How does plant biodiversity affect the structure and dynamics of plant-animal interaction networks?

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Abstract

The diversity-stability relationship depends critically on how species diversity affects the network structure of species interactions. However, research attempting to resolve the diversity-stability debate often neglects to examine the link between diversity and network structure. Here, we take a functional trait approach to predict how changes in plant functional diversity will affect the structure of plant-animal networks. Our model predicts that increasing plant functional diversity enhances the modular structure of the network; however, this relationship is dampened when interacting with a generalist animal community. Importantly, our model offers testable predictions that can be acquired readily from empirical data. Given the theoretical relationships between network structure and stability, our model indicates that plant functional diversity could stabilize or destabilize interaction networks, depending on whether interacting animals are antagonists or mutualists.

Diversity-Structure-Stability Debate

The relationship between species diversity and community stability has been debated for decades. Starting in 1955, Robert MacArthur used a simple graphical model to demonstrate that increasing the number of species or links in a food web should dampen population fluctuations in a community (MacArthur 1955). Around the same time, Charles Elton (1958) proposed that complex communities frequently prevented invasions from other species, drawing on evidence that biological invasions occurred frequently in boreal forests and agricultural fields, while invasions were unheard of in tropical forests. However, this notion of more diverse and complex communities being more stable was questioned in the 1970s with dynamical models of communities (Gardner and Ashby, 1970; May 1972). Robert May's (1972) work was particularly influential, where he showed that either increasing species diversity, connectance, or interaction strengths destabilized randomly assembled communities. May's work spurred an entire line of research trying to better understand how the apparently diverse and complex communities we observe in nature persist over time.

A key insight emerging from subsequent diversity-stability research is that the strength and organization of species interactions (network structure) is not random, as May's model assumed. In fact, many structural properties of real interaction networks appear to confer stability to diverse assemblages of species (McCann 2007; Bascompte 2009). For example, the large number of weak trophic interactions that link species in real communities can be a potent stabilizing force (Yodzis 1981; McCann 1998, 2000). Similarly, the modular structure frequently observed in food webs (Thebault & Fontaine 2010; Stouffer and Bascompte 2011) and nested architecture of mutualistic networks (Bascompte 2003; Thebault & Fontaine 2010; Rohr et al. 2014) enhance community persistence and resilience to perturbations.

Research linking network structure to community dynamics, however, has not been paralleled by active research linking species diversity to network structure. Understanding the relationship between diversity and network structure is just as critical though, if we want to resolve the diversity-stability debate. One key point that has been made though is that species diversity will only alter network structure if species are functionally different from each other (Ives 2005). Therefore, species diversity, *per se*, will not affect network structure, but functional diversity has the potential to. For example, the functional diversity of plant communities has been shown to be a better predictor of plant productivity than species diversity, because it better encapsulates the complementary trait differences between species in their ability to acquire different resources (Tilman et al. 1997; Cadotte 2017). Similarly, it has become clear over the years that a functional trait approach is critical for predicting interactions between species at different trophic levels (Ings et al. 2008).

Heuristic Model of Diversity-Structure Relationship



To help fill this knowledge gap, we developed a heuristic model to predict how changes in plant functional diversity will affect the architecture of plant-animal interaction networks. We focus on plant-animal networks because of their fundamental importance in determining regulating and provisioning ecosystem services in terrestrial environments. Our model explores how network assembly is influenced by plant functional trait diversity and the degree of specialization in animal communities. In particular, we were interested in how plant and animal trait distributions ￼affect the modularity and nestedness of plant-animal networks. Theoretical models suggest that the modular and nested architecture of plant-animal interactions play a key role in the persistence and resilience of these networks (Thébault & Fontaine 2011, Stouffer & Bascompte 2010, Rohr et al. 2014), which is why we focus on these structural properties.

Our model abstracts reality by representing plant and animal traits along a single trait dimension. We hold the number of species constant for this current simulation to focus on differences in trait diversity and composition of specialists. To create plant communities that varied in trait diversity, we randomly drew 20 plant species from a uniform trait distribution. Our lowest level of trait diversity sampled plants from a trait space ranging from 0 to 0.1, while our highest level of diversity varied from 0 to 1. Likewise, we randomly drew 20 animal species from the same uniform trait distribution used for the plants, but we also varied the proportion of specialists that comprised the community (0 to 100%). We arbitrarily assumed that specialist animals had a niche width of 0.05, while generalists had a niche breath of 0.5 for all the simulations. We determined pairwise interactions if an animal's niche width overlapped with the plant's position in functional trait space. We then calculated the nestedness (NODF, Almeida-Neto et al. 2008) and modularity (QB, Beckett 2016) of each plant-animal network. The code used to simulate this model and reproduce the figures is publicly available at https://github.com/mabarbour/network\_assembly.

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| **Figure 1 | Example of network assembly in our heuristic model.** For network (A), plant functional diversity = 0.5 and proportion of specialist animals = 0.25. For network (B), plant functional diversity = 1.0, and proprotion of specialist animals = 0.75. We used 20 species each of plants and animals for the actual simulations, but only show four species each here to make clear how we assembled plant-animal networks. |

Our model predicts that increasing plant functional diversity will reduce the nested architecture of the network (Fig. 1A). Given the strong trade-off between nestedness and modularity (Thébault and Fontaine, 2010), this also indicates that increasing functional diversity will result in a more modular network (Fig. 1B). This result is intriguing, because nestedness is thought to confer stability to mutualistic networks, whereas modularity stabilizes antagonistic networks (Thébault and Fontaine, 2010). Therefore, whether plant functional diversity is stabilizing or not may depend on whether the animal community consists of mutualists or antagonists. The strength of this diversity-structure relationship, however, is contingent on the specialization of the animal community (Fig. 1). For example, nestedness decreases much more rapidly with plant functional diversity when there are a higher proportion of specialists in the animal community. Therefore, plant functional diversity and trait composition of the animal community interact to determine network structure.

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| **Figure 2 | Predicted network architecture of plant-animal interactions due to variation in plant functional diversity and the proportion of specialist animal species.** |

Future Directions

Our heuristic model takes an important step toward predicting the relationship between plant diversity and network structure; however, these predictions need to be tested. One way to do this would be to leverage the large number of plant-animal networks that are publicly available (e.g. Web of Life, Fortuna et al. 2014). As an example, one could use the observed normalized degree distributions of the animal species as a proxy for their niche width in functional trait space. Modelling plant functional diversity poses a greater challenge for applying to real data, because prior studies often neglect to measure plant functional traits, although this is changing (Crea et al. 2015). If trait data is not available for the network, one could extract plant trait data from global databases (e.g. TRY, Kattge et al. 2011) and use an appropriate metric of functional trait diversity for the plant community. Alternatively, one could use phylogenetic relationships among plant species as a proxy for functional trait diversity. This actually might be the best way to go, seeing has how phylogenetic diversity can often encapsulate diversity of important, but unmeasured functional traits (Srivastava et al. 2012), and is often a better predictor of ecosystem function than species diversity or functional diversity (Cadotte et al. 2009). Taking advantage of these observational data will likely reveal much information about network assembly, but it will also be limited by the range of plant trait diversity and animal degree distributions observed in real networks. Perhaps the best test of our model would be to take advantage of plant-animal interactions that have been collected across the accumulating number of biodiversity-ecosystem function studies (Hooper et al. 2005 and Cardinale et al. 2012) or design an experiment that explicitly manipulates plant functional diversity and animal degree distributions.

By focusing on functional trait diversity rather than species diversity, our model could also integrate the effects of intraspecific trait variation. There is a growing empirical support for the important role intraspecific trait variation can play in shaping network structure (Barbour et al. 2016). However, there is currently little guidance on how we would expect inter- and intraspecific variation to scale up to affect interaction networks in diverse communities. We think this is an exciting direction that future research should explore.

An important issue that our model does not address is how the positive relationship between plant functional diversity and plant productivity (Tilman et al. 1997; Cadotte 2017) would modify the predictions from our model. From an interaction strength perspective, higher productivity can destabilize communities due to the "paradox of enrichment" (Rosenzweig 1971). However, productivity is often associated with increased habitat complexity in terrestrial environments, which can attract upper trophic levels that would prevent population outbreaks of insect herbivores. Indeed, empirical work from the Cedar Creek Biodiversity Experiment suggests that plant diversity stabilizes insect community dynamics (Haddad et al. 2011). Interestingly, our model suggests another mechanism – enhanced modularity – by which plant biodiversity enhances the stability of trophic networks.







# Conclusion

Resolving the diversity-stability debate requires a mechanistic understanding of the relationship between diversity, network structure, and stability. The heuristic model we propose takes us a step closer toward understanding the often-neglected link between diversity and network structure. Our functional trait model predicts that increasing plant functional diversity will enhance the modular structure of the network; however, this relationship is dampened when interacting with a generalist animal community. Importantly, our model offers testable predictions that can be acquired readily from empirical data. Given the theoretical relationships between network structure and stability, our model implies that plant trait diversity could stabilize plant-herbivore networks, but has the potential to destabilize networks of mutualistic interactions by eroding their nested architecture. If we want to predict how the loss of biodiversity will affect the stability of ecosystem services that humans rely upon, then future work needs to continue to understand the relationship between diversity, network structure, and ecosystem stability

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