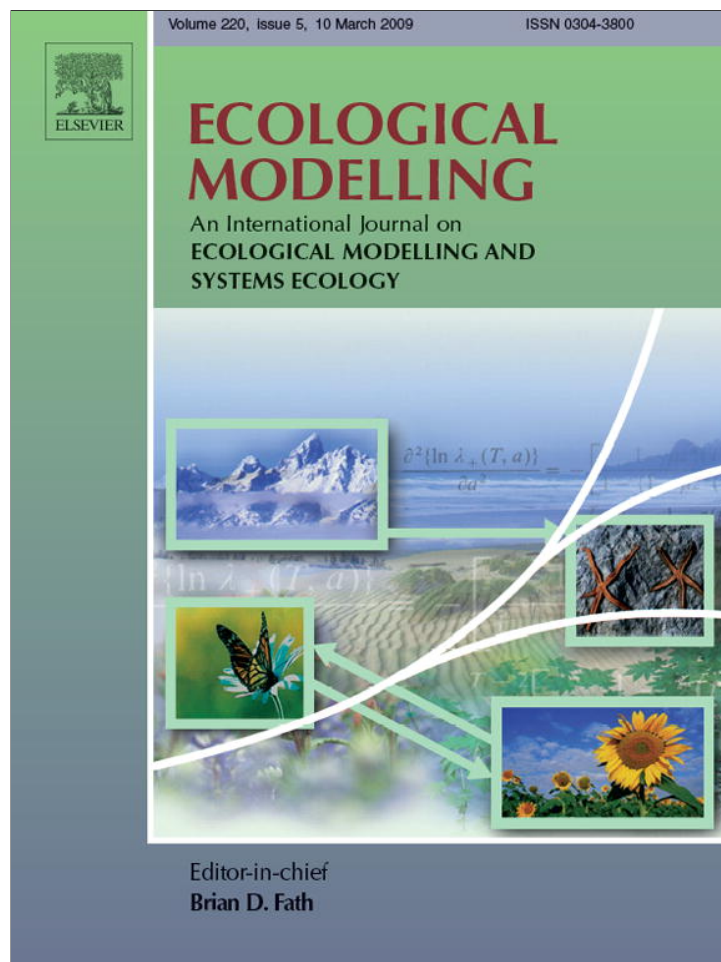


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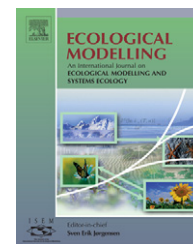


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Do plant–pollinator interaction networks result from stochastic processes?

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ABSTRACT

Plant–pollinator interaction networks are characterized by several features that cannot be obtained from a totally random network (e.g. nestedness, power law distribution of degree specialization, temporal turnover). One reason is that both plants and pollinators are active for only a part of the year, and so a plant species flowering in spring cannot interact with a pollinator species that is active only in autumn. In this paper we build a stochastic model to simulate the plant–pollinator interaction network, taking into account the duration of activity of each species. To build the model we used an empirical plant–pollinator network from a Mediterranean scrub community surveyed over four years. In our simulated annual cycle we know which plant and pollinator species are active, and thus available to interact. We can obtain simulated plant–pollinator interaction networks with properties similar to the real ones in two different ways: (i) by assuming that the frequency distribution of both plant and pollinator duration of activity follow an exponential function, and that interaction among temporally coexisting species are totally random, and (ii) by assuming more realistic frequency distributions (exponential for pollinators, lognormal for plants) and that the interaction among coexisting species is occurring on a per capita basis. In the latter case we assume that there is a positive relationship between abundance and duration of activity. In our model the starting date of the species activity had little influence on the network structure. We conclude that the observed plant–pollinator network properties can be produced stochastically, and the mechanism shaping the network is not necessarily related to size constraints. Under such conditions co-evolutionary explanations should be given with caution.

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1. Introduction

Plant–pollinator interaction webs are among the most intensively studied ecological networks. They are considered to be mutualistic networks consisting of many interacting species having a high variability in the degree of specialization. A number of studies documented that the degree of specializa-

tion in a community follows a power law distribution with exponential truncation (Jordano et al., 2003; Vázquez and Aizen, 2004; Petanidou and Potts, 2006; Guimarães et al., 2007). This means that most species are specialists (i.e. interacting with only one or just a few partners) whereas a few species have a number of interactions much higher than the average. Furthermore, plant–pollinator networks are shown to be

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nested, i.e. specialists tend to interact with sets of partners that are subsets of the partners interacting with the more generalists (Bascompte et al., 2003; Olesen et al., 2008; Petanidou et al., 2008). In addition, plant–pollinator networks are dynamic: there is considerable seasonal variability (Olesen et al., 2008; Basilio et al., 2006) and a high turnover in species composition and network topology from one year to the next (Petanidou et al., 2008; Alarcón et al., in press).

Nestedness and power law distribution in the degree of specialization are not expected from randomly assembled networks (Vázquez and Aizen, 2004; Santamaría and Rodríguez-Gironés, 2007). There should be some constraints or assembly rules in the interaction in order to get a scale free, nested network. Such a rule is the ‘preferential attachment’ in dynamic networks: new nodes prefer to attach to previously existing nodes that already have many links (Barabasi and Albert, 1999). Preferential attachment, exemplified for plant–pollinator networks as “specialists prefer to interact with generalists” can, indeed, produce the observed properties (Guimaraes et al., 2007). Different routes to the desired properties have been proposed by Vázquez and Aizen (2003, 2004), Stang et al. (2006), and Krishna et al. (2008). The observed network pattern can be obtained stochastically either by taking into consideration the abundance of each species (measured with the surrogate of frequency of interaction) as shown by Vázquez and Aizen (2004) and Krishna et al. (2008) or by explicitly considering the incompatibility of the biometric features of the organisms involved and the resulting forbidden links (e.g. between deep flowers and insects with short tongues) as proposed by Stang et al. (2006) and Santamaría and Rodríguez-Gironés (2007). In our study case, the biometric features of the flowers do not seem to explain the relations with their pollinators (Petanidou, 1991), and the abundance of each pollinator species is unknown. Still, there might be another path to allow us to model this interaction network, based on a very interesting observation by Olesen et al. (2008): a species degree of specialization is closely related to its phenophase, i.e. its duration of activity in the year.

The observation by Olesen et al. (2008) is important for at least two reasons: (a) it can explain, as we aim to show in this study, why we observe a power law distribution in degree of specialization (or perhaps another type of distribution in accordance with the distribution of the species phenophase in a community) and, (b) it is grounded on well known temporal patterns of organism activities that are shaped by evolutionary but not necessarily co-evolutionary processes.

The main point of this paper is to produce suitable theory linking network structure to dynamics. We aim to reproduce observed network properties (like nestedness and network temporal turnover) on the basis of simple stochastic rules, with the main focus on the role of the phenophase length as the main driver of the observed network patterns.

Stochastic models are often used in ecology since they offer a simple mechanism to describe complex phenomena and patterns. Currently much research focuses on the role of environmental and demographic stochasticity on population dynamics (among others Kallimanis et al., 2005; Garnier et al., 2006; Hovestadt and Poethke, 2006; Bode and Possingham, 2007). Furthermore, stochastic models are also used to describe interactions among individuals (e.g. Caplat

et al., 2008), among species (e.g. Roth et al., 2008), even among functional groups (e.g. Esther et al., 2008). They are also used to simulate community dynamics (e.g. Eppstein et al., 2006) and to plan for the selection of reserve networks (e.g. Moilanen et al., 2006; Sabbadin et al., 2007). In this paper we used stochastic modelling to examine whether the plant–pollinator interaction network is, in fact, just the result of random associations between partner species that happen to coexist in time.

To answer this question we model the plant–pollinator interaction on the premise that at each moment the plant–pollinator interaction web is formed stochastically by randomly pairing plant and pollinator species among the ones available for interaction at that point in time. The real system we used as a benchmark is the pollination network surveyed for four consecutive years by Petanidou (1991). This robust dataset, hereafter called “Daphni dataset”, consists of 132 plant and 665 pollinator species and originates from a Mediterranean scrub community ca. 10 km west of Athens, Greece, and has been used in many pollination studies (see Petanidou et al., 2008 for a concise review). We evaluated our model on the base of how close it produces the global properties of this real network (i.e. connectance, temporal turnover, degree distribution, and nestedness).

2. The models

The model is built on the assumption that each species (plant or pollinator) has a definite phenophase, i.e. its availability to act as a partner in the pollination network is limited in time. Indeed, pollination partner species differ significantly in the duration of plant flowering (Kochmer and Handel, 1986; Petanidou et al., 1995b; Tébar et al., 2004) and the duration of insect activity (O’Toole and Raw, 1991; Petanidou and Ellis, 1996). Flowering span is limited in time for most plant species populations with few of them showing a long-lasting flowering period. Similarly, very few insect species populations are active for prolonged periods of time, whereas most of them are active for only a short period. In addition, not all species flower or are active simultaneously. Thus, the phenophase is defined by two characteristics: (i) a starting day of flowering or pollinator activity during the annual cycle and (ii) the duration of flowering or pollinator activity.

The Mediterranean community under study shows a seasonal variation as to the phenophase of plant and pollinator species. This means that during part of the year (i.e. main season) most plant and pollinator species are simultaneously active, while during other parts of the year few species remain active. In order to simulate this seasonal effect, we assumed that the median dates of activity of each species are not uniformly distributed throughout the year, but they follow a normal distribution with a peak at the main season (Petanidou et al., 1995b). This model for the seasonal variation of phenophase introduces an additional layer of complexity; thus we have to test whether this added complexity is necessary. Therefore, we also examined the simple assumption that a species may commence its activity at any day of the year with equal probability, in other words that there is no seasonal activity pattern. This latter model may be less realistic, but if it produces the observed patterns then we might infer that sea-

sonality is not necessary for explaining the plant–pollinator interaction network.

The duration of activity is the most important feature in our model. A realistic choice for this trait is that for both plant and pollinator species it follows a right skewed distribution. Indeed, it is known that in real ecosystems there are many species with short and a few species with long duration of activity (O'Toole and Raw, 1991; Petanidou and Ellis, 1996) hence the frequency distribution of durations is right skewed.

From the Daphni dataset (Petanidou, 1991) it is evident that the frequency distribution of the pollinator species duration of activity is exponential (Fig. 1). In our dataset the minimum duration of pollinator activity was considered to be 14 days,

thus all species with shorter durations were assumed to be active for 14 days, and this might explain the small difference between the exponential distribution and the observed frequency distribution. We were unable to locate other studies documenting the frequency distribution of phenophase length of all pollinator species within a community. The plant species flowering durations follow a lognormal distribution (Fig. 1), which is also confirmed by other studies from various ecosystem types (Herrera, 1986; Kochmer and Handel, 1986; Bosch et al., 1997; Bawa et al., 2003; Tébar et al., 2004).

Based on the above considerations we built a model simulating random interactions among temporally coexisting plant and pollinator species, i.e. a mixed model of random interac-

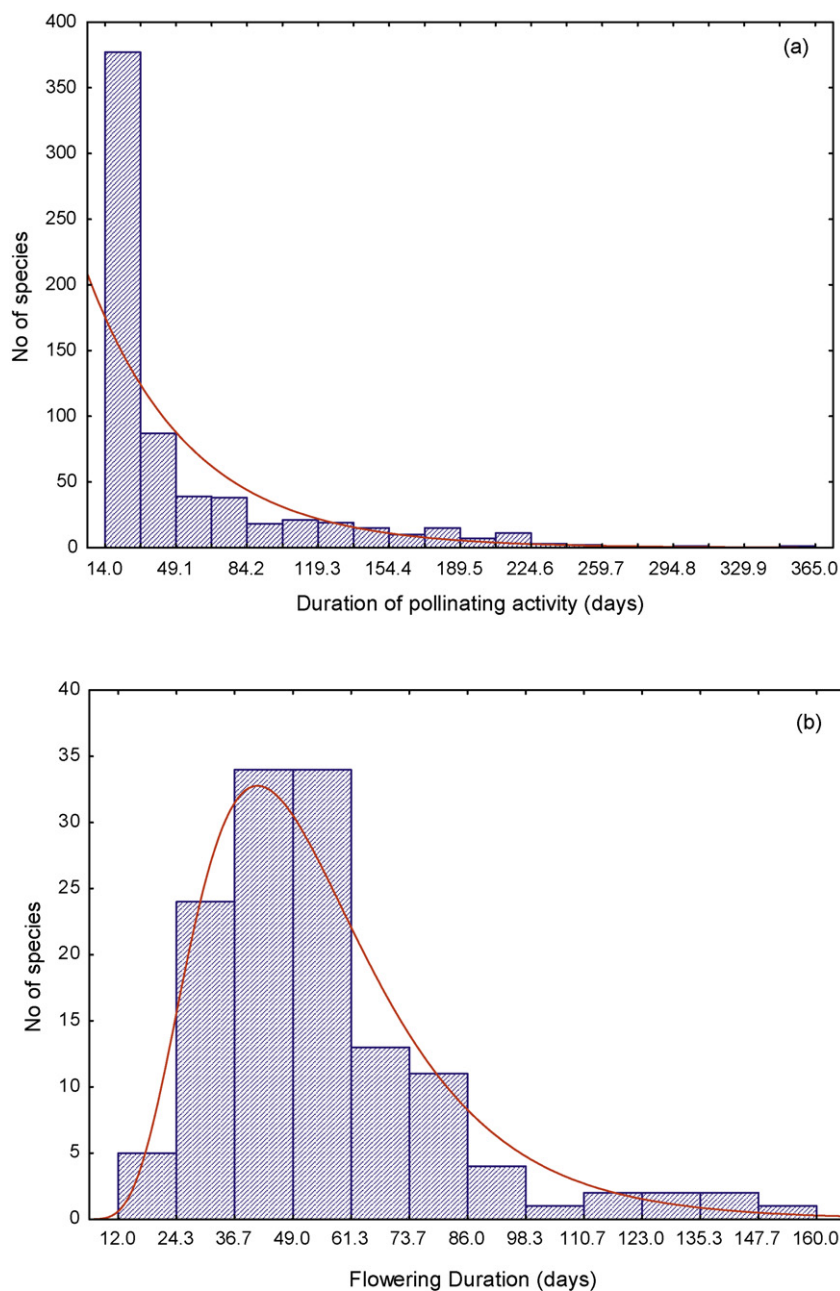


Fig. 1 – Observed frequency distributions of (a) the duration of pollinating activity of insects and of (b) the flowering duration of plants from the Daphni study site. The line represents the fitted frequency distribution: (a) exponential with rate parameter 0.198, and (b) lognormal with average 3.91 (approximately 50 days), standard deviation 0.44.

Table 1 – The assumptions of the three models examined, regarding the rule of choosing interaction partners and the frequency distribution in duration of plant flowering and pollinator activity.

	Model I	Model II	Model III
Frequency distribution of the duration of plant flowering	Exponential	Lognormal	Lognormal
Frequency distribution of the duration of pollinator activity	Exponential	Exponential	Exponential
Rule for choosing interaction partner each simulated day	Random per species, i.e. each species equal probability	Random per species, i.e. each species equal probability	Random per capita, i.e. probability proportional to species duration of activity
Detailed explanations are given in the text.			

tions and forbidden links (Jordano et al., 2003). We investigated three variants of the model. Table 1 shows the similarities and differences between the three alternatives examined. The first examined variant (Model I) is the simplest but less realistic, in the sense that the frequency distributions of the durations of both pollinator activity and plant flowering are exponential. In the other two examined variants (Models II and III) the duration of pollinator activity follows an exponential distribution whereas the duration of plant flowering is lognormal.

Once the starting date and the duration of activity of each species had been defined for an annual cycle, we estimated exactly which hypothetical plant and pollinator species are available/active at each simulated calendar day. Obviously if the starting date of activity of a species is at the end of the annual cycle its duration of activity goes into the next simulated year. At the end, we assigned links between plants and pollinators on a per day basis.

For each simulated day there are A pollinator species active and P plant species in flower. Each available pollinator species has a constant probability to form a link with one of the available plant species. So at any simulated day, pollinator species may form up to one link, but plants may accept as many links as the available pollinator species.

For models I and II there is not any kind of preference in either insects or plants to establish a link with a specific partner. The linking process is totally stochastic and each species has an equal probability to interact.

In model III, the probability to form a link is not equal among species, but is proportional to their duration of activity. This model resembles the Barabasi and Albert (1999) model of preferential attachment but it deviates in two important aspects. Firstly, the probability of interaction is not proportional to the species degree as it is in their model in which the “rich get richer”, but it is proportional to the species duration of activity. So in essence, a species in its first day of activity, despite the lack of links, may be the most likely to form interactions with other species, just because it is characterized by the longest duration of activity. Secondly, the rationale behind our rule is very different. We assume that a plant–pollinator interaction does not occur among species but among individuals; and that species with longer duration of activity/availability are more abundant at each point in time. The above assumptions are corroborated by Olesen et al. (2008) who also reported a correlation between species abundance and duration of phenophase. Further evidence in support of the assumption for a relationship between duration of activity

and abundance came from the analysis of our Daphni dataset. Petanidou and Ellis (1996) found that the highest duration of activity (average, per species) was that of Halictidae, a family known to encompass many primitively eusocial species sensu Michener (2000). It was followed by Anthophoridae, Colletidae, Megachilidae and Andrenidae (presentation in decreasing order of magnitude of the duration of activity), i.e. with families with a decreasing degree of sociality. Among all bee species the highest duration of activity was that of eusocial bees, viz. *Apis mellifera* (365 days per year). Primitively eusocial bee species scored also very high as it was with several halictids (among them *Lasioglossum malachurum* with 274 days and *L. marginatum* with 182 days), Apidae (*Bombus terrestris* with 143 days; and four *Ceratina* species with an activity of ca. 185 days). These data show that the duration of activity of a bee species reflects the population abundance and the degree of sociality of the species at the same time (Wilson, 1976; Petanidou and Ellis, 1996; O’Toole and Raw, 1991; Michener, 2000).

After establishing the daily links, we accumulated all these simulated daily networks over a simulated annual cycle and analyzed the properties of the cumulative annual plant–pollinator interaction network of the plant species that were available and the pollinator species that were active.

We ran each model for 100 iterations (i.e. simulated years). In each simulated annual cycle the interaction matrix was cleared and formed from scratch. Among different simulated years the starting date and the duration of activity of each simulated species, as well as the probability of interaction was held constant. So all simulated years were potentially identical and all differences were purely stochastic. In each year the potential species pool was 132 simulated plant species and 665 simulated pollinator species, as it was in our real Daphni dataset. For each simulated year we recorded the number of plant and pollinator species present in the interaction network (i.e. species with at least one link formed), as well as each species degree (i.e. the number of other species it interacted with in that simulated year). In the results we present the maximum and minimum number of species with a specific degree that was observed in any of the 100 simulated years, and compare these patterns with the observed degree distribution in the original Daphni dataset.

We calculated the similarity in the pairwise comparisons among years in the species composition using the Jaccard similarity index.

We quantified nestedness (N) using the matrix temperature (T). The temperature of the interaction matrix is calculated

as the ratio of sum of squared deviations from the boundary line (isocline of a maximally packed matrix) of unexpected presences and absences and the maximum value possible for an interaction matrix, multiplied by 100 (Atmar and Patterson, 1993). We followed Bascompte et al. (2003) and defined the degree of nestedness in terms of matrix temperature

$$N = \frac{100 - T}{100}$$

We calculated nestedness temperature using the BINMATNEST software package (Rodríguez-Gironés and Santamaría, 2006). In this analysis we were not interested to estimate if the observed nestedness pattern was greater than random, just that it was comparable to the observed nestedness of the Daphni dataset, therefore we did not use any null model for the nestedness analysis.

3. Results

Fig. 2 shows the results for model I. In particular it shows the degree distribution of the four annual interaction networks for pollinators (a) and for plants (b) observed in Daphni and the maximum and minimum number of species with

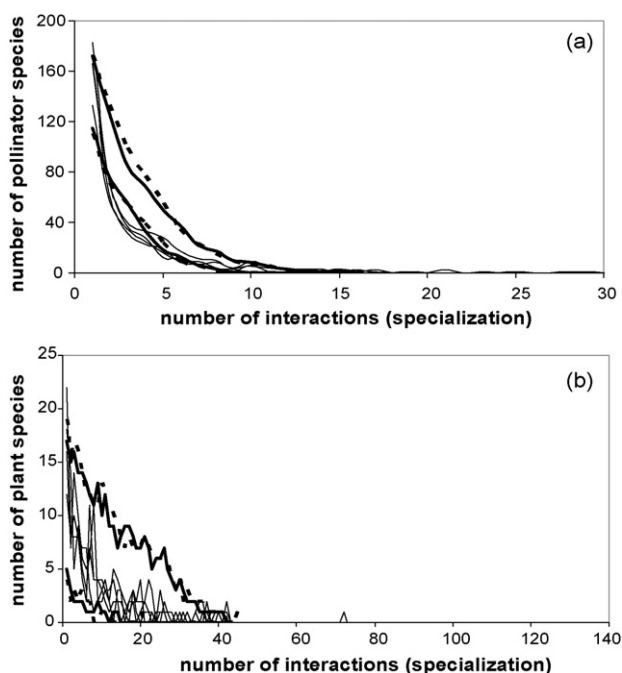


Fig. 2 – Frequency distributions of the number of interactions per species for the pollinators (a) and the plants (b) in the observed Daphni network and in the simulations of model I. The assumptions for the generated simulations were: (i) equal probability of interaction among coexisting species and (ii) frequency distribution for both plants and pollinators is exponential. The thick continuous lines represent the minimum and maximum number of species that had a number of interactions in the simulations; the thick dotted lines represent the simulation results with seasonal variation included; the thin lines show the frequency distribution of the four annual networks observed in nature.

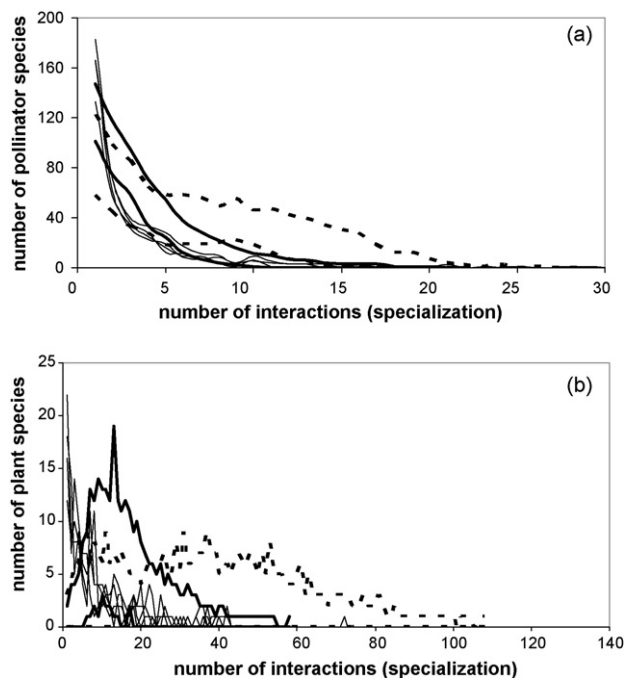


Fig. 3 – Frequency distributions of the number of interactions per species for the pollinators (a) and the plants (b) in the observed Daphni network and in the simulations of model II. The assumptions for the generated simulations were: (i) equal probability of interaction among coexisting species and (ii) frequency distribution is exponential for pollinators, and lognormal for plants. The thick continuous lines represent the minimum and maximum number of species that had a number of interactions in the simulations; the thick dotted lines represent the simulation results with seasonal variation included; the thin lines show the frequency distribution of the four annual networks observed in nature.

the same degree in the 100 simulated years. In this model I the general trend of the degree distribution among the simulated and observed networks is similar, but with quantitative differences. For both plants and pollinators there is an underestimation of the frequency of extreme specialists and generalists. The more generalist species of the simulated networks had approximately 40% less interactions than the observed ones. The most extreme specialists on the other hand were considerably fewer than observed. Fig. 2 also shows (with dashed lines), the results for model I with seasonal variation incorporated. The two lines differ only slightly, with the seasonal synchronization of the species phenophases only slightly increasing the number of species and links observed, but with the same qualitative behaviour of the model.

Model II (Fig. 3) is by far worse than model I as the differences between simulations and observations are more pronounced not only quantitatively, but also qualitatively. The major difference is for the case of plants, where the degree distribution reflects strongly the lognormal distribution of the period of flowering (Fig. 1), rather than the degree distribution of the observed networks. The same observations hold for the

version of model II that assumed species to follow a seasonal pattern (Fig. 3, dashed lines).

Finally, Model III (Fig. 4) provides a good agreement with the real network as the range of the simulated values include the observed ones in nature both for plants and pollinators. The existence of a seasonal pattern in the simulated date of activities only slightly increased the number of species present and the range of species that interacted with the most generalist ones (Fig. 4, dashed lines).

Some global properties of the simulated and the observed plant–pollinator annual networks are given in Table 2. Again, model III appears to perform best among the three simulated networks: (i) it is nested in a similar way as the observed ones; and (ii) the species richness within simulations for both plants and pollinators are closer to the observed ones compared with the other models. However, the similarity of the species composition among years is higher than the observed similarity, as indicated by both the number of species in common and by the Jaccard similarity index, but it is still lower than the values given by models I and II.

Table 2 also shows the effect of incorporating seasonal variability into our models. The main effect is that because during

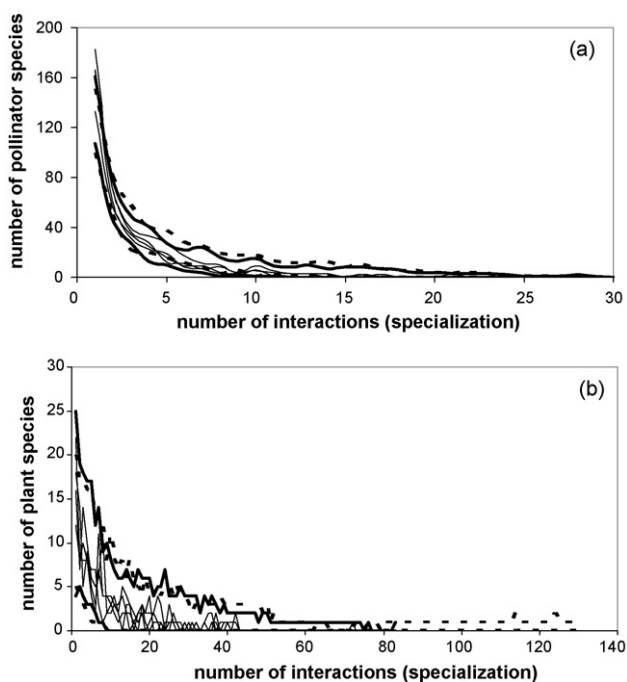


Fig. 4 – Frequency distributions of the number of interactions per species for the pollinators (a) and the plants (b) in the observed Daphni network and in the simulations of model III. The assumptions for the generated simulations were: (i) probability of interaction among coexisting species proportional to their duration of activity and, thus, to their abundance; (ii) frequency distribution is exponential for pollinators and lognormal for plants. The thick lines represent the minimum and maximum number of species that had a number of interactions in the simulations; the thick dotted lines represent the simulation results with seasonal variation included; the thin lines show the frequency distribution of the four annual networks observed in nature.

the main season more species coexist in time, the overall number of links observed and the number of species present each year increases compared to the model without seasonal variation. Despite that, the networks display similar values of nestedness and similar values of the Jaccard similarity index.

4. Discussion

Even though plant–pollinator interaction networks are usually analyzed as static network snapshots, in reality this is far from true. Recently some studies have started delving into the dynamic nature of these interactions (Medan et al., 2006; Guimaraes et al., 2007; Alarcón et al., in press; Olesen et al., 2008; Petanidou et al., 2008). They showed that as it has been studied so far, a plant–pollinator network is the accumulation of a number of observations at different points in time. At these different times, different assemblages of plant and pollinator species may be present and available to interact among each other. The kick-off question of this paper is whether the patterns observed in the plant–pollinator interaction networks (i.e. specialization, nestedness, temporal turnover) are in fact nothing more than the accumulation of random associations of temporally coexisting species.

Model I assumed that the frequency distribution of the duration of activity in both plants and pollinators follows an exponential distribution and produced patterns resembling the observed ones in nature. This model is the simplest way to produce the observed patterns with the smallest number of variables and rules needed to describe the system. However, this model had a serious flaw in our case. The distribution pattern of the frequency of flowering duration, both in our dataset and in other studies (Kochmer and Handel, 1986; Herrera, 1986; Petanidou et al., 1995b; Bawa et al., 2003; Tébar et al., 2004), is not exponential, but lognormal. The observed frequency distribution of the pollinator phenophase length observed in the Daphni dataset did not differ significantly from the exponential distribution. Since we were unable to find other studies documenting the frequency distribution of the duration of activity for any community of pollinators, we assume this distribution (exponential) to be the best approximation. Even though model I cannot be invoked as an explanation in this system, it might prove applicable in other systems where the assumptions are satisfied (e.g. is it possible that the nestedness of species assemblages in islands could be explained by such a model?).

Model II was built on more realistic assumptions, i.e. the frequency distribution of the flowering period was lognormal. However, the simulated networks differed quantitatively and qualitatively from the observed ones. Notably, the degree distribution of the plant species differs significantly from the observed one. This mismatch between simulations and observations indicates that this simple model is not enough to explain all the structure of the networks observed in nature.

In order to account for the discrepancy between the observed and simulated networks, and build an improved third model, we considered the fact that the plant–pollinator interaction does not occur among species but among individuals. Vázquez and Aizen (2003, 2004) and Krishna et al. (2008) have already shown that there is a relationship between

Table 2 – Values for the different components and characteristics of the plant–pollinator networks in the real and the simulated annual networks.

	Real networks		Model I		Model II		Model III	
	with	without	with	without	with	without	with	
Seasonality								
Minimum number of pollinator species	305	448	452	549	565	326	369	
Maximum number of pollinator species	430	485	568	595	611	375	408	
Minimum number of plant species	97	119	114	128	127	114	114	
Maximum number of plant species	119	128	131	132	132	125	126	
Minimum number of interactions	868	1294	1296	969	1013	1239	1480	
Maximum number of interactions	1493	1479	2012	1753	1972	1417	1721	
Minimum number of pollinator species shared between 2 simulated years	183	358	331	268	299	245	291	
Maximum number of pollinator species shared between 2 simulated years	238	399	414	317	364	283	320	
Minimum value of Jaccard similarity for pollinator species	0.39	0.81	0.71	0.71	0.75	0.55	0.60	
Maximum value of Jaccard similarity for pollinator species	0.45	0.94	0.93	0.85	0.93	0.64	0.68	
Minimum number of plant species shared between 2 simulated years	80	113	78	120	121	107	107	
Maximum number of plant species shared between 2 simulated years	106	124	119	129	131	120	120	
Minimum value of Jaccard similarity for plant species	0.66	0.88	0.72	0.92	0.91	0.85	0.85	
Maximum value of Jaccard similarity for plant species	0.84	0.99	1.00	0.99	0.99	0.97	0.96	
Minimum nestedness value	0.971	0.955	0.948	0.871	0.892	0.962	0.954	
Maximum nestedness value	0.982	0.973	0.974	0.933	0.954	0.991	0.990	

Values are given with and without seasonality.

species abundance and its frequency of interaction, and the random interaction should take into consideration the different availability of each species at each point in time. The rank–abundance graph of any real community shows that there are few abundant species and many rare ones (Hubbell, 2001). Krishna et al. (2008) demonstrate an application of neutral theory on building mutualistic networks. Therefore, the species probability of interaction with other species should be constant among individuals and not among species. Hanski (1982) core satellite hypothesis examines the relationship between a species local abundance and its geographic distribution. He defines core species as being both widely distributed and locally abundant and satellite species as being both narrowly distributed and locally rare. Henceforth this pattern has been confirmed by several studies (Bock, 1987; Gotelli and Simberloff, 1987; Bowers, 1988; Gaston and Lawton, 1988). Herewith we assume that a similar pattern may also apply in time as it does in space, i.e. a relationship between abundance and duration of activity. Species that are active for only a short period of time are also rare. For instance, in our data set all singletons have a short period of activity, while eusocial insects with large populations are the longest active species (i.e. honeybees; see model description).

Model III mirrors closely the degree distribution and the nestedness of the observed Daphni network. The close match between simulated and observed network structures implies that the observed network properties can be obtained as the accumulation of random associations (on a per capita basis and not per species) of temporally coexisting species. This third model is novel because it uses a single characteristic of the interacting species (its phenophase length) and defines both forbidden links (a flower in spring cannot be pollinated

by an insect active in autumn) and preferential attachment (a species that is active for long is assumed to be abundant throughout the period, and thus have more individuals to form interactions).

In all the above models the temporal turnover among years concerned both the species composition and the interaction identity, but in all cases the simulated turnover was lower than in the real networks. The reason for this discrepancy may be that the simulation models were exactly identical among simulated years, whereas environmental conditions (e.g. climate vicissitudes, ecological succession, human disturbance) vary from year to year. In real life, the plant and pollinator phenology (i.e. the starting at a certain time and duration of their flowering/activity) is shaped by a combination of parameters that fluctuate dramatically in time (Petanidou and Ellis, 1993; Petanidou et al., 1995a,b). This implies that each species not only is available for a limited period of the year, but also that this period is unpredictable to a certain degree. For instance, availability of pollinators within a year may affect the duration of flowering in a community (negatively as shown by Petanidou et al., 1995b). This implies that the duration of flowering is a trait dependent on the yearly fluctuations of both plants in flower and insects active (and might imply that phenophase is determined by biotic factors). A longer flowering duration in a year of fewer pollinators may result in a better service to both pollinators and plants in a community, but we are not yet in a position to tell whether and how this interferes with the structure of plant–pollinator interaction network. Similarly, a longer activity period of a pollinator species (thus, with larger population numbers) in a year with fewer pollinator species may equally result in a better service to both pollina-

tors and plants in that community (Petanidou and Potts, 2006). The lack of inter-annual variation in the simulations did not stop species richness and network topology from changing in the simulations: it just dampened the range of the fluctuation.

The common denominator of all our models is the assumption that species interactions are random in each point in time. In models I and II the randomness is assumed at the species level, in model III at the level of the individual. The latter model is similar to, but not identical with, the preferential attachment model of Barabasi and Albert (1999). However, our model differs from preferential attachment in important ways, especially it does not assume that highly connected species (i.e. generalists) will become more and more attractive to new species as potential partners, as is the case in the Guimaraes et al. (2007) model. In our model the simulated species are not destined (i.e. express no preference) to interact with other predefined species, as implied in models with biometric matching among plant and pollinator species (e.g. Stang et al., 2006; Santamaría and Rodríguez-Gironés, 2007). They just choose randomly among potential interaction partners depending on the availability of these partners. This would be more apparent if the nodes in our network were not species but individuals. As it is now, the nodes representing species are aggregations made up of nodes representing all the individuals. The lack of species preferences is strongly reflected in the lack of fidelity among interaction partners from one year to the next as recorded both in our simulations and in the real network (Petanidou et al., 2008). Species are associated with very different interaction partners in different years, even though the potential species pool is the same in each year, a phenomenon that has been also observed in several other natural communities (Herrera, 1988; Cane and Payne, 1993; Price et al., 2005). In addition, the number of species each partner species interacts with varies significantly among years. As a result, a species may appear as specialist in one year (e.g. they interact with only one partner species) but as generalist in another. This phenomenon is much more evident in the plant–pollinator webs observed in nature (Alarcón et al., in press; Olesen et al., 2008; Petanidou et al., 2008).

The apparent degree of specialization (measured as the minimum, maximum, mean, and range of number of interaction partners per year) is strongly correlated with the species duration of activity. Petanidou et al. (2008) and Olesen et al. (2008) report similar trends in dynamic pollination networks observed in nature. Perhaps this is a general trend that has been so far overlooked.

In this study we used a single dataset (the Daphni dataset) as a benchmark to test the realism of our model. Our dataset is one of the largest known in the literature, focusing, however, in a single community. This might limit the generalization of our findings. For example we found no published record for a community wide frequency distribution of the phenophase duration for pollinators and assumed the exponential distribution solely based on our own dataset. Perhaps such a distribution may be different in different community structures or other biogeographic regions. Therefore, we caution that our results need to be verified in other test communities before generalizations could be safely made.

Another caveat refers to the importance of seasonal variation. In the Mediterranean, there is a strong seasonal pattern in species activity, with many species coexisting during the main season (spring to early summer) and considerably fewer species being active during the rest of the year. Our results indicate that explicitly incorporating this seasonal variability has a quantitative effect, but the general trends reported (nestedness, degree distribution, temporal turnover) still hold. Therefore, we suggest that seasonality does not play a critical role in the formation of the plant pollinator interaction network. Thus, we argue that our model might work equally well in a community that is not seasonal.

4.1. Theoretical implications

In this paper we show how a simple model based solely on the species phenophase and its population abundance, can capture most of the features of the observed plant–pollinator interaction networks. Although our model captures many aspects of the behaviour of the real system, we should point out that it does not prove that the mechanism behind the real life phenomenon is the same as our model, just that it might be. And since it is the simplest explanation, we do not need to resort to more complicated explanations.

In our model we consider all the species more or less equivalent regarding their role as either pollinators or food sources on a per capita basis in concordance with Hubbell (2001) neutrality assumption. According to this theory, patterns of community organization could arise under the assumption that all species are identical on a per capita basis (e.g. He, 2005). Krishna et al. (2008) demonstrate how neutral communities may produce mutualistic networks with properties comparable to the known networks.

The dominant paradigm of plant–pollinator interactions is that the observed interactions have been predicted by co-evolution. However, Ollerton since 1996 highlighted the apparent paradox that although floral morphology often appears to reflect evolutionary adaptation to specific pollinator morphology, implying specialized interactions, such highly specialized interactions are rare in nature. Our simple model indicates that given the species phenophase, the observed interactions may be the result of purely stochastic processes; thus, co-evolutionary explanations are not necessary to explain the observed global network patterns. Here, we should point out that our model does not falsify co-evolution, it does not prove that predictions made by co-evolution do not hold, and also that the proposed model is not a test for the relevance of co-evolution in assembling mutualistic networks. However, our model offers a simple explanatory tool, a mechanism, to unravel how the plant–pollinator networks may be structured, once a species phenophase is taken into account. However, we have no explanation why species have evolved to be active for a certain period of time. It is possible that co-evolutionary theory may explain frequency distributions, but this cannot be concluded based on the data at hand. The literature on the relative importance of biotic and abiotic factors on shaping phenological patterns is ambiguous (e.g. Bolmgren et al., 2003; Cleland et al., 2007). The only conclusion that could be drawn so far is that co-evolution may shape phenological patterns, but it is not necessary that it does so.

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