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Evidence of structural balance in spatial ecological networks

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Despite recent advances in applying networks to study ecological systems, most of the network datasets are built attending only to a single type of interaction between nodes, which can be an oversimplification. In the present work, we built ecological networks that had positive and negative links for multiple plant communities based on the local spatial association between species. Then, we evaluated whether those networks were in balance, a hypothesis commonly formulated for real signed graphs but never tested in systems other than social networks. Specifically, we quantified the global and the local structural balance in the networks. We found that plant community networks were more balanced than expected by chance, and that this pattern was due to a large number of balanced triads to the detriment of unbalanced ones. Furthermore, this pattern was consistent among all of the types of the plant communities examined, which suggests that configurations that promote structural balance might be common in ecological signed networks. We also found that almost all networks had some unbalanced components, which might be responsible for the adaptation of the system. Mechanisms behind these structure and possible applications for community ecology are discussed. Our results encourage testing structural balance in other ecological networks to confirm if it is a widespread architecture of natural systems.

The use of network science to study ecological communities has become a rising trend in recent times (Heleno et al. 2014, Kissling and Schleuning 2015). Networks allow the analysis of the interaction patterns among the elements of complex systems (Albert and Barabási 2002, Newman 2003) and the role of the structural organization in the functioning of these systems (Boccaletti et al. 2006). Thus, it is not surprising that networks are nowadays a common tool to study the organization of biotic interactions in real ecosystems (Ings et al. 2009). However, despite of the advances achieved by applying networks to ecosystems, most of ecological networks are usually built attending only to one particular type of interaction between species, which could frequently represent an oversimplification of the true functioning of real communities.

In ecological communities, living organisms can interact with others positively (e.g. mutualistic and facilitative interactions) or negatively (e.g. competitive and parasitic interactions); and commonly these types of interactions occur at the same time within a given community (Kéfi et al. 2012, 2015). In ecology, however, there have been few empirical examples that have considered multiple types of interactions within the same network, probably because of the high logistic effort involved in documenting all the potential interactions present within a community (Melián et al. 2009, Pocock et al. 2012). Furthermore, the analysis of these networks presents some difficulties over the analysis of networks with only one type of interactions, being necessary the use of new methodologies or theoretical frameworks (like the use of multilayer networks, Mucha et al. 2010, Boccaletti et al. 2014, Kivelä et al. 2014). Networks which include positive and negative links are called signed networks and have been mostly considered theoretically (Harary et al. 1953, Zaslavsky 1982, Traag and Bruggeman 2009) and used to study social networks (Leskovec et al. 2010, Szell and Thurner 2010, Szell et al. 2010, Facchetti et al. 2011), while being ignored in other contexts such as ecological systems.

Signed networks exhibit a property called structural balance, which is based on how nodes organize in subgroups within the network (Cartwright and Harary 1956). A signed network is said to be balanced if it can be partitioned into groups of nodes in such a way that 1) every pair of connected nodes within the same group share a positive link, and 2) links between nodes within different groups have a negative sign (Doreian and Mrvar 2009). Structural balance is associated with the resilience of social networks because it prevents the appearance of conflicts that might disrupt the system (Cartwright and Harary 1956). However, real networks rarely organize in a perfectly balanced way (i.e. some links do not fulfill the criterion for structural balance), and the deviation from perfect balance is called 'frustration'

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Supplementary material (Appendix ECOG-02561 at <www.ecography.org/appendix/ecog-02561>). Appendix 1.