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

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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

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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.

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

Table 1. List of the 22 published flower–visitation network studies included in the review about the differences between the sampling methods used in each study (see Appendix A for references). The table summarizes: the link weight used in the network analysis, observation time (time spent observing a specific number of flowers of a plant species in each census) and study period (number of field work months per year, number of study years and, when it is know, number of total field work days in brackets).

Reference	Link weight	Observation time	Study period
Mosquin and Martin (1967)	No. of visits	na	3 days
Small (1976)	No. of visits	10 h/plant	3 months
Schemske et al. (1978)	No. of visits	na	3 months, 2 years
Motten (1982)	No. of visits/flower/h	30 min/census	5 years
Primack (1983)	No. of visits	na	2 seasons (18 days)
Primack (1983)	No. of visits	na	3 months, 2 years
Primack (1983)	No. of visits	na	3 months (24 days)
Barrett and Helenurm (1987)	No. of visits	na	5 months, 3 years
Kato et al. (1990)	No. of visits	10 min/census	7 months, 4 years (31 days)
Inoue et al. (1990)	No. of visits	6 h/day	8 months, 4 years (48 days)
Elberling and Olesen (1999)	No. of visits	10 h/plant	3 months
Memmott (1999)	No. of visits	Transects (no time)	1 month
Olesen et al. (2002)	No. of visits	30 min/census	1 month, 2 years
Olesen et al. (2002)	No. of visits	30 min/census	1 month
Vázquez and Simberloff, 2003; Vázquez and Simberloff (2002, 2003)	(Proportion of visits × total no. visits)/total census	10 min/census	1 season
Ollerton et al. (2003)	No. of visits	63 h	2 months
Ebeling et al. (2008)	No. of visits	6 min/census	2 years (17 days)
Bosch et al. (2009)	No. of visits	4 min/census	4 months (24 days)
Kaiser-Bunbury et al. (2009)	Total no. of visits/total no. of flowers/h	30 min/census	6 months (12 days)
Alarcón et al. (2008, 2010)	No. of visits	20–40 min per transect	6 weeks, 2 years (12 days)
Weiner et al. (2011)	No. of visits	na	4 months
Chacoff et al. (2012)	No. of visits	5 min/census	4 months, 4 years

exclusively explained by flower abundance. The only studies that integrate floral abundance into the link weight measure are those by Kaiser-Bunbury, Memmott, and Müller (2009) and Kaiser-Bunbury, Valentin, Mougal, Matatiken, and Ghazoul (2011). Although it would also be ideal to account for flower–visitor abundance, such information is hardly available, owing to the difficulty of tracking insects.

Our aim here is to examine how link weight may affect properties of mutualistic networks, possibly leading to different interpretations regarding their functional consequences for ecological communities (Gómez et al. 2011). By using new empirical data from two different communities during 2 years, we compare five different types of link weights, which include progressively more detailed information, available from studies based on plot observations, on the observed plant–pollinator interactions. The simplest weight we use is the number of insect visits to flowers. Then, we standardize this number by total observation time, getting a visitation rate measure. The third link weight considers the number of flowers observed in each census. In a next step, information on the flower–visitor's behavior is included, specifically the proportion of flowers visited per time unit. Finally, the fifth and most complex link weight additionally includes the independently estimated flower abundance of each flowering species. More than discerning which link weight is best to include

in pollination networks, which will depend on the question being addressed, the type of network descriptors chosen and the methodology applied in the fieldwork, our objective in this study is to assess the consistency of network parameters when different link weights are used for the same interactions. If such parameters do differ significantly, it will imply that link weight must be standardized when networks are compared, e.g. across habitats, through time or along ecological gradients.

Materials and methods

Study sites and sampling procedure

The study was carried out in two sites on Mallorca (Balearic Islands) in two consecutive years (2009 and 2010): Son Bosc (39°46′28.11″N; 3°07′45.34″E) is a diverse dune marshland in the north, whereas Sa Coma de n'Arbona (39°47′59.51″N; 2°47′07.81″E) is located on the western-exposed slope of Puig Major, the highest peak of the Serra de Tramuntana mountain range in the northwest of the island, at *ca.* 1200 m above sea level (see further description of the study sites in Appendix A). In Son Bosc, sampling took place between April and July whereas in Puig Major – where the

flowering season is delayed due to its higher altitude – the study was performed between May and August.

Flower abundance was estimated every two weeks at each site, counting the number of all open flowers of each flowering plant encountered within permanent belt transects. In Son Bosc, 13 and 10 belt transects (50 m × 2 m) in 2009 and 2010 were surveyed, covering a total area of 1300 m^2 and 1000 m^2, respectively. In Puig Major, 9 belt transects (three 20 m × 2 m, four 25 m × 2 m, one 30 m × 2 m and one 40 m × 2 m) were sampled both years, covering a total area of 460 m^2. Flower abundance was calculated for each species as the number of open flowers divided by the total area surveyed. For species with tightly clustered inflorescences (e.g. the capitula of Asteraceae) we scored only single inflorescences.

All plants in bloom were censused throughout the flowering season. Once or twice per week we made insect censuses on flowers from haphazardly selected individuals and from 10:00 am to 17:00 pm on calm and sunny days. Insect visits to flowers were recorded from a distance of approximately 1 m to minimize interference with insect behavior. We recorded contacts between insects and flowers during three-minute periods at Son Bosc and five-minute periods at Puig Major (longer here due to lower insect activity at high altitudes). During each census we recorded: (a) identity of flowering plant species, (b) number of open flowers of each individual plant observed; (c) identity of each flower–visitor (species name if possible or morphotype otherwise); (d) number of individuals of each species visiting flowers, and (e) number of flowers visited by each flower visitor. Unidentified insects in the field were collected for further identification by taxonomists. Plant identification followed Beckett (1993) and Western Mediterranean Virtual Herbarium (http:\\herbarivirtual.uib.es).

Total time spent censusing flower–visitor interactions was 42:18 h (2009) and 49:39 h (2010) in Son Bosc and 13:20 h (2009) and 38:15 h (2010) in Puig Major. Total number of censuses differed across species, sites, and years proportional to the duration of a plant species flowering period in the community.

Construction of quantitative flower–visitation networks

For each community, we built five types of matrices each one using a different link weight as follows:

M1: no. of visits. Number of visits of an insect species to flowers of a plant species was used as link weight.
M2: no. of visits/time. Number of visits was standardized by total observation period spent on each plant species during the entire season.
M3: no. of visits per flower/time. Same as M2 but number of visits was also standardized by number of open flowers observed in each censused individual. This is a way to quantify insect visits on a floral basis.

Table 2. Numbers of flower visitor species, flowering plant species and their interactions (individual visits) for each of the 12 temporal networks of each site.

Temporal networks	Flower–visitor species	Plant species	Total interactions
Son Bosc April 2009	30	40	756
Son Bosc May 2009	66	50	904
Son Bosc June 2009	60	22	539
Son Bosc July 2009	31	18	477
Son Bosc April 2010	42	33	814
Son Bosc May 2010	74	48	1233
Son Bosc June 2010	70	40	871
Son Bosc July 2010	41	21	277
Puig Major May–June 2009	35	17	181
Puig Major July–August 2009	31	11	221
Puig Major May–June 2010	41	21	121
Puig Major July–August 2010	48	19	376

M4: proportion of flowers visited/time. Same as M3 but considering number of flowers visited by each insect species instead of number of visits. Thus, this weighting of interactions considers the proportion of flowers of a given plant species visited by each flower–visitor species in each census (flowers visited/flowers observed).
M5: (Proportion of flowers visited/time) × flower abundance. Same as M4 but considering also the estimated total number of flowers of each plant species in the community that was available each day of census.

To minimize potential artifacts due to temporally "forbidden links" (*sensu* Jordano et al. 2003), we constructed a total of 12 temporal interaction networks ("temporal snapshots", Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch 2010), one per month in Son Bosc and one for every 2 months in Puig Major (as network sizes in the latter community were smaller; Table 2). The temporal snapshots reflect network structures more realistically than full-season networks as they include those species that coexist in time. Thus, a total of 60 matrices (12 temporal networks x five link weights) were analyzed.

Network parameters

For each of the 60 matrices we calculated eight of the most widely used quantitative descriptors of the structure of weighted ecological interaction networks. At network level we calculated nestedness (weighted NODF), complementary specialization H_2', plant generality (G_p), flower–visitor generality (G_{fv}), interaction evenness (IE) and interaction diversity (ID). At species level we obtained species specialization d' and strength for plants and flower visitors (see

Appendix B). We used the *bipartite* package version 1.17 (Dormann, Fründ, Blüthgen, & Gruber 2009) run in *R 2.11*.

Statistical analysis

General linear mixed models with link weight as a fixed factor, and month nested within year and year nested within site (Son Bosc and Puig Major) as random factors were used to test whether link weight explained significant variation in network parameters, one at a time, as response variables. If the minimal adequate model based on an AIC model selection procedure included the fixed factor link weight, a *posteriori* Tukey's test with the general linear hypothesis function (glht; 'many-to-one comparison procedure' [Dunnett 1955]) was performed to identify which matrices differed from each other. The response variables G_p, G_{fv}, mean d_p', mean d_{fv}', mean St_p, mean St_{fv}, mean weighted St_p, and mean weighted St_{fv} were log-transformed for a better fit with a normal distribution of the residuals. These analyses were done using the packages *lme4* (Bates, Maechler, & Bolker 2011) and *multcomp* (Hothorn, Bretz, & Westfall 2008) in *R 2.11*.

In order to confirm that our results describe patterns that are different from random, we compared them with an appropriate null model (Dormann et al. 2009) (see Appendix C: Figs. 1 and 2).

Results

The number of individual visits observed in one 'observation unit' (3 or 5 min census) varied much across plant species, ranging from 0 to 36. In Son Bosc, we observed a total of 164 flower–visitor species visiting 80 plant species and recorded a total of 5871 interactions (*i.e.* individual visits) during the 2 years, whereas in Puig Major we found 93 flower–visitor species visiting 34 plant species, recording a total of 899 interactions during the same 2 years. Table 2 shows this information for each of the 12 temporal networks.

Effect of link weight type on network properties

M1 vs. M2: Standardizing visitation frequency by total observation time resulted in an increase of H_2' (Fig. 1B; $z = 3.31$, $p < 0.01$), mean d_p' (Fig. 2C; $z = 3.83$, $p < 0.01$) and mean d_{fv}' (Fig. 2D; $z = 6.49$, $p < 0.001$), but no significant change was detected in other parameters (Figs. 1 and 2).

M2 vs. M3: When accounting for number of flowers of each individual plant observed in each census, four parameters decreased: IE (Fig. 1E; $z = -3.03$, $p < 0.05$), ID_{fv} (Fig. 1F; $z = -2.87$, $p < 0.05$), ID_p (Fig. 1F; $z = -5.63$, $p < 0.001$) and mean weighted St_p (Fig. 2E; $z = -4.87$, $p < 0.001$), while two parameters increased: weighted NODF (Fig. 1A; $z = 2.83$, $p < 0.05$) and mean d_{fv}' (Fig. 2D; $z = 4.95$, $p < 0.001$).

M3 vs. M4: When using number of visited flowers instead of number of visits as link weight (standardizing by time and flowers observed), parameters did not change significantly, except for mean weighted St_{fv}, which decreased (Fig. 2F; $z = -3.91$, $p < 0.001$).

M4 vs. M5: The inclusion of total flower abundance in link weight significantly modified three network-level parameters: G_{fv} (Fig. 1C; $z = -7.24$, $p < 0.001$), IE (Fig. 1E; $z = -7.01$, $p < 0.001$) and ID_p (Fig. 1F; $z = -3.61$, $p < 0.01$) decreased; and two species-level parameters: mean weighted d_p' (Fig. 2A; $z = 4.63$, $p < 0.001$) and mean weighted St_p (Fig. 2E; $z = 9.80$, $p < 0.001$) increased.

When comparing the simplest (M1) with the most complex link weight (M5), we found significant changes in all examined parameters but two (G_p and mean weighted d_{fv}'). A clear trend toward a higher weighted NODF, H_2', mean d_p', and mean d_{fv}' was found. By contrast, G_{fv}, IE, ID_{fv}, ID_p, and mean weighted St_{fv} tended to decrease (Figs. 1 and 2).

Discussion

Our findings show that the weight given to each interaction in quantitative flower–visitation networks affects most network properties. This indicates that using one or another indiscriminately is not a trivial decision, as the ecological interpretation of network structure may notably differ.

Standardizing the number of visits simply by census time (M2) could be important for those networks where sampling effort in time differed across plants during the whole flowering season, as it is in our case, as the number of visits to a plant could be mainly driven by the time spent observing it. However, we found that accounting for census time had only weak effects on network properties, probably due to the strong positive correlation between values in M1 and M2 ($r_s = 0.693$, $p < 0.01$), *i.e.* usually, more abundant insects show higher visitation rates. Similar results were obtained by Vázquez and Simberloff (2003).

When censusing flower visitors on plants, especially in those with many flowers, we usually observe only a limited area of the entire individual. We might expect that areas with more flowers might have a higher chance to receive more visits than others in which we observed only a few flowers. However, the correlation between visitation rate (no. visits/min) and number of visits per flower per minute was weak ($r_s = 0.262$, $p < 0.01$), and this is probably why we find significant differences in parameters between M2 and M3. Flower visitors appear to become more specialized (higher d' values) in M3, which indicates that at least some insects tend to visit plants even if these have less flowers. Interestingly, community interactions also become less diverse and more heterogeneous. Moreover, weighted strength of plants decreased in M3, which implies that the importance of any particular plant for flower–visitor community is lower. Finally, nested pattern of interactions became somewhat greater, suggesting that the community is more structured and organized (less abundant and specialized
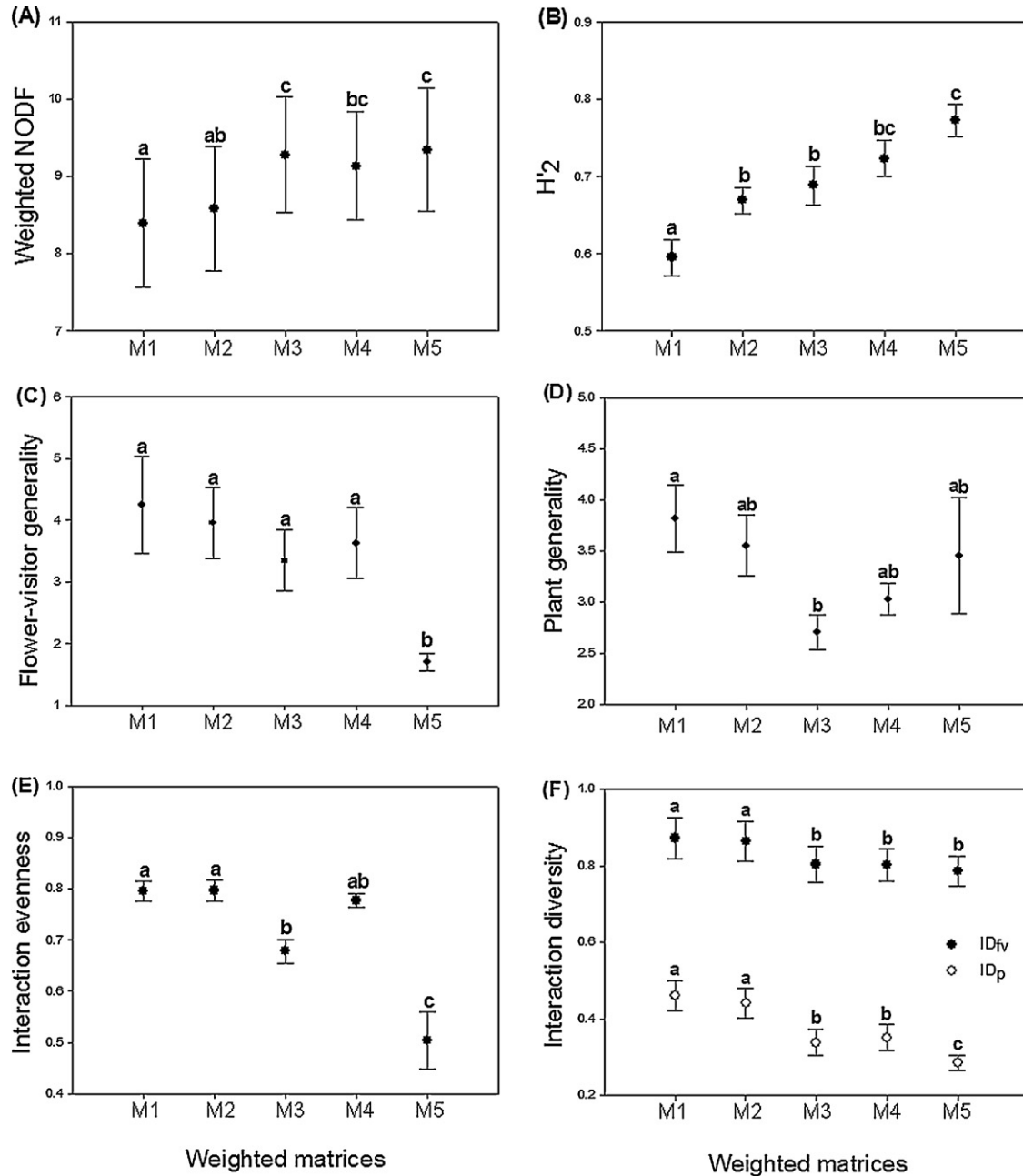
Fig. 1. Mean ± SE of the network-level parameters (A) weighted NODF, (B) H_2', (C) flower–visitor generality (G_{fv}), (D) plant generality (G_p), (E) interaction evenness and (F) interaction diversity (ID_{fv} and ID_p) of the 12 temporal networks (4 one-month networks for each of two subsequent years in Son Bosc, and 2 two-month networks for the same 2 years in Puig Major) for weighted matrices: M1 (no. of visits), M2 (no. of visits/time), M3 (no. of visits per flower/time), M4 (proportion of flowers visited/time) and M5 (proportion of flowers visited/time × flower abundance). For each parameter, values with the same letter are not significantly different from each other.

interactions tend to be proper subsets of more abundant and generalized ones) when accounting for number of flowers observed.

The link weight included in M4 is related to the number of flowers visited by each insect species. In a single foraging bout, the same visitor can visit one or many flowers, which can have important implications for plant reproductive success (*e.g.* Vázquez et al. 2005; Sánchez-Lafuente,

Rodríguez-Gironés, & Parra 2012); from the visitor's viewpoint, the amount of energy gained also depends on the number of flowers visited per plant and unit time. Quite surprisingly, however, network descriptors in M4 were quite similar to those found in M3. When testing the relationship between link weights used in M3 and M4, we again found a strong positive and significant correlation ($r_s = 0.895$, $p < 0.01$); the more visits (bouts) a plant receives the higher
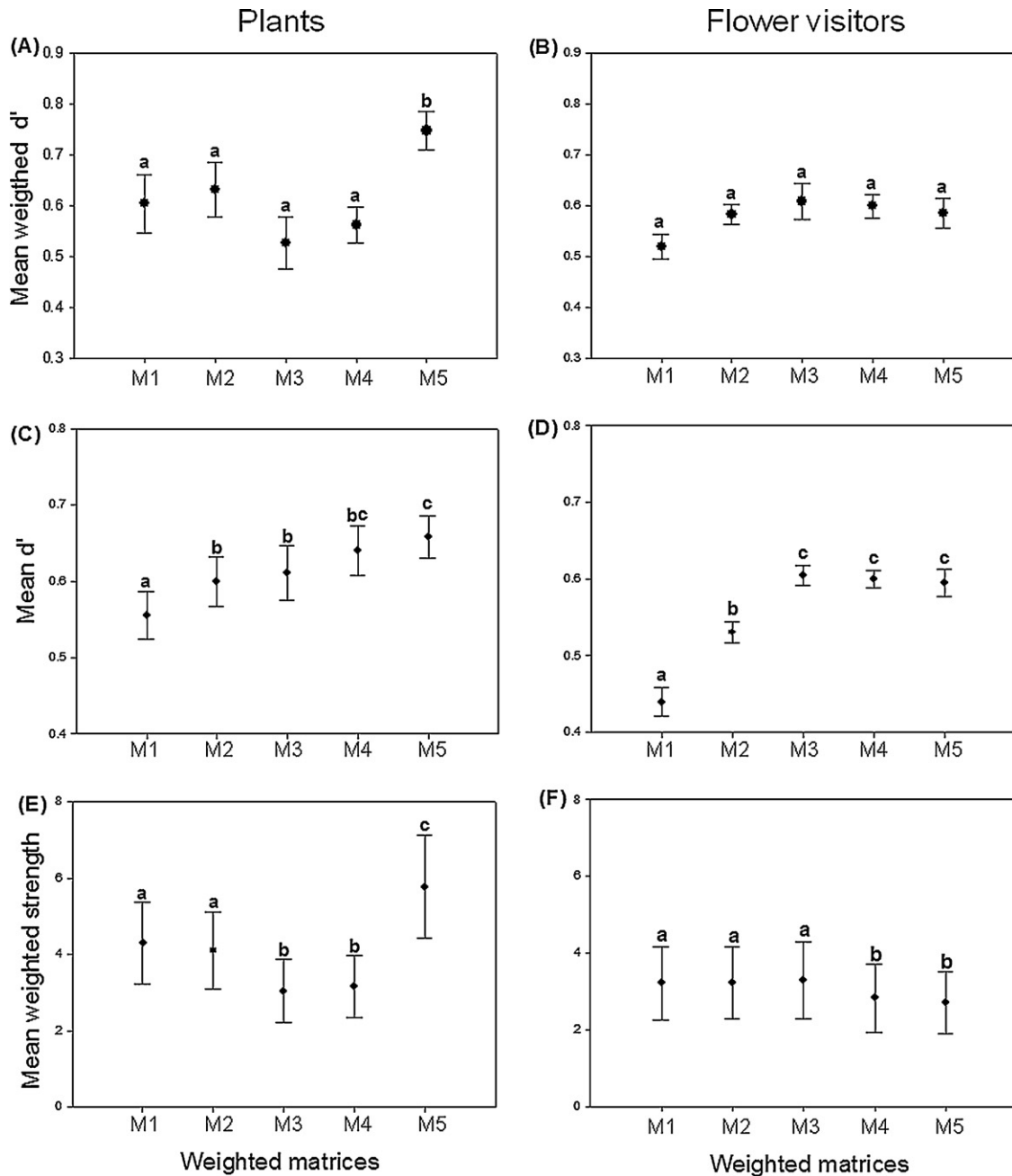
Fig. 2. Mean ± SE of the species-level parameters (A) mean weighted d_p', (B) mean weighted d_{fv}', (C) mean d_p', (D) mean d_{fv}', (E) mean weighted St_p and (F) mean weighted St_{fv} of the 12 temporal networks (4 one-month networks for each of two subsequent years in Son Bosc, and 2 two-month networks for the same 2 years in Puig Major) for weighted matrices: M1 (no. of visits), M2 (no. of visits/time), M3 (no. of visits per flower/time), M4 (proportion of flowers visited/time) and M5 (proportion of flowers visited/time × flower abundance). For each parameter, values with the same letter are not significantly different from each other.

will be the number of flowers visited on it. However, for each interaction, this relationship will depend upon the number of flowers visited in a single bout.

Finally, when accounting for flower abundance of each plant species in link weight, we are including information on its relative importance in the entire community. A particular flower visitor with a given flower visitation rate (*e.g.* 20 flowers/min) can be considered to be more specialized if it visits less-abundant flowers. This link weight (M5)

showed changes compared to M4. In particular, an overall higher heterogeneity of interactions at network level was detected; from the plants' perspective, there was a lower interaction diversity with their flower visitors and plant species appeared to be more specialized; from the animals' perspective, they appeared to visit a lower effective mean number of plants per species and the importance of plants for any particular flower–visitor in the community was also greater.

The only species-level parameter that was consistent regardless of link weight was mean strength (results not shown). Although plants' and flower–visitors' dependencies changed with weight given to an interaction, there was probably a compensatory effect, some species becoming more dependent on others whereas others becoming less dependent.

The differences between effects of link weight on plant and flower–visitor species parameters might be attributed to non-independent measurements of flower–visitor abundance in contrast to independent measurement of flower abundance. So far, however, most flower–visitation networks have been sampled from the plants' perspective, mainly due to methodological difficulties of tracking flower visitors. Only recently researchers have begun to include the pollinators' perspective on plant–pollinator interactions at the community level, for example by exploring the structure of pollen-transport networks (Gibson, Nelson, Hopkins, Hamlett, & Memmott 2006; Bosch, Martín-González, Rodrigo, & Navarro 2009; Alarcón 2010).

The parameters obtained using different link weights in our temporal network replicates showed that they do not only change in absolute values (or mean values for species level parameters) but also in rank order for the different weighted networks. The level of rank concordance of link weights between temporal networks (Kendall's W test) shows that most network parameters exhibit large differences in link weight rank (see Appendix C: Figs. 3–4 and Table 1). In other words, the rank of a particular link weight varies among the different temporal networks. However, there are some exceptions, like plant interaction diversity which shows high rank concordance between temporal networks regardless the link weight used (Kendall's $W = 0.839$, $p < 0.001$).

Recommendations for comparing weighted flower–visitation networks

A review of 22 published studies revealed a great variability in the way researchers have gathered data and constructed matrices of flower–visitation networks. On the one hand, there are large differences in census durations, ranging from 4 to 30 min, as well as in total observation time per plant species, from a few days to several years (Table 1). Our results show that this heterogeneity in total census time per plant is not crucial when describing the structure of quantitative flower–visitation networks. On the other hand, there are also differences in link weight used in such studies: Most consider the number of visits, though in some cases they account for time, flowers visited or total floral abundance. In this case, our findings lead us to recommend that if our goal is to compare topologies across networks, we should use the same link weight in all of them to reduce the risk of drawing erroneous conclusions.

The important question of which weight is most appropriate for a particular ecological network study is not trivial and ultimately depends upon the research objective, the sampling method used in field work and the indices calculated to describe network structure. However, it is clear that if we aim to move toward a more functionally relevant description of the structure of ecological networks, we need interaction weights that are as accurate as possible to avoid biases and misinterpretations and that are standardized across the entire network. A structure as much related to function as possible can help us, for instance, to better predict the community-wide impacts of species invasions or the consequences of the loss of species or interactions in the community.

Appendix A–C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2012.08.002.

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