



# Generalists are more specialized in low-resource habitats, increasing stability of ecological network structure

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**Linking mechanistic processes to the stability of ecological networks is a key frontier in ecology. In trophic networks, “modules”—groups of species that interact more with each other than with other members of the community—confer stability, mitigating effects of species loss or perturbation. Modularity, in turn, is shaped by the interplay between species’ diet breadth traits and environmental influences, which together dictate interaction structure. Despite the importance of network modularity, variation in this emergent property is poorly understood in complex natural systems. Using two years of field data, we quantified interactions between a rich community of lepidopteran herbivores and their host plants across a mosaic of low-resource serpentine and high-resource nonserpentine soils. We used literature and our own observations to categorize herbivore species as generalists (feeding on more than one plant family) or specialists (feeding on one plant family). In both years, the plant-herbivore network was more modular on serpentine than on nonserpentine soils—despite large differences in herbivore assemblage size across years. This structural outcome was primarily driven by reduction in the breadth of host plant use by generalist species, rather than by changes in the composition of species with different fundamental diet breadths. Greater modularity—and thus greater stability—reflects environmental conditions and plastic responses by generalist herbivores to low host plant quality. By considering the dual roles of species traits and ecological processes, we provide a deeper mechanistic understanding of network modularity, and suggest a role for resource availability in shaping network persistence.**

ecological networks | plant-herbivore interactions | network modularity | resource availability hypothesis | herbivore diet breadth

Over the past several decades, there has been a surge of interest in the structure of species interaction networks, the mechanisms that shape network topology, and the ecological function such emergent properties might confer (1). Network metrics related to stability have received particular attention (2, 3), as they provide information about persistence of communities and their potential resilience to environmental change. Recently, the degree to which interaction webs are modular, or composed of subsets of strongly interacting organisms, has been shown to be an important property conferring stability in antagonistic networks (2–4): More modular networks contain the effects of species loss (5) and competition (3) within subgroups of interacting organisms, and thus prevent the propagation of such disruptions throughout the network. However, despite the relevance of this property to the persistence of trophic communities, the abiotic and biotic factors that shape modularity remain poorly understood (6, 7). An important next step is to disentangle drivers of network modularity in trophic networks and to develop theoretical frameworks that will help predict variation in this topological property across natural landscapes.

Like all aspects of network structure, modularity is shaped by the interplay between evolutionary and ecological forces: Evolutionary processes dictate the potential, or “fundamental,”

breadth of trophic interactions in which a species might engage, and ecological filters shape the degree to which species “realize” those links within a network (7, 8). Thus, shifts in network structure across natural landscapes can arise in several ways: 1) change in the relative abundance of intrinsically generalized or specialized interactors (hereafter, fundamental generalists or specialists), including local extinction of one or more interactors; 2) change in the pattern of interaction between the same suite of species, such as species becoming more generalized or more specialized under different ecological conditions (hereafter, realized interaction structure); or 3) a combination of both processes (7).

Despite the joint roles of fundamental and realized processes in shaping modularity, these mechanisms are often investigated separately when they are explored at all (*SI Appendix, Fig. S1 and Table S1*). For example, many studies focus on species-level trait means as explanations for compartmentalized structure, ignoring the degree to which the observed patterns of interaction might be shaped by ecological context (but see ref. 9). These studies find that modular organization in food webs may be driven by phylogeny (10), trait matching (11), and evolved diet breadth constraints (e.g., fundamental specialization) (9). Others explore how modularity varies across ecological contexts, such as with season (12), anthropogenic habitat change (13, 14), host plant genotype (15), and presence of other organisms (9, 15). These latter

## Significance

The degree to which food webs are divided into “modules” of strongly interacting species is an important property conferring stability in ecological communities; however, the mechanisms causing variation in this emergent property are poorly understood in nature. Here, we document temporally consistent differences in plant-herbivore network modularity across two soil types. Next, we parse the mechanistic basis of this structural change between evolutionary constraint (e.g., prevalence of species with specialized versus generalized diet breadth) and interaction plasticity (e.g., shifts in “realized” diet breadth of generalist species). Our findings broaden understanding of abiotic context as a driver of food web structure, suggesting that higher modularity—and thus greater stability—may be a general network property in low-resource contexts.

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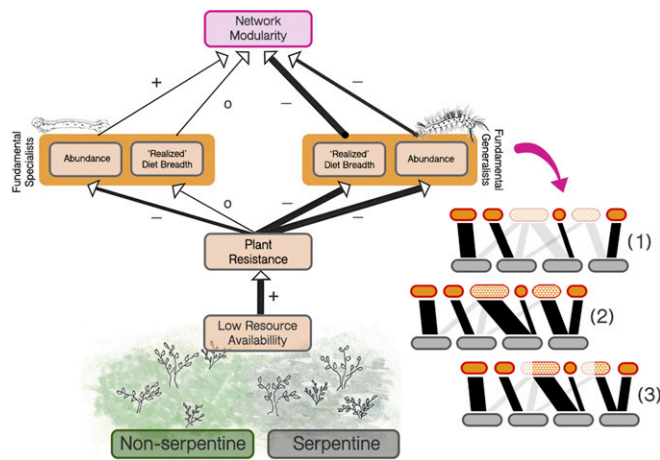
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studies focus on how environmental variation can shape network structure, but often lack important information about traits of species in the food web (7, but see ref. 9).

In the present study, we focus on communities where the fundamental diet breadth of interacting organisms is known (*SI Appendix, Table S2*), and use resource availability theory to inform hypotheses of how abiotic context might influence both species and interactions in plant-herbivore food webs, with ultimate effects on network modularity (Fig. 1). For example, low-resource contexts are predicted to increase plant resistance to herbivory, favoring species with long-lived tissues that are well-defended and low in nutrient content (16). Such resistance traits, in turn, influence abundance (17) and host plant choice (18, 19) of phytophagous insects, with potentially stronger effects on generalists than on specialists (20) (Fig. 1). Indeed, while recent theoretical work suggests that resource availability can have profound effects on network structure (21), it is unclear whether such effects manifest across natural landscapes of varying resource level (but see ref. 22).

We study these linkages in a system of woody chaparral shrubs, with their associated lepidopteran herbivores, which grow across a mosaic of low-resource serpentine and higher-resource non-serpentine soils. Prior work in this system has found that plant resistance varies with soil type in a manner consistent with resource availability theory (23). Our goal is to understand how natural variation in abiotic resources might shape network modularity, and to parse the mechanistic basis of such differences between evolutionary (fundamental) and ecological (realized) trophic characteristics of species.

Specifically, we hypothesize that



**Fig. 1.** Hypothesized relationship between abiotic resource availability and plant-herbivore network structure in the nonserpentine/serpentine system. Plus and minus signs and open circles indicate direction of effect (positive, negative, no effect, respectively); line thickness indicates magnitude; webs (1–3) illustrate network outcomes. Low resource availability (serpentine) increases plant resistance to herbivores. Plant resistance has a negative effect on abundance of all herbivores, but the magnitude of this effect is greater for generalists than for specialists. Lower abundance of generalists removes individuals whose interactions create links across modules. Lower specialist abundance can weaken their positive effect on interaction strength within modules and may reduce the number of modules, but it cannot add/remove links across modules. Plant resistance can also constrain generalist species’ interactions to a subset of potential host plant genera (i.e., reduce their “realized” diet breadth), but it cannot decrease the host range of specialists to fewer than one plant genus. Networks 1–3 illustrate (1) abundance effects on modularity; (2) effects of interaction plasticity on modularity; and (3) a combination of both processes—with a focus on the role of fundamental generalist species (patterned nodes).

- 1) Herbivores will decline in abundance on low-resource serpentine soils, where host plants are more resistant, and this effect will be greater for fundamental generalists than specialists.
- 2) Fundamental generalists will “realize” a narrower breadth of interactions in serpentine soils, where the host plant community is more resistant.
- 3) By reducing the abundance of generalist species and/or narrowing their realized interaction breadth, serpentine soils will be associated with more modular plant-herbivore networks than neighboring nonserpentine soils.

## Methods

**System.** This study was conducted across a naturally occurring mosaic of serpentine and nonserpentine soil patches at the University of California’s McLaughlin Reserve (*SI Appendix, Fig. S2*). Serpentine soils are generally characterized by low Ca:Mg ratios, deficiencies in essential nutrients (N, P, or K), and high heavy metal content (24). We focused on three pairs of congeneric woody shrubs that grow across soil types, as well as a single species (*Adenostoma*) that occurs in both soil types. Species were *Ceanothus cuneatus* (nonserpentine; hereafter, NS) and *Ceanothus jepsonii* (serpentine; hereafter, S) (Rhamnaceae); *Arctostaphylos manzanita* (NS) and *Arctostaphylos viscida* (S) (Ericaceae); *Quercus berberidifolia* (NS) and *Quercus durata* (S) (Fagaceae); and *Adenostoma fasciculatum* (NS, S) (Rosaceae). We chose these species because they are the dominant chaparral vegetation in the region (25, 26) and span a diverse phylogenetic range, and because prior work in this system has documented greater antitherbivore resistance overall in serpentine shrubs (23). At the study site, focal plant species comprise similar proportions of the woody plant species (40% and 44%, respectively) and families (26% and 24%, respectively) present in each soil type (*SI Appendix, Table S3*).

**Larval Collection.** In 2014, we established 12 transects (6 transects/soil type) across the McLaughlin Reserve (*SI Appendix, Fig. S2*). Study plants were selected by walking along each transect and randomly selecting 3 plants/species. This protocol resulted in 18 plants/soil type for all taxa with the exception of nonserpentine *Quercus berberidifolia*, which was absent from one site; replication of this species was  $n = 12$ . In spring 2014 and 2015, externally feeding lepidopteran larvae were collected from focal plants using a beat-sheet (*SI Appendix, Methods*).

**Larval Identification and Diet Breadth Designation.** We collected and reared a total of 2,337 larval Lepidoptera from seven families. Larvae were reared and photographed individually, and categorized into morphotypes with assistance from David L. Wagner (University of Connecticut). Morphotypes ( $n = 80$ ) were replaced by species identifications after the emergence of adults. Adult identification was confirmed by John DeBenedictis at the Bohart Museum of Entomology (University of California, Davis), and vouchers were pinned for accession to the Bohart Museum. We confirmed 53 morphotypes to species and used this subset of species in diet breadth analyses (*SI Appendix, Table S2*). We used published literature to assign species to one of two fundamental diet breadth categories: fundamental generalists ( $n = 24$  species), for species that feed on more than one plant family, and fundamental specialists ( $n = 29$  species), for species that feed within one plant family (*SI Appendix, Table S2*). If a species’ diet breadth was not established in the literature, we used our own records to assign diet breadth ( $n = 10$  species) under the condition that more than three individuals were collected from multiple plant individuals (*SI Appendix, Table S2*).

## Statistical Analyses.

**Sampling completeness.** To ensure that sampling completeness was comparable across networks, we calculated sampling and interaction accumulation statistics following Jordano’s designations (27):  $A$  = number of herbivore species;  $P$  = number of plant species;  $I_{max}$  = number of all potential pairwise interactions;  $n$  = number of records;  $I_{obs}$  = number of observed links in the network;  $I_{est}$  Chao and  $I_{est}$  ACE = two methods for estimating the asymptotic number of unique pairwise interactions (vegan package, function estimateR) (27, 28). We calculated the estimated percentages observed for Chao and ACE as  $(I_{obs}/I_{est})$ .

**Shifts in abundance of fundamental generalists and specialists.** To understand whether low-resource soils are associated with a greater decline in abundance of generalists than specialists, we quantified the abundance of each herbivore species in each soil network in each year ( $n = 4$  networks). If a species was absent from a network, we assigned it an abundance of 0. We fit

a negative binomial generalized linear mixed-effects model (glmer.nb in R) with the larval abundance of each species in each network as our response variable, and soil type and herbivore diet breadth as interactive main effects. We included year as an additional fixed effect and herbivore species as a random effect. (SI Appendix, Statistical Analysis).

**Shifts in realized interaction structure across soil types.** To assess whether generalist herbivores realize different diet breadths in different soil types, we quantified Shannon's partner diversity (H) for each fundamental generalist species in each soil type. This metric weights the partner richness ("degree" in network terminology) of each species by the strength of their interactions, down-weighting weak links (29). We focused this comparison only on fundamental generalists because they have the potential to link or separate modules by broadening or narrowing their diet breadth across host plants (Fig. 1).

For each soil network (nonserpentine, serpentine) in each year (2014, 2015), we calculated the H value for each generalist species (function specieslevel; R package bipartite). To avoid spurious values due to rarity, we excluded any species with fewer than three observations in each soil × year network. We then used generalized linear mixed models (GLMMs) to ask whether these generalist species exhibited differing levels of specialization (partner diversity H) across resource environments. We used year as a fixed effect and herbivore species as a random effect. We also included each species' abundance as a covariate, as more abundant generalists have the statistical "opportunity" to realize more links. To further account for differences in network size, we performed the same analysis after randomly subsampling all four networks to the same size ( $n = 200$  interactions).

**Modularity of serpentine and nonserpentine networks.** We used the DIRTLPAwb+ algorithm (30) to quantify the modularity (Q) of plant-herbivore networks in each soil and year ( $n = 4$  networks). Higher values of modularity, which scales between 0 and 1, indicate greater prevalence of within-module than between-module interactions (31). We then compared the modularity of each empirical network to networks generated by three null models: the Patefield algorithm r2dtable (null model I); shuffle.web (null model II); and swap.web (null model III) (32). Respectively, these three models test the role of species abundance distributions, interactions (connectance), and their combined effect in generating modular structure (SI Appendix, Statistical Analysis).

We also asked whether differences in network size explain modularity results. Because network-grouping algorithms, such as Q, can achieve larger values in networks with more species and links (31), this property was expected to change simply due to the difference in herbivore assemblage size between serpentine and nonserpentine soils. We addressed the role of network size using two approaches. First, we calculated  $Q_{norm}$ , where ( $Q_{norm} = Q/Q_{max}$ ). This standardizes each network's modularity by its theoretical maximum (30). Next, we randomly subsampled each network across a range of size intervals and compared values of  $Q_{norm}$  at a threshold size interval (one-half the size of the smallest network;  $n = 140$  interactions) using a two-sample t test (SI Appendix, Statistical Analysis).

**Shifts in interaction strength and plant resistance across soil types.** To explore whether changes in interaction structure might be associated with soil-mediated plant resistance, we asked whether plant genera with the greatest difference in plant resistance across soil types also exhibit the greatest difference in plant-herbivore interaction strength. To quantify plant resistance, we used published trait data in this system to calculate a "resistance index" (RI) for each plant species in each soil type, following the method of Fine et al. (33). We used five leaf traits found to be important to herbivores in other systems: leaf nitrogen content, leaf carbon content, leaf water content, leaf toughness, and leaf nickel content (34–37). For a given pair of congeners/conspecifics across soils, the difference in these RI values represented the difference in resistance across soil types (SI Appendix, Methods).

To quantify interaction strength (IS), we took the two-year average of the total number of plant-herbivore interactions for each plant species in each soil type. For this comparison, we focused only on interactions with fundamental generalists because of their role in linking or separating modules within the plant-herbivore network. For a given pair of congeners/conspecifics across soils, the difference in these IS values represented the difference in interaction strength across soil types.

All network properties (modularity, H) were calculated using the R package bipartite, version 2.08 (32). All regression analyses were conducted using the lme4 package (38) in R, version 3.3.0. We obtained P values for fixed effects using the car (39) and sjstats (40) packages. The significance of random effects was quantified using log-likelihood ratio tests (base R, function anova). Data visualization was performed using ggplot2 (41, SI Appendix, Statistical Analysis).

## Results

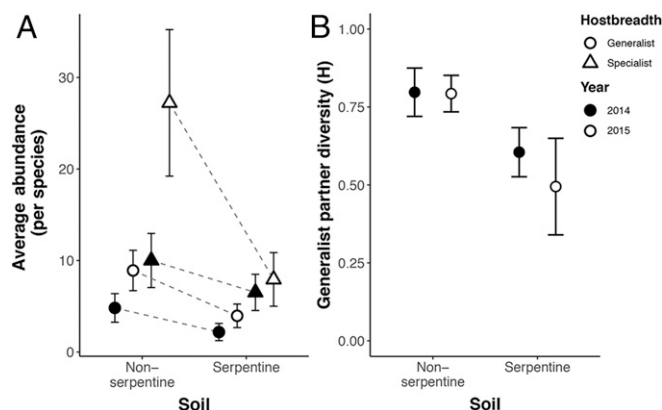
**Sampling Completeness.** Networks captured between 68 and 86% of estimated total interactions. In 2014, we sampled an estimated

68% of nonserpentine interactions and 77% of serpentine interactions. In 2015, we sampled an estimated 82% of nonserpentine interactions and 86% of serpentine interactions (SI Appendix, Table S4).

**Abundance of Fundamental Generalists and Specialists across Soil Networks.** Intrinsically generalized and specialized species declined similarly in abundance from nonserpentine to serpentine networks. Specifically, herbivore species were on average ~60% less abundant on serpentine than nonserpentine soil ( $F_{1,207} = 23.15$ ;  $P < 0.01$ ), but this effect did not differ between fundamental generalists and specialists (nonsignificant soil × host breadth interaction;  $F_{1,207} = 0.17$ ;  $P = 0.70$ ) (Fig. 2A and SI Appendix, Table S5). Species abundances were higher overall in 2015 than in 2014 ( $\beta = 0.75$ ;  $F_{1,207} = 19.22$ ;  $P < 0.001$ ). Abundance also varied by herbivore species (log-likelihood ratio test;  $\chi^2 = 60.7$ ,  $P < 0.001$ ) (SI Appendix, Table S5).

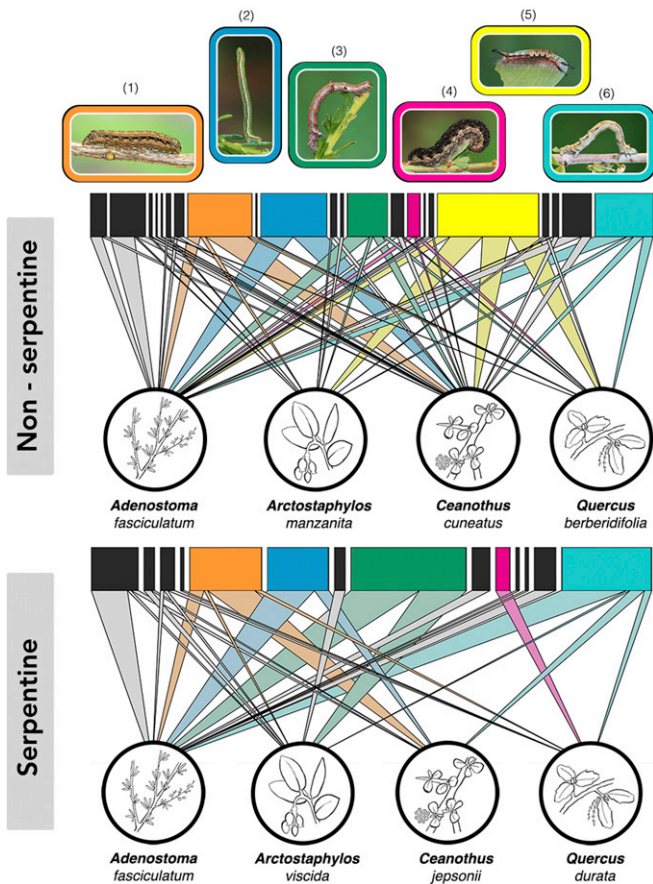
**Shifts in Realized Diet Breadth across Soils.** Shannon partner diversity, H, of generalist herbivores declined by ~33% between nonserpentine and serpentine soils ( $\beta = -0.22$ ;  $F_{1,27} = 5.81$ ;  $P = 0.02$ ) (Fig. 2B and SI Appendix, Fig. S3 and Table S6). There was a positive effect of species abundance on H, with each additional individual increasing this metric by 0.01 ( $\beta = 0.01$ ;  $F_{1,27} = 5.30$ ;  $P = 0.03$ ) (SI Appendix, Fig. S4 and Table S6). We calculated that the average difference in generalist species' abundance from nonserpentine to serpentine soil was ~3.5 individuals, which corresponded to a change of ~0.04 in Shannon partner diversity. Interestingly, despite herbivores being much more abundant overall in 2015 than in 2014 (23), there was no effect of year on partner diversity (Fig. 2B and SI Appendix, Table S6) nor any effect of herbivore species (log-likelihood ratio test,  $P = 1.0$ ). Results were similar when networks were randomly subsampled to control for differences in size (SI Appendix, Table S7).

**Ramifying Effects on Network Modularity across Serpentine and Nonserpentine Soils.** In both years, serpentine plant-herbivore networks were more modular than nonserpentine networks (Fig. 3 and SI Appendix, Figs. S5 and S6). Modularity scores were 12.5 and 5.6% higher in serpentine than in nonserpentine networks in 2014 and 2015, respectively. After accounting for differences in network size by dividing by each web's theoretical maximum



**Fig. 2.** Association between soil type, abundance, and diet breadth of herbivores. (A) Both generalists and specialists decline from nonserpentine to serpentine soil (error bars:  $\pm 1$  SEM). In each soil/year, sample sizes are  $n = 22$  species (generalists) and  $n = 31$  species (specialists). (B) For fundamental generalists, mean H is lower in serpentine than in nonserpentine soils (error bars:  $\pm 1$  SEM). Sample sizes are  $n = 8$  (2014) and  $n = 13$  (2015) species for nonserpentine and  $n = 4$  (2014) and  $n = 8$  (2015) species for serpentine.





**Fig. 3.** Ecological networks between host plants and fundamental generalist herbivore species from nonserpentine and serpentine soil, aggregated across years. We highlight six of these species to show how individual species realize different interaction structures across soils. Species are 1) *Egira perlubens* (orange); 2) *Eupithecia nevadata* (blue); 3) *Hesperumia sulphuraria* (green); 4) *Mesogona olivata* (pink); 5) *Orgyia vetusta* (yellow); and 6) *Tetracis hirsutaria* (teal). Note that species abundances (bar widths) are comparable within but not between networks (*SI Appendix, Fig. S5*).

( $Q_{max}$ ), this shift in modularity remained similar for both 2014 (12.8%) and 2015 (5.6%) (*SI Appendix, Table S8*).

All empirical plant-herbivore networks were significantly more modular than networks generated by our null models. Observed modularity scores of 0.55 to 0.64 were significantly higher than if network structure had been driven by species abundance distributions alone ( $Q = 0.09$ – $0.14$ ; null model I) or by both abundance and connectance ( $Q = 0.35$ – $0.51$ ; null model III). Interestingly, constraining only connectance (null model II) recapitulated the modularity of empirical soil networks (*SI Appendix, Fig. S7 and Table S9*). Together, these null model comparisons suggest that ecological or evolutionary processes are “forbidding links” (42) between some plants and herbivores, and that network structure is shaped independently of species abundances.

Herbivore species’ abundances were almost twice as high in 2015 as in 2014 (Fig. 2A). Despite this large difference, increases in network modularity were maintained from higher-resource nonserpentine soils to lower-resource serpentine soils. Further, when we subsampled all networks to the same size ( $n = 140$  interactions; equal to one-half of the size of the smallest network), serpentine networks retained their lower modularity in both years ( $P < 0.001$ ) (*SI Appendix, Fig. S6*). This temporal replication allowed us to more confidently link differences in network modularity to soil type, and to suggest that such network properties are

more invariant than other properties of the plant-herbivore community, such as assemblage size.

**Shifts in Interaction Strength with Plant Resistance.** We found that shifts in interaction strength across soil types paralleled differences in the resistance index between host plants. Using a total of 437 interactions between host plants and fundamental generalist herbivores, we found that interaction strength changed the most in *Ceanothus* ( $\Delta IS = 42.5$ ) followed by *Adenostoma* ( $\Delta IS = 20.5$ ), *Quercus* ( $\Delta IS = 13.0$ ), and *Arctostaphylos* ( $\Delta IS = 7.5$ ) (*SI Appendix, Table S10*). Similarly, *Ceanothus* exhibited the greatest difference in the resistance index between serpentine and nonserpentine soils ( $\Delta RI = 5.85$ ) followed by *Adenostoma* ( $\Delta RI = 2.82$ ), *Quercus* ( $\Delta RI = 1.59$ ), and *Arctostaphylos* ( $\Delta RI = -0.11$ ) (*SI Appendix, Fig. S8 and Table S10*).

## Discussion

We found that low-resource soils increase the modularity of plant-herbivore networks and that this structural change is largely due to differences in the realized, plastic pattern of species interactions rather than shifting abundances of species with intrinsically different diet breadths. Both fundamental specialists and generalists decline in serpentine soils, resulting in smaller trophic networks, and the generalist species that remain in serpentine networks interact with fewer host plants. These shifts in interactions mirror shifts in plant resistance across soils: Host plant genera that exhibit the greatest resistance increase in serpentine soil also lose the most interactions with generalist herbivores in that soil type. We find that such effects are consistent across years despite an almost twofold difference in overall herbivore assemblage size. Together, these findings highlight the importance of ecological filters in shaping network topology and suggest that abiotic resource availability may be a pervasive driver of network structure in nature.

We find that low-resource serpentine soil negatively affects herbivore abundance; however, contrary to our expectations, this effect was similar regardless of species’ evolved diet breadth. Plant defense theory predicts that generalist “jacks of all trades” are less able than specialists to consume resistant plants (20), and thus we hypothesized that fundamental generalists should decline more than specialists in the more resistant serpentine plant community. This has been found in theoretical studies, with well-defended hosts excluding generalist species in simplified food web models (21). In empirical systems, magnified effects of plant resistance on generalist herbivore species have been documented in *Brassica oleraceae*, with induced plant defense affecting generalist but not specialist herbivores (43). More broadly, toxic plants often host specialized herbivore species and exclude generalists (44). We developed two ideas that can explain why we find similar declines in specialist and generalist herbivores across soils.

First, woody plants such those studied here may rely more on quantitative and physical defenses than on qualitative toxins; such defenses are thought to impede and deter, but not physiologically exclude, generalist herbivores (45). Second, our study uses pairs of closely related (congeneric and conspecific) plant species across soils which are likely to share major classes of chemical and physical defense (46, 47). In sum, resistance traits may differ primarily in magnitude rather than identity across soils—making it less likely that generalist herbivore species would be excluded entirely from a congeneric or conspecific host plant in the other soil type. In systems with more distantly related host plants across environments, we might expect greater decline or turnover of generalists to underlie shifts in network structure rather than interaction plasticity of shared herbivore species. Similarly, if low-resource environments are dominated by toxic plant species, these plant communities can exclude generalists entirely, with even stronger effects on network-level modularity.

While generalists did not experience disproportionate decline across soil types, they exhibited narrower diet breadth (lower partner diversity) in low-resource serpentine soil, even after accounting for changes in abundance. We found that contraction (e.g., *Hesperumia sulphuraria*, *Mesogona olivata*; Fig. 3) or skewing (e.g., *Eupithecia nevadata*, *Tetracis hirsutaria*; Fig. 3) of generalist diet breadth was the primary driver of differences in network modularity across food webs.

Shifts in hostplant use by generalists may, in turn, be shaped by the different levels of plant resistance in serpentine and non-serpentine soil. We found that plant genera or species with the greatest difference in their plant resistance index across soils also exhibited the greatest change in interaction strength with generalist herbivores (SI Appendix, Table S10). A similar effect of plant resistance on realized diet breadth was found across elevational gradients, with generalist butterfly species consuming fewer host plant taxa in more resistant low-elevation host plant communities and broadening their host breadth at higher elevations, where potential hosts were more benign (48). However, other studies found the opposite relationship: In the Brazilian *cerrado* and *cerradão*, caterpillar diet breadth increases as the dry season progresses (49) and as soil fertility declines (22). In these systems, such temporal and spatial shifts in diet breadth are associated with lower host plant richness and density, suggesting that generalists may become less selective when options are few (22). In contrast, when shifts in plant quality occur independently of changes in quantity, generalists may realize more specialized links with higher-quality host plants. Because woody host plants were similarly available across serpentine and nonserpentine soils and sampling occurred simultaneously across environments, our study may reflect shifts in realized diet breadth that occur when plant availability is more constant. Together, these findings provide a framework for predicting plastic change in generalist diet breadth, and subsequent effects on network structure, across different types of environmental variation.

More broadly, linking species-level processes to network outcomes can deepen our understanding of how modularity might confer stability within food webs. For example, herbivores may compete via shared enemies on common host plants (apparent competition) (50), with species loss or gain altering attack rates on neighbors. Modular networks, like those on our resource-poor soils, may lessen such indirect effects among species by limiting co-occurrence of the same species—and their accompanying predators or parasitoids—to fewer food web modules (3). Traits like diet breadth may also affect the likelihood of sharing enemies: Fundamentally generalized herbivores may be attacked by more (and more generalized) enemy species than fundamental specialists (51). Thus, a modular network composed of fundamental specialists may contain fewer indirect links through shared enemies, within or among modules, than one composed of fundamental generalists acting as “realized” specialists. Future studies should consider how the potential for indirect effects within networks—and consequences for stability—may be shaped by emergent network structure in concert with traits of constituent species.

The ability of species in a network to reorganize the links they form with resource nodes—topological plasticity—has been found

to increase stability in both mutualistic (52) and trophic (53) networks. Identifying fundamental generalists within networks, and understanding the circumstances under which they rewire their interactions, is thus an important frontier in network ecology. We find that networks are topologically plastic across two resource contexts, becoming more modular in low-resource serpentine soil due to narrower “realized” diet breadths of shared generalist species. Interestingly, this shift toward a more stable interaction structure (2, 3) occurs even as herbivore species’ local abundance declines, which should otherwise increase extinction risk and decrease community robustness (54). Together, these findings suggest that the importance of network plasticity per se should be considered in conjunction with the stability that resulting topologies (and abundances) may confer. In addition, aside from increasing network stability in the present, this plastic narrowing of diet breadth may be a precursor to the evolution of specialists from generalists (e.g., the “oscillation hypothesis of diversification”) (55). Thus, dietary shifts can be both a driver of plant-herbivore network structure in the short term, which is our focus here, and linked to evolutionary outcomes for herbivores over longer timescales.

A common critique of network analysis is that it is disconnected from community ecological theory (8). To date, most empirical studies of modularity in antagonistic and mutualistic ecological networks have focused on significant deviation from random structure. Fewer studies explore potential mechanisms leading to structural variation (SI Appendix, Table S1). When mechanisms generating modularity are explored, the focus is often on the role of phylogenetic constraint (10) and trait matching (11) as processes that fundamentally prevent organisms from interacting across modules, leaving processes that shape presence and strength of realized links underexplored (SI Appendix, Table S1, but see ref. 9). Here, we use the theoretical frameworks of resource availability (16, 33) and plant defense theory (20) to understand how and why modularity varies in plant-herbivore networks. We find that fundamental generalists realize more specialized interactions in low-resource serpentine soils, increasing modularity at the scale of the entire network. Shifts in generalist interaction strength mirror differences in host plant suitability across soils, consistent with theoretical predictions of trophic structure in more resistant host plant communities. These structural differences persist across years despite variation in overall herbivore assemblage size. Together, these findings suggest that greater modularity—and thus stability (2, 3, 5)—may be a general property of plant-herbivore networks in low-resource contexts.

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