

## ABSTRACT

### **Network structure modulates evolutionary dynamics in resource competition networks**

Augusto N. Carvalho and Paulo R. Guimarães Jr.

Competition for limited resources is an important phenomenon limiting species abundance and promoting niche variation across evolutionary timescales. We have a solid body of empirical and theoretical work exploring how simple, pair-wise competitive interactions affect trait evolution. Because competitors rarely interact with resources in isolation, since species are often inserted in complex networks of interactions, a fundamental problem to solve is how competition shapes trait evolution in a multispecies context. Here, we integrated network theory with a trait-based evolutionary model to investigate how competition and network structure affects trait evolution in resource-sharing networks. By using simple theoretical networks, we described how traits and trait matching between species and resources evolve in response to competition. Specifically, we analyzed the role of network structure — connectance, centrality and centralization — to the evolutionary dynamics. Our results show that trait shifts and trait mismatching due to competition were positively correlated with the importance of the shared resource as a selective pressure to the consumers. Species centrality and network centralization significantly influenced trait evolution, whereas the impact of connectance was weaker. Notably, core species in star-shaped networks experienced the greatest trait shifts under competition but showed smaller trait mismatches due to their ability to fall back on a subset of their resources. Similar patterns were not observed in linear networks. These results highlight the potential role of network structure to the competitive evolutionary dynamics. We hypothesize that the invasion by supergeneralists will strongly impact peripheral species that interact with more isolated resources in the trait-space, due to propagation of competitive effects through the network.

**Keywords:** Competition, evolution dynamics, resource-sharing networks, trait matching, centrality.

## MATHEMATICAL MODEL:

The evolutionary dynamics of the trait  $Z$  of competitor  $i$  in the network can be described as:

$$Z_i^{t+1} = Z_i^t + \varphi \left\{ m_i \left[ \sum_{u=1}^R \frac{q_{iu}^t}{K_i^t} (Z_i^t - Z_u^t) + \sum_{u=1}^R \sum_{j=1}^C \frac{q_{iu}^t q_{ju}^t}{K_i^t} (Z_j^t + \varepsilon_{ii}^t - Z_i^t) \right] + (1 - m_i)(\theta_i - Z_i^t) \right\}$$

Where  $K_i^t = \sum_{u=1}^R q_{iu}^t + \sum_{u=1}^R \sum_{j=1}^C q_{iu}^t q_{ju}^t$ , in which  $Z_i^t(Z_j^t)$  is the mean trait values of a competitor  $i$  ( $j$ ),  $\varphi_i$  is a scaling parameter proportional to the amount of genetic variance in the population,  $q_{iu}^t$  is the strength of selection imposed by the resource  $u$ ,  $\sum_{u=1}^R q_{iu}^t$  is the sum of the selective effects of all resources and  $\sum_{j=1}^C q_{iu}^t q_{ju}^t$  is the sum of the selective effects of all competitors,  $\varepsilon_{ii}^t$  is the trait difference between species  $i$  and its competitors, determining the threshold for alleviating the negative fitness impacts of competition,  $\theta_i$  is the trait values favored by all other environmental pressures, and  $m_i$  represents the overall strength of the biotic interaction (resource use and competition) as selective pressures and.  $\varepsilon_{ii}^t$  is a positive number if  $Z_i^t > Z_j^t$  and negative otherwise:

$$\begin{cases} \varepsilon_{ii}^t > 0, & \text{if } Z_j^t < Z_i^t, \\ \varepsilon_{ii}^t < 0, & \text{if } Z_j^t > Z_i^t, \end{cases}$$

In which  $\varepsilon$  is a  $S \times S$  diagonal matrix in which  $\varepsilon_{ii}^t$  describes the trait distances that eliminate the negative effects of competition for species  $i$ . We define  $q_{iu}^t$  and  $q_{ju}^t$  as a function of trait matching. In first place,  $q_{ij}^t$  depends on a suite of traits not explicitly modeled by us that define if the interaction between two species can even occur. Second, if traits are similar between species and resources, the interaction should be stronger, and not relevant if species traits are too different. Combining these two components, we arrive at our equation for  $q_{iu}^t$  and  $q_{ju}^t$ :

$$q_{iu}^t = \frac{a_{iu} e^{-\alpha(Z_u^{(t)} - Z_i^{(t)})^2}}{\sum_{k=1}^N a_{ik} e^{-\alpha(Z_k^{(t)} - Z_i^{(t)})^2}}$$

where  $\alpha$  controls the sensitivity of  $q_{iu}^t$ .

## REFERENCES

- Andreazzi, C. S., Thompson, J. N., & Guimarães, P. R. (2017). Network Structure and Selection Asymmetry Drive Coevolution in Species-Rich Antagonistic Interactions. *The American Naturalist*, 190(1), 99–115.  
<https://doi.org/10.1086/692110>
- Dormann, C. F., Gruber, B., & Fruend, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, 8(2), 8–11.
- Poisot, T., Canard, E., Mouillot, D., Mouquet, N., & Gravel, D. (2012). The dissimilarity of species interaction networks. *Ecology Letters*, 15(12), 1353–1361. <https://doi.org/10.1111/ele.12002>
- R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org>
- Tim Tinker, M., Guimarães, P. R., Novak, M., Marquitti, F. M. D., Bodkin, J. L., Staedler, M., Bentall, G., & Estes, J. A. (2012). Structure and mechanism of diet specialisation: Testing models of individual variation in resource use with sea otters: Network structure of individual resource use. *Ecology Letters*, 15(5), 475–483. <https://doi.org/10.1111/j.1461-0248.2012.01760.x>