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The effects of intraspecific and interspecific diversity on food web stability

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Abstract

Although the effects of species diversity on food web stability have long been recognized, relatively little is known about the influence of intraspecific diversity. Empirical work has found that intraspecific diversity can increase community resilience and resistance, but few theoretical studies have attempted to use modeling approaches to determine how intraspecific diversity will affect food web stability. To begin to address this knowledge gap, we added intraspecific diversity to May's classic random food web model. We found that, like species diversity, intraspecific diversity decreased stability. These effects on stability were not simply attributable to changes in interaction strengths, suggesting that intraspecific diversity can have its own independent effects on stability. Its effect depends on the relationship between inter- and intra-genotype interactions; when competition within genotypes was stronger than among them, food webs were generally more stable than when the converse was true. Overall, our model suggests that determining the direction and the magnitude of intraspecific diversity's effects on stability in natural systems will require more empirical information about how its inclusion alters patterns of interaction strength and food web topology.

Keywords Intraspecific diversity · Genetic diversity · Diversity-stability relationship · Food webs

Introduction

The relationship between biodiversity and the stability of trophically structured communities has long been a topic of interest in ecology. Empirical work and early intuitions suggested that greater species diversity would stabilize communities (reviewed by McCann, 2000). For example, Elton (1958) observed that diverse natural communities were less frequently invaded by herbivorous pests than species-poor, human-altered habitats such as agricultural fields. Yet early theoretical work on community stability by May (1972) found that increasing the number of species in a randomly constructed food web was destabilizing. Thus, there seemed to be substantial contradictions between empirical observations and theoretical predictions about biodiversity's impact on stability.

In the years following May's seminal study, scientists sought to resolve this discrepancy between empirical and theoretical expectations. One avenue of research found that diversity often promotes the occurrence of weak species interactions in real food webs (Wootton 1997; Kokkoris et al. 1999; McCann 2000). Weak interactions can stabilize communities by dampening the fluctuations induced by strong interactions between consumers and resources (McCann et al. 1998; McCann 2000). May (1972) made a similar argument from a mathematical perspective by showing that randomly assembled communities are stable when $\alpha < 1/\sqrt{CN}$, where α, C, and N respectively represent mean interaction strength, connectance (proportion of all species interactions realized), and the number of species. Thus, if interactions are weak on average, there is a greater chance that the inequality will hold and that the community will be stable. These studies collectively support the idea that promoting weak species interactions may be one mechanism by which species diversity increases stability in real communities.

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Other aspects of food web topology can also contribute to stability. For instance, consumer-resource interactions, particularly omnivory, can promote food web stability (Hastings and McCann 1997; Allesina and Pascual 2008; Allesina and Tang 2012; Caravelli and Staniczenko 2016), while mutualistic and competitive interactions can be destabilizing (Allesina and Tang 2012). Compartmentalization also leads to greater stability because in compartmentalized food webs, subsets of species interact more among themselves than with others, and perturbations thus tend to propagate within but not between compartments (Krause et al. 2003; Stouffer and Bascompte 2011). Because this is more common in empirical than randomly assembled food webs, it may help explain the discrepancy between the two (Krause et al. 2003; Rezende et al. 2009; Stouffer and Bascompte 2011). The nested structure of an interaction web may also relate to stability; nestedness is often stabilizing, but webs that are nested such that generalist resources are preferred by all consumers while specialist resources are neglected by all consumers are generally unstable (Staniczenko et al. 2013). Hence, diversity could indirectly affect stability by altering (i) the frequency of different types of interactions, (ii) the degree of compartmentalization, or (iii) the type of nestedness in food webs.

The discrepancy between empirical and theoretical expectations about the impact of diversity on stability may also be due in part to differences in how complexity and stability are defined (Pimm 1984). In this study, we will focus on local stability, which determines whether a community is able to return to its interior equilibrium following an infinitesimal perturbation. Local stability thus differs from global stability which refers to a community returning to its interior equilibrium following a perturbation of any size (Pimm 1984). Assuming infinitesimal perturbations, local stability is directly related to community persistence in that a locally stable interior equilibrium necessarily entails the persistence of all species. Under those conditions, local stability can thus be seen as a conservative estimate of community persistence because a locally stable interior equilibrium implies the persistence of all species, whereas not all scenarios leading to the persistence of all species will necessarily yield a locally stable interior equilibrium.

Although the effects of species diversity on food web stability have received much attention, little is known about the influence of diversity within species. However, intraspecific diversity is ubiquitous, and empirical studies often show that it promotes resilience and resistance (Hughes and Stachowicz 2004; Reusch et al. 2005); affects food web structure, potentially by making it more complex or less connected (Quevedo et al. 2009; Rudolf and Rasmussen 2013; Barbour et al. 2016; Clegg et al. 2018); and supports more species-rich communities (Crutsinger et al. 2006). The magnitude of these effects may even be comparable to that of species diversity (Des Roches et al. 2018). The few theoretical studies that exist show that intraspecific diversity changes food web structure or interaction strengths (Moya-Laraño 2011; Gibert and Brassil 2014; Gibert and Delong 2017), suggesting that it could subsequently affect stability. Intraspecific diversity can also stabilize competitive networks (Maynard et al. 2019) or increase species coexistence in consumer-resource systems (Gibert and DeLong 2015). However, aside from these few studies, the effect of intraspecific diversity on food web stability has rarely been addressed from a modeling perspective (Bolnick et al. 2011). Given the similarities in the community-level impacts of species and intraspecific diversity, it is likely that the latter could have analogous effects on food web stability.

All things being equal, we may then predict that increasing intraspecific diversity in a random community will be destabilizing if it does not cause concomitant changes in food web properties that increase stability. However, theoretical studies have shown that, like species diversity, intraspecific diversity in predator-prey interactions can cause several changes associated with increased stability. For instance, intraspecific diversity can decrease interaction strengths and increase connectance and omnivory (Moya-Laraño 2011). It can also enhance food web complexity (Moya-Laraño 2011; Barbour et al. 2016), which increases stability in real food webs (Dunne et al. 2002). Importantly, an empirical study of food webs found that differences between food webs that accounted for intraspecific diversity due to ontogenetic shifts and those that did not were due in part to real differences in structure and function, not simply increased complexity (Clegg et al. 2018). Intraspecific diversity is likely to have real effects on food web structure, but because it can change food web topology in several different dimensions, it may not be easy to predict how it will ultimately impact stability.

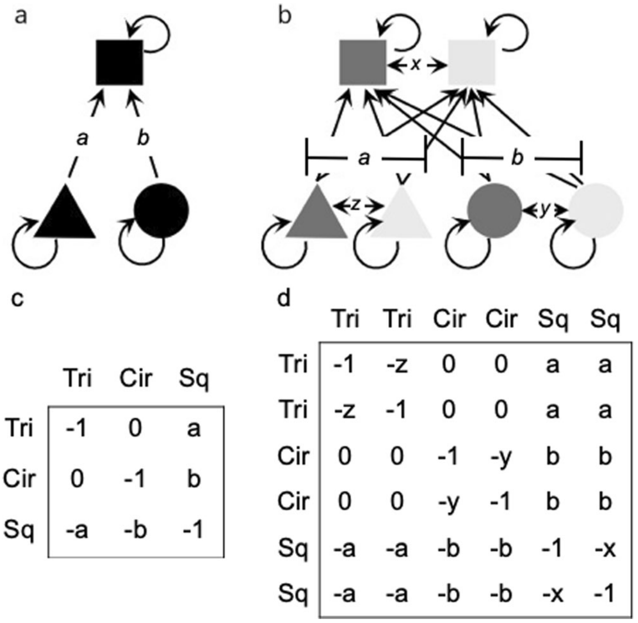
In addition, the effect of intraspecific diversity on food web stability may also depend on relative interaction strengths in the food web. Theory suggests that for two species to coexist, the strength of intraspecific competition must be greater than that of interspecific competition (Chesson 2000). An analogous rule may apply for multiple genotypes of the same species to coexist stably in a food web, but there is not yet strong evidence for or against this rule. Intraspecific diversity could result in different patterns of interaction strengths between and among genotypes, so determining how the relationships between those interactions relate to stability will be important for fully understanding the impact of intraspecific diversity.

Because the effect of intraspecific diversity in food webs is not yet well understood, we sought to use the most basic (random) food web model to determine whether inter- and intraspecific diversity affect food web stability differently. Specifically, we asked the following questions: (1) How does intraspecific diversity affect stability in randomly assembled food webs? (2) Does the effect of intraspecific diversity depend on the relative strengths of inter- and intragenotype interactions? These results will help inform directions for future research to better understand how and when intraspecific diversity should be incorporated into ecological research.

Methods

We modified May's random food web model (May 1972) by adding intraspecific diversity. In May's classic model, random values were used to populate a matrix of pairwise interactions, α_{ij}, between each species i and j. Intraspecific interactions found along the diagonal of the matrix were set to -1 such that each species exhibited negative density dependence. All other interactions were set to zero with probability $1 - C$ (where C is connectance, the proportion of all species interactions realized) or a non-zero random number with probability C. Random values for interaction strengths were drawn from a standard normal distribution (mean $\mu = 0$ and standard deviation $\sigma = 1$). We made an adjustment to the May model following Allesina and Pascual (2008) by making all interspecific interactions predator-prey (or host-parasite) interactions. Predator-prey interactions are represented by a positive effect of the prey on the predator and a negative effect of the predator on prey.

We built on that model by adding intraspecific diversity to each interaction matrix (Fig. 1), following similar methods to those used to establish interspecific interactions. Although we will use the term "genotypes" to refer to intraspecific diversity throughout this paper, our results apply equally well to ecotypes or any other form of variation within species. We added a row and column to the food web matrix for each additional genotype in each species (Fig. 1d). For simplicity, intraspecific variation was only added to interaction coefficients governing competition between genotypes of the same species, not to predator-prey interactions among species. Specifically, if there was a predator-prey interaction between two species in the original food web matrix without intraspecific diversity, all genotypes of those two species interacted according to the same α_{ij} where i and j represent species (not genotype) identity (Fig. 1). As in May's model, the diagonal elements (here, intragenotype competition) were constant for all genotypes and species. For intraspecific competition among genotypes, interaction strengths were either 0 or a random value with probability $1 - C$ or C, respectively, to remain consistent with the way species interactions were assigned. The results based on this scheme hold when all genotypes within a species are allowed to interact with each other, rather than interactions being assigned with probability C, although trends are more difficult to discern as the effect of genotypic richness is more extreme (Supplementary Fig. 1). Hence, our results are robust to the specific scheme used to determine whether genotypes are allowed to interact. The strength of intraspecific competition among genotypes was assigned using random values drawn from a normal distribution with mean -1 so that interactions among genotypes within species were constrained to be largely competitive. As with species diversity, the standard deviation was set to 1. Food webs with more genotypes are said to have greater intraspecific variation.



	Tri	Cir	Sq
Tri	-1	0	a
Cir	0	-1	b
Sq	-a	-b	-1

	Tri	Tri	Cir	Cir	Sq	Sq
Tri	-1	-z	0	0	a	a
Tri	-z	-1	0	0	a	a
Cir	0	0	-1	-y	b	b
Cir	0	0	-y	-1	b	b
Sq	-a	-a	-b	-b	-1	-x
Sq	-a	-a	-b	-b	-x	-1

Fig. 1 Conceptual figure of a random food web model **a** without and **b** with intraspecific variation. Letters next to arrows indicate the strength of that interaction. Food web models are used to build adjacency matrices for food webs **c** without and **d** with intraspecific variation. When intraspecific variation is added to food webs, predator-prey interactions and self-limitation remain unchanged while competition within species varies among genotypes and species

We sampled the parameter space by varying connectance, C, from 0.1 to 0.3 by steps of 0.1; species richness, S, from 10 to 50 by steps of 5; and genotypic richness, G, from 1 to 10 by steps of 1. G was constant across all species in the food web. We ran 500 simulations for each combination of parameters. We also ran 100 simulations with the standard deviation of the distribution of interactions within species set to 0.1 instead of 1 to see how outcomes changed when interactions among species were more similar than interactions between species, a condition that seems likely to be common in the real world.

To determine how the relative strengths of inter- and intragenotype competition relate to stability, we also established three versions of the model in which these relationships varied. Specifically, simulations were carried out such that average strengths of competition fell into one of the following categories: (I) intragenotype competition > intergenotype competition, (II) intra- and intergenotype competition are equal, and (III) intragenotype competition < intergenotype competition. In reality, average intragenotype competition was always stronger than intergenotype competition, but the ratio of intra- to intergenotype competition was greatest in model version I and least in model version III. We will continue to use our above descriptions as shorthand because it is a clear way to describe that we varied the relative strength of inter- and intragenotype competition. All competition strengths were selected randomly from normal distributions, but their means, μ, varied so that the above conditions would hold true on average ($\mu_{\mathrm{I}} = -1$, $\mathrm{diagonals}_{\mathrm{I}} = -2$; $\mu_{\mathrm{II}} = -1$, $\mathrm{diagonals}_{\mathrm{II}} = -1$; $\mu_{\mathrm{III}} = -2$, $\mathrm{diagonals}_{\mathrm{III}} = -1$).

Each randomly assembled community was then assessed for stability using a local stability analysis. A system like this is locally stable only when the real part of all eigenvalues is negative, meaning that all species and genotypes return to their non-zero equilibrium abundance following an infinitesimal perturbation. We used this metric to compare food web stability across parameter space and among the three models. We also determined mean α values for each simulation to see whether stability was related to interaction strengths.

Results

In the simple random model, increasing genotypic and species richness were both destabilizing (Fig. 2), and increasing genotypic richness was more destabilizing than increasing species richness (Table 1). Both species and genotypic richness had the same effects on the proportion of eigenvalues with negative real parts, but increases in either type of richness caused less dramatic changes in the proportion of eigenvalues with negative real parts than in stability (Fig. 2a–f).

The relationship between inter- and intragenotype competition strength had a substantial effect on stability. When intragenotype interactions were stronger than intergenotype interactions, stability was generally greater (Fig. 2b) than in simulations in which intragenotype interactions were weaker than or equal to intergenotypic interactions (Fig. 2a, b vs. Fig. 2c–f).

Genotypic richness may affect stability via changes in interaction strength as previous work has shown that food webs dominated by weaker interactions tend to be more stable. Surprisingly, high stability was associated with stronger mean interaction strengths (Fig. 3a). However, in general, stability varied substantially with very little change in interaction strength (e.g., Fig. 3i), suggesting that differences in interaction strengths did not drive differences in stability associated with genotypic richness. In addition, if we changed the mean of the distributions from which interaction strengths were drawn to make mean interactions stronger, food webs were somewhat destabilized, but the overall pattern of decreasing stability with increased intraspecific diversity was maintained (Supplementary Fig. 2).

Discussion

Our simulation results suggest that diversity within species affects the stability of random food web models, just as species diversity does. Stability generally decreases with intraspecific richness, but the relative strength of intraspecific interactions also matters. As with competition among species, food webs that have stronger intra- than intergenotype competition are less destabilized by intraspecific diversity than those that have weaker intra- compared with intergenotype competition. Thus, the magnitude but not the direction of the effect of intraspecific diversity on stability will depend on the balance of interactions among and within genotypes.

The decrease in stability that we observed with increasing intraspecific diversity likely occurred because intraspecific diversity can affect multiple aspects of the inequality governing stability. In completely random communities, stability occurs when $\alpha < 1/\sqrt{CN}$ (May 1972). Although our communities were not entirely random because species were only allowed to engage in predator-prey interactions, the lack of any constraint on the relationship between genotypes within species means that May's criterion is likely a more useful heuristic for predicting the effects of diversity, connectance, and mean interaction strength on stability in our study than the more recent criterion derived for pure predator-prey systems (Allesina and Tang 2012). Overall, intraspecific diversity can increase the likelihood of stability by decreasing interaction strengths, but it can also decrease the likelihood of stability by increasing complexity (by effectively increasing the number of species, N). It follows that if intraspecific diversity has no other effects on food web structure, it is only expected to increase stability when it reduces mean interaction strength (since it necessarily increases effective N). Additionally, because the right-hand side of this inequality is a nonlinear decreasing and decelerating function, initial increases in intraspecific diversity via higher N will tend to promote instability more than increases at larger values of N, unless intraspecific diversity also greatly reduces mean interaction strength. In our model, stability decreased with intraspecific diversity regardless of any changes in interaction strength (Fig. 3), suggesting that, given changes in interaction strength of this magnitude, stability was mainly governed by N. Thus, the default expectation should be that increasing intraspecific diversity will generally reduce stability, particularly at the low end of the complexity spectrum, unless it severely constrains interaction strength or alters the topology of the food web in other ways.

This result suggests that intraspecific diversity alone does not necessarily stabilize food webs. However, as with species diversity models, adding intraspecific diversity in real systems may alter food web topology, affecting stability in ways that are not reflected in our model. For instance, intraspecific niche partitioning in a generalist fish predator promotes food web

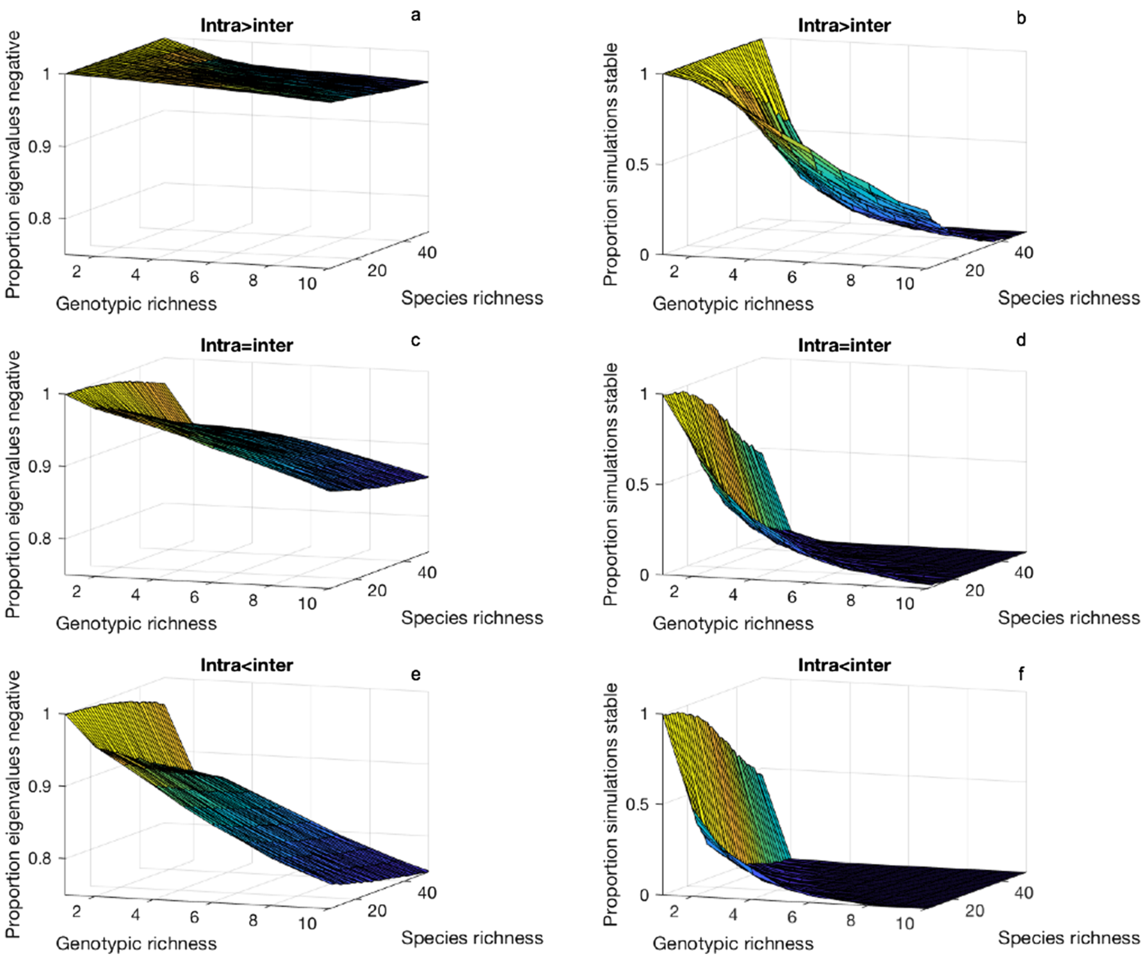


Fig. 2 Effects of species and intraspecific richness on the proportion of eigenvalues in simulations whose real parts are negative (left column) and the proportion of simulations that are locally stable (right column). Competition within genotypes was constrained to be stronger than among genotypes (I; top row), unconstrained (II; middle row), or weaker than among genotypes (III; bottom row). Values are averaged across all connectance levels. Note that z-axis ranges differ in the right and left columns

modularity or compartmentalization (Quevedo et al. 2009) which is known to promote stability (Krause et al. 2003; Stouffer and Bascompte 2011). In our model, modularity would not be meaningful as interactions were randomly generated so any modules found would simply be artifacts of that process. However, this may be a way in which our simple model lacks realism as modularity or compartmentalization likely exists in real food webs. Similarly, intraspecific diversity has been shown to decrease interaction strength, increasing species persistence in a consumer-resource model (Gibert and Brassil 2014). However, intraspecific diversity may also decrease stability in real systems by causing species interactions to be less generalized (Fagan 1997; Clegg et al. 2018). Finally, food webs are stabilized by asymmetrical interactions characterized by differences in the magnitude of the interaction strengths between species pairs (Jordán et al. 2003; Bascompte et al. 2006). Interaction asymmetry is affected by species abundances and spatial distributions (Vázquez et al. 2007; Morales and Vázquez 2008), which intraspecific diversity could also change, thereby stabilizing or destabilizing the food web depending on the particular direction of its effects. These topological changes that intraspecific diversity imposes

Table 1 Slope estimates from multiple regression of local stability against standardized species and intraspecific richness in simulations with competition within genotypes more than among (intra > inter; I), unconstrained (II) or less than among genotypes (intra < inter; III)

	Intra > inter (I)	Unconstrained (II)	Intra < inter (III)
Species richness	− 0.14	− 0.075	− 0.042
Intraspecific richness	− 0.28	− 0.18	− 0.15

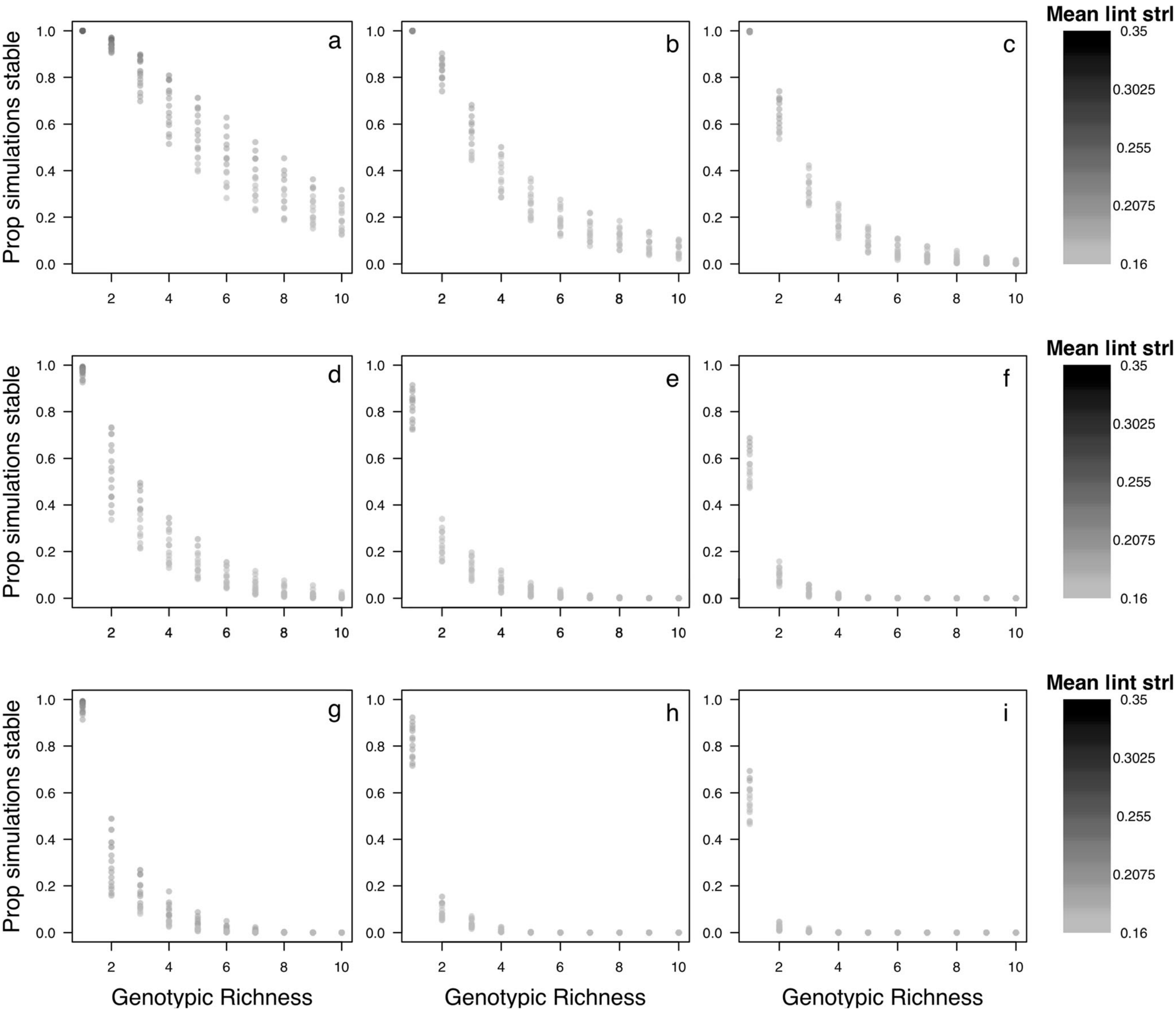


Fig. 3 Mean proportion of simulations that are locally stable at each level of genotypic richness in low species diversity (left column), medium species diversity (middle column), and high species diversity (right column) simulations. Points are colored according to the mean absolute value of interaction strengths with darker points indicating stronger interactions and lighter points indicating weaker interactions. Competition within genotypes was constrained to be stronger than among genotypes (I; top row), unconstrained (II; middle row), or weaker than among genotypes (III; bottom row). Values are averaged across all connectance levels

on real food webs suggest that it could be more stabilizing than our results suggest.

It is important to note that systems were only locally stable by our measure if all genotypes of all species had negative real parts of their eigenvalues. However, in real systems, we might also be interested in knowing whether all species persist even if some genotypes go extinct. This is analogous to metrics often used in empirical studies in which measuring species-level persistence is more feasible than genotype-level persistence, and empirical studies using this measure often find that intraspecific diversity promotes stability via resilience and resistance (Hughes and Stachowicz 2004; Reusch et al. 2005; Agashe 2009). This is in contrast to the results from our model and is likely due to a sampling effect as the probability of including a genotype capable of persisting increases as more genotypes are added (Aarssen 1997; Huston 1997).

Intraspecific diversity may enhance community persistence in real systems by providing redundancy, but as our model results demonstrated, local stability may decrease since all genotypes are unlikely to persist as intraspecific diversity increases. In the long run, if multiple genotypes are not conserved, intraspecific diversity decreases, and the community will become less stable at each point in time as the likelihood of including a genotype capable of persisting decreases. A loss of genetic diversity has also been shown to lead to different community and ecosystem outcomes (Olden et al. 2004), suggesting that not only will persistence of all species not be guaranteed but community function may also be altered. These results thus suggest that ignoring genotypic diversity as a source of redundancy and species persistence may eventually lead to an elevated risk of extinction.

Other effects of intraspecific diversity

Intraspecific diversity may have different effects on stability depending on the context. We found that the relative strength of inter- and intragenotype competition affected stability in a way that was analogous to expectations based on species interactions. Stronger interactions within genotypes than among them promoted stability just as stronger intraspecific than interspecific competition promotes coexistence of multiple species (Chesson 2000). However, little work has compared inter- and intragenotype interaction strengths empirically, so which relationship is most common in the real world remains unclear. Contrary to our model predictions of the conditions that lead to stability, the limited data that exist show that competitive interactions are stronger among genotypes than within (Andalo et al. 2001; Chang and Smith 2014) or do not show a clear pattern (Fridley and Grime 2010). Although these results come from few studies in few systems, our model suggests that if this pattern is common in real systems, intraspecific diversity may often destabilize communities via its effect on the relative strength of interactions among and within genotypes.

We saw little difference in the effect of species richness compared to intraspecific richness, with the only apparent distinction being in the magnitude of their effects on stability. This is unlikely to be due purely to an increase in complexity as models with the same number of taxonomic units (e.g., $S = 40$ and $G = 1$ compared with $S = 10$ and $G = 4$; Fig. 2), and hence the same number of interactions, were consistently less stable when G was large than when S was. This may be partly because greater genotypic richness shifted the relative balance of inter- and intragenotype competition towards greater relative strength of intergenotype competition in our model (Supplementary Table 1), which was destabilizing. Empirical work will be required to determine whether or not that shift occurs in real systems.

In addition, the difference in the magnitude of the effect of the two types of diversity on stability could be because intra- and interspecific interaction strengths varied by the same amount in this model, a simplification that may be unrealistic. For instance, in terrestrial plants, intraspecific trait variation accounts for on average 25% of trait variation in a community, while interspecific variation accounts for the rest (Siefert et al. 2015). As trait variation is closely related to niche variation and competition strength, this suggests that making intra- and interspecific interaction strengths equal may not be entirely representative of reality. However, when we decreased the amount of variation in intraspecific interactions to 10% of variation in interspecific interactions, the most extreme change that occurred was that the effects of genotypic diversity and species diversity became equal (Supplementary Table 2). Thus, our results suggest that under realistic patterns of trait variation, intraspecific richness may often have a stronger effect on stability than does species richness. However, further study of how much variation each source contributes in other taxa may be necessary to better understand how these model predictions apply in different situations.

Our simple random model is a useful starting point for understanding how intraspecific diversity affects food web stability, but additional empirical research is needed to help inform more realistic models that address the mechanisms by which intraspecific diversity affects stability. A particularly useful area of research would be to investigate how inter- and intraspecific diversity affect the strength of species interactions in order to elucidate real-world patterns of interactions and the conditions under which various constraints on species interactions apply. For instance, future research could address how inter- and intraspecific interaction strengths compare, how the effects of intraspecific diversity on species interactions differ from those of interspecific diversity, and realistic patterns of inter- relative to intragenotype competition. In addition, the theoretical research that exists on the community-level effects of intraspecific diversity to date tends to focus on very simplified systems or intraspecific variation due to ontogenetic changes (Rudolf and Rasmussen 2013; Clegg et al. 2018). Extending beyond simple systems and discrete differences among ecotypes or stages to investigate how more common amounts of intraspecific diversity affect more complex communities would be a productive next step. Finally, the degree of intraspecific variation may not be equal among all trophic levels (Svanbäck et al. 2015), and incorporating more realistic patterns of intraspecific variation may contribute to a better understanding of the effect of intraspecific variation on stability. The future research avenues suggested here would help build more realistic modeling frameworks to tease apart the relative importance of the different mechanisms by which intraspecific diversity alters stability in trophically structured communities.

We have shown that intraspecific diversity in random food webs can decrease stability, even as empirical studies tend to show the opposite. This contradiction makes clear the importance of being explicit about what aspect of stability a study seeks to understand and why one metric or another was chosen. These patterns could change in direction or magnitude as more realism is added to the model; for instance, the relative balance of inter- compared to intragenotype competition can affect how stabilizing or destabilizing intraspecific diversity is. However, in general our results suggest that species and intraspecific diversity have qualitatively similar effects in agreement with the few empirical studies that compare their effects (Cook-Patton et al. 2011; Des Roches et al. 2018). Overall, developing a better understanding of how intraspecific interactions differ from their interspecific counterparts will help explain how these two types of diversity jointly influence the stability of natural food webs.

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