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# Herbivore diet breadth mediates the cascading effects of carnivores in food webs

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**Predicting the impact of carnivores on plants has challenged community and food web ecologists for decades. At the same time, the role of predators in the evolution of herbivore dietary specialization has been an unresolved issue in evolutionary ecology. Here, we integrate these perspectives by testing the role of herbivore diet breadth as a predictor of top-down effects of avian predators on herbivores and plants in a forest food web. Using experimental bird enclosures to study a complex community of trees, caterpillars, and birds, we found a robust positive association between caterpillar diet breadth (phylogenetic diversity of host plants used) and the strength of bird predation across 41 caterpillar and eight tree species. Dietary specialization was associated with increased enemy-free space for both camouflaged ( $n = 33$ ) and warningly signaled ( $n = 8$ ) caterpillar species. Furthermore, dietary specialization was associated with increased crypsis (camouflaged species only) and more stereotyped resting poses (camouflaged and warningly signaled species), but was unrelated to caterpillar body size. These dynamics in turn cascaded down to plants: a metaanalysis ( $n = 15$  tree species) showed the beneficial effect of birds on trees (i.e., reduced leaf damage) decreased with the proportion of dietary specialist taxa composing a tree species' herbivore fauna. We conclude that herbivore diet breadth is a key functional trait underlying the trophic effects of carnivores on both herbivores and plants.**

ecological specialization | host specificity | plant–herbivore interactions | tritrophic interactions | trophic cascade

**P**redicting the strength of trophic interactions is a major goal in ecology. Because most natural ecosystems contain numerous coexisting species at each trophic level, achieving this goal necessarily involves the integration of theory in evolutionary, community, and food web ecology. In this context, evolutionary ecology explains how traits of organisms adapt them to a fundamental trade-off between resource acquisition and mortality risk from natural enemies (1, 2); community ecology theory links the many patterns and consequences of species interactions to the diversity of traits of those species (2); and food web ecology subsumes this diversity into patterns of trophic structure and dynamics, such as a trophic cascade (3). The recognition that functional traits of species can drive the indirect positive effect of carnivores on plant biomass [trophic cascades broadly defined (4, 5)] provides important insight into the causes of variation in these dynamics (1, 6). An emerging understanding of the functional traits mediating trophic cascade strength includes traits of herbivores that facilitate predator avoidance (7–10), or provide constitutive (11, 12) or induced resistance to predation (13). These examples identify antipredator traits of herbivores as an important mediator of top-down effects on plants within individual tritrophic food chains. However, the role of antipredator (or other) traits of herbivores is currently unclear because there is little work comparing a sufficient number of species within a community to causally implicate particular traits. Such comparative analysis of functional traits within a community

could reveal the effects of herbivore community structure on trophic cascade strength. Herbivore community structure is likely to influence cascading effects (14), especially on plants hosting species-rich herbivore assemblages, such as insect herbivores on woody plants (15, 16).

Here, we test the hypothesis that herbivore diet breadth—specifically, the diversity of plant species consumed—is a functional trait that predicts both the strength of top-down effects of predators on herbivores and the strength of trophic cascades. Insect herbivores are notable for their species richness and great variation among species in dietary specialization (17, 18). According to the enemy-free space (EFS) hypothesis, dietary specificity has evolved in response to generalist predators because specialist herbivores can more effectively use their host plants for defense or refuge (i.e., EFS) than can generalist herbivores (19). Antipredator traits associated with dietary specificity in herbivorous insects include sequestration of plant toxins (20, 21), aposematism [warning signals coupled with unpalatability (22, 23)], as well as superior crypsis (19). Therefore, herbivore diet breadth, by serving as a surrogate for this suite of antipredator traits, might succeed in predicting the strength of top-down control. We thus extend the EFS hypothesis to link theory in evolutionary, community, and food web ecology through the prediction that plants with herbivore communities dominated by dietary specialists will experience weak trophic cascades, compared

## Significance

**This study shows the far-reaching effects of herbivore dietary specialization on the ecological and evolutionary dynamics of carnivore–herbivore–plant interactions. First, we test the long-standing hypothesis that dietary specialization of insect herbivores mediates the strength of bird predation on herbivores. Accounting for phylogenetic nonindependence of herbivores and plants, we show for the first time (to our knowledge) that dietary specialization of herbivore species is associated with reduced bird predation across an herbivore phylogeny, and that dietary specialization of herbivores increases the antipredator effects of camouflage and aposematism. Second, this study develops and finds support for the novel hypothesis that the proportion of dietary specialist species in a plant's herbivore community predicts the degree of antiherbivore protection birds provide to plants.**

Author contributions: M.S.S., I.H.L.-M., E.A., and K.A.M. designed research; M.S.S., I.H.L.-M., and T.E.F. performed research; E.A., K.D.W., and K.A.M. contributed new reagents/analytic tools; M.S.S., I.H.L.-M., K.D.W., and K.A.M. analyzed data; and M.S.S., K.D.W., and K.A.M. wrote the paper.

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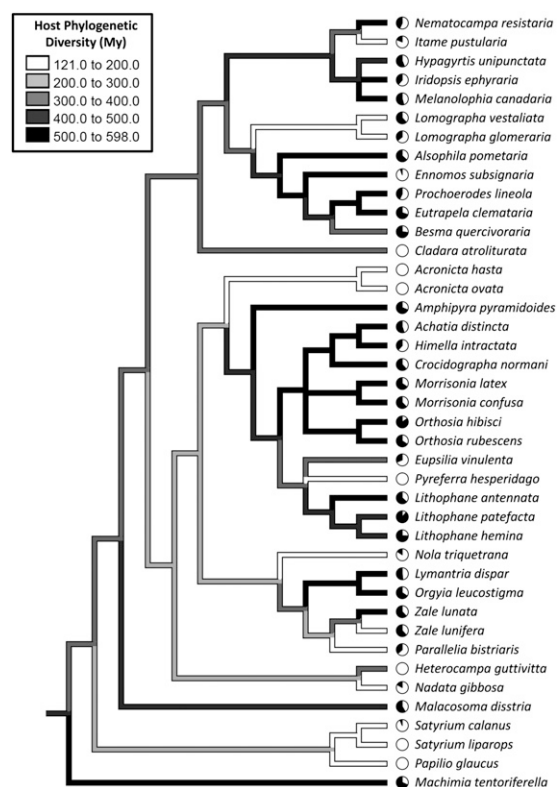
with those dominated by dietary generalists (hereafter the “EFS-cascade hypothesis”).

Although past work provides support for the EFS hypothesis, experimental tests have been limited in several regards. Comparative tests using multiple herbivore species in the same community show reduced attack rates by predators on dietary specialist vs. generalist species (e.g., refs. 20 and 22–24). These studies typically do not account for phylogenetic nonindependence among the herbivore taxa studied (but see ref. 21), thus leaving open the possibility that inferences are biased by nonindependent comparisons (25). In addition, all tests of the EFS hypothesis have focused on predatory insects (predatory wasps, ants, and hemipterans), and it is unknown whether dietary specialization provides EFS from generalist vertebrate predators such as insectivorous birds, bats, and lizards; these vertebrates are important consumers of plant-feeding insects and are known to indirectly benefit plants (26–28). Finally, past empirical work has been limited to predation trials in which herbivores are presented to predators divorced from the full context of their host plants or habitat, thus preventing herbivores from fully using their host plant for EFS. Consequently, a more thorough testing of the EFS hypothesis is warranted and necessary before extending its predictive power to the strength of top-down effects on herbivores and plants.

Studying a food web of trees, caterpillars, and insectivorous birds, we evaluated the EFS hypothesis by comparing the effects of bird predation on the 41 most abundant dietary specialist and generalist caterpillar species in a single forest ecosystem. Notably, our test of the EFS hypothesis assesses vertebrate predator effects on herbivores in situ, i.e., naturally occurring on plants, accounts for phylogenetic nonindependence of herbivores, and investigates mechanisms of EFS by analyzing associations between antipredator traits and herbivore diet breadth. Finally, we tested the EFS-cascade hypothesis for the first time (to our knowledge), using a metaanalysis to determine whether variation in the diet breadth of caterpillar assemblages among 15 tree species is associated with variation in the indirect effects of birds on plants, while accounting for the phylogenetic nonindependence of plants. Importantly, by including data from a total of eight geographic locations, this analysis expanded the scope of inference beyond a single ecosystem.

## Results

**Field Experiment Testing the EFS Hypothesis.** To test the EFS hypothesis, we measured the effect of bird predation over 4 y on the 41 most abundant forest caterpillar species (84% of all individual caterpillars collected) in central Connecticut. These herbivores span a range in diet breadth from specialists, feeding on a single plant species, to broad generalists, feeding on multiple families of plants (29). For each of these caterpillar species, we compared caterpillar densities (individuals per square meter of foliage) on tree branches or entire saplings with netted enclosures (bird exclusion) to those on branches exposed to birds (control). The effect size of bird predation on caterpillars was calculated as a log response ratio (LRR) (30) such that a negative value indicates bird suppression of caterpillar density. We found strong support for the EFS hypothesis, as dietary specialization of herbivores, indicated by small values of host phylodiversity (HPD) (31), was associated with reduced predation across the herbivore phylogeny (Fig. 1); as caterpillar diet breadth (HPD) decreased, the effects of birds on caterpillar density ( $LRR_{\text{herbivore}}$ ) became less negative, both in the raw data ( $R^2 = 0.36$ ;  $P < 0.0001$ ) and in phylogenetically independent contrasts (PICs) (32) of caterpillar taxa (PIC,  $R^2 = 0.14$ ;  $P = 0.017$ ). When the caterpillar species were grouped into putative defensive strategies based on appearance (camouflaged vs. warningly signaled), the analysis of  $LRR_{\text{herbivore}}$  using raw data revealed an interaction between appearance and diet breadth [Fig. 2; analysis of covariance (ANCOVA),  $P = 0.036$ ]. However, this interaction was not significant in the PIC ANCOVA



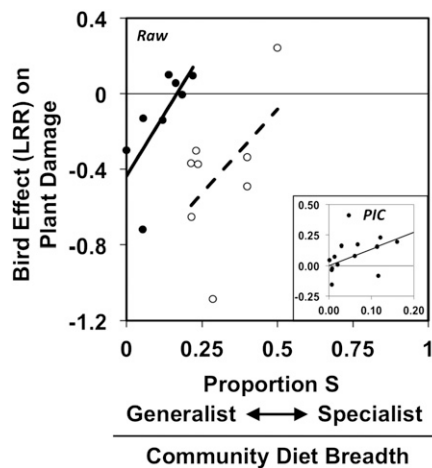
**Fig. 1.** A reconstruction of caterpillar diet breadth [host phylodiversity (HPD) in millions of years] mapped onto the caterpillar phylogeny (see *Relationship Between Bird Predation and Herbivore Diet Breadth: Accounting for Phylogeny* for detailed methods). HPD represents the aggregate phylogenetic distance among hosts, here derived from branch lengths on a dated phylogeny. Higher values of HPD indicate more generalized diets. The black area of each pie chart at the branch tips shows the magnitude of the bird predation effect [percentage density reduction, calculated by exponentiating the LRR,  $\ln(\text{control caterpillar density}/\text{bird exclusion caterpillar density})$ ], for each caterpillar species in the field experiment.

(HPD by appearance,  $P = 0.357$ ) and was dropped from the final model, which showed independent EFS benefits of dietary specialization (Fig. 2, *Inset*;  $P = 0.005$ ) and warning signals for caterpillars ( $P = 0.041$ ).

**Antipredator Traits Associated with Diet Breadth.** To elucidate mechanisms underlying the EFS benefit of dietary specialization, we analyzed the association between diet breadth and other caterpillar traits known or hypothesized to influence the magnitude of bird predation. The latter set of traits included stereotypy of resting location within a plant (proportion of observations in most frequent resting location), body size (mean length), and crypsis [latency (time) to discovery against the plant background in a human subject assay]. We determined whether variation in diet breadth predicted stereotypy or body size for warningly signaled ( $n = 8$ ) and camouflaged species ( $n = 33$ ), with the expectation that dietary specialization would be associated with reduced bird predation due to greater stereotypy or smaller body size (33, 34). Analyses of raw and PIC data detected no significant interactions between the effects of species traits (body size or stereotypy) and appearance (warningly signaled vs. camouflaged) ( $P > 0.20$  in all cases), so the interaction terms were excluded from the models reported here. As expected, dietary specialization was positively related to stereotypy in ANCOVAs using raw data (Fig. 3; HPD,  $P = 0.035$ ; appearance,  $P = 0.21$ ;  $n = 35$ ) and PIC data (Fig. 3, *Inset*; HPD,  $P = 0.020$ ; appearance,  $P = 0.35$ ;  $n = 34$ ). Dietary specialization was not significantly related to mean body length in the ANCOVA using either







**Fig. 4.** Indirect effect of bird predation on plant damage [LRR:  $\ln(\text{control}/\text{bird exclusion})$ ] in relation to the diet breadth of the assemblage of caterpillars [proportion of specialist caterpillar species (proportion S)] associated with each of 15 tree species. The main panel shows this relationship based on raw data from this study (filled symbols, solid line) and data from other studies (open symbols, dashed line). The *Inset* depicts this relationship via a partial regression plot of phylogenetically independent contrasts (PICs) among tree taxa, showing the effect of proportion S on bird LRR<sub>plant</sub> after removing the effect of data source.

for details) and used this index of host plant quality to predict the indirect effect of birds on plant damage (bird LRR<sub>plant</sub>). This regression showed no overall association between host plant quality and the indirect effect of birds on plant damage ( $R^2 = 0.09$ ,  $P = 0.47$ ; PIC,  $R^2 = 0.17$ ,  $P = 0.30$ ). Despite previous work in this system showing a significant effect of host plant species quality on bird predation of generalist caterpillars (29), we find here that high-quality tree taxa also hosted proportionally more specialist (predator-resistant) caterpillar species (high proportion S; linear regression, raw data  $R^2 = 0.44$ ,  $P = 0.071$ ; PIC,  $R^2 = 0.59$ ,  $P = 0.03$ ). Hence, the nonsignificant net effect of host plant species quality on the indirect protective effect of birds on plants (mediated by the entire herbivore assemblage) is likely a result of these countervailing influences.

## Discussion

**Support for the EFS Hypothesis.** Our results show that larval dietary specialization among several lineages of Lepidoptera is associated with reduced larval mortality from avian predators. This finding, together with prior work (20, 22–24), indicates that the acquisition of EFS from generalist predators is an ecologically and phylogenetically widespread evolutionary advantage of dietary specialization in Lepidoptera, the most species-rich taxon of herbivores (38–40).

**Antipredator Traits Associated with Diet Breadth: Underlying Mechanisms of EFS Effect.** In accord with the original exposition of the EFS hypothesis (19), we find that dietary specialization entailed superiority in herbivore antipredator defenses, such as aposematism and crypsis. For camouflaged species, we show evidence that crypsis underlies the benefit of specialization through a negative association between diet breadth and latency to detection. Among camouflaged species, the greater visibility (reduced crypsis and occurrence on multiple tree species) of dietary generalists might facilitate search image formation and learning by birds, thus subjecting these caterpillar species to especially efficient predation. That the small set of warningly signaled species also gained EFS with increasing dietary specialization shows that the antipredator benefits of narrow diet also operate in ways other than superior crypsis. Indeed,

caterpillar species with narrow diets and warning signals gained the most EFS, a pattern most parsimoniously consistent with aposematism (39). In addition, behavioral stereotypy of caterpillar species was associated with dietary specialization in both warning signal and camouflage groups, suggesting that behavioral specialization in microhabitat selection is another trait contributing to the enhanced EFS of dietary specialization. Although the significance of behavioral stereotypy to the EFS hypothesis needs further investigation, it is plausible that it acts as an “amplifying trait” in the context of aposematism (40). Behavioral stereotypy is likely to enhance the defensive effect of warning signals by maximizing the signal-to-noise ratio perceived by avian predators as they search on individual plants. In the context of crypsis, behavioral stereotypy might similarly maximize the background matching upon which crypsis relies. Finally, we discount the alternative possibility that caterpillar body size is actually driving the EFS effect of dietary specialization through size-dependent predation because our raw and PIC analyses found no correlation between body size and diet breadth. However, in some cases the association between dietary specialization and small body size (33) coupled with greater bird predation on larger herbivore prey (34) could generate a pattern of increased EFS for specialist herbivores.

**Support for the EFS–Cascade Hypothesis.** In support of the EFS–cascade hypothesis, we found that the effect of herbivore diet breadth cascaded down to the first trophic level, implicating herbivore diet breadth as a potentially widespread source of variation in the indirect effects of generalist predators on plant damage due to herbivory. Recent metaanalyses of the indirect beneficial effect of vertebrate insectivores on plants were unable to explain significant variation seen across tritrophic studies based on ecosystem properties [climate zone, agricultural vs. natural (28, 41)], plant growth stage (41), or intraguild predation (26). Based on the evidence presented here, we suggest that diet breadth of the herbivore assemblage and the defensive traits associated with dietary specialization may provide some missing explanatory power.

Our findings build upon past food web theory positing a role of herbivore diet breadth and antipredator traits in mediating food web structure. For example, Schmitz (1) argues for the central importance of the fundamental foraging trade-off herbivores face between nutrient acquisition and predation risk as a driver of the impacts of carnivores on plant communities. In particular, generalist grazing herbivores facing a trade-off between food quality and predation risk are likely to mediate strong top-down effects on plant communities by virtue of dietary switching in response to predation risk, whereas dietary specialist herbivores have reduced capacity to do so (1, 42). The present study argues for an alternative mechanism by which generalist herbivores mediate strong top-down food web dynamics: the evolved association between dietary specialization and superior antipredator traits. The temperate forest ecosystem studied here contains species-rich herbivore communities with few abundant grazers. Nevertheless, top-down effects of vertebrate carnivores on arthropod herbivores and plants are well documented in such ecosystems (26, 28). Our evidence suggests that the EFS–cascade hypothesis is an important predictor of these top-down dynamics.

Although we show that the diet breadth of herbivore assemblages predicts the strength of indirect effects of plant damage for individual plant species [species-level cascades *sensu* (43)], we further suggest that differences in the dietary specialization of herbivores among ecosystems (18) might inform variation among ecosystems in the strength of trophic cascades (44, 45). For example, some of the unexplained variation in top-down control of plant production in terrestrial vs. aquatic (5, 46) and managed vs. unmanaged (46) ecosystems could be explained by the observed differences between these systems in herbivore diet breadth. Other differences among ecosystem types notwithstanding (45),

small-bodied herbivores in terrestrial ecosystems (mostly insects) tend to have narrower diets than the small-bodied grazing herbivores (amphipods, fishes, gastropods) that dominate many marine ecosystems (47, 48). Further quantification of herbivore diet breadth or feeding modes across ecosystem types would enable more general tests of the role of diet breadth as a mediator of trophic cascade strength (1).

## Materials and Methods

**Field Experiment Testing the EFS Hypothesis.** We conducted a bird exclusion field experiment to quantify the magnitude of bird predation on forest caterpillars. The bird exclusion treatment consisted of nylon nets (13- or 20-mm mesh size) fashioned into bags with fishing line and fitted around experimental branches or entire saplings (49). Paired control branches or saplings were chosen to match treatment units based on spatial proximity, branch size and height, and plant species. These experimental units were replicated across 18 spatially independent blocks (with respect to bird foraging ranges), each with a different set of treatment and control branches of eight abundant tree species, in each of 4 consecutive years (2008–2011) in a temperate deciduous forest (Connecticut) (see *Field Experiment Testing the Enemy-Free Space Hypothesis* for further details, and Table S1 for the full list of caterpillar species and their host trees). Each of the 41 caterpillar species was sampled 10 or more times ( $n = 10\text{--}783$ ) from the total of 1,824 sampled tree branches or saplings. Limited sample sizes of most caterpillar species necessitated that counts of each species be pooled across all years to get a single population density value for each treatment, and bird effect sizes were calculated as LRRs (30) according to the following formula:  $\text{bird LRR}_{\text{herbivore}} = \ln(\text{control population density/exclusion population density})$ . The diet breadth of each caterpillar species, as indicated by its use of the eight studied tree species, was then calculated as HPD (31), the total phylogenetic branch length (in million years) required to join the set of host plants observed for a caterpillar species during the 4-y study. This metric is equivalent to phylodiversity, from the biodiversity literature, and phylogenetic host specificity, from the parasitology literature (31). We then performed ANCOVA on  $\text{LRR}_{\text{herbivore}}$  with HPD as the covariate, caterpillar appearance (warningly signaled vs. camouflaged; see next section) as a main factor, and the interaction between them. Separate ANCOVAs were run on raw data and PICs (see *Relationship Between Bird Predation and Herbivore Diet Breadth: Accounting for Phylogeny* and Table S2 for detailed phylogenetic methods). For continuity with analyses testing the EFS–cascade hypothesis (see below), we show mean ( $\pm 1$  SE)  $\text{LRR}_{\text{herbivore}}$  in relation to diet breadth as a categorical variable (dietary specialist species restricted to host plants in one family, generalist species feed on more than one plant family). Analyses of the effect of caterpillar diet breadth on bird  $\text{LRR}_{\text{herbivore}}$  were conducted without regard to host plant species, as preliminary analyses showed that host plant did not mediate the differential effects of birds on specialists vs. generalists (i.e., no diet breadth by host plant interaction on  $\text{LRR}_{\text{herbivore}}$ ).

**Antipredator Traits Associated with Diet Breadth.** First, we classified each caterpillar species as possessing or lacking warning signals based on visual inspection of caterpillars from our field experiment as well as from descriptions in field guides (50–52). Specifically, caterpillar species with bright coloration dominated by white, red, or yellow, hair-like setae conspicuous from a distance of 30 cm without magnification, and/or an osmeterium (defensive organ that is conspicuous when everted) were assigned to the warning signal group. Those species lacking these characters were in turn classified not only as lacking warning signals, but also as camouflaged because they all had coloration dominated by green, brown, or gray, generally resembling the coloration of the vegetation on which they lived.

For a subset of camouflaged species for which we had appropriate images ( $n = 26$ ), we quantified the magnitude of crypsis with a computer-based assay. Following previous studies (53), we used human subjects as surrogate predators in our crypsis assay. To quantify crypsis, we presented 52 human subjects (hereafter “participants”) with 99 standardized digital grayscale photographic images of caterpillars on their host plants and measured their ability to find each caterpillar. Grayscale images were used to avoid possible human bias due to color perception differences between humans and birds (54), and a random set of 40 images was presented in a random order to each participant. We used our own original program written in JavaScript (Netscape Communications Corporation) that used Mozilla Firefox to display images and record the latency (in hundredths of a second) from initial display until a participant mouse-clicked on the photograph (code of program available upon request). For each caterpillar species, we calculated the mean

detection latency as a metric of crypsis. See *Antipredator Traits Associated with Diet Breadth: Latency* for further methodological details.

For another subset of the caterpillar species for which we had prior data ( $n = 35$ ), we characterized the behavior of caterpillar species in nature because aposematism and crypsis have behavioral as well as morphological components (40). We specifically considered the possibility that microhabitat selection by caterpillars might modify the effects of warning signals or camouflage. During field surveys in 2004–2007, we conducted systematic sampling of caterpillars by visually inspecting sampled branches (detailed methods in ref. 18). On each occasion when we located a caterpillar on its host plant, we recorded its resting substrate, according to the following six categories: under surface of leaf blade, upper surface of leaf blade, edge of leaf blade, petiole, within leaf shelter, woody tissue (including branches and the trunk). To quantify the magnitude of behavioral specialization, we calculated the variable “stereotypy” for each caterpillar species as the proportion of observations in which the species was found at rest on its most frequently used resting substrate (see *Antipredator Traits Associated with Diet Breadth: Stereotypy* for further details).

We measured the body length of all surviving caterpillars collected during the bird exclusion field experiment to the nearest 0.5 cm (2008–2010) or the nearest 0.1 cm (2011). To avoid confounding bird effects on caterpillars with average body size, we calculated the mean body length of each caterpillar species from samples in the bird exclusion treatment only to estimate average body size per caterpillar species.

To elucidate mechanisms of the EFS benefit of dietary specialization, we analyzed the association between diet breadth and other caterpillar traits known or hypothesized to influence the magnitude of bird predation. The latter set of traits included stereotypy, mean body length, and latency. We used separate ANCOVA models to determine whether variation in HPD and caterpillar appearance (warningly signaled vs. camouflaged) predicted stereotypy or body size, respectively. Parallel ANCOVAs were performed on raw and PIC data (for details on the latter method, see *Relationship Between Bird Predation and Herbivore Diet Breadth: Accounting for Phylogeny*). After initial ANCOVA models showed no significant interaction between HPD and appearance ( $P > 0.20$  in all cases), we dropped the interaction term in a subsequent set of tests to gain statistical power. We expected that dietary specialization would be associated with reduced bird predation due to greater stereotypy or smaller body size (33). For camouflaged species only, we regressed mean latency on HPD to test the prediction that dietary specialization entails superior crypsis.

**Testing the EFS–Cascade Hypothesis.** Our measures of effects on plants came from years 2008 and 2009 of the bird exclusion field experiment (described above). We estimated herbivore damage as the percentage of leaves from each experimental branch damaged by caterpillars, calculating the LRR on plant damage per tree species as the mean bird  $\text{LRR}_{\text{plant}} = \ln(\% \text{ damage control}/\% \text{ damage exclusion})$ . We then quantified herbivore assemblage diet breadth for each tree species as the proportion of specialist to species in its fauna (proportion  $S$ ), i.e., the number of specialist caterpillar species (those feeding on a single host plant family; Table S1) divided by the total number of caterpillar species recorded from each tree species. We used the proportion  $S$  (as opposed to average HPD of a caterpillar assemblage or proportion  $S$  density) in this analysis so as to combine our own data with data from the published literature, which does not provide relative caterpillar densities among host plants. We identified seven additional tree species for which published values for bird effect sizes and proportion  $S$  could be compared (Table S3). Bird  $\text{LRR}_{\text{plant}}$  values were taken from a metaanalysis of bird exclusion studies (26). Plant damage responses varied among multiple studies of individual tree species and, where applicable, we averaged multiple responses to produce a single value per tree species. For these seven tree species, the proportion  $S$  of the caterpillar assemblage was calculated from caterpillar–host plant records using the HOSTS database (35) (see *Testing Enemy-Free Space–Cascade Hypothesis* for details). To test our prediction, we regressed bird  $\text{LRR}_{\text{plant}}$  upon proportion  $S$ . Because measures of plant damage from the literature were mostly estimated as percentage damage per sampled leaf, whereas the estimates from our experiment were estimated as percentage damaged leaves per branch, the literature estimates had the potential to differ significantly from ours due to this methodological difference. Therefore, we also included data source (this study vs. other studies) as a factor in the model. We first examined an ANCOVA on the raw data, followed by an ANCOVA on PICs (55), which accounted for the phylogenetic non-independence among the tree species (see *Testing Enemy-Free Space–Cascade Hypothesis* and Fig. S1 for detailed phylogenetic methods).

We conducted further analyses of the data from the eight tree species in our field experiment to assess alternatives to the EFS–cascade hypothesis.

We again performed parallel analyses on the raw data and on PICs calculated using phylogenetic relationships of the tree species. First, we considered the bitrophic possibility that herbivore proportion  $S$  might by itself determine levels of plant damage. Therefore, we analyzed the mean level of leaf damage per tree species (from bird exclusion branches only) as a function of herbivore proportion  $S$ . Host plant quality could also mediate predator effects on plants; we therefore regressed bird  $LRR_{\text{plant}}$  on host plant quality, which was quantified as the average growth performance per tree species of the seven most abundant generalist caterpillar species in the community (29). High host plant quality was previously found to strengthen bird predation of generalist caterpillars (only) in this system (29), leading to

the prediction of stronger predator effects on plant damage with increasing host plant quality.

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- Schmitz OJ (2010) *Resolving Ecosystem Complexity* (Princeton Univ Press, Princeton).
- Mittelbach GG (2012) *Community Ecology* (Sinauer Associates, Sunderland, MA).
- Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecol Lett* 7(2):153–163.
- Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J (2000) When is a trophic cascade a trophic cascade? *Trends Ecol Evol* 15(11):473–475.
- Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. *Am Nat* 155(2):141–153.
- Terborgh J, Estes JA (2010) *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature* (Island Press, Washington, DC).
- Beckerman AP, Uriarte M, Schmitz OJ (1997) Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc Natl Acad Sci USA* 94(20):10735–10738.
- McIntosh AR, Townsend CR (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: A trophic cascade mediated by fish induced changes to grazer behaviour? *Oecologia* 108(1):174–181.
- Wojdak JM, Luttjeb B (2005) Relative strengths of trait-mediated and density-mediated indirect effects of a predator vary with resource levels in a freshwater food chain. *Oikos* 111(3):592–598.
- Stief P, Hölker F (2006) Trait-mediated indirect effects of predatory fish on microbial mineralization in aquatic sediments. *Ecology* 87(12):3152–3159.
- Wootton JT, Parker MS, Power ME (1996) Effects of disturbance on river food webs. *Science* 273(5281):1558–1561.
- Bridgeland WT, Beier P, Kolb T, Whitham TG (2010) A conditional trophic cascade: Birds benefit faster growing trees with strong links between predators and plants. *Ecology* 91(1):73–84.
- Van der Stap I, Vos M, Verschoor AM, Helmsing NR, Mooij WM (2007) Induced defenses in herbivores and plants differentially modulate a trophic cascade. *Ecology* 88(10):2474–2481.
- Schmitz OJ (1998) Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am Nat* 151(4):327–342.
- Futuyma DJ, Gould F (1979) Associations of plants and insects in a deciduous forest. *Ecol Monogr* 49(1):33–50.
- Strong DR, Lawton JH, Southwood R (1984) *Insects on Plants: Community Patterns and Mechanisms* (Harvard Univ Press, Cambridge, MA).
- Schoonhoven LM, Loon JJA, Dicke M (2005) *Insect-Plant Biology* (Oxford Univ Press, New York), 2nd Ed.
- Dyer LA, et al. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature* 448(7154):696–699.
- Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology* 69(4):886–892.
- Dyer LA (1995) Tasty generalists and nasty specialists: Antipredator mechanisms in tropical lepidopteran larvae. *Ecology* 76(5):1483–1496.
- Vencl FV, Nogueira-de-Sá F, Allen BJ, Windsor DM, Futuyma DJ (2005) Dietary specialization influences the efficacy of larval tortoise beetle shield defenses. *Oecologia* 145(3):404–414.
- Bernays EA (1989) Host range in phytophagous insects—the potential role of generalist predators. *Evol Ecol* 3(4):299–311.
- Bernays EA, Cornelius ML (1989) Generalist caterpillar prey are more palatable than specialists for the generalist predator *Iridomyrmex humilis*. *Oecologia* 79(3):427–430.
- Dyer LA (1997) Effectiveness of caterpillar defenses against three species of invertebrate predators. *J Res Lepid* 34:48–68.
- Harvey PH, Pagel MD (1991) *The Comparative Method in Evolutionary Biology* (Oxford Univ Press, New York).
- Mooney KA, et al. (2010) Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proc Natl Acad Sci USA* 107(16):7335–7340.
- Boyles JG, Cryan PM, McCracken GF, Kunz TH (2011) Conservation. Economic importance of bats in agriculture. *Science* 332(6025):41–42.
- Mäntylä E, Klemola T, Laaksonen T (2011) Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia* 165(1):143–151.
- Singer MS, Farkas TE, Skorik CM, Mooney KA (2012) Tritrophic interactions at a community level: Effects of host plant species quality on bird predation of caterpillars. *Am Nat* 179(3):363–374.
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80(4):1150–1156.
- Poulin R, Krasnov BR, Mouillot D (2011) Host specificity in phylogenetic and geographic space. *Trends Parasitol* 27(8):355–361.
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125(1):1–15.
- Davis RB, Ünay E, Javois J, Gerhold P, Tammaru T (2013) Degree of specialization is related to body size in herbivorous insects: A phylogenetic confirmation. *Evolution* 67(2):583–589.
- Rommel T, Davison J, Tammaru T (2011) Quantifying predation on folivorous insect larvae: The perspective of life-history evolution. *Biol J Linn Soc Lond* 104(1):1–18.
- Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernandez LM (2012) *HOSTS—A Database of the Hostplants of the World's Lepidoptera*. Available at [www.nhm.ac.uk/research-curation/research/projects/hostplants/](http://www.nhm.ac.uk/research-curation/research/projects/hostplants/). Accessed April 30, 2012.
- Ali JG, Agrawal AA (2012) Specialist versus generalist insect herbivores and plant defense. *Trends Plant Sci* 17(5):293–302.
- Mooney KA, Halitschke R, Kessler A, Agrawal AA (2010) Evolutionary trade-offs in plants mediate the strength of trophic cascades. *Science* 327(5973):1642–1644.
- Scoble MJ (1995) *The Lepidoptera: Form, Function and Diversity* (Oxford Univ Press, Oxford).
- Santos JC, Coloma LA, Cannatella DC (2003) Multiple, recurring origins of aposematism and diet specialization in poison frogs. *Proc Natl Acad Sci USA* 100(22):12792–12797.
- Ruxton GD, Sherratt TN, Speed MP (2004) *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry* (Oxford Univ Press, New York).
- Van Bael SA, et al. (2008) Birds as predators in tropical agroforestry systems. *Ecology* 89(4):928–934.
- Trussell GC, Schmitz OJ (2012) Species functional traits, trophic control and the ecosystem consequences of adaptive foraging in the middle of food chains. *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives*, eds Ohgushi T, Schmitz OJ, Holt RD (Cambridge Univ Press, New York), pp 324–338.
- Hunter MD, Price PW (1992) Playing chutes and ladders—heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73(3):724–732.
- Rodríguez-Castañeda G (2013) The world and its shades of green: A meta-analysis on trophic cascades across temperature and precipitation gradients. *Glob Ecol Biogeogr* 22(1):1180130.
- Shurin JB, Markel RW, Mathews B (2010) Comparing trophic cascades across ecosystems. *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, eds Terborgh J, Estes JA (Island Press, Washington, DC), pp 319–336.
- Halaj J, Wise DH (2001) Terrestrial trophic cascades: How much do they trickle? *Am Nat* 157(3):262–281.
- Hay ME, Steinberg PD (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. *Herbivores: Their Interaction with Secondary Metabolites, Evolutionary and Ecological Processes*, eds Rosenthal GA, Berenbaum M (Academic, San Diego), pp 371–413.
- Poore AGB, Hill NA, Sotka EE (2008) Phylogenetic and geographic variation in host breadth and composition by herbivorous amphipods in the family Amphithoidae. *Evolution* 62(1):21–38.
- Mooney KA (2006) The disruption of an ant-aphid mutualism increases the effects of birds on pine herbivores. *Ecology* 87(7):1805–1815.
- Wagner DL (2005) *Caterpillars of Eastern North America: A Guide to Identification and Natural History* (Princeton Univ Press, Princeton).
- Wagner DL (2011) *Owlet Caterpillars of Eastern North America* (Princeton Univ Press, Princeton).
- Wagner D, Ferguson D, McCabe T, Reardon R (2002) Geometroid caterpillars of Northeastern and Appalachian Forests. *USFS Technology Transfer Bulletin* (US Forest Service, Morgantown, WV).
- Karpestam E, Merilaita S, Forsman A (2013) Detection experiments with humans implicate visual predation as a driver of colour polymorphism dynamics in pygmy grasshoppers. *BMC Ecol* 13:17.
- Endler JA, Mielke PW (2005) Comparing entire colour patterns as birds see them. *Biol J Linn Soc Lond* 86(4):405–431.
- Garland T, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic analysis of co-variance by computer-simulation. *Syst Biol* 42(3):265–292.