Ecological Indicators 14 (2012) 7–10

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Short communication

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

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ARTICLE INFO

Article history:
Received 11 February 2011
Received in revised form 6 May 2011
Accepted 28 June 2011

Keywords:
Community
Complexity
Food web
Rare species
Stability

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.

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 conservations 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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doi:10.1016/j.ecolind.2011.06.032

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 convencional 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 convencional 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)

of connectance: its calculation is debatable (Cohen et al., 1993) and it is dependent on network size, sampling effort, and to the inclusion of interaction strengths (Banasek-Richter et al., 2004; Blüthgen et al., 2008), However, connectance remains the main measure of network complexity (e.g. Banasek-Richter et al., 2009; Estrada, 2007).

One of the broadly accepted generalizations involving connectance is that high connectance is a characteristic of pristine or near pristine communities that tends to protects them from secondary extinctions (Dunne et al., 2002; Thébault and Fontaine, 2010). An important corollary to this view is that highly connected communities are implicitly accepted to be "desirable" from a conservationist view point, i.e. a positive relationship between connectance and conservation value is generally assumed (Gilbert, 2009). Although the ubiquity of this relationship has been questioned (Tylianakis et al., 2010), connectance has been suggested as an important and holistic biological indicator (Gilbert, 2009) and that conservation efforts should be orientated to protect and promote highly connected communities.

We conducted a literature review to test for an empirical relationship between perceived conservation value of species interaction networks and their connectance.

2. Methods

We conducted a literature search for studies where connectance was compared between communities differing in their conservation status, such as due to pollution, biological invasions or habitat fragmentation. We conducted online searches for the term "connectance" on *ISI Web of Knowledge*, *Science Direct* and *Google Scholar*, (search conducted in June 2010).

The relative conservation value of the compared communities is case-specific and (by definition) subjective and was inferred from each study. As a general rule, communities which undergone degredation, i.e. alterations as a consequence of external environmental threats (e.g. acid rains, biological invasions, overfishing) are considered to have lower conservation value than near-pristine communities.

3. Results and discussion

The search yielded 287 studies of which only 20 discussed the effect on connectance of some form of ecological degradation. These 20 studies presented data for 23 systems (Table 1).

Only 12 studies express any *a priori* expectation (even if implicitly) towards the relationship between connectance and conservation value, and these cover the whole range of possible relationships (Table 1). Six studies (26%) found that connectance increased with environmental degradation (a negative relationship between connectance and conservation value), seven studies (30%) found that connectance was reduced with environmental degradation (a positive relationship), and nine studies (43%) did not detect any relationship.

Only five studies (22%) considered interaction frequency on the calculation of connectance and only ten studies (43%) considered the effect of network size in the comparison of connectance between communities. While these hinder the statistical comparison of conservation values *per se* it is less important when only the direction of the change in connectance is compared.

The empirical finding of a positive relationship of conservation value with connectance fits the assumption that pristine communities are more complex, which protects them from environmental threats. On the other hand, a negative relationship can be predicted since connectance quantifies the average generalization of species (Dunne et al., 2004; Warren, 1994), i.e. connectance decreases when specialists are lost or generalists are gained. Both situations are likely under an ecological threat because specialists tend to face increased risk of extinction (Devictor et al., 2008), while generalists are better able to resist extinction and better able to become expand their ranges (McKinney and Lockwood, 1999). Our results suggest that there is not sufficient empirical evidence of a general relationship between ecological degradation and connectance, as might be naively expected. Instead the relationship is context-specific, which requires the development of context-specific hypotheses.

Unfortunately, a formal meta-analysis on the relationship between connectance and conservation value is not yet possible as most studies do not include replicates for their networks, and therefore no measures of data dispersal (e.g. standard deviation) can be calculated. Nevertheless our review clearly suggests that the way that ecological degradation affects connectance is highly context-specific.

4. Conclusion

In the face of the ongoing biodiversity crisis, we must understand the consequences of species loss for the conservation of ecosystem functions (Kremen and Hall, 2005). However, network studies often assume all nodes (i.e. species), to differ only in their ecosystem function (Thébault and Fontaine, 2010), a simplification which equally weights the conservation of all species: from critically endangered endemic species to weeds (e.g. Heleno et al., 2009). Given the conflicting empirical evidence revealed in this study, it is clear that connectance, applied on its own and interpreted simplistically, cannot be used as an indicator of conservation value, in the way that value is normally ascribed. We believe that descriptors of species interaction networks clearly have an important role to play in guiding conservation efforts and their use should be encouraged However, while ecologists are developing increasingly robust measures of network complexity and network robustness (Blüthgen, 2010), to date, such measures have not included basic considerations of species conservation value. Although this remains a heady goal, such step would largely benefit the application of ecological network theory in conservation practice.

Acknowledgments

We thank S. Pearce, L. Carvalheiro, D. Evans, R. Gibson and K. Henson for discussion on the topic and J. Memmott, J. Ramos, J. Olesen and A. Traveset for comments on the manuscript.

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