	147	-3.87E+00	0.061	ns
	Premna sp.1	2	13	-1.67E-06	0.661	ns
	Trichospermum pleiostigma	22	17	2.89E-05	0.931	ns
	Melochia sp.1	131	28	-3.94E+01	0.000	decrease
	Melanolepis multiglandulosa	71	66	1.71E+00	0.162	ns
	Macaranga tanarius	17	3	4.03E+00	0.425	ns
	Cordyline terminalis	4	3	5.42E+00	0.858	ns
	Breynia cernua	6	7	9.45E+00	0.350	ns
	Trema orientalis	64	40	6.94E-01	0.137	ns
	Manihota esculenta	10	10	-3.40E+01	0.047	decrease
Homoptera	Trema orientalis	24	17	1.45E-06	0.422	ns
	Pipturus argenteus	47	106	-4.42E-05	0.093	ns
	Melanolepis multiglandulosa	34	81	-4.21E-05	0.293	ns
	Trichospermum pleiostigma	8	15	-5.58E-05	0.893	ns
	Macaranga tanarius	2	2	8.20E-01	0.617	ns
Heteroptera	Trichospermum pleiostigma	8	28	-1.40E+00	0.379	ns
	Melanolepis multiglandulosa	356	60	-3.83E-01	0.105	ns
	Pipturus argenteus	262	213	7.24E-05	0.963	ns
	Melochia sp.1	111	7	-1.92E+00	0.254	ns
	Trema orientalis	27	26	1.39E+01	0.002	increase
	Melochia sp.1	84	5	-4.37E+00	0.001	decrease
	Trema orientalis	61	62	-8.06E-01	0.061	ns
Aranea	Pipturus argenteus	80	146	-1.35E+00	0.000	decrease
	Melanolepis multiglandulosa	56	55	-6.57E-01	0.189	ns
	Cordyline terminalis	12	8	-3.26E-01	0.561	ns
	Breynia cernua	10	8	2.05E+00	0.032	increase
	Trichospermum pleiostigma	25	29	2.56E-01	0.459	ns
	Macaranga tanarius	6	7	-1.07E+00	0.668	ns
Mantodea	Pipturus argenteus	11	67	1.62E-01	0.025	increase
	Melanolepis multiglandulosa	3	18	-1.48E-06	1.000	ns
	Trichospermum pleiostigma	5	24	4.98E+01	0.000	increase
Coleoptera	Trema orientalis	30	12	-3.07E-05	0.740	ns
	Pipturus argenteus	393	662	-3.65E-05	0.000	decrease
	Trema orientalis	107	44	5.80E-05	0.485	ns

Order	Plant	NC	NEx	HL	P	Direction
Lepidoptera	Trichospermum pleiostigma	50	79	-4.99E-05	0.347	ns
	Macaranga tanarius	43	20	-3.36E-05	0.860	ns
	Melanolepis multiglandulosa	148	81	8.67E-01	0.046	increase
	Melochia sp.1	341	11	-2.31E+00	0.078	ns
	Premna sp.1	16	17	-1.05E+00	0.824	ns
	Piptrus argenteus	31	234	-3.07E-01	0.002	decrease
	Trema orientalis	218	417	3.64E-05	0.000	increase
	Trichospermum pleiostigma	36	13	-2.86E-01	0.527	ns
	Melanolepis multiglandulosa	12	7	4.31E-05	0.966	ns
	Macaranga tanarius	4	4	9.71E+00	0.142	ns
	Melochia sp.1	66	4	5.22E+00	0.323	ns
	Breynia cernua	2	8	-3.02E-01	0.891	ns

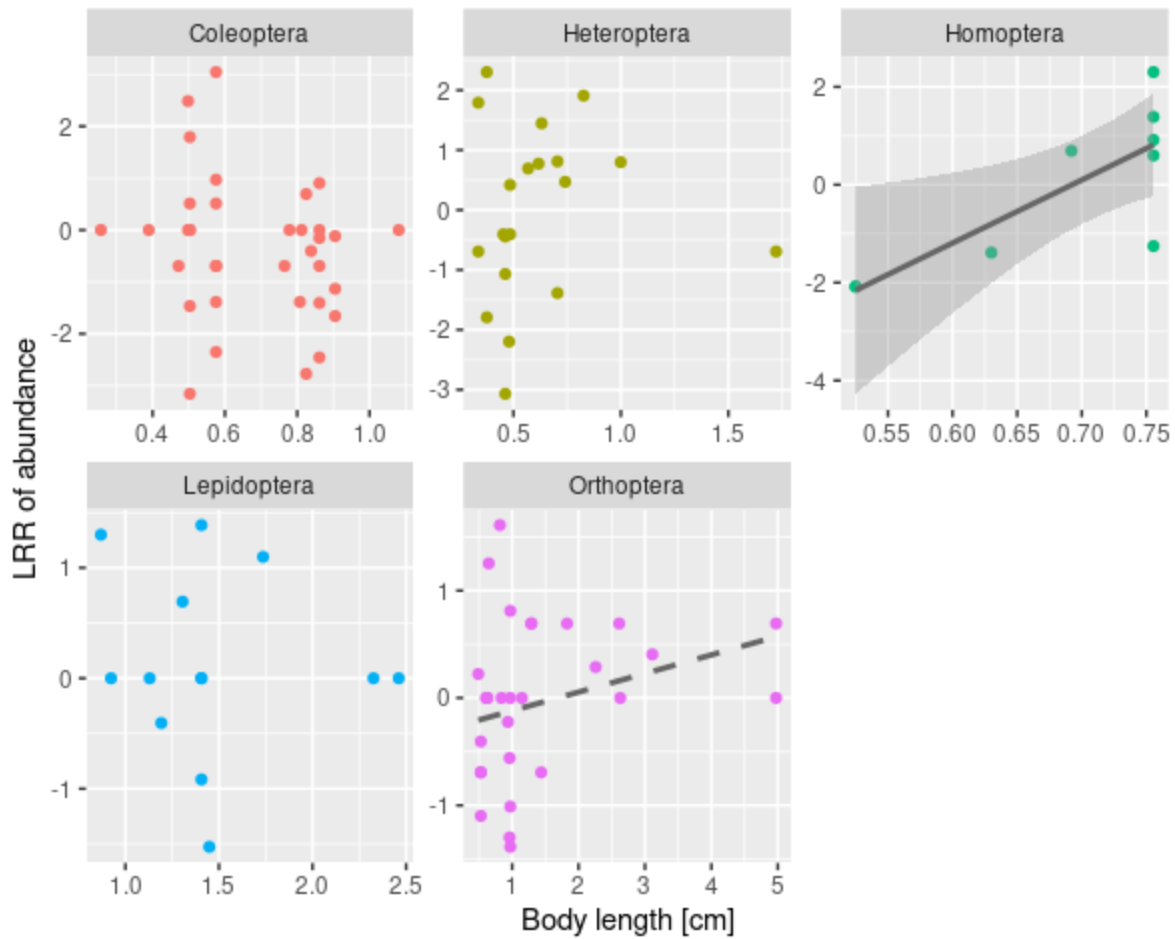
For Review Only

**Table S5.** Arthropod individual body lengths at individual experimental blocks (g1, ..., g6) analysed with the Mann-Whitney's tests. Abbreviations: NC – number of individuals in the control, NEx - number of individuals in the exclosure plots, HL – Hodges-Lehman centrality estimator (median of the differences between individuals from control and exclosure), ns – not significant. 'Direction' indicates how median changes from predator exclosure (no focal predators: birds, bats and ants) to the control plot (predators present).

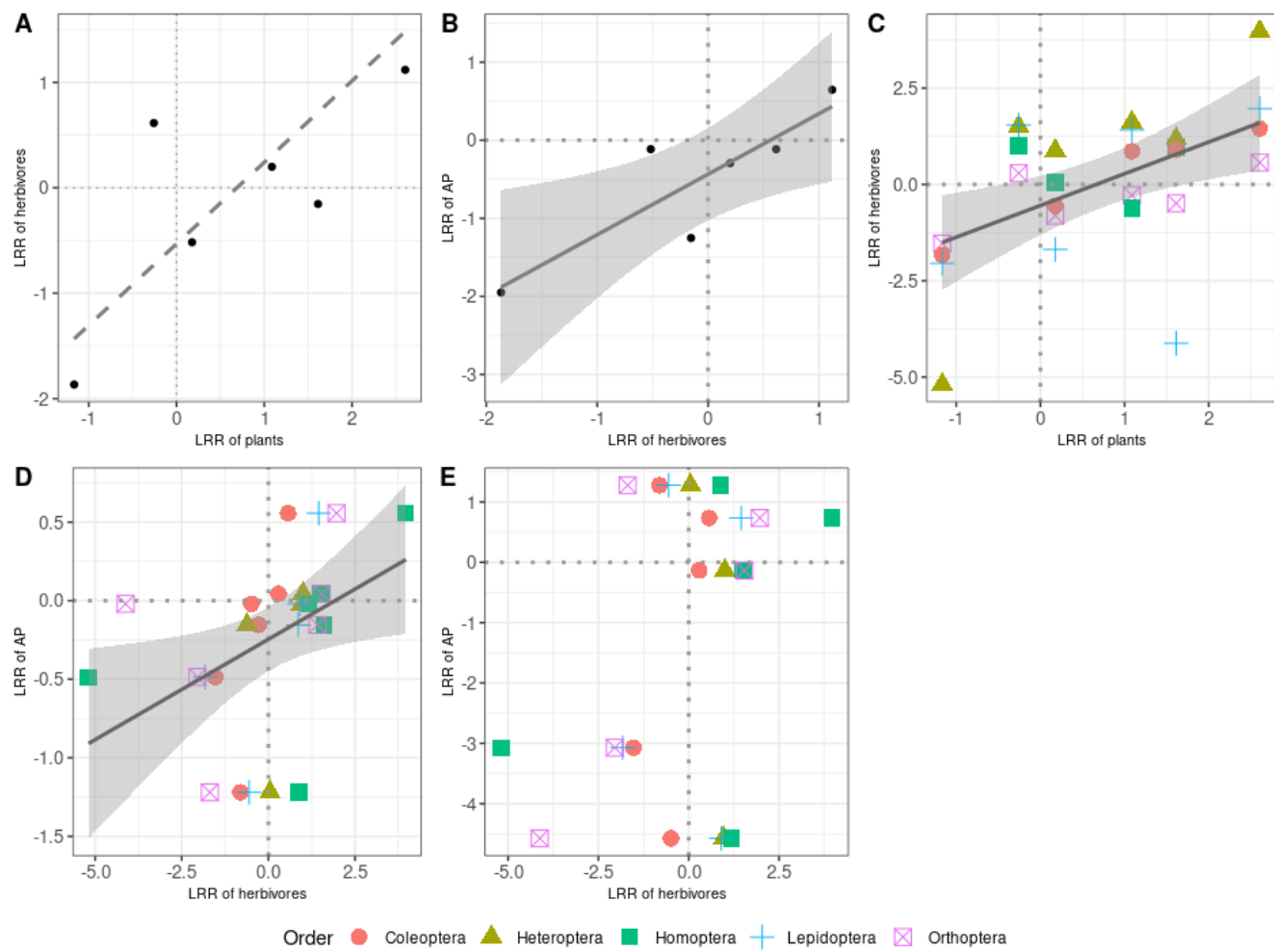
Order	Block	NC	NEx	HL	P	pred.eff
Orthoptera	g5	78	24	-1.20E+01	0.010	decrease
	g4	152	74	-2.39E+01	0.000	decrease
	g2	37	19	-3.03E+01	0.072	ns
	g1	60	42	4.53E-01	0.384	ns
	g3	69	116	-5.01E-01	0.560	ns
	g6	26	94	2.06E+00	0.145	ns
Homoptera	g1	29	17	1.83E+00	0.000	increase
	g4	11	17	-2.67E-05	0.145	ns
	g2	8	3	-5.03E-05	0.737	ns
	g3	63	62	6.31E-05	0.788	ns
Heteroptera	g5	168	4	-4.22E-01	0.734	ns
	g3	156	143	2.19E+00	0.000	increase
	g1	28	36	4.74E+00	0.000	increase
	g6	3	109	-3.02E+00	0.025	decrease
	g2	263	22	-1.34E+00	0.000	decrease
	g4	167	48	-6.91E-01	0.242	ns
Aranea	g4	89	82	-8.06E-01	0.050	decrease
	g6	35	63	7.62E-01	0.047	increase
	g3	76	103	-2.02E+00	0.000	decrease
	g2	49	25	-2.92E+00	0.001	decrease
	g1	66	59	-7.54E-02	0.458	ns
	g5	47	19	-1.90E+00	0.003	decrease
Mantodea	g3	7	6	7.96E-05	0.382	ns

	g6	2	96	1.62E-01	0.000	increase
	g5	6	2	-1.47E+01	0.371	ns
	g2	2	3	-6.35E-05	0.683	ns
	g1	38	24	-4.87E-05	0.179	ns
Coleoptera	g2	165	45	-4.01E+00	0.000	decrease
	g3	320	445	-4.86E-05	0.000	decrease
	g4	362	151	-5.04E+00	0.000	decrease
	g5	198	37	-1.26E+00	0.000	decrease
	g6	65	315	1.62E-06	0.294	ns
Lepidoptera	g1	101	24	1.30E-01	0.658	ns
	g2	5	379	5.21E-05	0.000	increase
	g3	18	94	6.24E-05	0.965	ns
	g4	70	40	2.35E+00	0.001	increase
	g5	177	15	-1.81E+00	0.000	decrease
	g6	18	150	1.48E+00	0.070	ns

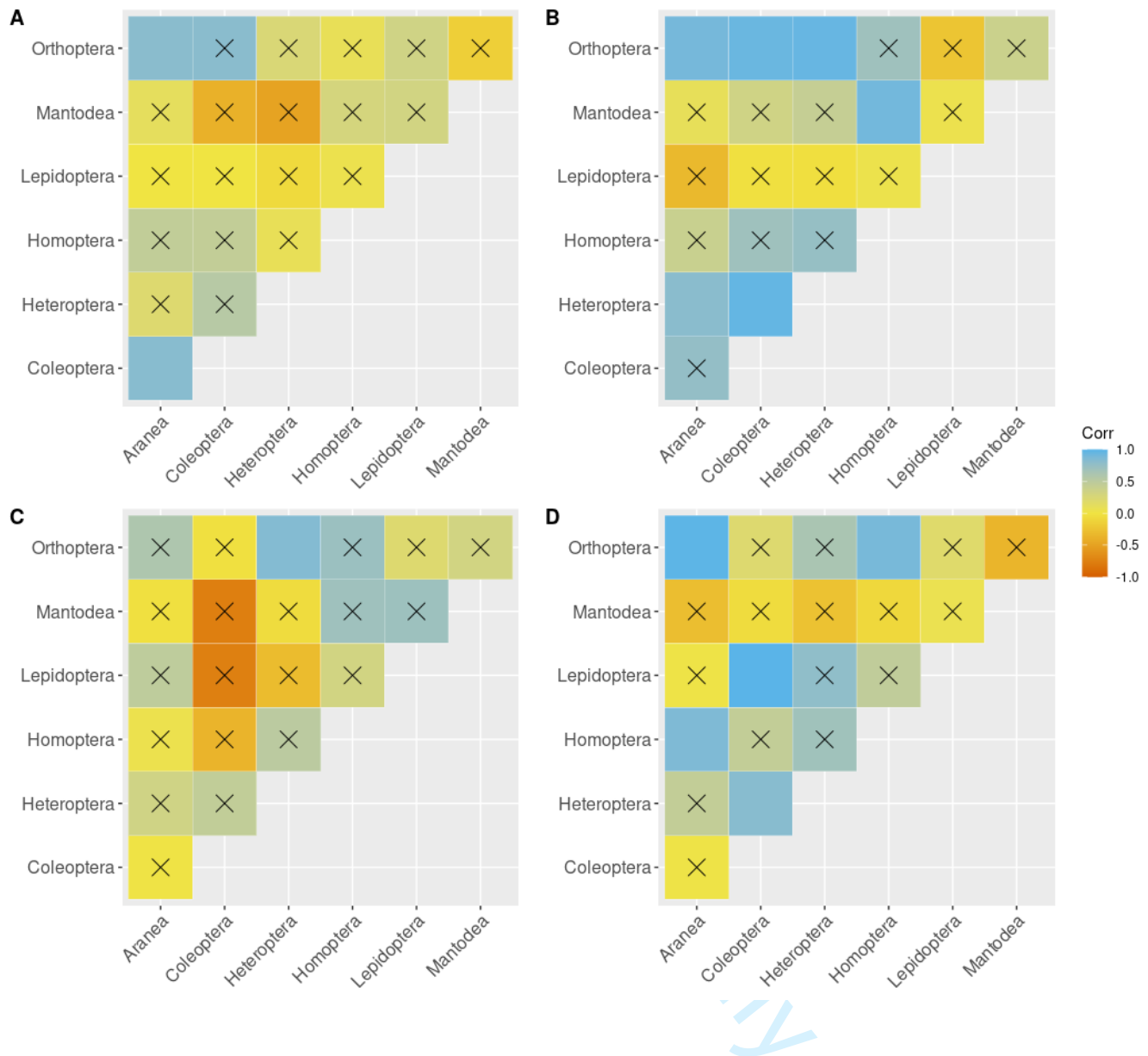




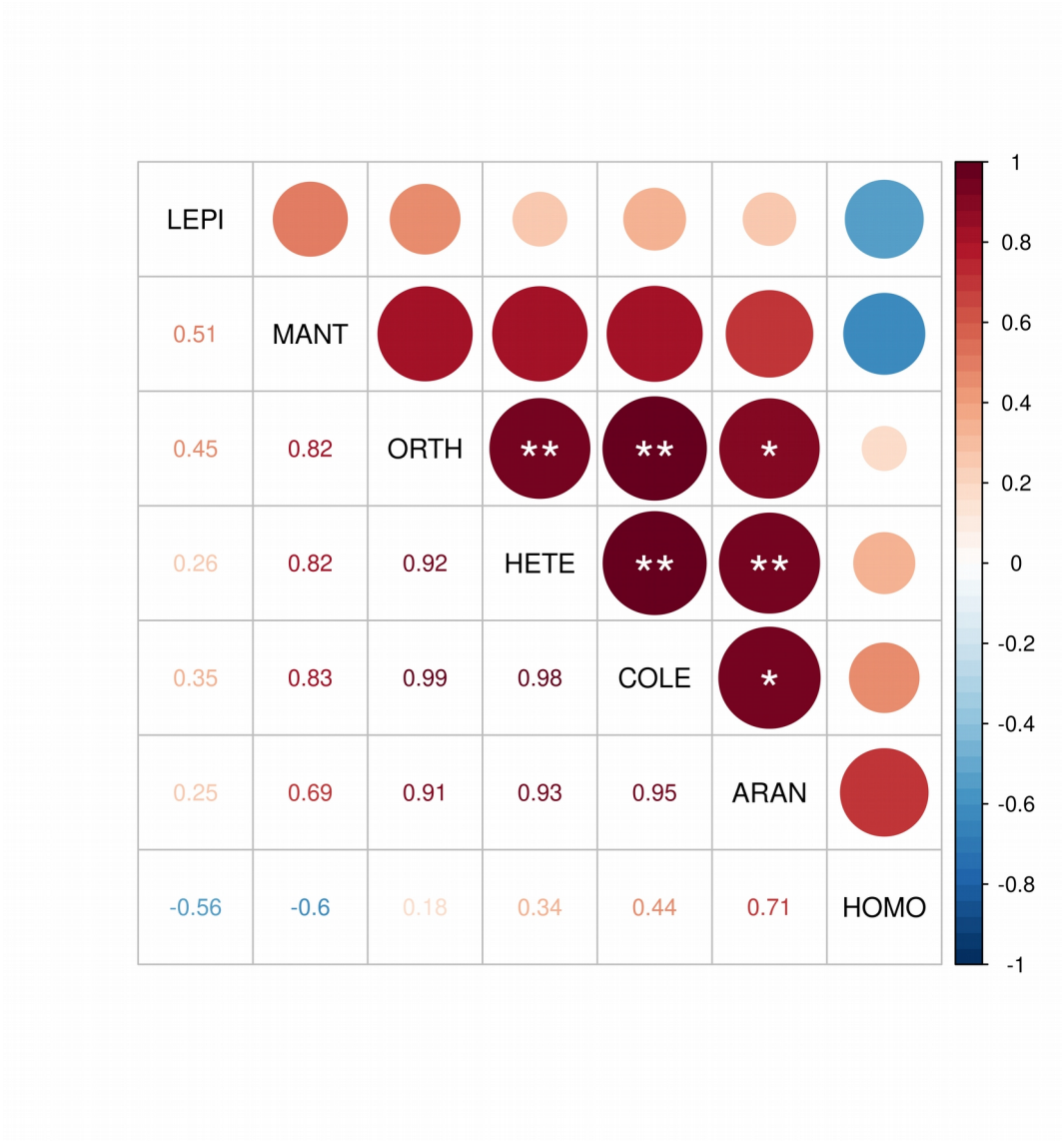
**Figure S7.** Relationships between body length of herbivorous insects and the effect of birds, bats and ants represented as logarithm of the control:exclosure abundance ratio for studied arthropod herbivore orders. Significance is indicated with the line type: solid line:  $\alpha = 0.05$ , dashed line  $\alpha = 0.1$ . In case of a significant regression 95% confidence intervals are plotted.



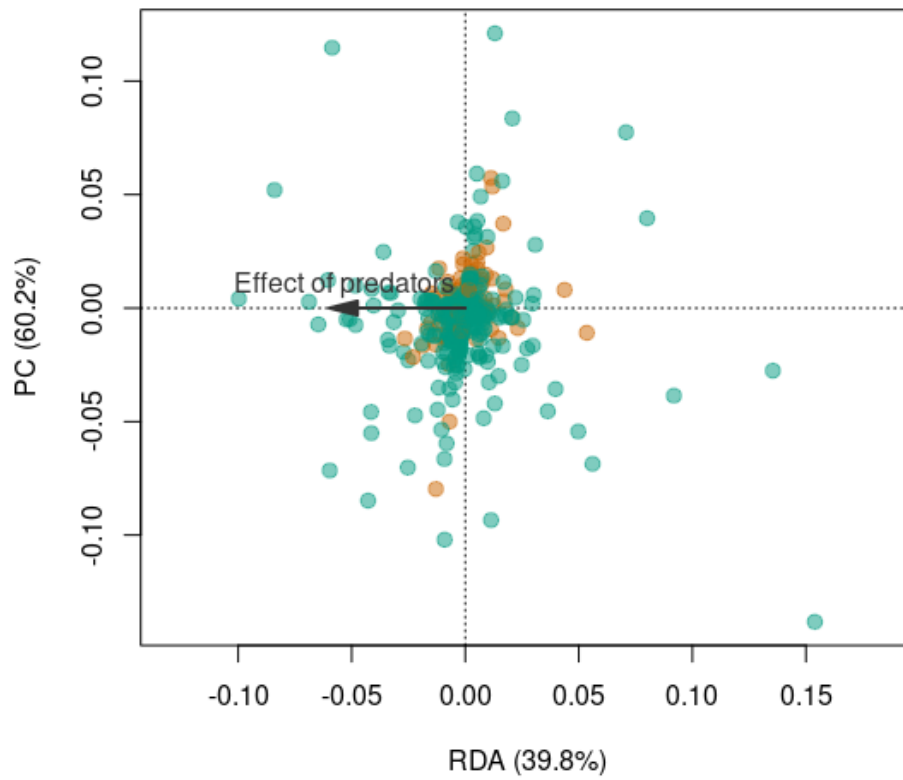
**Figure S8.** Relationships of predator (birds, bats and ants) effects on biomass between different trophic levels in individual plots: A – herbivores vs plants; B – herbivores vs arthropod predators (AP); C) herbivore Orders vs plants; D – spiders vs herbivores; E – mantoids vs herbivores. Predator effects were evaluated using log response ratios (LRR): the logarithm of the ratio between the biomass at the control and predator exclosure treatment within the same experimental block. Positive/negative values of the LRR indicate increase/decrease in biomass of a given trophic level in the presence of predators. Solid line represents significance at the  $\alpha = 0.05$  level and dashed line at the  $\alpha = 0.1$  level. 95% CIs also plotted for significant relationships.



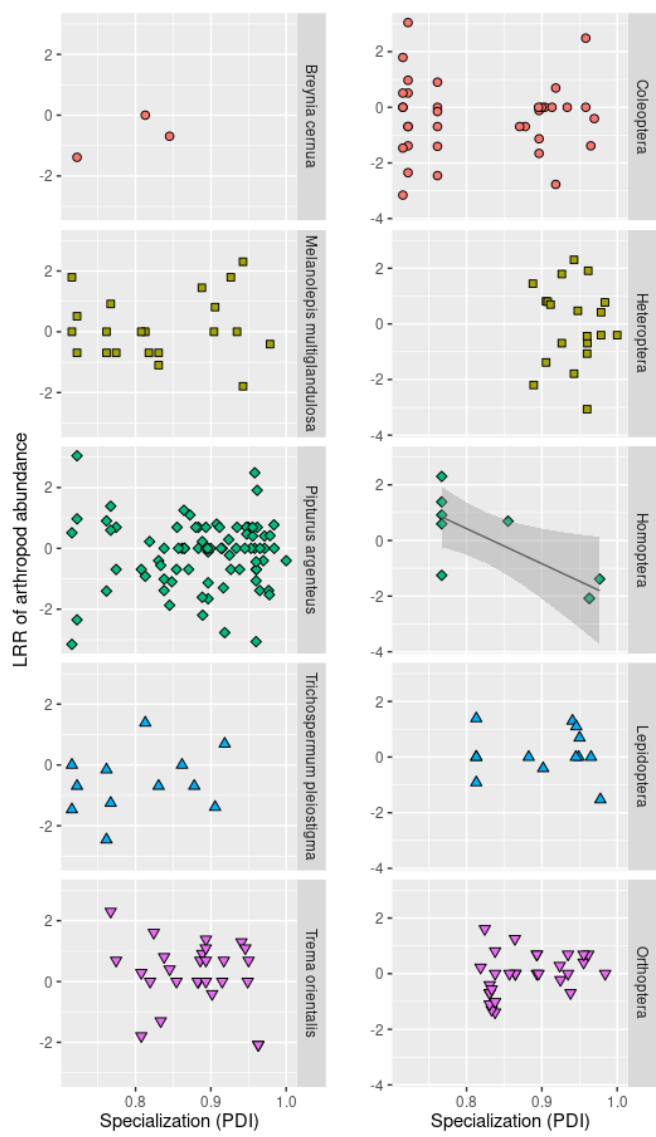
**Figure S9.** Pearson's correlation plots for the raw abundance (A,B) and biomass (C,D) values of studied arthropod orders for each of the six control (A,C) and exclosure (B,D) plots. Barrage indicates non-significant correlations.



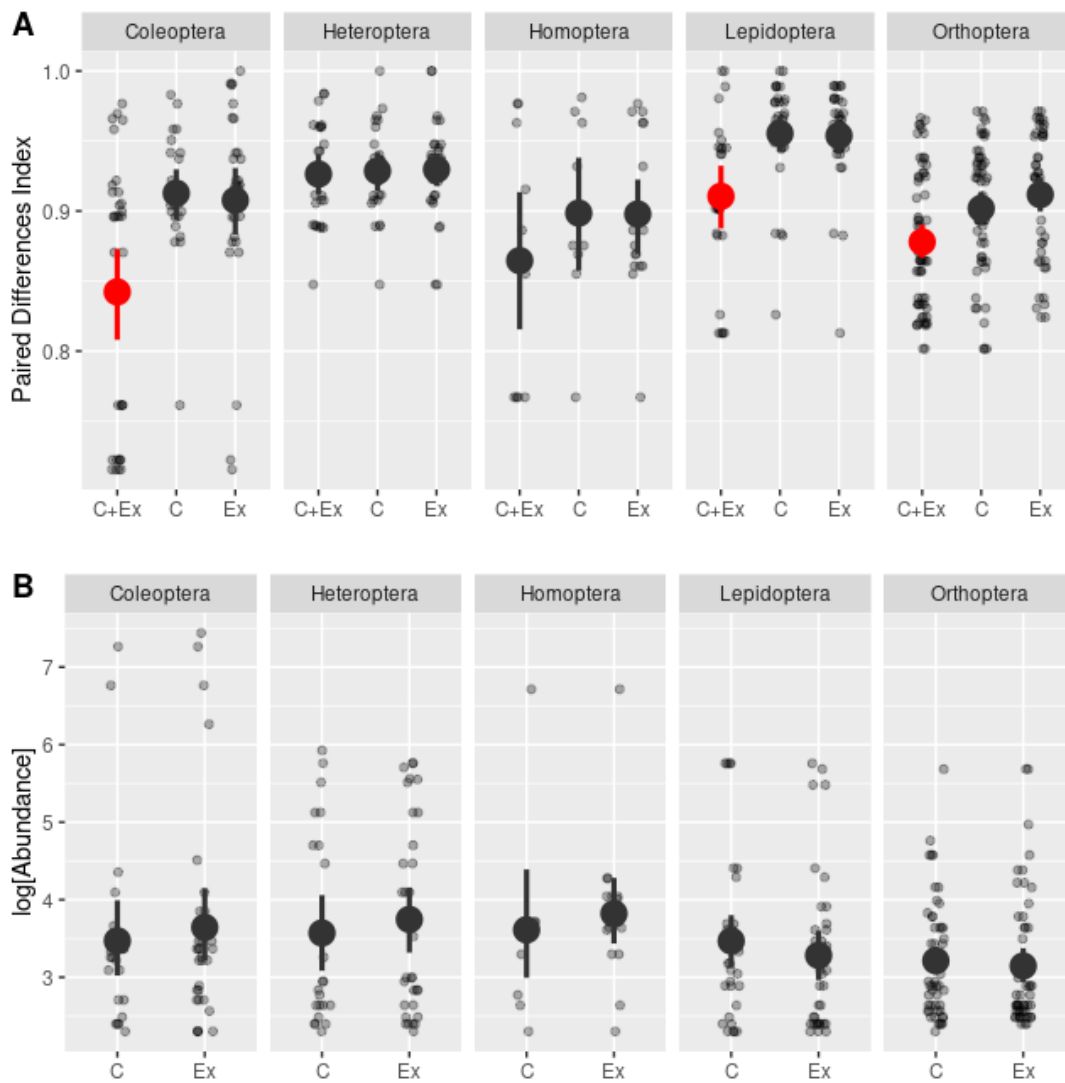
**Figure S10.** Pairwise Pearson correlations of the effects of birds, bats and ants on arthropod abundance between studied orders, Predator effects were evaluated using log response ratios (LRR): the logarithm of the ratio between the abundance at the control and predator exclosure treatment, within the same experimental block: LEPI – Lepidoptera; MANT – Mantodea; ORTH – Orthoptera; HETE – Heteroptera; COLE – Coleoptera; ARAN – Aarneae; HOMO – Homoptera. Significance is indicated with asterisks:  $P < 0.001$  (\*\*\*);  $P < 0.01$  (\*\*);  $p < 0.05$  (\*).



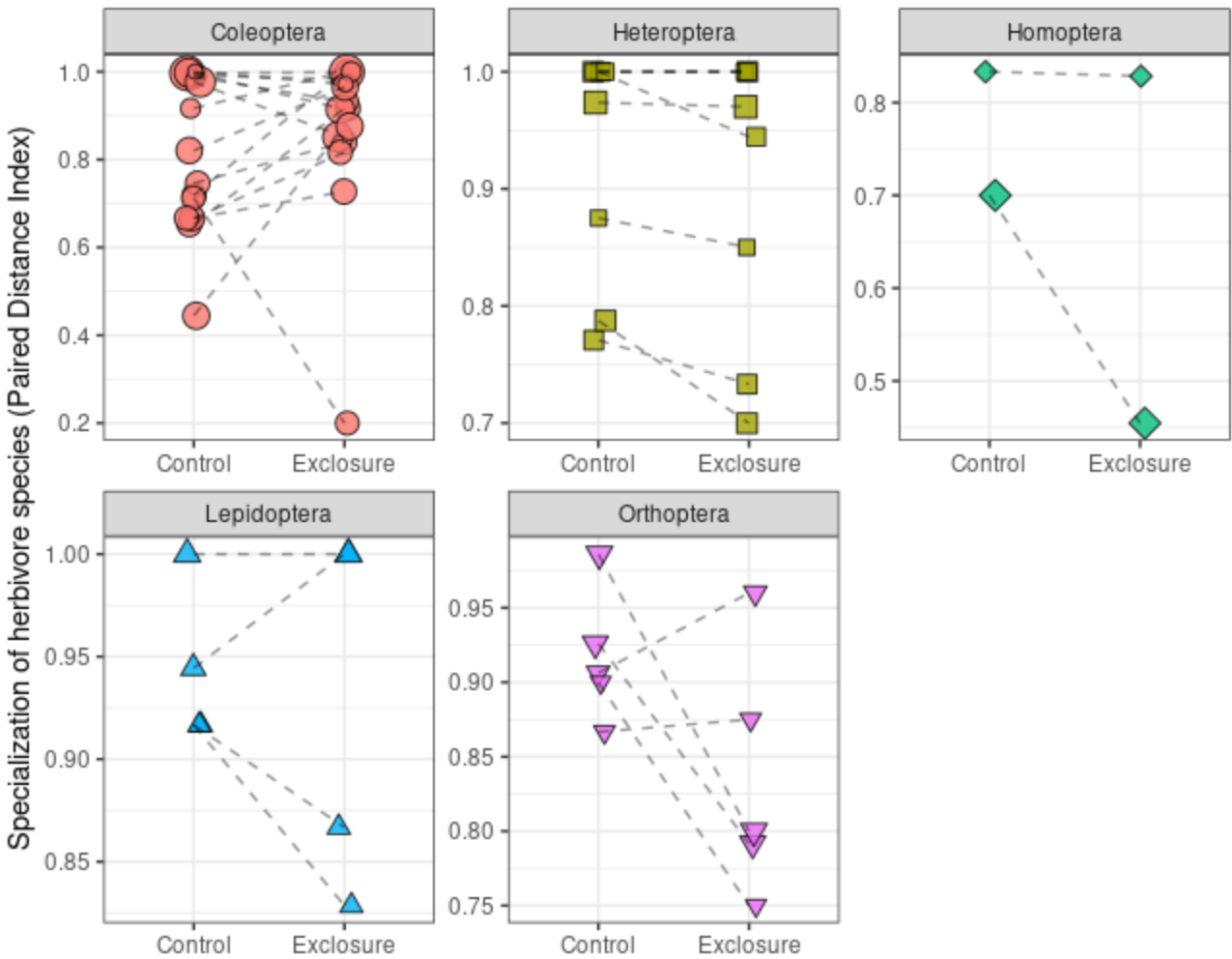
**Figure S11.** pRDA diagram for the predator effect on the abundance-based arthropod community composition. Analysis is constrained on the block (site) effect and first four plant composition PC axes, that together explained  $\sim 91\%$  of variation in vegetation composition (evaluated using pPCA on plant community composition constrained on the block effect). RDA axis represents the effect of birds, bats and ants on individual herbivore (green) and arthropod predator species (gold). Negative coordinates indicate reduced arthropod species' abundance in presence of vertebrate predators. Conditional variables explained  $\sim 87.1\%$  of (conditioned) variation. Effect of predators was not significant overall and explained merely  $\sim 5.16\%$  variation in the arthropod community composition. The residual variance amounted to  $7.8\%$ . Qualitatively similar results were obtained for biomass based community analysis.



**Figure S12.** Effect of specialization (measured with the Paired Differences Index - PDI) on herbivore species performance (logarithm of control:exclosure abundance ratio) for most common plant species and studied herbivorous orders. Each point represents a herbivore species for which  $\geq 5$  individuals sampled. Significance of the regression coefficient at the  $\alpha = 0.05$  level is indicated by a solid line and for those 95% CIs are plotted. For each herbivore species its cumulative abundance at control and exclosures was used as a weighting factor in the regression.

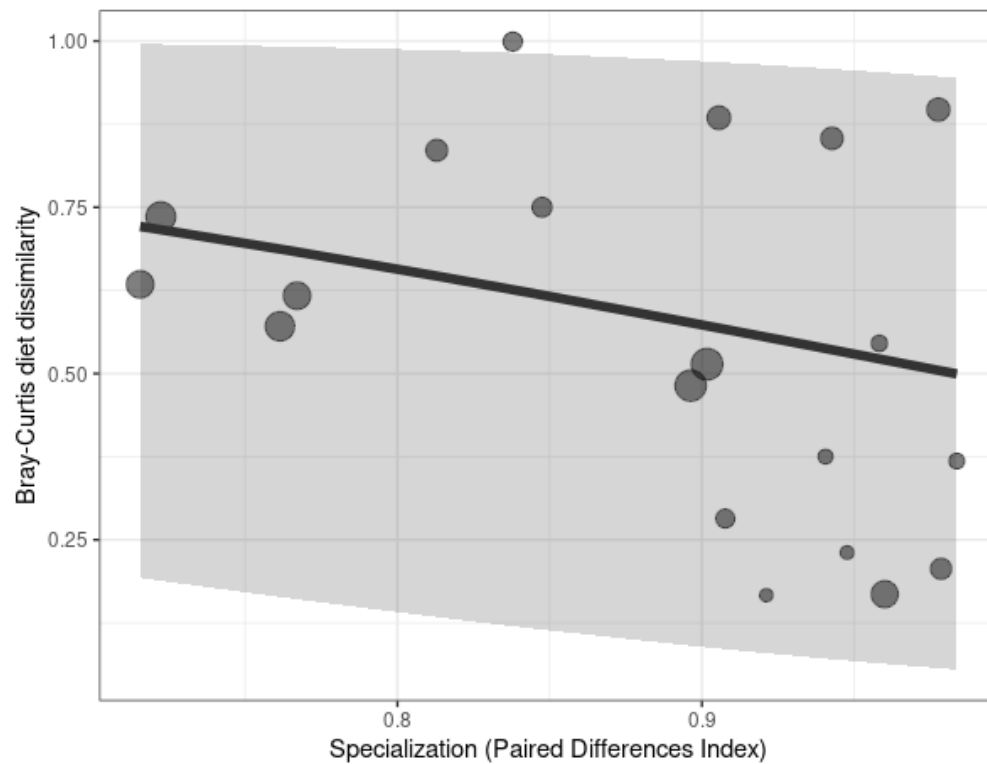


**Figure S13.** Specialization (measured with the Paired Differences Index - PDI) of herbivore species assigned to three groups (A) based on whether their incidence: present in both enclosure and control plot (Ex+C), exclusively in the control (C) or exclusively in the enclosure (Ex) plots. Abundance comparison for species found exclusively in control and experimental plots (B). Minimal abundance for a species included in this analysis was 10 individuals. Red color indicates significant differences from any other group within the order.

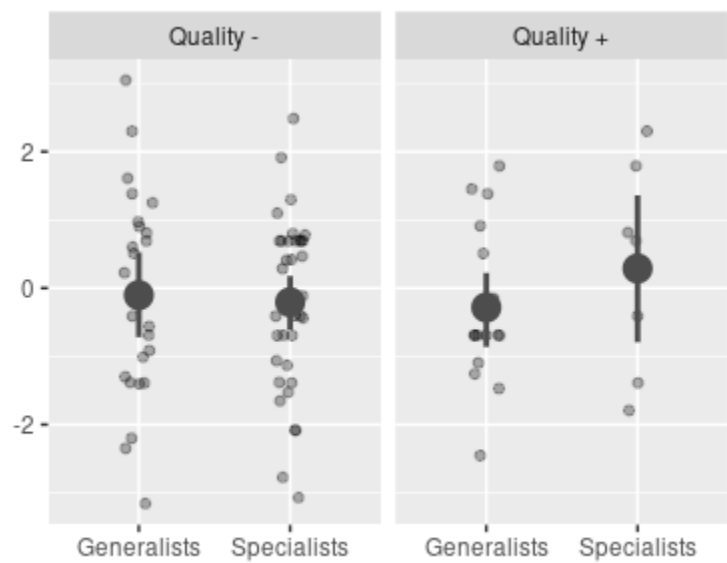


**Figure S14.** Specialization values, measured with the Paired Differences Index – PDI for comparable species in control vs predator exclosure plots for individual insect morpho-species from studied herbivorous orders. Statistical significance of differences between means between the treatments was evaluated using linear mixed effect models with block treated as a random effect. Only Orthoptera was marginally significant ( $T = -2.13$ ,  $P = 0.066$ ). Lines connect herbivore species in both control and exclosure within the same experimental block. Only species with minimum total abundance of 10 individuals were used for the analysis.

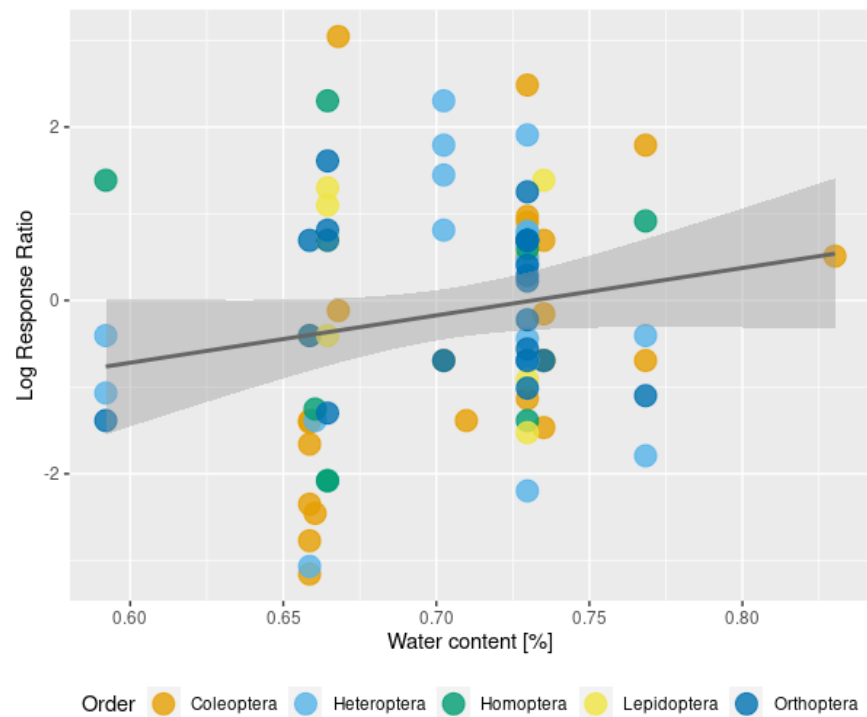




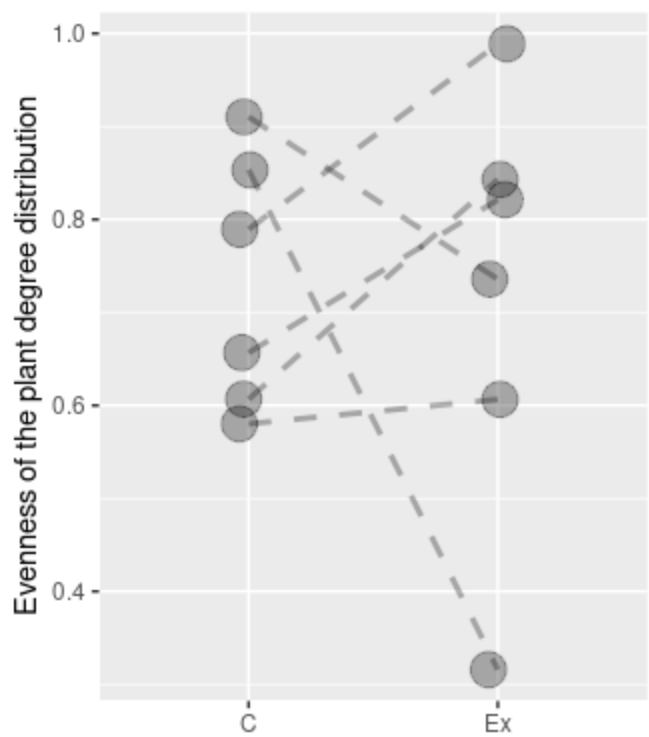
**Figure S15.** Weighted correlation between diet shifts (Bray-Curtis dissimilarity in resources use between exclosure and control plots) and specialization (Paired Differences Index – PDI). Line indicate predicted values of a weighted beta regression model with 95% prediction quantiles are shown. Model is significant but explains only ~9% of variation. Each point represents a herbivore species, and point size is proportional to natural logarithm of its species abundance, which was also used as weights in the regression. Herbivore species with a minimum total of five individuals were included in the analysis.



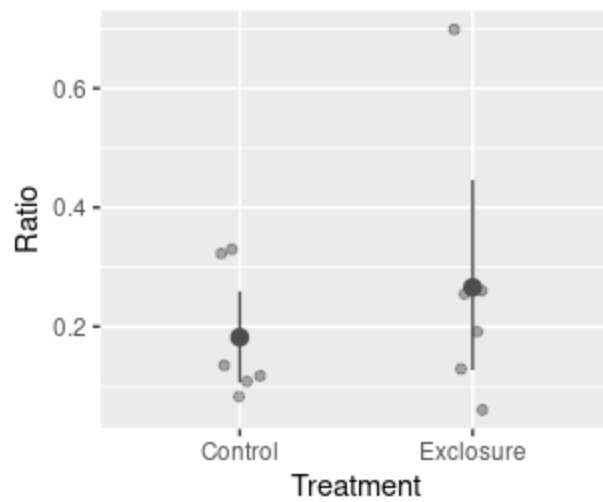
**Figure S16.** Interaction between plant quality (- low, + high, measured as the coordinates along a first axis of PCA performed on SLA and WATER content, i.e. predicted values of their correlation) and specialization (measured as the Paired Differences Index – PDI) in predicting individual species responses to predation (y axis), measured with the logarithm of control:exclosure abundance within the same experimental block. Positive/negative values indicate positive/negative effect of predators presence on given herbivore species. Each insect species was assigned to generalists/specialists group if their PDI value was to the left/right from the mean PDI value for all herbivorous species. Mean values between groups and their interactions were not significantly different.



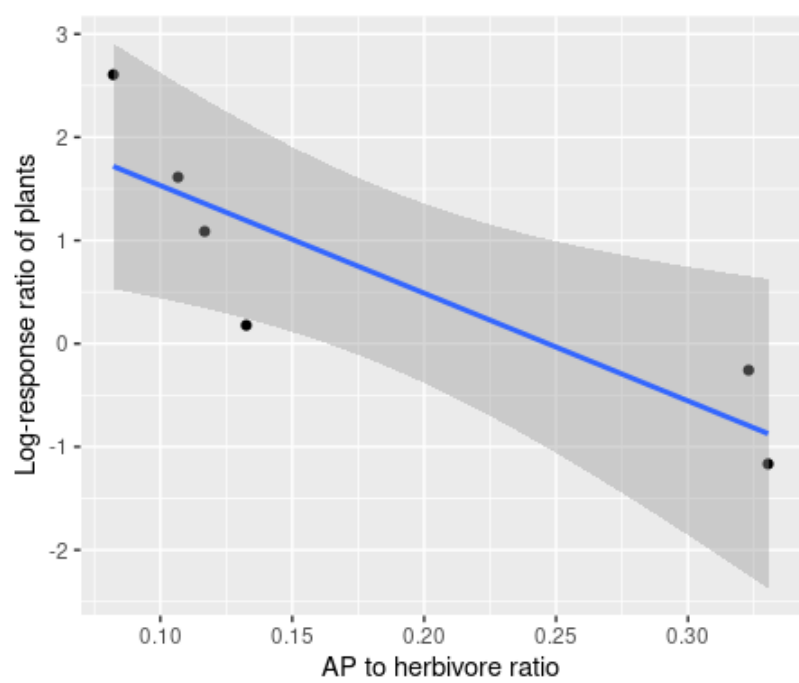
**Figure S17.** Correlation between leaf water content (a proxy for the leaf quality) and the effect of predators (measured with logarithm of control:exclosure abundance ratio). Points indicate individual herbivorous species from different experimental blocks, divided into different orders (colours). Model includes random effect of the block. Significant regression line ( $T = 3.341$ ,  $P = 0.001$ ) and 95% CIs are plotted.



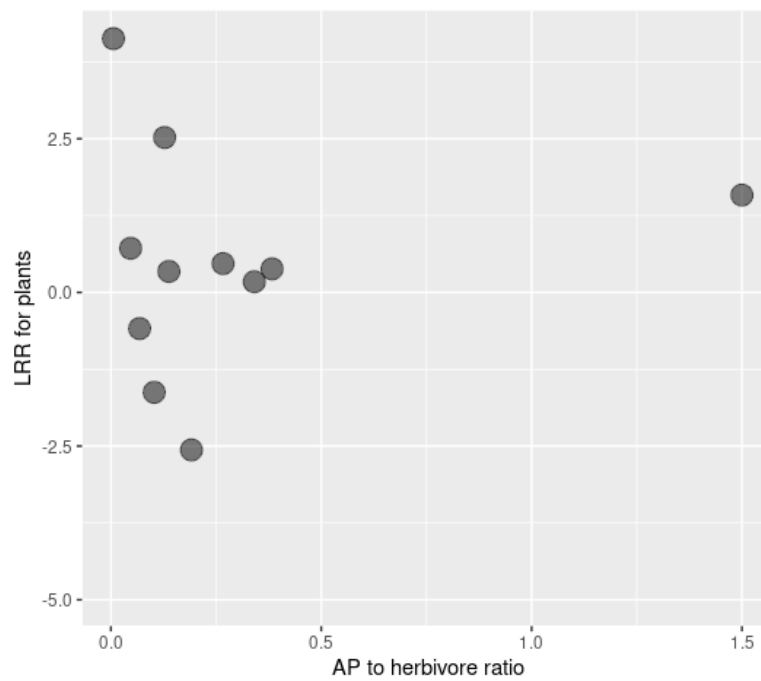
**Figure S18.** Comparison of the evenness values calculated from the degree distribution of plants (used as a measure of distribution of links) in plant-herbivore interaction networks between control (C) and exclosure (Ex) plots. Lines connect network descriptors within the same experimental block. Statistical significance of the difference was evaluated using a beta mixed-effect models with the logit link function and block treated as a random effect.



**Figure S19.** Comparison of the arthropod predators:herbivores ratio between control and focal predator exclosure plots. Mean and 95% bootstrapped CIs are present. The ratio was not significantly affected by the exclosure treatment. Significance was evaluated using mixed effect model with a random effect of block.



**Figure S20.** Correlation between the arthropod community trophic composition (ratio of arthropod predators to herbivores in the presence of focal predators: birds and bats, and ants) and indirect effect of focal predators on the woody plant biomass for each experimental block. Solid line indicates significance at the  $\alpha = 0.05$  level. Individual experimental block as points and 95% CIs are plotted.



**Figure S21.** Trophic community composition of arthropods (ratio of arthropod predators to herbivores in the presence of focal predators: birds and bats, and ants) vs indirect effect of focal predators on the woody plant biomass (logarithm of the control:exclosure abundance ratio) on individual plant species (grey points). Correlation was not significant.