GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 13 (2012) 500–508
Basic and Applied Ecology
www.elsevier.com/locate/baae

How different link weights affect the structure of quantitative flower–visitation networks

Rocío Castro-Urgal*, Cristina Tur, Matthias Albrecht[1], Anna Traveset

Institut Mediterrani d'Estudis Avançats (CSIC-UIB), C/Miquel Marqués 21, 07190 Esporles, Mallorca, Balearic Islands, Spain

Received 6 March 2012; accepted 9 August 2012

Abstract

Despite the considerable work carried out to assess the structure of weighted and unweighted mutualistic networks, little is known about how different ways to measure the weight of interactions can influence network parameters used to describe such structures. The use of an appropriate 'link weight' is especially important if we want to move toward a more functional perspective in ecological network studies. Here, we evaluated how the use of five different link weights, starting with the simplest one – the number of visits – and including progressively information on total census time, number of flowers observed, number of flowers visited and total flower abundance of each species in a plant community, influences widely used descriptors of network structure. We analyzed different network-level properties: weighted nestedness, flower–visitor generality, plant generality, complementary specialization H_2', interaction evenness and interaction diversity, as well as species-level parameters: specialization index d' and strength. We built two quantitative flower–visitation networks from two different communities sampled during two consecutive years, in which we also measured independently flower abundance of each plant species. Results showed that the type of link weight used can significantly alter network structure. A clear trend toward more specialized interactions (decreased flower–visitor generality, increased H_2' and d'), higher heterogeneity in the frequency of interactions (lower evenness and diversity of interactions) and higher weighted nestedness was found as interaction weight gained in complexity. However, standardizing only for total censusing time had only weak effects on network parameters. Our findings highlight the importance of carefully considering the most appropriate link weight for each ecological network study, emphasizing that comparisons across networks that use different weights might lead to flawed results and thus to ecological misinterpretations of network structures.

Zusammenfassung

Trotz der erheblichen Anstrengungen, die gemacht wurden, um die Struktur von gewichteten und ungewichteten mutualistischen Netzwerken zu bewerten, ist wenig darüber bekannt, wie die unterschiedlichen Wege, um die Gewichtung von Interaktionen zu messen, die Netzwerkparameter beeinflussen, die benutzt werden, um solche Strukturen zu beschreiben. Der Gebrauch einer passenden link-Gewichtung ist besonders wichtig, wenn wir eine stärker funktionale Perspektive in ökologischen Netzwerk-Untersuchungen erreichen wollen. Hier untersuchten wir, wie fünf verschiedene link-Gewichtungen weithin genutzte Deskriptoren von Netzwerkstrukturen beeinflussten. Ausgehend von der einfachsten Gewichtung (Anzahl Blütenbesuche) nahmen wir immer mehr Informationen hinzu: Beobachtungsdauer, Anzahl der beobachteten Blüten, Anzahl der besuchten Blüten und die gesamte Blütenabundanz aller Arten in der Pflanzengesellschaft. Wir analysierten verschiedene Eigenschaften auf

*Corresponding author. Tel.: +34 971 611 719; fax: +34 971 611 761.
E-mail address: rocio.castro@uib.es (R. Castro-Urgal).
[1]Present address: Research Station Agroscope Reckenholz-Tanikon ART, Reckenholzstrasse 191, 8046 Zurich, Switzerland.

http://dx.doi.org/10.1016/j.baae.2012.08.002

Netzwerkebene: gewichtete nestedness, Generalisierung von Blütenbesuchern und Pflanzen, komplementäre Spezialisierung H_2', Interaktions-Evenness und Interaktions-Diversität. Und wir untersuchten Parameter auf der Artebene: Spezialisierungsindex d’ und -stärke. Wir konstruierten zwei quantitative Blütenbesuchsnetzwerke für zwei unterschiedliche Gemeinschaften, die über zwei Jahre hinweg beprobt worden waren, und in denen wir auch unabhängig die Blütenabundanz aller Pflanzenarten bestimmten. Die Ergebnisse zeigten, dass die eingesetzte link-Gewichtung die Netzwerkstruktur signifikant beeinflussen kann. Ein klarer Trend hin zu stärker spezialisierten Interaktionen (abnehmende Generalisierung der Blütenbesucher, zunehmendes H_2' und d'), größere Heterogenität in der Häufigkeit der Interaktionen (geringere Evenness und Diversität der Interaktionen) und höhere gewichtete nestedness ergab sich, wenn die Wichtung der Interaktionen an Komplexität zunahm. Dagegen hatte die Standardisierung durch die Gesamtbeobachtungsdauer nur geringen Einfluss auf die Netzwerkparameter. Unsere Befunde unterstreichen, wie wichtig es ist, die passendste link-Gewichtung für jede Netzwerkuntersuchung sorgfältig zu bedenken, und sie betont, dass Vergleiche zwischen Netzwerken, die unterschiedliche Gewichtungen benutzen, zu fehlerhaften Ergebnissen und damit zu ökologischen Fehlinterpretationen von Netzwerkstrukturen führen können.

Keywords: Flower abundance; Interaction strength; Plant-pollinator interactions; Network parameters; Quantitative networks

Introduction

In the last decades, the focus of research in mutualistic plant–animal interactions has shifted from traditional studies on interactions between pairs of species to community-level studies. This change in perspective was promoted by increasing evidence that reciprocal specialization between species is rather rare and that most species interact with multiple mutualistic partners (Waser, Chittka, Price, Williams, & Ollerton 1996). The community perspective in ecology was further fueled by developments in complex network analysis techniques profitably used in a multitude of research disciplines (Borgatti and Everett 1997; Strogatz 2001; Montoya, Pimm, & Solé 2006).

Early studies of mutualistic interactions at the community level only considered the presence or absence of an interaction between species. In these binary networks, all realized links are considered equally ‘important’ (e.g. Jordano 1987; Memmot & Waser 2002; Bascompte, Jordano, Melián, & Olesen 2003). This first “generation” of networks allowed the identification of some general patterns, such as the right-skewed distribution of links per species (Waser et al. 1996; Jordano, Bascompte, & Olesen 2003), nestedness (Bascompte et al. 2003), asymmetry of interactions (Vázquez & Aizen 2004; Bascompte, Jordano, & Olesen 2006) and modularity (Olesen, Bascompte, Dupont, & Jordano 2007). These network properties may play important roles for the functioning of the systems they describe (Gómez, Perfectti, & Jordano 2011). However, it was soon widely recognized by ecologists that the accuracy of such binary networks was limited as they fail to describe the strong heterogeneity in the frequency of interactions among species observed in the field. Thus, the development of weighted measures that describe the intensity of exchange of benefits between partners in mutualistic interactions (their interaction strength) has become necessary, increasing the reliability of network properties and facilitating their biological interpretation (Bersier, Banašek-Richter, & Cattin 2002; Blüthgen, Menzel, & Blüthgen 2006).

The number of studies using a quantitative network approach has also grown in recent years. In food webs, interaction strength is usually based on the energy flow through the system. In mutualistic networks, by contrast, there is great variability in the way researchers gather field data and construct interaction matrices owing to the huge heterogeneity in habitat types (forest, savannahs, meadows, *etc.*) and to particular study aims. Such variability makes comparisons across studies difficult. Moreover, Gibson, Knott, Eberlein, and Memmott (2011) have recently shown that the topology of plant–pollinator networks can be affected by methodological biases. A review of 22 published studies analyzing the structure of weighted plant–pollinator networks shows the heterogeneity across these studies, which differ both in link weight as well as in total census time (Table 1).

The simplest and most commonly used link weight in pollination networks is the number of pollinator visits to each plant species. The number of flowers visited by a pollinator is another measure claimed to be a good predictor of the per capita reproductive performance of insect-pollinated plants and used as a proxy of the functional impact of an interaction (Vázquez, Morris, & Jordano 2005). Still, another measure of link strength takes into account the abundance of available resources (flowers in the case of pollination networks) in the entire community, which may be important in determining which flowers are visited by a given flower–visitor. The recently developed species-level (d') and network-level (H_2') complementary specialization indices (Blüthgen et al. 2006) represent an attempt to account for such resource availability. However, floral abundance is usually estimated indirectly based on visitation frequency totals, which are not necessarily good proxies of actual resource availability. One recent study has tested the effect of independently measured flower availability on several network properties such as network specialization, species richness and flower–visitor abundance (Weiner, Werner, Linsenmair, & Blüthgen 2011), finding that flower abundance is important for the distribution of visitors within a site. However, Lopezaraiza-Mikel, Hayes, Whalley, and Memmott (2007) found that higher visitation rate is not