



Short communication

Connectance of species interaction networks and conservation value: Is it any good to be well connected?

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ABSTRACT

Recently, the focus of conservation efforts gradually changed from a species-centred approach to a broader ambition of conserving functional ecosystems. This new approach relies on the understanding that much ecosystem function is a result of the interaction of species to form complex interaction networks. Therefore measures summarising holistic attributes of such ecological networks have the potential to provide useful indicators to guide and assess conservation objectives. The most generally accepted insight is that complexity in species interactions, measured by network connectance, is an important attribute of healthy communities which usually protects them from secondary extinctions. An implicit and overlooked corollary to this generalization is that conservation efforts should be directed to conserve highly connected communities. We conducted a literature review to search for empirical evidence of a relationship between connectance (complexity) and conservation value (communities on different stages of degradation). Our results show that the often assumed positive relationship between highly connected and desirable (i.e. with high conservation value) communities does not derive from empirical data and that the topic deserves further discussion. Given the conflicting empirical evidence revealed in this study, it is clear that connectance on its own cannot provide clear information about conservation value. In the face of the ongoing biodiversity crisis, studies of species interaction networks should incorporate the different 'conservation value' of nodes (i.e. species) in a network if it is to be of practical use in guiding and evaluating conservation practice.

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1. Introduction

In recent decades the focus of conservation has gradually changed from a species-centred approach into protecting ecosystem functions and their impact on human wellbeing through the provision of ecosystem services (Millennium Ecosystem Assessment, 2005). Intrinsic to this approach is the understanding that much ecosystem function is a result of the interaction of species with each other (Duffy et al., 2007). Not only does human welfare depends on species interactions, but it is through interactions that disturbance can cascade through whole communities. The structure of ecological networks can therefore influence the resilience and robustness of ecosystems (Dunne et al., 2002; Thébault and Fontaine, 2010). In order to conserve ecosystem function, it is important that these species interaction networks are robust to cascading species loss, and it has been suggested that highly connected networks are at earlier stages of ecological

degradation and better prepared against it (Gilbert, 2009). But what does this mean, in practice, for the conservation of species and habitats? Can the connectance of these species interaction networks give an indication of their conservation value?

Species interaction networks depict groups of species that interact with each other, and these interactions can be trophic, as in food-webs, or mutualistic, such as pollination and seed dispersal networks. Framing important conservation problems into this community-oriented viewpoint has been argued to be a powerful tool in order to direct conservation planning, particularly when this seeks to conserve ecosystem function (Heleno et al., 2010).

One of the earliest and most popular metrics proposed to characterise species interaction networks is "connectance": the proportion of realized interactions from the pool of all possible interactions between the species of a network (May, 1973). Connectance was central to the initial "complexity begets stability" debate (May, 1973, 1999; Pimm, 1984) and despite considerable criticism, continues to be broadly used as a measure of community complexity (Banasek-Richter et al., 2009; Gilbert, 2009; Tylianakis et al., 2010). There are several caveats regarding the use

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Table 1

Summary of published studies evaluating the relationship between Connectance (C) and communities under some form of ecological degradation affecting Conservation Value (CV). A positive relationship assumes that CV increases as C increases, a negative relationship assumes the contrary. Connectance calculation indicates the method used to calculate connectance in each study. Effect of network size indicates whether the size of the networks was considered when comparing connectance values between communities. Question marks highlight data that are not unequivocal.

System	Ecological correlate of degradation	Expected relation of C and CV	Result	Relationship of C and CV	Connectance calculation	Effect of network size	Reference
40 published food webs (marine, estuarine, terrestrial)	Disturbance	No expectation	C lower on disturbed	Positive	Qualitative	Yes	Briand (1983)
Zooplankton food webs on lakes	Acidification	Positive	C lower on acidic	Positive	Qualitative	No	Locke and Sprules (1994)
Periphyton-macroinvertebrates on stream	Invasion by crayfish	No expectation	C higher on invaded	Negative	Qualitative (?)	No	Charlebois and Lamberti (1996)
Fish-macroinvertebrates-algae on stream	Disturbance	Positive	No effect	None	Qualitative	Yes	Townsend et al. (1998)
Stream food web	Invasion by dragonfly	No expectation	C higher on invaded	Negative	Qualitative	No	Woodward and Hildrew (2001)
Plant-pollinator (visitation networks)	Alien vs native plants	No expectation	C lower on aliens	Positive	Qualitative	Yes	Memmott and Waser (2002)
Zooplankton-copepods on ponds	Insecticide application	Positive	C lower on sprayed	Positive	Qualitative	No	Kreutzweiser et al. (2004)
Crustacean zooplankton-copepods on ponds	Insecticide application	Positive	C higher on sprayed	Negative	Qualitative	No	Kreutzweiser and Thomas (1995) in Kreutzweiser et al. (2004)
Marine food web	Overfishing	No expectation	C higher on overfished	Negative	Qualitative (?)	No	Heymans et al. (2004)
Plant-pollinators on hay meadows	Restoration	No expectation	C marginally higher on old meadows	None (?)	Qualitative	No	Forup and Memmott (2005)
Bees/wasps-parasitoids on agricultural land-forest gradient	Agricultural intensification	No expectation	No effect	None	Quantitative	Yes	Tylianakis et al. (2007)
Bees/wasps-parasitoids on agricultural land-forest gradient	Agricultural intensification	No expectation	C higher on degraded	Negative	Qualitative	No	Tylianakis et al. (2007)
Plant-herbivores-carnivore on grasslands	Disturbance	No expectation	C lower on disturbed	Positive	Qualitative	No	Voigt et al. (2007)
Plant-pollinator visitation web on heathlands	Restoration	Positive	C higher on ancient	Positive (?)	Qualitative	Yes (?)	Forup et al. (2008)
10 published Plant-pollinator webs (forest, 2 insular)	Plant invasion	No expectation	No effect	None	Qualitative	Yes	Aizen et al. (2008)
Marine food web	Disturbance/degradation	Positive	C lower on degraded	Positive	Qualitative	No	Coll et al. (2008)
Plant-herbivores-parasitoids on forest	Plant invasion	No expectation	No effect	None	Quantitative	Yes	Heleno et al. (2009)
Plant-pollinator-parasitoids on heathlands	Restoration	Positive	No effect	None	Quantitative	No	Henson et al. (2009)
Organic vs conventional farms	Biodiversity loss	Negative	No effect	None	Quantitative	No (?)	MacFadyen et al. (2009)
Plant-pollinator	Plant invasion	Negative	No effect	None	Qualitative	Yes	Vilà et al. (2009)
Organic vs conventional farms	Biodiversity loss	Negative	C marginally lower on organic farms	Negative	Qualitative	No	MacFadyen et al. (2009)
Plant-pollinator	Plant invasion	No change	No effect	None	Qualitative	Yes	Padrón et al. (2009)
Plant-herbivores-parasitoids on forest	Restoration	Negative	C marginally lower on restored	None (?)	Quantitative	Yes	Heleno et al. (2010)

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