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Effect of temporal data aggregation on the perceived structure of a quantitative plant–floral visitor network

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Abstract

Seasonal turnover in plant and floral visitor communities changes the structure of the network of interactions they are involved in. Despite the dynamic nature of plant–visitor networks, a usual procedure is to pool year-round interaction data into a single network which may result in a biased depiction of the real structure of the interaction network. The annual temporal dynamics and the effect of merging monthly data have previously been described for qualitative data (*i.e.* describing the occurrence of interactions) alone, while its quantitative aspect (*i.e.* the actual frequency with which interactions occur) remain little explored. For this, we built a set of 12 monthly networks describing year-round plant–floral visitor interactions in a 30-hectare planted forest and its adjacent agricultural landscape at Bahauddin Zakariya University Multan, Pakistan. A total of 80 plant and 162 insect species, which engaged in 1573 unique interactions, were recorded. Most network properties (particularly the number of plants, visitors and unique interactions) varied markedly during the year. Data aggregation showed that while animal species, plant species, unique interaction, weighted nestedness, interaction diversity and robustness increased, connectance and specialization decreased. The only metric which seemed relatively unaffected by data pooling was interaction evenness. In general, quantitative metrics were relatively less affected by temporal data aggregation than qualitative ones. Avoiding data aggregation not only gives a more realistic depiction of the dynamic nature of plant–visitor community networks, but also avoids biasing network metrics and, consequently, their expected response to disturbances such as the loss of species.

Key words: network descriptors, plant–floral visitor network, qualitative, quantitative network, seasonal variations.

Introduction

The study of ecological networks has shed light on our understanding of the organization of biodiversity in ecological systems. Particularly, plant-pollinator[1] networks describe the interactions that occur between flowers and their visitors at a given place and time (Memmott 1999). These networks have been used, among other things, to describe variations in properties along ecological gradients (Olesen & Jordano 2002; Devoto *et al.* 2005), to assess the success of habitat restoration (Forup & Memmott 2005; Forup *et al.* 2008; Devoto *et al.* 2012), to understand the mechanisms and consequences of invasion by exotic species (Memmott &

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[1] The terms 'pollinator' and 'floral-visitor' are used interchangeably, although we realize not all flower visitors pollinate (Kevan & Baker 1983).

Waser 2002; Morales & Aizen 2002; Lopezaraiza-Mikel *et al.* 2007), to generate recommendations on the conservation of rare species (Gibson *et al.* 2006), and to predict the possible consequences of global warming (Devoto *et al.* 2007; Memmott *et al.* 2007).

The quality of the data sets used to build plant-pollinator networks has been continually improved in recent years. While early networks described only the presence or absence of interactions (thus called qualitative networks`, *e.g.* Jordano 1987), an increasing number of networks now contain information on the frequency or weight of each interaction recorded in the field (quantitative networks`, *e.g.* Memmott 1999). Describing plant-pollinator networks in a quantitative fashion is now the standard in ecology as they depict interactions more appropriately than qualitative attempts and their properties are more robust against sources of bias such as sampling intensity, species richness and plant-to-visitor species ratio (Dormann *et al.* 2009).

The intricate patterns of interaction between species in plant–floral visitor networks have inspired a wealth of metrics that attempt to describe this complexity. Thus, network descriptors such as connectance, nestedness, degree distribution, interaction diversity, interaction strength and interaction evenness among many others have been proposed, debated and extensively used in the analysis of plant-pollinator networks in recent years. These descriptors have revealed the tantalizing structural complexity inherent to these networks (Bascompte & Jordano 2007). However, the bulk of studies are static descriptions of the structure of pollination networks, and only a few studies have explored their temporal dynamics. These studies show evidence that many network properties have strong temporal dynamics and exhibit changes on an hourly (Baldock *et al.* 2011), daily (Olesen *et al.* 2008), monthly (Basilio *et al.* 2006) and annual (Petanidou *et al.* 2008) basis.

One noteworthy consequence of the temporal dynamics shown by networks is that most network descriptions will be biased in some way as they all aggregate temporal data to some extent. Basilio *et al.* (2006) illustrated the effect of aggregating temporal data by identifying three potential sources of bias when merging a whole year of observations into a single network. First, species that apparently have the potential to interact may actually have non-overlapping phenologies (Olesen & Jordano 2002; Jordano *et al.* 2003; Basilio *et al.* 2006). Second, species with prolonged phenologies may appear to have more interactions than they typically have at any particular moment (Waser *et al.* 1996). Third, possible seasonal changes that may occur in system size, symmetry, connectance, species turnover and degree of generalization of the species involved may be overlooked (Basilio *et al.* 2006).

A limitation shared by most temporal descriptions published so far (but see Baldock *et al.* 2011) is that, because of the way the data was gathered in the field, only qualitative networks can be constructed. This limits our ability to understand changes in the quantitative aspects of these networks and, equally important, the effect of data aggregation on quantitative metrics. In this context, the aims of the present study are two-fold: (i) to describe the temporal dynamics of a quantitative plant–floral visitor network along a whole year; and (ii) to assess the effect of temporal data aggregation on qualitative and quantitative network properties. These aims were addressed in the context of a subtropical forest park in Punjab, Pakistan.

Materials and methods

Study site

The study was done at a 30-hectare forest plot within the campus of Bahauddin Zakariya University Multan, Pakistan (30.255°N; 71.513°E; 114 ± 6 m above sea level). Aside from some supplementary plantation of *Eucalyptus camaldulensis*, *Dalbergia sissoo*, *Acacia nilotica*, *Albizzia procera* and *Leucaena leucocephala* the forest remains uncultivated, and a large array of herbs, shrubs and trees naturally grow in it, the most common being *Capparis deciduas, Tamarix aphylla*, *Ziziphus jujuba*, *Prosopis juliflora*, *Launae audicaulis, Raphanus sativus*, *Cirsium arvense*, *Haloxylon recurvum, Salsola baryosma, Pulicaria crispa, Achyranthes aspera*, *Heliotropium europaeum*, *Sonchus asper*, *Lantana camara*, *Carthamus oxycantha, Cleome viscose, Oxalis corniculata*, *Portulaca oleracea*, *Stellaria media*, *Alhagi graecorum* and *Abutilon indicum*. The forest is located in the Southern Irrigated Zone of Punjab (PARC 1980). The area has subtropical climate with hot summer and cold winters; the mean daily maximum and minimum temperatures are in the range of 30 to 35°C and 15 to 20°C, respectively. The highest temperature (45 to 51°C) is recorded in May and June while the lowest (3 to 0°C) is recorded in January (Khan *et al.* 2010). The mean annual rainfall is around 300 to 500 mm (PARC 1980).

Monsoon lasts from July to September and contributes nearly half of the total annual rainfall. The region has four distinct seasons: winter (December to February), spring (March to May), summer (June to August) and autumn (September to November). In the study area most plant species (about 60%) flower during spring followed by summer, autumn and winter (Sajjad *et al.* 2010; 2012). Geographically, it is an alluvial plain with fertile soils deposited by the flood regime of the rivers over thousands of years. Most of the land is cultivated and irrigated by canals or underground waters. Cotton-wheat rotation is traditionally the most common in the area, among a variety of other crops grown.

Network construction

The interactions between plants and their floral visitors were recorded on a wide array of vegetation types which comprised 75 naturally occurring species of trees, shrubs or annuals and five crop species, grown unevenly on a total of 2 hectares along forest margins. These crops were *Brassica napus*, *Raphanus sativus* and *Allium cepa*, which flowered in spring, and *Helianthus annuus* and *Abelmoschus esculentus*, which flowered in summer.

Visitor censuses were done during the first fortnight of each month from January to December 2007. It was ensured that each plant species was sampled once every 30 days. During a census, thirty individuals of each plant species in bloom were randomly selected and each observed for 60 seconds. Thus, a total of 30 minutes of observations per plant species per census were done. During each census the number of individuals of each floral visitor species that visited the flowers of the focal plant was counted. Observations encompassed the entire flowering period of all plant species in the area. Only diurnal floral visitors were recorded. Total sampling effort was 121 hours. Since plant species belonged to different categories *i.e.* (trees, shrubs, herbs *etc.*) and had different inflorescence types (*i.e.* umbels, heads, *etc.*), we defined the sampling units for each plant species separately, and each time recorded observations from those sampling units *i.e.* entire plant, specific number of branches per tree, one square meter of an individual plant, *etc.*

During field observations, all the visitor insects were first morphotyped and a few individuals of each morphotype were collected for further identification to the lowest possible taxonomic level. The identification to family level of Diptera and Coleoptera was done following Borror *et al*. (1981). Bee genera were identified following Michener (2000). Syrphid fly and butterfly species, and plant specimens were identified by taxonomists (see Acknowledgments). Voucher specimens were deposited at the Agricultural Museum of the University College of Agriculture, Bahauddin Zakariya University Multan, Pakistan.

Data analysis

To describe the temporal changes in network structure along the year (Objective 1), interaction data for each month was analyzed as a separate network. Nine properties were calculated for each monthly network: animals (number of visitor species), plants (number of plant species), number of unique interactions, connectance, weighted nestedness, interaction evenness, interaction diversity, network-level of specialization and robustness to species loss.

The number of unique interactions was calculated as the number of non-zero cells in the matrix representation of the interaction network. Connectance was calculated as the fraction of all potential interactions that were actually observed (Jordano 1987). Weighted nestedness was calculated following the method developed by Galeano *et al.* (2009) which, unlike the original nestedness (Bascompte *et al.* 2003), considers interaction frequencies in its calculation. The interactions in a network are nested when specialists (species with few interaction partners) interact with species that form well-defined subsets of the species with which generalists (species with many interaction partners) interact (Bascompte *et al.* 2003).

Interaction evenness treats the interactions between each pair of species in a matrix, which occur at different frequencies, as “species” which occur at different “abundances”. In this way, applying the Shannon’s evenness to an entire matrix calculates the evenness of interactions in the same way the evenness of a community would be calculated (Bersier *et al.* 2002; Blüthgen *et al.* 2006). Interaction diversity, which is also based on Shannon’s diversity index, calculates the diversity of pairwise interactions (Blüthgen *et al.* 2006; Blüthgen *et al.* 2008). The network-level of specialization is a measure of specialization based on the deviation of a species’ realized number of interactions and that expected from each species’ total number of interactions (Blüthgen *et al.* (2006). The robustness of a network measures its response (*i.e.* occurrence of secondary extinctions) to the loss of species (Burgos *et al.* 1981). All network metrics were calculated with the R package ‘bipartite’ (Dormann *et al.* 2008). Monthly values of each metric were plotted for a whole year.

To assess the effect of temporal data aggregation on network properties (Objective 2) networks encompassing time periods of increasing length were constructed, from 1 to 6 months (following Medan *et al.* 2006). We started by merging interaction data from all possible pairs of consecutive months (January + February, February + March, *etc.*). Mathematically, this is done by adding together the corresponding elements (*i.e.* entries) of the matrices. We repeated the process for periods of 3 to 6 months. For each network of merged data we computed the same properties that were used to describe the monthly networks. The coefficient of variation of the grouped means across all aggregation levels was used as a measure of the degree to which each network property was affected by data aggregation.

Results

Overall, we recorded 1573 unique interactions between 80 plant and 162 insect species. On average, each insect species visited 7.2 ± 9 plant species (mean ± SD) and each plant species was visited by 15 ± 8.6 insect species. Overall, species rich families of visitors were Syrphidae (14 species), Apidae (10), Megachilidae (8) and Halictidae (5). There were significant changes of the abundances of four insect orders over the sampling months (χ^2 test, $P < 0.0001$, Fig. 1). During winter, flies (Diptera) were more abundant than bees and wasps (Hymenoptera) but in spring, summer and autumn, bees and wasps remained dominant over flies (Fig. 1). The number of flowering plant species with at least one interaction was 3, 12, 38, 38, 37, 28, 24, 21, 20, 12, 6 and 3 from January to December, respectively.

The maximum number of species of floral visitors recorded in 1 month on a single plant species was 31 species in April on *Calotropis procera*, which year-round comprised 4.57% of the total interactions. *C. procera* also had the highest number (46) of visitor species of the system followed by *Malvastrum coromandelianum*, *Launaea procumbens*, *Tribulus terrestris* and *Cucumis prophetarum* which represented about 3 % of all interactions each. The number of species of floral visitors of a plant species was positively correlated to the length of its flowering periods ($r^2 = 0.616$, $P < 0.0001$).

The maximum number of species of plants recorded in 1 month for a single visitor species was 26 species in April for *Sphaerophoria bengalensis* (Syrphidae), which comprised 1.8 % of the total interactions of the system. The most interaction-rich flower visitors included *Eristalinus aeneus* (Syrphidae), *Halictus* sp. (Halictidae), *Apis dorsata* (Apidae), *Apis florea* (Apidae), *Ischidon scutellaris* (Syrphidae) and *Ceratina sexmaculata* (Apidae) (comprising 3 to 4.4 % of all interactions). These generalist flower visitors had long activity periods (>9 months; except for Syrphidae, which mainly occur in spring) during which they interacted with no less than 40 plant species each. The number of plant species visited by a floral visitor species was positively correlated to the length of the visitor's period of activity (months) ($r^2 = 0.624$, $p < 0.0001$).

The maximum number of active insect species was recorded in April, while March, April and May were the months with the highest species richness of flowering plants (Fig. 2). Coincidentally, the highest numbers of unique interactions were recorded in the period March–June (Fig. 2). After the sharp increase in the period January–April, a gradual decline in the number of flowering plant species was observed between May and December. The number of visitor species, however, remained at a plateau from June to October followed by a sharp decline in the following 2 months (Fig. 2).

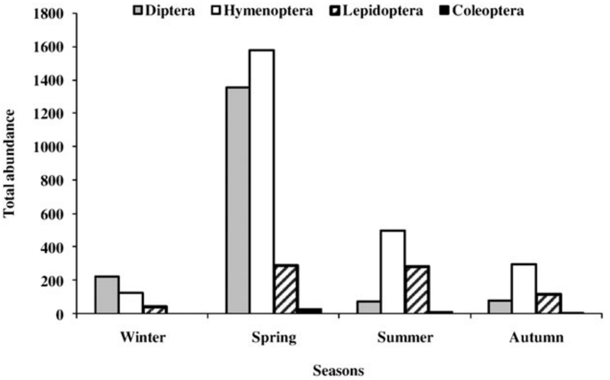

Figure 1 Seasonal variation in population size of the main orders of flower visitors of a plant community sampled year-round at a planted forest in the campus of Bahauddin Zakariya University Multan, Pakistan.

Connectance ranged from 9.63 % to 52.38 % (average, 19.43 %) and was negatively associated to the total number of active plant and visitor species in the community ($r^2 = 0.307$, $P = 0.062$). Seasonal variations in weighted nestedness and interaction diversity seemed to oppose the variations in number of plant and insect visitor species. Interaction evenness was lower in December and January; thereafter it gradually increased until June. The maximum interaction diversity was recorded in December, when there was a maximum number of plant and visitor species. The most specialized interactions occurred between October and February (Fig. 2).

Regarding the effect of monthly data aggregation, the number of floral visitor species and plant species and the number of unique interactions among them were the properties most affected by data aggregation (as shown by their high coefficients of variation across aggregation levels, Fig. 3). Interaction evenness was by far the property least affected by data aggregation. The rest of the properties measured (connectance, weighted nestedness, interaction diversity, specialization and robustness) showed intermediate coefficients of variation.

Regarding the direction of the change in network properties caused by data aggregation, the number of plants, number of floral visitors, number of unique interactions, weighted nestedness, interaction diversity and robustness increased, while connectance and specialization decreased with increasing data aggregation. Finally, interaction evenness showed no clear trend in response to data aggregation (Fig. 3). In general, the quantitative properties (weighted nestedness, interaction evenness, interaction diversity, specialization and robustness) were least affected by temporal data aggregation than qualitative properties (floral visitor species, plant species, unique interaction and connectance).

Discussion

This study described monthly variations in the structure of a quantitative plant–visitor network and explored the effect on network descriptors of aggregating monthly data. While previous studies based on temporal dynamics have focused on the seasonal turnover of interactions (*e.g.* Olesen *et al.* 2008; CaraDonna *et al.* 2017), this is the first study to provide a quantitative description of the seasonal changes in the metrics of a plant–visitor interaction network. To our knowledge, it is also the first study to assess the effect of

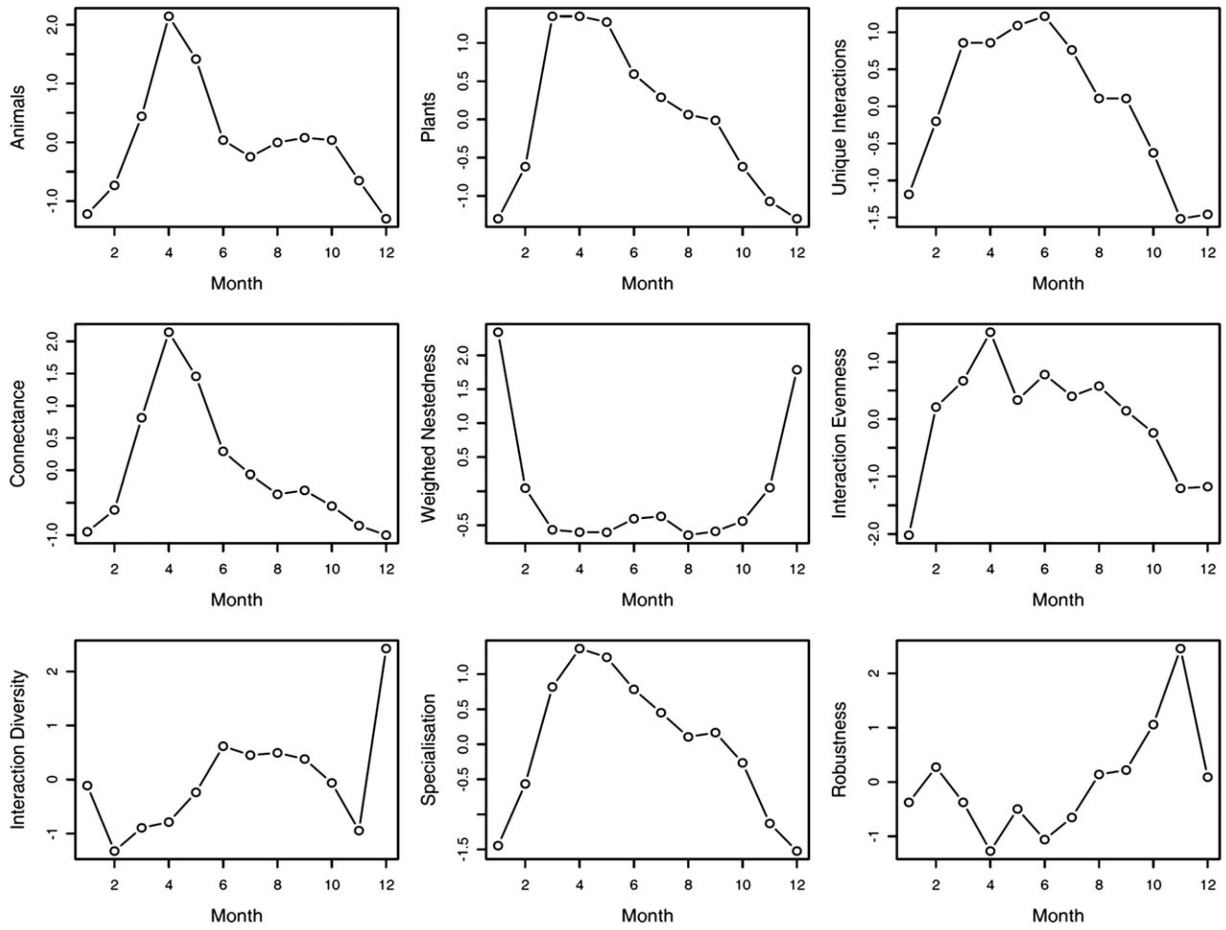

Figure 2 Monthly variation of nine properties of a year-long plant-pollinator network. For each property data points represent the values of individual monthly network (month 1 = January). Values are shown centered on the annual means and divided by their standard deviation.

temporal data aggregation on quantitative network descriptors. In this section, we will first discuss our results in the context of our objectives and then address the main limitations of this study.

In this study all network properties (both qualitative and quantitative) showed significant seasonal variations. This is consistent with previous studies that show that qualitative network properties (connectance, nestedness, modularity, *etc.*) vary significantly within a single year (*e.g.* Basilio *et al.* 2006). The present study thus strengthens the idea that a proper description of the interactions in a plant–visitor community with year-round activity should include all seasons and not just the few months of spring and summer.

Different studies have shown variable levels of temporal variations on network properties (Olesen *et al.* 2008; Petanidou *et al.* 2008); however, seasonal variations are more prominent than interannual variations (Olesen *et al.* 2008). In this study, the seasonal variations in nestedness and interaction diversity opposed the variations in number of plant and insect visitor species. The seasonal changes in weighted nestedness and network-level specialization suggest that species exhibited more specialized interactions during the time of the year when the number of species and interactions were at a minimum. Since specialization is not affected by system size and sampling intensity (Blüthgen *et al.* 2006) our finding regarding seasonal changes in specialization seem robust. Although counterintuitive, this could mean species behave as generalists and forage less selectively when resources are abundant, but become more selective when resources are scarce.

Our analysis of data aggregation (Objective 2) showed that most properties, both qualitative and quantitative, are affected by temporal aggregation. While animal species, plant species, unique interaction, weighted nestedness, interaction diversity and robustness increased, connectance and specialization decreased. The only metric which seemed relatively unaffected was interaction evenness. Our findings are in accordance with previously reported qualitative studies of plant–visitor networks (Basilio *et al.* 2006; Medan *et al.* 2006). Their results suggest that the analysis of a

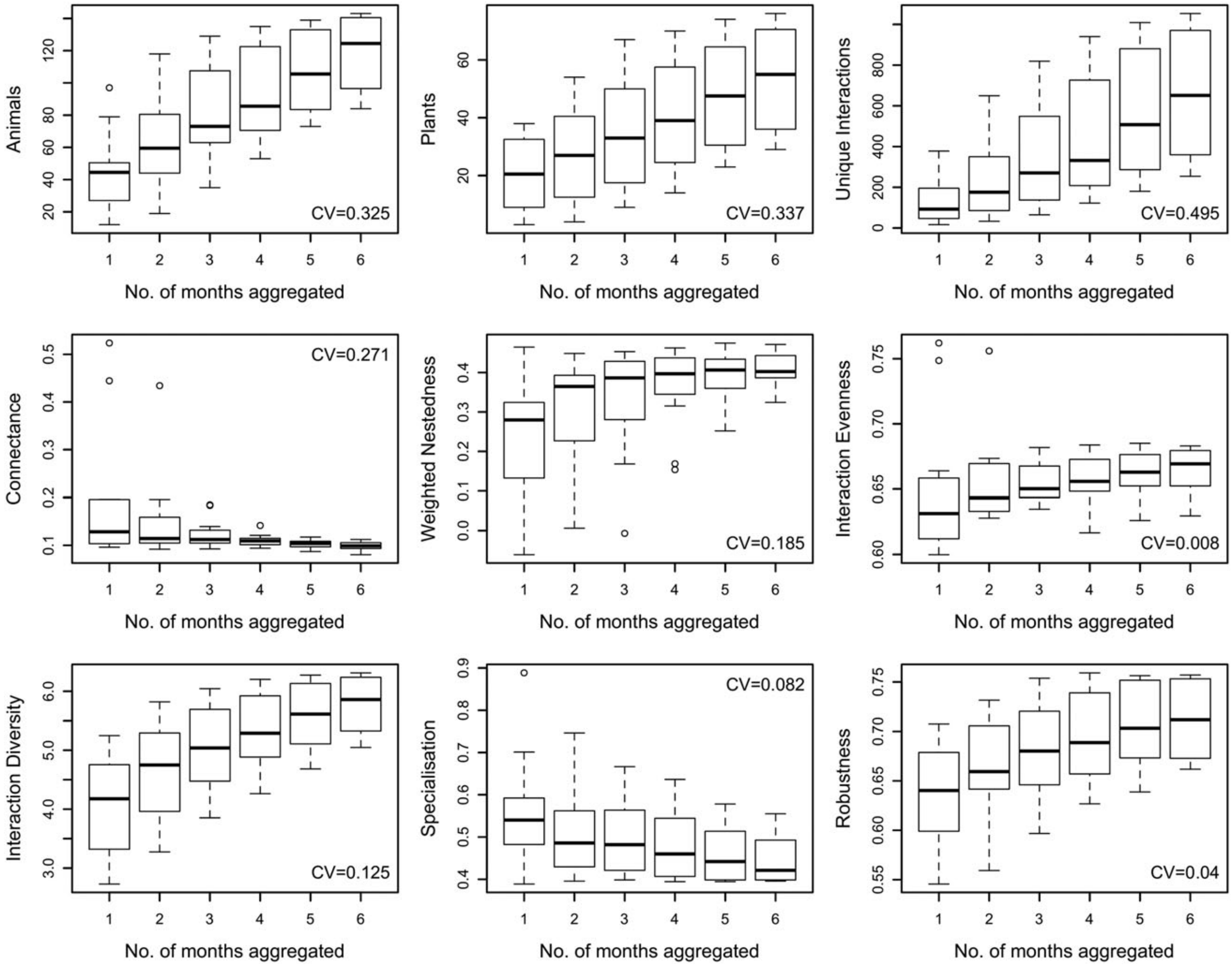

Figure 3 Variation of nine properties of a year-long plant-pollinator network as a function of the number of months of which data was aggregated for calculations. The coefficient of variation of the mean value of each property across aggregation levels is shown.

plant–visitor community which is active along the whole year should be done at shorter, biologically relevant periods due to the introduction of “forbidden links” which may bias the results when longer periods are considered (Jordano *et al.* 2003). The aggregation of network data for long periods may give rise to many non-coincidental plants and pollinator phenologies, resulting in, for instance, decreased network connectance. Cumulative webs may bias the results whereas comparing seasonal or sequential webs more explicitly shows network dynamics and interaction turnover (CaraDonna *et al.* 2017).

In general, quantitative properties (weighted nestedness, interaction evenness, interaction diversity, specialization and robustness) were relatively less affected by temporal data aggregation than qualitative properties (floral visitor species, plant species, unique interaction and connectance). This is in accordance with previous studies in food webs showing greater robustness of quantitative network properties compared to their qualitative versions against variable sampling efforts (Banasek-Richter *et al.* 2004). Temporal aggregation can be seen as a form of increasing sampling effort since interaction data contained in networks of each individual month is considerably less compared to their aggregated versions. In addition, as the species with higher interaction frequencies tend to be the ones most abundant and/or with longer phenophases (Olesen *et al.* 2008; Vázquez *et al.* 2009), individual monthly networks therefore tend to be dominated by these species and their reciprocal interactions. Because the temporal turnover in dominant species (and their interactions) between months will tend to be small, this core of dominant interactions, which drive quantitative network metrics, is unlikely to change abruptly with the aggregation of temporal data. As quantitative network metrics have been shown to be rather insensitive to changes in any cell of the interaction matrix apart from those with high values (Dormann *et al.* 2009) it is perhaps not surprising that the aggregation of temporal data has a smaller effect on quantitative properties than on qualitative ones.

Limitations

A potential limitation of our study (*i.e.* impact of merging temporal data on quantitative and qualitative network properties) is that sampling effects may have influenced observed network structure in at least two possible ways. First, some network properties such as connectance clearly scale with the number of species in the network analyzed (Dormann *et al.* 2009). For instance, connectance tends to decrease with increasing species richness of the network (Jordano 1987). This implies that the variations in connectance may be an artefact and do not reflect a seasonal shift in the behavior of the species in the network (Blüthgen *et al.* 2008). Second, previous studies dealing with temporal dynamics of plant-pollinator networks (*e.g.* Basilio *et al.* 2006; Alarcón *et al.* 2008; Olesen *et al.* 2008; Petanidou *et al.* 2008; Baldock *et al.* 2011) have pointed out that abundance and phenophase length (*i.e.* the length of a species' period of activity) can influence the detection probability of pairwise interactions and ultimately network structure (Blüthgen *et al.* 2008; Vázquez *et al.* 2009). Thus, interactions involving abundant species with long phenophases may be easier to observe than those involving rare species with short phenophases (Vázquez *et al.* 2009), which results in that the latter may appear as more specialized simply because of this sampling bias. In our study, however, the most interaction-rich species were Syrphidae, although species in this family tended to have rather short phenophases (March to April). In this case, their short phenophase was compensated by their large abundances in the field (Stang *et al.* 2006; Dormann *et al.* 2009; Vázquez *et al.* 2009).

Concluding remarks

Plant–visitor networks, and more generally ecological networks, are dynamic entities that constantly reshape their structure both at small and large time frames (Trøjelsgaard & Olesen 2016). In the wake of climate change, recording interactions between species at fine temporal scales is a useful tool for predicting phenological shifts and the resulting temporal mismatches expected to arise (Dixon 2003; Memmott *et al.* 2007; Kaiser-Bunbury *et al.* 2010). In this context, it is essential to gather field data in a way that it describes temporal dynamics and it can be used in climate change simulations. In addition, in the light of the effect reported here of temporal data aggregation on network structure, and considering network structure may affect the way it responds to species loss (Memmott *et al.* 2004; Devoto *et al.* 2007), the aggregation of temporal data should be done cautiously.

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