

The temporal dimension in individual-based plant pollination networks

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The pollination success of animal-pollinated plants depends on the temporal coupling between flowering schedules and pollinator availability. Within a population, individual plants exhibiting disparate flowering schedules will be exposed to different pollinators when the latter exhibit temporal turnover. The temporal overlap between individual plants and pollinators will result in a turnover of interactions, which can be analyzed through a network approach. We have explored the temporal dynamics of individual-based plant networks resulting from pairwise similarities in pollinator composition. During two flowering seasons, we surveyed the phenology and pollinator fauna of the individual plants from a population of *Erysimum mediohispanicum* (Brassicaceae). We analyzed the topology of these networks by means of their modularity, clustering, and core–periphery structure. These metrics are related to network functional properties such as cohesion, transitivity and centralization respectively. Afterwards, we analyzed the influence of each pollinator functional group on network topology. We found that network topology varied widely over time as a consequence of the differences in plant phenology and the idiosyncratic and contextual effect of pollinators. When integrating all temporary networks, the network became cohesive (non modular), transitive (locally clusterized), and centralized (core–periphery topology). These topologies could entail important consequences for plant reproduction. Our results highlight the importance of considering the entire flowering season and the necessity of making comprehensive temporal sampling when trying to build reliable interaction networks.

Phenology is crucial to understand plant–pollinator interactions (Elzinga et al. 2007). Most plant populations are composed of individuals showing different flowering schedules (Primack 1980, Marquis 1988) which vary in flowering intensity, timing, and duration (Augspurger 1983, Mahoro 2002). These individual flowering schedules entail important effects on plant reproduction (Munguía-Rosas et al. 2011). For example, flowering synchrony among conspecific can influence seed siring (Herrera 1992), or create intrapopulation assortativity in mating (Weis et al. 2005, Elzinga et al. 2007, Ison et al. 2014) as mating probabilities are related to the level of synchrony (Hendry and Day 2005, Devaux and Lande 2008). Pollinators also display specific phenological patterns (Cane et al. 2005), which create temporal variations in pollinator availability (Herrera 1988). These variations in pollinator availability may cause differences in the subset of pollinator species interacting with those individual plants differing in flowering schedules. Consequently, and similarly to what occurs at the community level (Olesen et al. 2008, Rasmussen et al. 2013), a turnover of interactions is expected to emerge when individual plants flower at different moments and interact with different pollinators.

Plant–pollinator interactions have been widely analyzed during the last decades using network tools (Bascompte and

Jordano 2013). In pollination networks, links depict pollinator visits to plant reproductive organs. Accordingly, the occurrence and intensity of these links would be affected by plant and pollinator phenologies, since they can restrict pollination events to certain time windows (Olesen et al. 2011). Despite some overall network properties appearing to be constant among years (Olesen et al. 2008, Petanidou et al. 2008), recent studies have evinced the turnover of interactions within a flowering season, emphasizing the necessity of considering the seasonal dynamics to obtain a better understanding of these networks (Baldock et al. 2011, Simanonok and Burkle 2014). In this sense, the temporal dynamics of these interactions have been shown to influence some network properties. For example Olesen et al. (2008) found that the complexity of an arctic pollination network increased through time to reach a maximum before the network collapsed at the end of the season. Moreover, compartmentalization in Mediterranean pollination networks increased due to the mismatch of species phenophases (Bosch et al. 2009, Martín González et al. 2012), an effect that has been demonstrated to be enhanced when downscaling to pollinator individuals (Tur et al. 2015).

Most pollination studies using network tools have focused on the community level. These studies do mostly

use bipartite networks, which are composed of two sets of nodes: plant and pollinator species (Bascompte and Jordano 2013). Currently, there is a growing interest in downscaling the study of pollination networks to the individual level. This downscaling can be done for either plants or pollinators separately (Gómez et al. 2011, Gómez and Perfectti 2012, Tur et al. 2014), or even both simultaneously (Dupont et al. 2011, 2014). Contrasting with classic ecological networks, individual-based networks are able to reflect processes taking place at the population level. Some of these processes are even better analyzed when bipartite individual-based networks are projected into unipartite networks, a type of networks characterized by links connecting individuals of the same set and widely used to analyze social interactions. Interesting functional properties emerge in unipartite individual-based plant networks since links can serve as a proxy of mating probabilities among plants (Gómez et al. 2011). However, studies considering individual-based unipartite networks are scarce (but see Gómez et al. 2011, Gómez and Perfectti 2012, Dáttilo et al. 2014), even though this approach could produce novel insights about how interactions are structured within populations. For example, similarly to species in pollination network at the community level (Olesen et al. 2007), individual plants can be organized into cohesive groups or modules by having similar pollinator assemblages. Moreover, if plants with similar flowering schedules are structured in clumps, a modular structure may appear only at some temporal periods. In individual-based pollination networks high values of clustering, a metric measuring transitivity (Newman 2003a), could indicate a structure in the interaction with pollinators and the presence of groups of individuals that tend to mate frequently among themselves (Gómez et al. 2011). Other metrics are related to the centralization of the networks (Newman 2003b). Centralized networks are characterized by a core of nodes highly connected surrounded by a periphery of less connected nodes. We think that a core–periphery structure may emerge as a consequence of the differences in pollinator sharing. This network topology may be due in part to differences in flowering synchrony among plants, resulting in differences in the number of links per plant and, therefore, in their position in the center or periphery of the network.

In this study we address, during two flowering seasons, how the interplay between individual-plant phenology and pollinator availability shape the topology of the individual-based plant network in a population of *Erysimum mediobispanicum* (Brassicaceae). This species is highly generalist, pollinated by a myriad of insect species belonging to disparate taxonomical and functional groups (Gómez et al. 2014). The interaction with pollinators vary spatially at different scales, such as between regions, between populations, and even between co-occurring individuals (Gómez et al. 2009). The presence of interindividual variation in pollinators has been successfully investigated using individual-based networks (Gómez et al. 2011, Gómez and Perfectti 2012). Another feature of the pollinator assemblage of *E. mediobispanicum* is that it is composed of insects differing in their foraging periods. This generates an important seasonal turnover of the composition of *E. mediobispanicum* pollinator assemblages (Valverde et al. 2014). Taking into account this preliminary information, in this study we aim to 1) explore

the phenology of individual plants and their pollinators, 2) assess the between-plant differences in pollinator assemblage due to the temporal pollinator turnover, 3) determine the temporal shifts in the individual-based network topology described by modularity, weighted clustering and assortative mixing, three metrics related to network cohesion, transitivity and centralization, respectively (Borgatti et al. 2013), and (4) estimate the influence of different types of pollinators on the topology of these networks. The main goal of this study is to explore how intra-seasonal variation in plant and pollinator phenologies determines the temporal variation in individual-based plant networks.

Material and methods

Study system

Erysimum mediobispanicum (Brassicaceae) is a biennial, semelparous herb endemic to the Iberian Peninsula (Nieto-Feliner 2003). They grow vegetatively for 2–3 years and then develop 1–8 flowering stalks bearing up to several dozens of flowers. The flowering season occurs from May to the end of June. Flowers display a bright-yellow corolla with separate petals that facilitate pollinator access. Flowers are hermaphrodite and partially self-compatible, although they need the assistance of pollinators to produce full seed set (Gómez 2005). The pollination system of this species is extremely generalist, having several hundreds of pollinator species (Gómez et al. 2009, 2014).

Sampling design

During 2010 and 2011, a 20 × 20 m plot was set up in a population of *E. mediobispanicum* at 1723 m a.s.l. in a pine forest in the Sierra Nevada (southeastern Spain; 37°8'07"N, 3°21'71"W). Each year, one hundred plants were randomly selected within the plot, which represented the 80–90% of the total flowering plants in the population. To avoid interferences with other individuals, remaining individuals were removed or excluded from pollinators by bagging their flowering stalks.

We monitored the flowering phenology of each plant during the two study years. For this we recorded daily the flowering status of plants and periodically counted their open flowers (16 times in 2010 and 28 times in 2011). In addition, we counted the insects visiting the flowers of each plant during five minutes intervals, performing between one to four surveys per day, totaling 58 surveys in 2010 and 62 in 2011. Floral visitors were clumped into functional groups (FG herein), groups of species presumably exerting similar selective pressures on floral phenotype (Fenster et al. 2009). We considered only those insects contacting legitimately the plant reproductive organs at least during some foraging bouts. Based on morphological characteristics such as body size, proboscis length, floral fit or foraging behavior, we considered 23 FGs (see Table 1 for a description of FGs). Ants are not good pollinator in this system, but we decided to include them in the analyses not for their per-visit effectiveness but for their high abundance.

Table 1. Functional groups considered in this study, indicating a description of resource use (NC: nectar consumer, PC: pollen consumer, P: pollen collector) and the legitimacy of their interaction (Leg: legitimate visitor, Ileg: illegitimate visitor). Fulfillment of the conditions are indicated with a + symbol.

Functional group	Acronym	Size (mm)	Taxons	Resource			Legitimacy	
				NC	PC	P	Leg	Ileg
Long-tongued large bees	LtLB	> 10	Hymenoptera: Anthophoridae (<i>Anthophora</i>), Apidae (<i>Apis mellifera</i> , <i>Bombus</i>)	+			+	
Short-tongued large bees	StLB	> 10	Hymenoptera: Halictidae, Andrenidae	+		+	+	
Short-tongued medium-sized bees	StMB	5–10	Hymenoptera: Halictidae (<i>Lasioglossum</i> , <i>Halictus</i>), Megachilidae (<i>Osmia</i>), Andrenidae (<i>Andrena</i>)	+		+	+	+
Short-tongued small bees	StSB	< 5	Hymenoptera: Halictidae (<i>Lasioglossum</i>), Colletidae (<i>Hylaeus</i>), Andrenidae (<i>Andrena</i>), Apidae (<i>Ceratina</i>)	+		+	+	+
Large ants	LA	> 2	Hymenoptera: Formicidae (<i>Formica</i> , <i>Camponotus</i> , <i>Proformica</i> , <i>Cataglyphis</i>)	+			+	+
Small ants	SA	< 2	Hymenoptera: Formicidae (<i>Plagiolepis</i> , <i>Leptothorax</i>)	+			+	+
Pollen wasps	PW	variable	Hymenoptera: Vespidae. Masarinae (<i>Ceramius</i>)	+		+	+	
Small nectar-collecting wasps	SncW	< 3	Hymenoptera: Ichneumonidae	+			+	+
Long-tongued bee flies	LtBf	variable	Drptera: Bombyliidae (<i>Bombylius</i>), Nemestrinidae	+	+		+	
Short-tongued bee flies	StBf	variable	Diptera: Bombyliidae (<i>Anthrax</i>)	+	+		+	
Large hoverflies	LH	> 5	Diptera: Syrphidae (Eristalini)	+	+		+	
Small hoverflies	SH	< 5	Diptera: Syrphidae (Syrphini, Meodontini, Bacchini)	+	+		+	+
Large flies	LF	> 5	Diptera: Muscidae, Calliphoridae, Tabanidae, Scatophagidae, Anthomyiidae	+	+		+	+
Small flies	SF	< 5	Diptera: Muscidae, Anthomyiidae, Empididae, Bibionidae, Drosophilidae.. among others	+	+		+	+
Large beetles	LB	> 7	Coleoptera: Lagridae, Mylabridae, Alleculinae		+		+	+
Small beetles	SB	< 7	Coleoptera: Melyriade, Cleridae, Oedemeridae, Elateridae, Bruchidae, Buprestidae, Chrysomelidae		+		+	+
Small diving beetles	SDB	< 3	Coleoptera: Nitidulidae, Dermestidae, Phalacridae	+	+		+	+
Butterflies	Btfly	variable	Lepidoptera: Pieridae, Nymphalidae, Lycaeidae, Hesperidae	+			+	+
Large moths	LM	> 3	Lepidoptera: Crambidae, Noctuidae	+			+	
Small moths	SM	< 3	Lepidoptera: Adelidae	+	+		+	+
Hawkmoths	Hwk	> 7	Lepidoptera: Sphingidae	+			+	
Bugs	Bugs	variable	Hemiptera: Miridae, Lygaeidae, Pentatomidae (<i>Eurydema</i>)	+			+	+
Others	Oth	variable	Orthoptera, Raphidioptera, Neuroptera, among others		+		+	

Plant phenology and flowering synchrony

We described the phenology of the studied plants by means of flowering curves, estimated using local polynomial functions (Supplementary material Appendix 1). Flowering pairwise synchrony of each individual plant with the rest of conspecifics was determined by means of two indices: 1) unweighted synchrony ($X_{i,j}$; Eq. A1 in Supplementary material Appendix 2). This index measures the overlap in flowering and was calculated using Augspurger (1983) index considering the number of co-flowering days. 2) Weighted synchrony (J ; Eq. A2 in Supplementary material Appendix 2). This index weights the flowering overlap by the number of open flower and was calculated using the Jaccard-type Chao dissimilarity index (Chao et al. 2005) over the flowering curves. This index ranges from 0 to 1 and can be interpreted as the probability of two flowers chosen at random from two individuals being open the same day.

Temporal variation in pollinators

We analyzed the temporal variation in richness and diversity of FGs, calculated as the Hurlbert's PIE (D_{Hurlbert} ; Hurlbert 1971) (Eq. A3 in Supplementary material Appendix 2),

by pooling all surveys within 3-days overlapping temporal windows (Supplementary material Appendix 3). We visualized the temporal turnover in the FGs using spindle diagrams (Valverde et al. 2014). Here, turnover refers to the temporal change in the frequency of the interactions of pollinators and *E. mediobispicum* plants, independent of the local abundance of pollinators. To check the occurrence of this temporal turnover we calculated for each pair of surveys the dissimilarity in FG composition using the Morisita–Horn index (S_{M-H} ; Eq. A4 in Supplementary material Appendix 2), and compared these distances with the temporal distances, in days, using a Mantel test. We complemented this analysis by constructing a Mantel correlogram using the same distance matrices. This analysis allowed us to detect the minimum temporal distance at which the correlation in pollinator species composition disappear. Using this temporal distance we partitioned each flowering season in discrete non-overlapping temporal windows (τ_1, \dots, τ_n , herein). Each temporal window spanned a number of days higher than that minimum and contained an equitable number of surveys. Finally, we tested whether the composition in pollinators varied more between- than within-years using a PERMANOVA (Anderson 2001), nesting temporal windows within year and using days as replicates.

Between-plant differences in pollinator composition

We calculated the dissimilarity between plants in the composition of pollinator faunas using the Morisita–Horn index. The resulting distance matrices were compared with the flowering schedules distance matrices, which were calculated using the Jaccard-type Chao distance index. The comparisons were made by means of Mantel tests based on Spearman correlation index. We also performed a Mantel correlogram using the compositional dissimilarity as a response variable to identify correlation trends of pollinator composition with asynchrony classes. With this procedure we assessed if there was plant–plant isolation in pollinator composition due to their flowering asynchrony.

Temporal shifts in the topology of the individual-based plant networks

Each study year and temporal window resulted in an adjacency matrix of individual plants-FGs, showing the number of visits of each FG per individual plant. As our aim is to describe the individual-based plant networks, for each temporal window (t_1, \dots, t_n) we projected the plants-FGs adjacency matrix into a plant–plant matrix using the pairwise similarity in pollinator assemblages. Similarity was calculated as $1 - \text{Morisita-Horn index}$. Links in these networks indicate the probability of two plants sharing the same pollinators. Due to the high sampling effort, no single plant was unlinked, resulting in a massive network that may obscure some network properties (May 2006). To overcome this problem, we used percolation theory to find the simplest network while maintaining its percolation capacity (Rozenfeld et al. 2008). From a starting network, links are sequentially removed starting from the weakest, until the step before the network breaks down into isolated subgraphs. This is the so-called percolation threshold, beyond which the network breaks down into disconnected sub-networks. Percolation is a useful tool to simplify networks' complexity while maintaining the important connections and nodes involved in information flow (Muñoz-Pajares 2013). With the resulting percolated networks we made a topological description in terms of their modularity, weighted clustering and assortative mixing by degree.

Modularity (Q ; Eq. A5 in Supplementary material Appendix 2) measures to what extent a network is organized into modules. Modules are defined as groups of nodes with a higher link density within the group than among groups (Newman 2004). This metric measures the deviation from a random link distribution by calculating the observed fraction of links within each group minus the fraction expected at random (Newman 2004). We used the heuristic walktrap community detection method based on random walks (Pons and Latapy 2006) to find the most modular network structure. Here, modularity will give information on how the population is structured in groups of plants sharing similar pollinators.

Weighted clustering coefficient (C_w ; Eq. A6 in Supplementary material Appendix 2), a metric measuring transitivity, was estimated as the extension proposed by Opsahl and Panzarasa (2009) of the Newman's (2003a) global clustering coefficient. While the clustering coefficient informs about

the proportion of groups of three nodes (triad) fully interconnected, C_w weights each triad with the geometric mean of the links forming it. This metric measures the tendency of nodes to cluster together into tightly connected local groups. If node A shares a link with nodes B and C, in a network with a high value of C_w , nodes B and C will also share a link between them with a higher probability than with a node picked at random (i.e. high transitivity; Junker and Schreiber 2008). High values of this metric are expected in individual-based networks built on pollinator similarity. High values indicate that individual plants share the same pollinators producing a very compact network, while low values indicate sparse networks formed by plants visited by different subsets of the entire fauna of pollinators.

Assortative mixing by node degree (r ; Eq. A7 in Supplementary material Appendix 2) measures to what extent nodes tend to be connected with nodes of similar degree. This metric works as a correlation parameter among degree values of interconnected nodes (Newman 2003b). This metric takes a value of 1 if there is a perfect assortative mixing, 0 if there is no assortative mixing and close to -1 when the mixing is disassortative. Values close to -1 describe star-like networks while values close to 1 describe networks with a core of highly connected nodes against a periphery of nodes with lower degree (Newman 2010). In the context of our work, positive values will denote a network topology formed by a core of plants highly similar in pollinator composition and a periphery of less connected plants.

For all measured network metrics we analyzed their deviations from what is expected under the null hypothesis of pollinators foraging randomly. We constructed 500 random adjacency matrices maintaining the marginal values of the FGs per survey (i.e. total number of contacts). Through this type of randomization, we maintain FGs overall abundances and restrict plants sampling only in their flowering days. After this, we obtained the individual-based plant network as described previously (random networks herein) and calculated the mean and the 0.025 and 0.975 percentiles of the network metrics. We chose 500 replicates because beyond 400 replicates the mean and standard deviations of the metrics stabilized.

Influence of different FGs on network topology

We assessed the differential effect of each FG on network topology by comparing the empirical network with simulated networks where only insects belonging to a particular FG foraged randomly. For each bipartite matrix (total and temporary), the visits of a given FG were reshuffled among plants while maintaining the observed visitation distribution of the remaining FGs. The resulting matrix was percolated and network metrics were obtained as described before. We repeated this procedure 500 times for each FG and empirical matrix to obtain a distribution of simulated values for each network metric. We report the standardized effect sizes (SES herein) of each FG (Eq. A8 in Supplementary material Appendix 2). The sign and strength of SES indicates how the behavior of a given FG modifies the network metrics, with values close to 0 denoting similar effects to those produced when a FG forages randomly.

All analyses were performed under the R statistical analysis platform (<www.r-project.org>), using the packages ‘vegan’ (Oksanen et al. 2014), ‘igraph’ (Csardi and Nepusz 2006), ‘network’ (Butts et al. 2014), ‘tnet’ (Opsahl 2009), and ‘forraGEO’ (Valverde et al. unpubl.). We developed personalized codes modified from Muñoz-Pajares (2013) for some of the network analyses (Supplementary material Appendix 4). Supplementary material Figure A1 resumes the workflow followed to perform the network analyses.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.jf2c0>> (Perfectti et al. 2015).

Results

We did 120 pollinator surveys of the whole population (58 in 2010 and 62 in 2011), distributed over 70 flowering days (32 in 2010 and 38 in 2011), and totaling 43 975 minutes of observation. We recorded 7421 pollinator–flower interactions in both years (2949 visits, 21 735 minutes in 2010; 4472 visits, 22 240 minutes in 2011). We recorded 23 FGs, with a predominance of large ants (24% of total visits), long tongued bees (21%), small beetles (13%), and small ants (12%). The rest of functional groups did not exceed 10% of the overall visits.

Plant phenology and flowering synchrony

Individual plants differed in their phenologies (Fig. 1; Supplementary material Appendix Table A1). Unweighted synchronies showed intermediate values ($X_{i,j} = 0.62 \pm 0.18$ in 2010, $X_{i,j} = 0.69 \pm 0.14$ in 2011), which decreased when considering flowering intensity ($J = 0.25 \pm 0.21$ in 2010, $J = 0.14 \pm 0.14$ in 2011).

Temporal variation in pollinators

Pollinator richness and diversity showed similar temporal trends in both years (Supplementary material Appendix Fig. A2). The number of functional groups ranged from a minimum of seven at the onset of 2011 flowering season to 16 in the middle of the 2011 flowering season. Hurlbert’s PIE ranged from 0.18 in 2010 to 0.86 in 2011. Maximum values of diversity were found in the same temporal interval both years (140–155 julian days). However, temporal changes in richness were less congruent between years. Spindle diagrams showed contrasting patterns as a consequence of the temporal replacement of pollinators (Fig. 1b). This replacement was evidenced by a significant positive correlation between temporal distance among surveys and dissimilarity in pollinator composition (2010: $r = 0.014$, $R^2 = 0.35$, $DF = 1651$, $p < 0.001$; 2011: $r = 0.011$, $R^2 = 0.22$, $DF = 1828$, $p < 0.001$; Supplementary material Appendix Fig. A3). There was a positive and significant correlation between compositional dissimilarity and temporal distance across surveys ($r_M = 0.597$, $p = 0.001$ in 2010; $r_M = 0.458$, $p = 0.001$ in 2011). Mantel correlograms

indicated positive and significant correlation at the first distance classes (Fig. 2). However, this autocorrelation was lost beyond an interval of 5–6 days suggesting the occurrence of temporal isolation of the community of pollinators at this time span. Consequently, we grouped the surveys in periods of six days, resulting in a partition of six temporal windows (t1 to t6) each year. Variation in pollinator composition was higher within year than between years (PERMANOVA, SS between years = 0.506, $p = 0.008$; SS among temporal windows within year = 7.483, $p = 0.001$; SS within temporal windows = 8.841).

Between-plant differences in pollinator composition

The correlation between flowering asynchrony and pollinator dissimilarity was significant for both years (2010: $r_M = 0.079$, $p = 0.033$, 2011: $r_M = 0.21$, $p = 0.001$). Moreover, when analyzing the correlation patterns of pollinator dissimilarity along asynchrony classes using Mantel correlograms, we found a significant positive correlation for the two first distance classes (asynchrony ≤ 0.1 ; Fig. 3). In 2010 this correlation was lost from the third distance class while, in 2011, the correlation was shifted to a significant negative one from the fourth distance class on (asynchrony ≥ 0.23).

Temporal shifts in the topology of the individual-based plant networks

The total networks were composed of 95 and 89 connected plants in years 2010 and 2011 respectively (Fig. 4). However, the temporary networks varied widely in size (42 to 96 connected plants in 2010; 35 to 93 connected plants in 2011). Some plants were removed from some networks during the percolation process because they were visited by none or just a few insects (Table 2).

Modularity varied widely in both years (Fig. 5). In 2010, this metric showed higher and significant values only at the fourth temporary (t4) network ($Q = 0.39$, $p < 0.05$, Table 2). In 2011, modularity only reached marginally significant values at t5 and t6 networks ($Q = 0.41$ and 0.40 , $p < 0.1$). By contrast, weighted clustering exhibited a marked positive deviation from the null model, reaching significance at the t4 network in 2010 ($C_w = 0.86$, $p < 0.05$, Table 2) and marginal significance at the t4 network in 2011 ($C_w = 0.68$, $p < 0.1$). This metric showed a marginal significant value for the 2010 total network ($C_w = 0.61$, $p < 0.1$), reaching significance in 2011 ($C_w = 0.61$, $p < 0.05$). Finally, assortative mixing by node degree exhibited positive deviations through the whole time period, reaching marginal significance at the t4 network in 2010 ($r = 0.43$, $p < 0.1$, Table 2) and significance at the t4 network in 2011 ($r = 0.45$, $p < 0.05$). This metric showed positive and significant values for this metric in both total networks ($r = 0.51$ and 0.48 , $p < 0.05$ in 2010 and 2011 respectively).

Influence of different FGs on network topology

Only eight functional groups (long-tongued bees, large ants, small ants, bugs, small beetles, small moths, short tongued medium-sized bees and short-tongued small bees) showed a relative frequency higher than 0.10 in at least

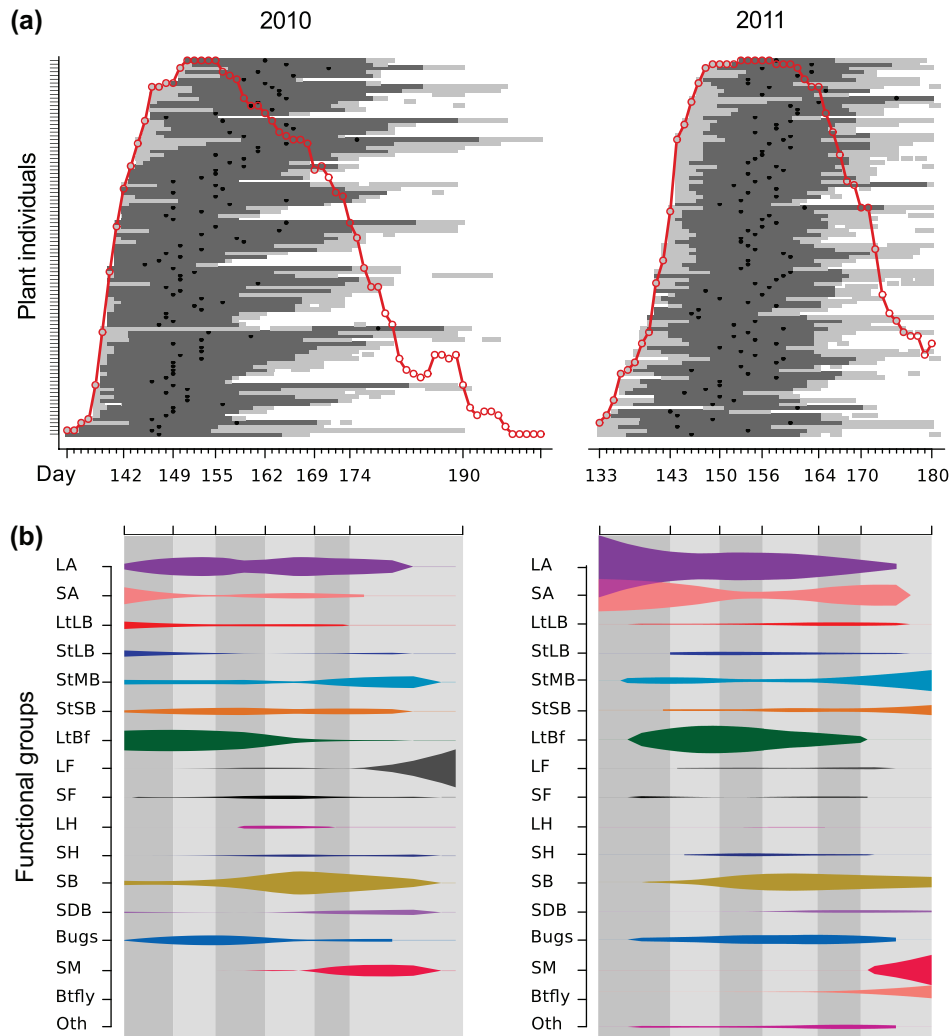


Figure 1. Flowering schedules and pollinator visits through time. (a) phenogram showing for each individual its flowering span (light gray bars), time period within the 25–75% cumulative open flowers (darker bars), and flowering peak (black dots). The number of flowering plants per day (red circles and lines) is also shown. (b) bundance of pollinator functional groups. The width of the spindle diagrams denotes the relative abundance of each pollinator group (see Table 1 for acronyms).

one network. Short tongued small bees did not exceed this threshold in 2011, therefore its effect sizes are only reported for year 2010. The effects of these functional groups on network metrics were not temporally consistent, neither in size nor in sign (see Fig. 5 for details). For example, modularity

was inconsistently affected by small ants which exerted significant effects of different sign at some temporary networks ($SES = -1.53$ and 2.84 at t_4 and t_6 networks in 2011). For weighted clustering, effect sizes also shifted in sign through both seasons. Only large ants, bugs and small beetles showed

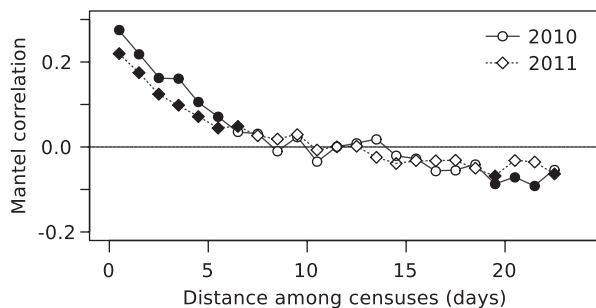


Figure 2. Temporal turnover of functional groups in both years. Mantel correlogram of Morisita–Horn dissimilarity index over temporal distances among surveys. Filled circles and diamonds indicate significant values ($p < 0.05$) of the Mantel correlation tests.

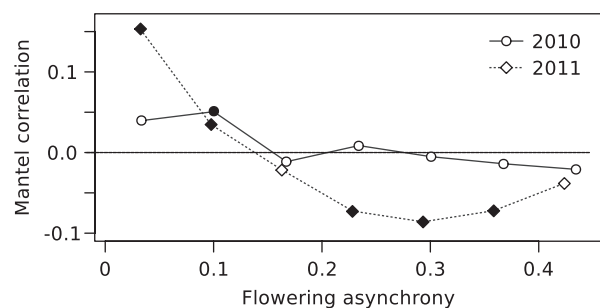


Figure 3. Mantel correlograms of pairwise dissimilarities in pollinator composition (Morisita–Horn dissimilarity index) against flowering asynchrony (Jaccard-type Chao distance index). Significance values ($p < 0.05$) obtained after 999 simulations are pointed out as filled circles and diamonds.

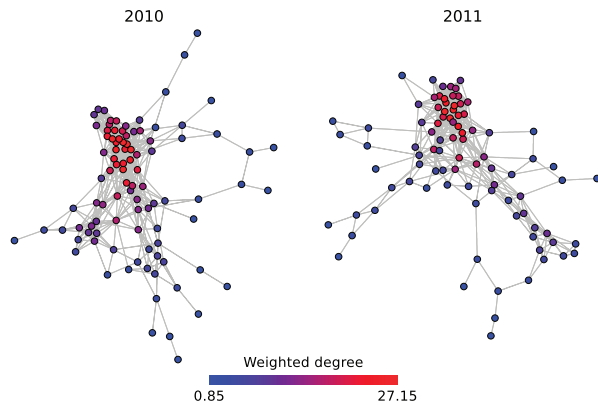


Figure 4. Total networks for both years. Each node represents an individual plant. Links among plants indicate similarities in pollinator composition. Colors of each node represent its weighted degree calculated as the sum of all link weights pertaining to that node. Note the core–periphery topology denoted by the distribution of node degrees.

significant effect sizes on this metric in some networks, particularly large ants which exerted significant positive effect sizes on two temporary networks (SES = 3.16 and 2.77 at t2 and t5 networks in 2010) and at both total networks (SES = 3.11 and SES = 3.66 in 2010 and 2011, respectively). Likewise, the effects of the functional groups on assortative mixing by degree shifted in sign through both years (Fig. 5). The functional group large ants stands out, again, showing significant positive effect sizes at one temporary network (SES = 2.00 at t2 network in 2011) and at both total networks (SES = 3.88 and 2.58 in 2010 and 2011, respectively).

Discussion

Exploring the phenology of individual plants and their pollinators

Erysimum mediohispanicum exhibited intermediate values of flowering synchrony during both years of study when

calculated using the Augspurger's index. These values are similar to those found in montane plants (Gómez 1993, Crimmins et al. 2013) and correspond with the higher values observed for other species (Primack 1980, Buide et al. 2002, San Martín-Gajardo and Morellato 2003, Samuel de Avila and Freitas 2011). Nevertheless, the variation in flower intensity among individuals resulted in low values of weighted synchrony. Under these circumstances we expect that the probability of interacting with the different pollinators will vary among plants. These findings emphasize the need of considering flowering intensity to obtain more accurate estimates of pairwise synchrony (Freitas and Bolmgren 2008) and individual plant–pollinator interactions (Encinas-Viso et al. 2012). Several factors may influence flowering phenology, including genetic variation (Mitchell-Olds 1996, Leinonen et al. 2013) and microenvironmental heterogeneity (Herrera 1988). Mediterranean open woodlands and shrublands, where populations of *E. mediohispanicum* grow, exhibit high microenvironmental variability (Gómez et al. 2004, Valladares and Guzmán 2006). Specifically, the plot maintains different microenvironments mainly related to the shaded areas that some pine trees produce. These microenvironmental differences occur at meter scales and translate in variation in resources and specially in humidity. We have observed that plants located in shaded areas flower for more time than exposed plants. We think that this heterogeneity may explain at least in part the observed variability in flowering and pairwise synchrony, and therefore could be a factor influencing plant–pollinator interactions.

The insects visiting the flowers of *E. mediohispanicum* also showed temporal changes in the relative occurrence of their visits, resulting in a turnover of interactions. This was reflected in the observed temporal variation in richness and diversity. Temporal changes in pollinator fauna have been reported mainly among years (Cane et al. 2005, Price et al. 2005, Dupont et al. 2009) and between populations (Price et al. 2005, Petanidou et al. 2008, Dupont et al. 2009). Moreover, temporal variations in pollinator fauna have also been recorded intra-annually for plant species having extended flowering (Herrera 1988, Ashman and Stanton

Table 2. Sampling effort and topological metrics for each network and year. Network size includes the number of flowering plants for a time period (flowering), the number of plants visited by pollinators (visited) and the connected plants in the similarity network after the percolation process (connected). 1-threshold denotes the lower limit of link weights remaining in each network after percolation.

Year	Network		Sampling effort			Network size				Network metrics		
	Time lap	Days	Surveys	Pollinator visits	flowering	visited	connected	1 - threshold	Modularity (Q)	Weighted clustering (C_w)	Assortative mixing by node degree (r)	
2010	142–147	6	8	691	93	88	88	0.56	0.03	0.7	0.23	
	149–154	5	11	873	100	98	96	0.62	0.06	0.73	0.33	
	155–159	5	10	630	100	92	92	0.66	0.07	0.67	0.34	
	162–168	5	9	297	90	67	66	0.57	0.39*	0.86*	0.43 [†]	
	169–173	5	9	274	72	62	59	0.52	0.25	0.7	0.4	
	174–189	6	11	162	61	42	42	0.40	0.08	0.69	0.09	
	Total	32	58	2927	100	100	95	0.85	0.34	0.61 [†]	0.51*	
2011	133–142	7	8	149	49	36	35	0.66	0.43	0.78	0.47	
	143–149	6	11	212	100	94	93	0.75	0.08	0.70	0.41 [†]	
	150–155	6	8	844	100	96	91	0.75	0.26	0.64	0.33	
	156–163	6	12	1178	100	94	93	0.70	0.04	0.68 [†]	0.45*	
	164–169	6	14	858	96	84	74	0.72	0.41 [†]	0.57	0.31	
	170–180	6	8	207	66	50	49	0.40	0.40 [†]	0.70	0.18	
	Total	37	61	4448	100	100	89	0.88	0.23	0.61*	0.48*	

Significant values are reported as *for $p < 0.05$, and [†]for partially significant ($p < 0.10$).

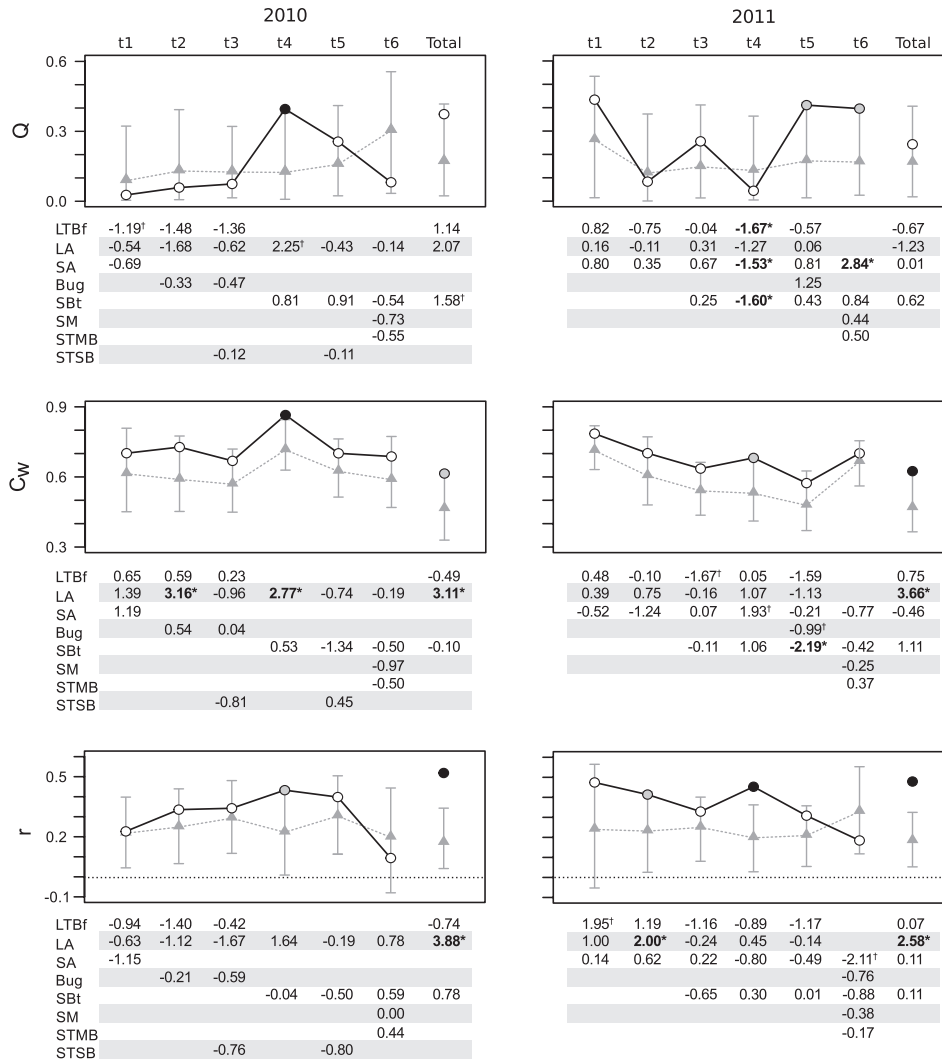


Figure 5. Intra-seasonal variation in network metrics (Q , modularity; C_w , weighted clustering; r , assortative mixing by node degree) and effect sizes for the most important pollinator functional groups. For each temporary (t1 to t6) and total network, empirical values (dark circles and lines) and 95% confidence intervals obtained from the null model of pollinators behaving randomly (gray triangles and lines) are drawn. Black filled circles indicate significance ($p < 0.05$) and gray filled circles marginal significance ($p < 0.1$). Values of effect sizes are denoted as *when significant ($p < 0.05$) and † when marginally significant ($p < 0.1$).

1991). In our case we have found a high intra-seasonal pollinator turnover in a plant without extended flowering. This fine-grain temporal variation has been previously detected at community level (Olesen et al. 2008, Baldock et al. 2011, Simanonok and Burkle 2014), for specific plants (Hurd and Linsley 1975), and previously reported in *E. mediohispanicum* (Valverde et al. 2014). Remarkably, this turnover was even stronger than the inter-annual variation, as could be expected for an extremely generalist plant when pollinator availability changes throughout the flowering season. Several intrinsic and extrinsic factors can influence pollinator turnover. Some important intrinsic factors are changes in insect population dynamics and emergence date (Ellwood et al. 2011, Kudo 2013), altitudinal migration (Stefanescu 2001, Gutiérrez and Wilson 2014), and temporal changes in their feeding habits (Faegri and van der Pijl 1979). On the other hand, extrinsic factors can include displacement by competition with other pollinators (Brosi and Briggs 2013),

or changes in local plant composition that may promote shifts in pollinator preferences (Cane and Sipes 2006). Regardless of the specific reasons, they ultimately affect the composition of pollinator assemblages visiting a plant species and thus the pollinating scenario within a population (Herrera 1988, Horvitz and Schemske 1990).

The interplay among plant and pollinator phenologies affects the likelihood of their interaction (Kudo 2013). Our results show that the variability in the phenologies of co-occurring individual plants and the turnover of pollinator visits lead to among-plant dissimilarities in their pollinator assemblages. Plants exhibiting disparate flowering schedules will be visited by different pollinators, resulting in a decoupling of interactions (Memmott et al. 2007, Hegland et al. 2009). Moreover, as pollination effectiveness can vary among pollinators (Sahli and Conner 2007), and even temporally within the same species (Fishbein and Venable 1996, Rafferty and Ives 2012), this decoupling of interactions can

entail variation in plant fitness (Schemske 1977, Mahoro 2002). Since in *E. mediohispanicum*, pollinators vary widely in effectiveness (Valverde et al. unpubl.), we hypothesize that plants flowering when the most effective pollinators are available may have their reproductive fitness enhanced. On the other hand, because plant fitness has been positively correlated with pollinator diversity (Klein et al. 2003, Gómez et al. 2007, Perfectti et al. 2009), plants flowering during the period of maximum diversity of pollinators may have their fitness enhanced. Further research should incorporate pollination performance to produce a more realistic view of how the interplay of plant and pollinator phenologies affects plant reproduction.

Temporal shifts in the topology of the individual-based plant networks

The patterns of node linkage can result in a non-random network topology (Newman 2010). Shared characteristics among nodes can partition the network into cohesive modules, a common feature of pollination networks (Lewinsohn et al. 2006, Olesen et al. 2007, Martín González et al. 2012). In individual-based pollination networks, plants having similar pollinator assemblages would be more connected and thus will group together into modules. For this to happen, individual differences in pollinator assemblages are required, a common phenomenon occurring in generalist systems (Herrera 1995, Thompson 2001). However, the presence of abundant shared pollinators will make these groups fuzzy. We have not found significant differences in modularity between the total empirical networks and the random networks, suggesting the absence of well defined groups of plants. Although modularity was significant in some temporary networks, most of them showed non-significant values. The high variation in the value of this metric suggests that the groups of plants sharing pollinators are temporally labile, meaning that network modules are not static, but divide and merge through time (Stanoev et al. 2011). In this sense, the integration of the temporary networks in the total network is surely canceling out the formation of modules. We believe that this pattern will be common in generalist plants visited by many disparate pollinators that vary temporally in their frequency of interaction.

Weighted clustering values, although not significant, were high in all temporary networks and consistently above the mean values obtained in the random networks. Because this metric measures the proportion of closed triplets in a network (Opsahl and Panzarasa 2009), our results indicate that the temporary networks were compact and enriched in closed triplets. Plants flowering at the same time will have higher likelihood of forming local clusters because of their higher probabilities of interacting with the same set of pollinators. This pattern is reinforced in the total network, where the temporary interactions between individual plants and pollinators are integrated. As a consequence, weighted clustering reached significance in the total network (Table 2, Fig 5). Under these circumstances, we would expect non-random mating among individual plants as a consequence of the pattern of pollinator sharing. High values of weighted clustering have been related to family aggregation in social networks

(Fowler et al. 2011). Detailed genetic studies, however, are needed to corroborate this idea.

Assortative mixing by node degree indicates whether there exists a pattern of node linkage based on node degree (Newman 2002). The positive values found for this metric in our system indicate that temporary networks had a core-periphery topology that is significant in the total networks (Table 2, Fig. 4, 5). We think that the core-periphery structure found in the total network could be in part due to the overlapping of temporary networks, in a similar way as Yang and Leskovec (2014) demonstrated for overlapping communities. In this sense, the network core would be enriched with plants flowering during the entire season and thus appearing in most temporary networks. These plants are more likely to be visited by a higher diversity of pollinators and therefore have high multiple similarities in pollinator composition with other plants. On the other hand, the periphery will be mostly composed of plants visited by singular pollinator assemblages, reducing their multiple similarities (Juraski et al. 2012), and decreasing the probabilities of being connected with more plants. Because being visited by a highly diverse pollinator assemblage enhances fitness (Klein et al. 2003, Gómez et al. 2007, Perfectti et al. 2009), we presume that core plants will have high values of fitness. Moreover, because core plants are highly inter-connected, they would receive more diverse pollen loads and would also donate pollen to many other plants (Gómez and Perfectti 2012), implying that their progenies will have higher genetic diversity. These mating patterns and the evolutionary consequences however should be verified using paternity analyses.

We have explored the effect that the non-random foraging behavior of pollinators may have on the topology of the networks. We did not find any consistent effect, measured as standardized effect sizes, for the temporary networks. Only for the total networks the effects of some type of pollinators became consistent (Fig. 5). Large ants, although varying the sign of their effect through the temporary networks, significant and positively affected weighted clustering and assortativity metrics in the total networks. However the lack of a consistent effect for the rest of pollinators suggests that the foraging pattern of pollinators varies temporally. Changes in pollinator behavior can be due to changes in feeding habits (Faegri and van der Pijl 1979), but also to the response to other pollinators' behavior. The arrival of new pollinator species can displace preexisting ones or change their foraging behavior as a result of competitive interactions (Morse 1982, Brosi and Briggs 2013). Moreover, aggressive resource consumers like ants (Blüthgen and Fiedler 2004), might deplete floral resources and thus may provoke important changes in the intensity of interaction of this plant species with other pollinator types. We think that the observed pollinator turnover supports that the effects of different pollinators on network topology are context-dependent, i.e. the effects of a pollinator type on network topology depends on the abundance of other pollinator types. This context-dependence has been previously suggested as an important driver of ecological interaction networks (Poisot et al. 2014) and could also be an important factor when downscaling to individual-based pollination networks.

Conclusions

Our study suggests that the interplay between plant phenology and pollinator availability shape the topology of the individual-based plant networks based on similarities in pollinator composition. Our networks were cohesive (non modular), transitive (locally clusterized), and centralized (core–periphery topology). These particular topologies could entail functional consequences for the persistence and evolution of plant populations. Nevertheless, our study shows that the network properties changed over time, indicating that the effects of different types of pollinators on network topology are contextual. This finding demonstrates the importance of considering the entire flowering season and highlights the necessity of making comprehensive temporal sampling when trying to build reliable interaction networks.

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Supplementary material (available online as Appendix oik-02661 at <www.oikosjournal.org/appendix/oik-02661>. Appendix 1–4.