

Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants

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Theory on trophic interactions predicts that predators increase plant biomass by feeding on herbivores, an indirect interaction called a trophic cascade. Theory also predicts that predators feeding on predators, or intraguild predation, will weaken trophic cascades. Although past syntheses have confirmed cascading effects of terrestrial arthropod predators, we lack a comprehensive analysis for vertebrate insectivores—which by virtue of their body size and feeding habits are often top predators in these systems—and of how intraguild predation mediates trophic cascade strength. We report here on a meta-analysis of 113 experiments documenting the effects of insectivorous birds, bats, or lizards on predaceous arthropods, herbivorous arthropods, and plants. Although vertebrate insectivores fed as intraguild predators, strongly reducing predaceous arthropods (38%), they nevertheless suppressed herbivores (39%), indirectly reduced plant damage (40%), and increased plant biomass (14%). Furthermore, effects of vertebrate insectivores on predatory and herbivorous arthropods were positively correlated. Effects were strongest on arthropods and plants in communities with abundant predaceous arthropods and strong intraguild predation, but weak in communities depauperate in arthropod predators and intraguild predation. The naturally occurring ratio of arthropod predators relative to herbivores varied tremendously among the studied communities, and the skew to predators increased with site primary productivity and in trees relative to shrubs. Although intraguild predation among arthropod predators has been shown to weaken herbivore suppression, we find this paradigm does not extend to vertebrate insectivores in these communities. Instead, vertebrate intraguild predation is associated with strengthened trophic cascades, and insectivores function as dominant predators in terrestrial plant-arthropod communities.

bottom-up and top-down control | intraguild predation | meta-analysis | trophic cascade | vertebrate predator exclusion

Research demonstrates that predators, by feeding on herbivores, can increase plant biomass via the indirect interaction commonly labeled a trophic cascade (1). In recent years, meta-analyses have quantified trophic cascades separately in terrestrial (2, 3) and aquatic systems (4, 5) and in multiple habitats together to compare the strength of trophic cascades among ecosystem types (6). Although the strengths of trophic cascades vary across ecosystem types, explanations for the significant residual variation within ecosystems remain enigmatic (6–8).

Vertebrate insectivores such as birds, bats, and lizards often feed as top predators on terrestrial arthropod communities, but based upon current theory it is unclear whether their effects should cascade down to affect plant biomass. Because of their large body size relative to arthropod prey, vertebrate insectivores can consume both predatory and herbivorous arthropods (9, 10). As a consequence, vertebrate insectivores may feed as so-called intraguild predators (11), simultaneously consuming intermediate

arthropod predators and herbivores. Theory predicts that any direct negative effect of vertebrate insectivores on herbivores would be counterbalanced, in part or in whole, by the simultaneous suppression of the arthropod predators of those herbivores (12, 13). Consequently, predicting the net effects of vertebrate insectivores on plants requires knowledge of their relative effects on both predatory and herbivorous arthropods (11). Resolving the functional role of vertebrate insectivores is increasingly important in light of their vulnerability to global change (14).

Despite the expectation that intraguild predation dampens the strength of trophic cascades, past meta-analyses have not tested this prediction. Meta-analyses of experiments from terrestrial systems have focused primarily on the top-down effects of predaceous arthropods (Table 1) (2, 3). To the extent that these meta-analyses included vertebrate insectivores, they emphasized effects on herbivores, and the role of predatory arthropods as mediators of trophic cascade strength has not been studied. Vance-Chalcraft et al. (15) investigated the consequences of intraguild predation for herbivore suppression, but their review included few studies on vertebrate insectivores and did not address the indirect effects of such dynamics for plants. Consequently, fundamental aspects of how vertebrate insectivores affect arthropods and plants remain unclear, despite extensive evidence for the importance of vertebrate insectivores (10, 16, 17).

To redress these gaps, we conducted a meta-analysis of 113 published studies from 63 publications in which vertebrate insectivores (birds, bats, or lizards) were removed, and their effects quantified not only for herbivores and plants but also for predaceous arthropods (for a summary table and list of source publications, see Table S1). With these data, we tested a set of predictions arising from theory on trophic interactions (12, 18) for the effects of vertebrate insectivores on arthropod predators (also referred to as intermediate predators), herbivores, and plants: (P1) generalist predators such as vertebrate insectivores should suppress both predatory and herbivorous arthropods, supporting our assertion that they feed as intraguild predators; (P2) because of the buffering influence of intermediate predators, the effect strengths of vertebrate insectivores on herbivores and plants should attenuate in communities where intermediate predators are more abundant relative to herbivores; (P3) Because intermediate predators should diminish the indirect effects of vertebrate insectivores, the

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Table 1. Summary of results from published trophic cascade meta-analyses involving terrestrial communities

Source	Arthropods		Plants	
	Predators*	Herbivores*	Damage*	Biomass*
(3)	—	−0.49 (−0.63 −0.35) 22%	−0.95 (−1.18 −0.72) 32%	+0.22 (+0.11 +0.33) 0%
(2)	—	−0.41 (−0.49 −0.33) 37%	−0.53 (−0.64 −0.42) 48%	+0.12 (+0.03 +0.20) 10%
(6) [†]	—	−0.44 (−0.72 −0.16) 17%	—	+0.11 (−0.06 +0.27) 17%
(9)	−0.71 (−0.95 −0.49) 100%	−0.60 (−0.90 −0.30) 100%	−0.32 (−0.45 −0.20) 100%	—
This study	−0.49 (−0.69 −0.29) 100%	−0.47 (−0.66 −0.28) 100%	−0.34 (−0.46 −0.22) 100%	+0.13 (−0.02 +0.28) 100%

*Values reported in each cell: log response ratios, 95% confidence intervals, and % of studies with vertebrate predators.

[†]Based on studies measuring plant biomass of whole communities, limited to grassland and agricultural fields, found stronger effects of vertebrate predators (across terrestrial and aquatic communities). Other meta-analyses use responses of individual plant species and show no effect of predator type.

net effects of vertebrate insectivores should be more strongly negative upon intermediate predators than herbivores, and these effects should tradeoff such that strong effects on intermediate predators are associated with weak effects on herbivores; (P4) as a result of this asymmetry in their net effects on intermediate predators and herbivores, vertebrate insectivores should alter the trophic composition of the communities on which they prey; and (P5) the results of our analysis should show relatively weak indirect effects on plant biomass as compared to past meta-analyses focused on experimental exclusions of arthropod predators that may more often feed directly upon herbivores without intraguild predation.

Results and Discussion

Tests of Predictions. Consistent with P1, vertebrate insectivores suppressed the abundance of both predaceous and herbivorous arthropods (Fig. 1 and values presented in Table S2). The meta-analysis of Van Bael et al. (9), which was based upon a subset of the data presented here ($n = 48$ studies), found parallel results for bird effects on predaceous and herbivorous arthropods in trees and understory shrubs. Although negative effects of vertebrate insectivores on arthropod predators may arise in part from competition for a shared prey base of herbivores, diet studies clearly demonstrate that vertebrate insectivores also directly consume predatory arthropods (10, 19, 20). This first result—that vertebrate insectivores act as intraguild predators, suppressing both intermediate predators and herbivores—thus sets the stage for our test of the subsequent predictions.

Contrary to our second prediction (P2), trophic cascade strength was correlated with the relative abundance of intermediate predators to herbivores in a community (Fig. 2 and Table S4). Among the studies where authors reported comprehensive arthropod community sampling and assigned all arthropods to a trophic role, the relative abundance of intermediate predators (IP) to herbivores (H) varied by over three orders of magnitude, from herbivore-dominated communities with ratios (IP:H) as low as 1:167 to predator-dominated communities with values as high as 4:1, with a mean ratio of 1.0 ± 0.4 intermediate predators for every herbivore. We calculated the natural log of the ratio of intermediate predators to herbivores in the presence of vertebrate insectivores (experimental control treatments), annotated here as $\ln(IP:H+)$, as a

metric of arthropod community trophic composition under natural conditions. In communities deficient in intermediate predators (low values of $\ln(IP:H+)$), vertebrate insectivores had relatively weak effects on intermediate predators, herbivores and plants (Fig. 2 and Table S4). In contrast, in communities with a high relative abundance of intermediate predators (high values of $\ln(IP:H+)$) trophic cascades were strong, with strong negative effects of vertebrate

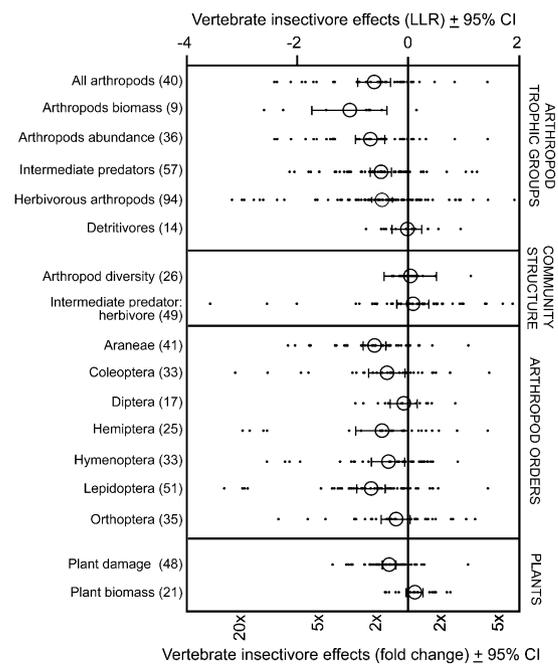


Fig. 1. Natural log ratio effect sizes ($=\ln[\text{control} / \text{predator exclusion}]$; $\pm 95\%$ CI) of insectivorous birds, bats, and lizards on arthropods and plants. Hollow circles show effect means, dots show values from individual studies. Sample size provided in parentheses. The bottom axis presents back-transformed effect sizes presented as untransformed proportional change. Summary statistics provided in Table S2. For intermediate predators: herbivores, a single study value of +2.2 is not shown.

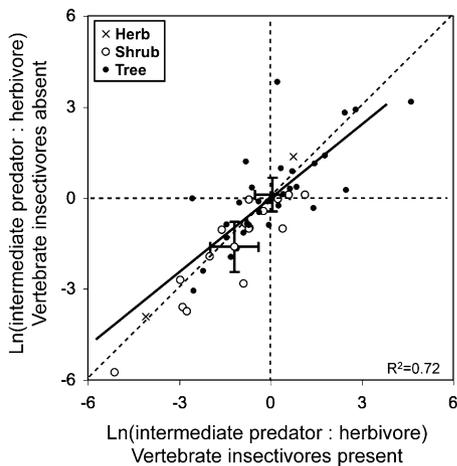


Fig. 3. Effect of vertebrate insectivores on arthropod community trophic composition. Each datum shows the natural log of the intermediate predator: herbivore ratio ($= \ln[\text{IP:H}]$) in treatments with and without vertebrate insectivores. Symbols with error bars show mean community composition for shrubs and trees \pm 95% confidence intervals. Trees have a significantly higher $\ln(\text{IP:H})$ than shrubs (Table S3). There were only two studies on herbs. Data are presented with study as the replicate and multiple studies per field site. Dashed vertical and horizontal lines show arthropod communities with an equal abundance of intermediate predators and herbivores.

but we found little evidence for a correlation between damage and biomass responses among the 16 studies that measured both ($r = 0.38, P = 0.16$; Fig. S2). As with previous meta-analyses, effects on herbivores were stronger than effects on plants, suggesting a progressive attenuation of top-down effects (25).

All of the above conclusions were robust with respect to the type of vertebrate insectivore studied, plant growth form, and several aspects of experimental design. Due to sample size restrictions, we were only able to compare the strength of bird and bat effects (combined) with those of lizards, and only upon arthropods. We found no detectable effect of top predator type upon predatory or herbivorous arthropods, or for all arthropods combined (Table S3). Similarly, we found no difference in plant or arthropod responses based upon whether the studied plants were trees or shrubs (Table S3), although insufficient data prevented a comparison of these woody plants to herbs. Finally, there were no indications that arthropod or plant effects varied as a function of the scale of predator exclusions, experimental duration, or sample size used in the examined studies (Table S3).

Summarizing our results, we show that vertebrate insectivores suppressed both intermediate predators and herbivores to an equal extent and that the effects of these vertebrate insectivores on herbivores and plants strengthened with increasing relative abundance of intermediate predators. This result is especially noteworthy given the overwhelming evidence that arthropod predators and parasitoids themselves are capable of suppressing herbivore populations (2, 3, 26). Theory on intraguild predation predicts that intermediate predators should buffer and weaken the net effects of top predators upon herbivores (21), and empirical evidence from arthropod food webs supports this prediction (15). Our contrary findings thus suggest that current models of trophic interactions do not adequately describe dynamics involving vertebrate insectivores.

Why Does Theory Fail for Vertebrate Insectivores? First, resource availability and primary productivity may cascade up food webs (27), leading to a parallel increase in the abundance of intermediate predators and to an increase in the strength of top predator effects. In the exploitation ecosystems hypothesis, Oksanen et al. (28) proposed that increasing primary productivity

of a system should result in progressive lengthening of food chains and increasing abundance at higher trophic levels. Empirical evidence also supports the hypothesis that bottom-up and top-down factors can interactively determine trophic structure (29, 30). To test this possibility, we investigated whether variation in primary productivity was associated with the relative abundance of intermediate predators and the strength of top predator effects on arthropods and plants. We used mean annual precipitation and the Normalized Difference Vegetation Index (NDVI) as indicators of primary productivity and also examined latitude (absolute value) with which mean annual precipitation and NDVI are negatively correlated. Although we found no evidence for an influence of precipitation or latitude, our analyses reveal that $\ln(\text{IP:H}+)$ increased significantly with NDVI (Fig. 4 and Table S3). We also found that $\ln(\text{IP:H}+)$ was significantly higher in trees than in shrubs (herbaceous plants yielded insufficient replication for analysis) (Fig. 4 and Table S3). If trees represent a higher-quality resource for arthropods than shrubs (e.g., because of higher productivity in the canopy vs. understory) a similar productivity effect may also explain these differences. In combination, host plant growth form and NDVI explained one-third of the overall variation in the relative abundance of intermediate predators to herbivores (Table S3). However, we failed to detect the predicted positive association between NDVI (or precipitation or latitude) and the effects of vertebrate insectivores on arthropods and plants (Table S3). Consequently, our analyses provide mixed support for the hypothesis that variation in primary productivity drives the positive association between the abundance of intermediate predators and the strength of top predator effects on arthropods and plants.

Second, an influx of allochthonous arthropods into structurally complex plant canopies might simultaneously subsidize predaceous arthropods and provoke functional and numerical responses of vertebrate insectivores (31). As mobility and foraging behavior tend to scale with trophic position (32), trophic subsidies might simultaneously increase the abundance of predaceous arthropods and the foraging intensity of vertebrate insectivores that in turn reduce herbivore abundance and benefit plants (13, 33). Predaceous arthropods were frequently present at densities that may not be sustained on herbivore prey alone (Fig. 3), suggesting such subsidies are likely important. Although some studies in our analyses reported abundances of detritivores (Fig. 1), there were insufficient data to rigorously test whether the relative abundance of detritivores was correlated with the abundance of intermediate predators and the strength of vertebrate insectivore effects.

Third, the effects of intermediate and vertebrate insectivores may operate synergistically to suppress herbivore abundance to the benefit of plants (34, 35). Under this hypothesis, intermediate predators may enhance the effects of vertebrate insectivores if each predator group forces herbivores to engage in behaviors that increase their vulnerability to attack by the other. Several studies have tested for interaction between the effects of vertebrate and arthropod predators, with synergistic effects demonstrated in some (36) but not all systems (37, 38). Such explanations would similarly explain the stronger effects of vertebrate insectivores on intermediate predators if interactions among those intermediate predators increase their vulnerability to vertebrate insectivores. Indeed, functional diversity among vertebrate insectivores within communities, in terms of body size, foraging strategy, foraging strata, and dietary preferences, can enhance prey suppression (9, 39).

Fourth, the parallel effects of vertebrate insectivores on predatory and herbivorous arthropods could arise through competition for a shared prey base of herbivores. None of the experiments included in this meta-analysis documented the extent to which vertebrate insectivores reduced predatory arthropods directly via consumption versus indirectly by consuming shared herbivorous prey. On Bahamian islands, experimental studies in our database

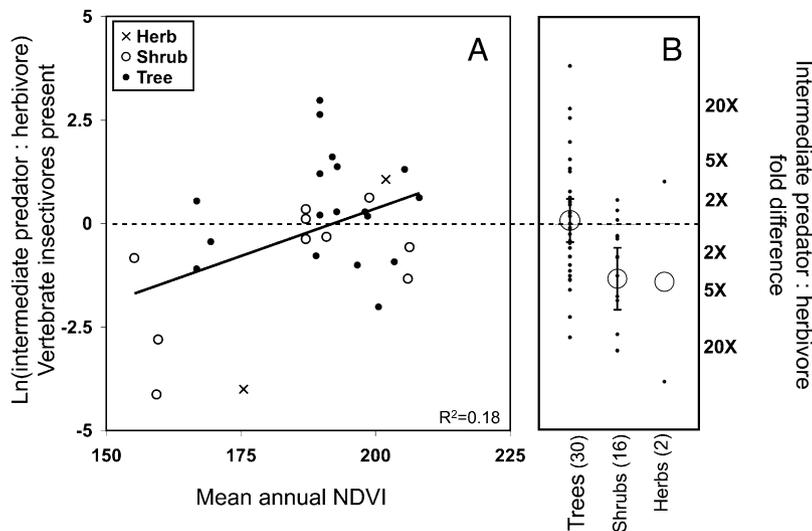


Fig. 4. Effects of NDVI (A) and host plant growth form (B) on the relative abundance of intermediate predators to herbivores in the presence of vertebrate insectivores ($=\ln[\text{IP:H+}]$). (A) Filled circles indicate trees, hollow circles shrubs, x herbaceous plants. Data are presented with field site as the replicate, compiling multiple studies in some cases. (B) Hollow circles show effect means (\pm 95% CI), and dots show values from individual studies. Sample sizes are provided in parentheses. Data are presented with study as the replicate, and multiple studies per field site.

that documented the negative effects of lizards on spiders (38, 40) were insufficient to disentangle these mechanisms, but parallel mechanistic studies demonstrated these effects occur via both predation and competition (19). If vertebrate insectivores fed exclusively upon herbivores, a parallel indirect effect on predatory arthropods would be expected (Figs. 1 and 3). However, such an explanation would not explain the strengthening of top-down controls by vertebrate insectivores with the increasing relative abundance of predatory arthropods (Fig. 2). Most importantly, there is extensive evidence that vertebrate insectivores do consume predatory arthropods (10, 19), and there is little reason to assume vertebrate insectivores would consume arthropods selectively with respect to their trophic level.

Although the above hypotheses seek to explain the positive association between intermediate predators and trophic cascades strength, the pattern that intermediate predators did not dampen herbivore suppression also requires exploration. We propose that vertebrate insectivores may, in fact, release herbivores from consumption by intermediate predators, but these relatively large and highly mobile vertebrates in turn switch among trophic groups opportunistically and dynamically. Previous studies suggest that many avian and mammalian insectivores show frequency-dependent pressure on prey groups to the extent that those prey are abundant relative to other potential prey (41). If vertebrate insectivores dynamically switch to the most abundant trophic groups (42), this frequency-dependent predation may equalize their effects on predatory and herbivorous prey, resulting in little net effect on the trophic composition of arthropod communities. Accordingly, the failure of intraguild predation theory to predict vertebrate insectivore effects may arise from aspects of their biology that facilitate dynamic switching between consumption of predaceous and herbivorous trophic groups, namely their large size relative to both arthropod groups, high mobility, and behaviorally sophisticated foraging strategies that vary within and among individuals and species.

Future Directions. Although our analysis of the published literature clearly documents patterns in the top-down cascading effects of vertebrate insectivores, limitations of the available data prevent definitive conclusions on the precise mechanisms at work. We outline multiple, nonmutually exclusive hypotheses that can only be tested with additional experimentation. In this regard, two issues are of paramount importance. First, more studies are needed that factorially manipulate both vertebrate insectivores and arthropod predators to definitively determine the role of intermediate predators as mediators of top-down effects. Here, it

will be critical to document not only the net effects of vertebrate insectivores on predatory arthropods but also the extent to which such effects are due to direct consumption versus competition for a shared prey base (40). To separate intraguild predation into its competitive and predatory components, studies must determine the overlap in diets of vertebrate insectivores and predatory arthropods in terms of prey taxonomic identity and size and also document per capita herbivore consumption when vertebrate and arthropod predators act alone and in combination (19, 43).

Second, studies must be conducted over significantly larger scales than those published to date. Although we observed no significant effects of the size of experimental units or the duration of studies (Table S3), we note that there are no published studies carried out at a scale relevant to the home ranges of the vertebrate insectivores or that ran for sufficient duration to encompass more than a single generation of the host plants. Our ability to “scale-up” results from relatively small-scale manipulations remains unclear for most systems.

Current theory successfully emulates the trophic dynamics operating within arthropod communities (15), but our findings show they are not extensible to predict effects of vertebrate insectivores in these terrestrial systems. Vertebrate insectivores such as birds, bats, and lizards reduce the densities of both predaceous and herbivorous arthropods according to their proportional representation in the arthropod community. Because terrestrial vertebrate insectivores are large and mobile, they may rapidly compensate for herbivore release, thus leading to an emergent equality in their top-down effects (41, 42). However, other factors may lead to a positive association between intermediate predators and top-down control from vertebrate insectivores, perhaps including—but not limited to—the bottom-up effects of resource availability, trophic subsidies, multiplicative predator effects, and competition for shared prey. As a result of these dynamics, vertebrate insectivores play a key role in suppressing arthropods and increasing plant biomass that was not anticipated by theory.

Methods

We searched the literature for manipulative field studies where (i) birds, bats, or lizards were experimentally excluded or enclosed with field cages or netting, (ii) matched with appropriate open-access controls, and (iii) effects were measured on terrestrial plants and with naturally occurring arthropod populations or communities. In some instances, multiple studies from a single publication were treated as independent experiments (see *SI Appendix 1* for details).

Tests for all hypotheses were based upon unweighted LRR (44), calculated from mean responses in the presence (\bar{Y}_{I+}) and absence (\bar{Y}_{I-}) of vertebrate insectivores ($\ln[\bar{Y}_{I+}/\bar{Y}_{I-}]$). We tested for effects of vertebrate insectivores on all arthropods, arthropod trophic groups, abundant arthropod orders, arthropod

diversity, arthropod community trophic composition (defined as the relative abundance of predaceous and herbivorous arthropods [IP:H]), plant damage by herbivores, and plant biomass. If a study included multiple responses of differing units, we averaged the LRRs within that study to generate a single LRR. When a study reported effects over time, we used the final time point.

For responses with sufficient sample sizes, we used general linear models to test for the effects of biological and methodological covariates (Table S3). We investigated whether LRRs were dependent upon methodological covariates (exclusion area, sample size, experimental duration), host plant growth form (herb, shrub, or tree), and insectivore taxon (birds and bats vs. lizards) with each study serving as the unit of replication (study-based covariates). In separate analyses, we tested for an influence of latitude (absolute value), mean annual precipitation, and site productivity (NDVI) using study sites as the replicate by averaging the responses of multiple studies as needed (site-based covariates). Latitude and longitude were taken directly from papers or extracted using the software application Google Earth (Google Inc.). Data on total annual precipitation were obtained from the WorldClim database (45) and mean annual NDVI from the National Oceanic and Atmospheric Administration Advanced Very High Resolution Radiometer satellite (46). When investigating the influence of covariates on plant responses, we conducted a single analysis in which biomass responses were preferentially taken when available, but otherwise used plant damage responses multiplied by -1 to convert the sign of these effects to parallel those of plant biomass responses. In these models, we included an indicator term for response metric (damage, biomass) to account for any difference between these measures. In all analyses we modeled LRRs as a linear function of all predictors and then discarded any terms where $P > 0.15$ to arrive at a final reduced model. Because of small sample sizes and difficulties in interpretation, we did not test for interactions among covariates in effects on LRRs.

Our analyses of arthropod community trophic composition were based upon 49 studies where the abundance of intermediate predators and herbivores were reported in the same units and were thus comparable. We quantified

arthropod community trophic composition as the natural log of the ratio of intermediate arthropod predators to herbivores ($\ln[IP:H]$), taking the value of this ratio in the presence of vertebrate insectivores ($\ln[IP:H+]$) to be a descriptor of each studied community. For 33 of the 49 studies the authors reported comprehensive sampling of the arthropod community. The value of $\ln(IP:H+)$ did not differ based upon complete versus incomplete sampling ($F_{1,48} = 2.56, P = 0.12$). In 26 of these 49 studies, there were arthropods not assigned to a trophic group by the authors and that were trophically ambiguous based solely upon their taxonomy. In these studies, trophically ambiguous taxa constituted 45% of arthropod abundance or biomass. Here we based our analyses only upon trophically assigned arthropods only. We did not detect a relationship between $\ln(IP:H+)$ and the proportion of the community consisting of unassigned arthropods ($r = -0.11, n = 26, P = 0.58$).

We investigated both the determinants of $\ln(IP:H+)$ and the association between $\ln(IP:H+)$ and trophic cascade strength (Tables S3 and S4, respectively). Tests for the determinants of $\ln(IP:H+)$ proceeded as described above, with separate tests for the influence of site- and study-based covariates on $\ln(IP:H+)$ (Table S3). When testing for the effects of arthropod community upon trophic cascade strength we used linear regression with $\ln(IP:H+)$ as a predictor and LRRs for top predator effects as the dependent variables (Table S4). Results were qualitatively identical when these analyses were repeated using the ratio of intermediate arthropod predators to herbivores in the absence of vertebrate insectivores ($\ln[IP:H-]$) or averaged across treatments. Finally, we compared the intermediate predator to herbivore ratio between treatments with $(IP:H+)$ and without $(IP:H-)$ vertebrate insectivores using the log response ratio $\ln(IP:H+/IP:H-)$.

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