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

Ruben Heleno[a*], Mariano Devoto[b] and Michael Pocock[c]

[a] Mediterranean Institute of Advanced Studies (CSIC-UIB), c/ Miquel Marqués 21, 07190 Esporles, Mallorca, Balearic Islands, Spain

[b] Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina.

[c] School of Biological Sciences, University of Bristol, Bristol BS8 1UG, United Kingdom

*Corresponding author:

E-mail: ruben_huttel@hotmail.com

Tel: 0059383129292

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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.

## 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 1999; May 1973; 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 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 generalisation 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.

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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. See Appendix 1 for table references.

Table 1.

| 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 | Vilá 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 |

**Appendix 1 -** List of references for Table 1.


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