Optimizing size thresholds in a plant–pollinator interaction web: towards a mechanistic understanding of ecological networks

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Abstract Using functional traits together with abundance effects strengthens the prediction of interactions between pairs of species in ecological networks. Insights into the way species interact as well as prediction accuracy can be gained when thresholds for trait value combinations that make interactions possible are optimized through model selection. I present novel data of two subalpine plant–pollinator communities and build several stochastic models integrating flower abundance and morphological threshold rules that allow or restrict interactions between species. The number of correctly predicted interactions was highest when thresholds were set so that the insect’s proboscis was not shorter than the nectar-holder depth minus 1–1.6 mm, and not wider than the nectar-holder width minus 0.5 mm. In comparison with models based solely on plant abundance effects, the model incorporating optimized size thresholds better predicted the distribution of the trait differences between plants and insects. This indicates that a mechanistic approach of interaction webs based on optimized

size thresholds provides valuable information on community structure. The possible implications for community functioning are discussed.

Keywords Functional traits · Mutualistic networks · Morphology · Model selection · Plant abundance

Introduction

The structure of mutualistic interaction webs is well known (Waser and Ollerton 2006; Bascompte and Jordano 2007), and the amount of accessible data is increasing due to, e.g., the interaction web database <http://www.nceas.ucsb.edu/interactionweb/>. Such datasets provide information about “who interacts with whom”, and sometimes with what frequency, and can be used for comparative studies (Jordano et al. 2003; Thébault and Fontaine 2008). Several attempts to predict the structure of the webs using simulation models have taken into account the abundance of the species (Vázquez and Aizen 2003; Burns 2006; Vázquez et al. 2009). However, the assemblage of species into communities is likely to depend on their functional traits (McGill et al. 2006), defined as the measurable properties of individuals that strongly affect their performance. For example, in food webs, diet breadth is known to increase with body size (Woodward and Hildrew 2002; Petchey et al. 2008), which is a key functional trait in interaction webs (Woodward et al. 2005). Similarly, body size can predict species degree, i.e., the number of interacting species, in an ant–plant web (Chamberlain and Holland 2009).

In community ecology to date, little research has taken into account functional traits (McGill et al. 2006). Mechanistic models based on these traits are needed to predict web structure so that neutral and mechanistic models can

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be compared (Santamaría and Rodríguez-Gironés 2007; Mason et al. 2007; Stang et al. 2009). Species interact through a large number of interacting traits. The resulting ecological complexity, therefore, needs first to be simplified in order to predict the probability of interactions. One way of achieving this is to consider pairs of traits that directly interact and then to derive mechanistic hypotheses that can be included in models. For example, in plant–pollinator webs, one of the most striking pairs of interacting traits is the length of an insect’s proboscis and the depth of a plant’s nectar-holder (Stang et al. 2006, 2007, 2009). In this study, I focus on this pair of functional traits and on an additional pair which relates the width of an insect’s proboscis to the width of a plant’s nectar-holder.

The straightforward hypothesis for both pairs of traits is that the insect’s proboscis must be both longer and narrower than the flower’s nectar-holder. However, the value of the morphological thresholds might vary depending on the insect’s behavior, the ability of the proboscis to expand, and other floral properties besides width and depth, such as flexibility, shape and hairiness. Similarly, the effects of plant abundance on the network structure can be measured with various indices, based on the abundance of inflorescences, the number of flowers per inflorescence, and the height and size of inflorescences. In order to determine the value of the thresholds and the abundance index that lead to the best network predictions (Rohr et al. 2010), I built algorithms integrating the effects of plant abundance and morphological thresholds, and selected the models a posteriori, depending on their prediction performances (Csillery et al. 2010). The morphological threshold values might vary among the plant and insect pairs, so the size thresholds I used here should be taken as a first step towards obtaining a detailed mechanistic understanding of plant–pollinator interactions.

One great challenge in the study of interaction webs is to be able to measure and predict the outcome of the functioning of the networks. For pollination networks, this means studying the pollination service provided by the insects. One factor affecting pollination efficiency is whether the flower’s and the insect’s morphological traits ‘match’ (Herrera 1987; Nilsson 1988; Johnson and Steiner 1997; Kobayashi et al. 1999; Hiei and Suzuki 2001; Nattero et al. 2010). The degree of size matching between plants and insects might explain part of the discrepancy that has been found between visitation and pollen-load data (Bosch et al. 2009; Alarcón 2010). Therefore, the prediction of the distribution of trait differences between plants and insects can be a first step towards the prediction of the pollination outcome of a network.

The datasets used are two previously unpublished networks established for neighboring subalpine meadows in the French Alps, including measurements of plant and

insect morphological traits. More specifically, I addressed the following three questions:

1. What are the abundance measure and size thresholds that lead to the best prediction of the network structure of these subalpine communities? What can we learn about the mechanisms of plant–pollinator interactions from the optimal abundance measure and optimal size thresholds?
2. Which simulation models correctly predict the distribution of size differences between plants and insects, and which influence the pollination process?
3. Do these new datasets confirm previous findings that integrating abundance and morphological threshold effects leads to a better prediction of network properties (Stang et al. 2009; Vázquez et al. 2009)?

Materials and methods

Study site and observational design

The field site is located in the upper Romanche valley of the central French Alps, on the south-facing aspect of the village of Villar d’Arêne (45.34° N, 6.34° E), near the “Station Alpine Joseph Fourier” on the Lautaret Pass. Two 500-m² terraced fields 1,000 m apart were chosen, one close to the hamlet “Les Cours” and one at a site called “La Guindaine”. The climate is subalpine with a continental influence.

At Cours, 25 plant species were chosen to observe insect visits between 9 June and 30 July 2008. At Guindaine, 23 species were observed between 12 June and 24 July 2008. In total, 32 different species were observed, 16 in both fields, 9 only in Cours and 7 only in Guindaine (ESM 1). The observed species represented 79 % of the total number of inflorescences in Cours and 84 % in Guindaine (the measurement of inflorescence abundances is described below). The remaining species in the fields studied were either rare (e.g., *Nigritella nigra*, *Gentianella campestris*) or hidden in the vegetation and difficult to observe (e.g., *Thesium alpinum*, *Euphrasia* sp.).

In both fields, each selected species was observed on two different days around its peak of flowering under sunny conditions with no wind, during two 15-min sessions. A permanent grid pattern of transects 3 m apart was established in both fields, and the observer walked along the grid looking for the focal plant flowers. If an insect was observed consuming nectar on this species, it was captured for trait measurements and identification. The few insects that fed only on pollen were ignored. Only five individuals of *Apis mellifera* were captured, and the remaining individuals were just counted. Ants and the proliferating

bibionid fly *Dilophus femoratus* were counted, but not included in the analysis. In total, 192 observational sessions of 15 min each took place, i.e., 48 h in total, during which 1,206 insect visits were observed in Cours and 918 in Guindaine.

Insect identification and trait measurements

The insects were identified to the species level wherever possible (98 species), but in some cases only to the genus level (33 genera). I defined morphospecies when they could only be identified to the family level (mainly Tenthredinidae, Ichneumonidae, Empididae, 74 morphospecies) or to the order level (dipterans that were damaged, 36 morphospecies). In total, 241 taxonomic entities were used (see ESM 2). The proboscis length and width of five individuals per species were measured to the nearest 0.1 mm under a dissecting microscope, as described in Stang et al. (2006). If fewer than five individuals per species were observed, then all of them were measured. A total of 765 insects were measured.

Once the observational sessions had been completed for a given plant species, ten inflorescences were collected in each field. I measured the inflorescence height, the number of flowers per inflorescence, and the depth and width of the nectar-holder of ten randomly chosen flowers per inflorescence. The depth and width of the nectar-holders were measured as in Stang et al. (2006).

Inflorescence abundance

Every week, the abundance of inflorescences in each field was measured using a point quadrat method. A 1-m² square wooden frame was randomly thrown onto the field and the number of mature inflorescences of each entomophilous species within the square was counted. The operation was repeated 20 times, and the 20 measurements were then pooled. General additive models (GAMs) implemented on R software (R Development Core Team 2009) in the “gam” package (Wood 2004) were used to interpolate the abundance of inflorescences for each observation day. R software was used for all the statistical analyses and simulations.

Insects may respond more to the abundance of flowers than to the abundance of inflorescences. This was checked by multiplying the abundance of inflorescences by the number of flowers per inflorescence. Alternatively, insects might respond to the abundance of flowers in a non-linear, saturating way, which was tested by using the logarithm of the number of flowers. Insects might also respond more to the size of inflorescences (their diameter or length) and where they occur in the herbaceous strata. A “visibility index”, defined as the product of inflorescence abundance, height and size was therefore built. In total, four indices were used: (1) the abundance of inflorescences, (2) the

abundance of flowers, (3) the logarithm of the abundance of flowers, and (4) the visibility index. Color can also be useful to define visibility, but insects’ response to color depends on their taxa (Faegri and Pijl 1966), so this criterion was not used. The abundance of insects could not be estimated independently of the flower visit observations in this study, and the abundance effects in the network prediction, therefore, only concern plant abundances.

Size thresholds definition

Two pairs of morphological traits were used to predict interactions between plants and insects: nectar-holder depth/proboscis length, and nectar-holder width/proboscis width. A flower and an insect can interact provided that:

$$\text{Proboscis length} - \text{nectar-holder depth} > \text{length threshold} \quad (1)$$

and

$$\text{Proboscis width} - \text{nectar-holder width} < \text{width threshold}. \quad (2)$$

A simple “null” hypothesis would be to claim that both length and width thresholds equal zero, i.e., that visits may occur if the proboscis length is greater than the nectar-holder width, and if the proboscis is narrower than the nectar-holder.

Algorithm predicting the interactions

The algorithm simulating the predicted networks was designed to follow the sampling method used in the field as closely as possible (see ESM 3 for details). The procedure involves distributing all the observed insects over the plants, taking into account the plants’ abundances and the species’ functional traits. The probability that a focal plant and a focal insect chosen at random will interact is assumed to be equal to the abundance index of the focal plant relative to the abundance of all the plants the focal insect can visit when the threshold criteria are taken into account. Whether there is an interaction or not is then chosen at random given this probability, and the procedure is repeated until all the observed insects have been attributed to a plant. As a consequence, the total number of interactions and the number of insect species are the same in the observed data and in the predicted matrices, but the number of plants can be different.

Parameters optimisation and model selection

The first step of the modelling procedure aimed at finding the optimal threshold values. The most complete model, which includes the length threshold (L), the width threshold

(*W*), and the plant abundance effects (*A*), hereafter called the “full model” (LWA), was used to determine the combination of the size threshold values that lead to the best prediction of the observed network. For each community, 1,000 LWA models were simulated using different size threshold values and the three different indices of plant abundance. The length threshold values were sampled uniformly from the interval (−10 and 7 mm), and the width threshold values from the interval (−2 and 2 mm). The proportion “*R*” of correctly predicted visits was then calculated for each simulated network and regressed against the size thresholds and the abundance indices using GAMs.

The second step aimed at finding the most adequate model. Alternative models that were simpler than the full model were simulated, using the optimal size threshold values and plant abundance indices determined during the first step. In total eight models that correspond to all the possible combinations of *L*, *W* and *A* were simulated: LWA (full model), LW, LA, *L*, WA, *W*, *A*, and the null model. One hundred networks were simulated for each of the eight model types and for each community (2 × 800 networks in total). Following an approximate Bayesian computation approach, which consists in fitting the model to data and then improving the model by checking its fit and comparing it with other models (Csillery et al. 2010), the models were selected according to the proportion “*R*” of visits they correctly predicted. In total, 3,600 networks were simulated during the parameters optimization step and the model selection step.

Network statistics

Three common summary statistics were used to describe the observed and predicted networks: connectance, nestedness, and evenness. ‘Connectance’ is the number of interactions that occurred divided by the number of all possible interactions. ‘Nestedness’ reflects the fact that specialists species tend to interact with generalist species. It measures the tendency of species to interact with a subset of the partners of more generalized species. Nestedness was calculated using the weighted-interaction nestedness estimator (WINE), proposed by Galeano et al. (2009) and implemented in the “bipartite” R package (Dormann et al. 2008). Compared with other nestedness estimators (Rodríguez-Girones and Santamaría 2006; Ulrich et al. 2009), WINE has the advantage that it takes into account the frequency of interactions between species, which is of particular importance in the present case because the distribution of the frequency of interactions is highly dispersed. ‘Evenness’ is the Shannon index of the distribution of interaction frequencies (Tylianakis et al. 2007; Vázquez et al. 2009). When a network is dominated by a few pairs of strongly interacting species, its evenness index is low.

Finally, the quality of the fit of simulated networks was measured using the proportion “*R*” of correctly predicted visits.

Results

Optimization of the parameters of the full model (LWA)

In both communities, the way plant abundance was calculated significantly affected the *R* of the simulations (Cours: $F_{3,980} = 90.58$, $p < 2e-16$; and Guindaine: $F_{3,980} = 126.10$, $p < 2e-16$). The *R* of models using the number of inflorescences or the number of flowers as an estimate of plant abundance was lower than the models using either the log of the number of flowers or the visibility index in both communities ($p < 2e-16$ in all cases, details not shown). In Cours, models using the visibility index performed better ($t = 6.39$, $p < 1e-9$), whereas in Guindaine the models using the log of the density of flowers had the highest *R* ($t = 2.75$, $p = 0.006$).

The value of the size thresholds also significantly affected the *R* of the simulations. The significance of the GAMs was $< 2e-16$ for both communities and both size thresholds (details not shown). Overall, the GAMs explained 80.1 % of the *R* deviance in Cours and 90.7 % in Guindaine. The remaining deviance was due to the stochastic properties of the simulation model.

A simulation’s *R* was low when the threshold conditions were highly restrictive and required an insect’s proboscis to be either very long or very narrow relative to the flower’s morphology (Fig. 1, top left), because in such cases only a few insects with a very long and narrow proboscis can interact with flowers. A simulation’s *R* was maximized when insects were able to visit flowers, provided that their proboscis was not shorter than the nectar-holder depth minus 1.05 mm in Cours or 1.64 mm in Guindaine, and not larger than the nectar-holder width minus 0.49 mm in Cours or 0.54 mm in Guindaine (Table 1). When the threshold conditions were very permissive, i.e., when insects with a wide and short proboscis could interact with virtually any kind of flower, the *R* decreased slightly, although in a less severe way than when conditions were restrictive (Fig. 1, bottom right).

Network statistics of the models

Using full models (LWA) resulted in better *R* in both communities (0.25–0.30; Fig. 2). The next best were with the models using size thresholds but not flower abundance. When only one size threshold was included in the models, those using the length threshold usually did better than

Fig. 1 Influence of the length and width of morphological threshold values on the proportion of correctly predicted interactions in the **a** Cours, and **b** Guindaine communities. The contour lines are produced by generalized additive models and correspond to the proportion of correctly predicted interactions (*dark* low proportions, *white* high proportions). The *top parts* correspond to restrictive length thresholds, whereas the *bottom parts* allow more interactions. The regions on the *left* correspond to restrictive width thresholds, whereas the regions on the *right* allow more interactions. The optimal threshold values are presented in Table 1

those using the width threshold. Models using flower abundance alone resulted in particularly low *R*, and in Guindaine they even performed worse than the null models. Network connectance was over-estimated and nestedness was under-estimated by all the models. The observed connectance and nestedness values were not included in any of the 95 % confidence intervals. However, the connectance and nestedness estimated by the full model were closer to the observed connectance value than those estimated by the other models. The evenness of the

interactions was over-estimated by all the simulation models. The full model correctly predicted evenness in Cours, and was close in Guindaine, and the other models performed gradually worse. The width and abundance model in Cours was, however, an exception. It led to better estimates of connectance, nestedness, and evenness than the full model (Fig. 2b–d, compare models WA and LWA), but it correctly predicted a smaller proportion of the observed interactions (Fig. 2a).

Size matching between plants and flower visitors

Of the observed interactions, 90 % respected the length optimal threshold, but only 2/3 respected a length threshold of zero, for which an insect's proboscis must be at least as long as the depth of the nectar-holder (Table 1). In contrast, 70–80 % of the observed interactions respected the width optimal threshold, and 90 % respected a width threshold of zero, where the insect's proboscis must be at least as narrow as the nectar-holder. This is because the length optimal threshold is more permissive than the length null threshold, whereas the width optimal threshold is more restrictive than the width null threshold. Violations of the width optimal threshold are more frequent (~20–30 %) than violations of the length optimal threshold (~10 %). When the width and length thresholds are considered simultaneously, about 70 % of the observed interactions met both optimal threshold criteria, while only 1/3 of the interactions predicted by the flower abundance model fulfilled these conditions (Table 1). Overall, the functional pattern predicted by the full model matched the observed pattern much better than the pattern predicted by the abundance model, which was very dispersed (Fig. 3).

Discussion

The full model performed better than the simpler ones in predicting the pollination networks. The fewer the mechanisms integrated by the models, the stronger was the difference between the predicted connectance, nestedness, and evenness and the observed values. In the simple models, if species can interact without morphological constraints, the degree of generalization of the species is over-estimated and the nested properties of the interaction webs are reduced. Functional traits, therefore, play a decisive role in the general properties of the two pollination networks documented here.

Several mechanisms can explain why the optimal threshold values were different from those expected under the null hypothesis, where the size thresholds equal zero, and from previous work (Stang et al. 2009). First, the two flower and insect traits considered were measured

Table 1 Threshold values and the percentage of interactions respecting them

	Population	Threshold values (mm)		Percentage of interactions respecting the thresholds								
		Length	Width	Length threshold			Width threshold			Both thresholds		
				Data	LWA	A	Data	LWA	A	Data	LWA	A
Null thresholds	Cours	0	0	64	63	40	89	100	84	56	63	27
	Guindaine	0	0	69	86	55	93	100	83	63	86	42
Optimal thresholds	Cours	−1.64	−0.54	91	100	61	71	100	69	66	100	35
	Guindaine	−1.05	−0.49	88	100	64	83	100	61	72	100	32

Threshold values of the null and optimal thresholds: under the null hypothesis all the threshold values are zero and the optimal thresholds are derived from Fig. 1. *Percentage of interactions* respecting the null and optimal thresholds, either the length threshold only, the width threshold only, or both thresholds; according to the observed data (*Data* columns), to the interactions predicted by the full model (*LWA* columns) and to the interactions predicted by the abundance model (*A* columns)

Fig. 2 Mean proportion (circles) and 95 % confidence intervals (horizontal bars) of correctly predicted interactions “R” according to the model type (a, e), connectance (b, f), weighted-interaction nestedness (c, g), and evenness (d, h) of the predicted networks. Dashed vertical bars the observed network values. Null null model, A abundance, W width threshold, L length threshold. Different combinations of the letters, A, W and L, indicate which mechanisms are included in the simulated networks

according to how I expected them to function, but it is impossible to be completely certain that they really function like this in nature. For example, the difference between the proboscis length and the nectar-holder depth of the species found to visit *Campanula rhomboidalis* was greater than 8 mm (large circles at the bottom of Fig. 3d).

The bell-shape of *C. rhomboidalis* raises the question of how to define the nectar-holder. Does the whole bell correspond to the nectar-holder, or is the nectar-holder limited to the base of the bell? Clearly, small insects are able to enter the bell and exploit the nectar despite having a short proboscis. However, *C. rapunculoides*, which belongs to the same genus and presents the same flower morphology, was visited by large insects that were unable to enter the bell completely and therefore had to rely on their long proboscis to reach the nectar (*Empis* sp, *Bombus pratorum*, *Bombus soroeensis*, *Apis mellifera*). In this case, the whole bell corresponds to the nectar-holder. Another aspect is that insects often have special ways of behaving to overcome morphological limitations (Waser 1986; Papaj and Lewis 1993). For example, most pollinators of *Erysimum*

mediohispanicum have mouth parts shorter than the corolla tube depth (Gómez et al. 2009).

Floral structures differ in how flexible, hairy, or glandular they are, which could affect the theoretical morphological constraints on reaching the nectar (Safa et al. 1984; Vargas et al. 2010). In the dataset presented here, the importance of pollinator behavior when confronted with more or less flexible floral structures is illustrated by the interaction between *Bombus ruderarius* and *Pedicularis foliosa*, where the difference between the proboscis length of the bumble bee and the nectar-holder depth is −11 mm (isolated circle at the bottom of Fig. 3a). This insect species is able to push apart the floral structures that prevent it from reaching the nectar (but nectar robbing was never observed during the field work). Note that the energy an insect is ready to spend on exploiting a flower might also depend on the nectar rewards it expects. Moreover, flower color and odor (Dudareva and Pichersky 2006) also affect insect choice (Gumbert et al. 1999). Pollinators tend to choose flowers that offer them enough nectar and/or pollen rewards in relation to their body mass (Heinrich 1975;

Fig. 3 Differences between insect and plant functional traits (proboscis length minus nectar holder depth, and proboscis width minus nectar holder width) in the observed (a, d) and predicted networks (full model LWA b, e; abundance model c, f) in both communities (Cours a–c; Guindaïne d–f). Each circle represents an interaction between a plant and an insect. The diameter of the circles

is proportional to the square-root of the number of individual interactions. The dashed horizontal and vertical lines represent the optimal length and width thresholds, respectively. The areas in gray represent the trait differences that are not allowed in the full model (LWA). All the interactions of the communities predicted by the full model respect the optimal size thresholds

Brown et al. 1978; Pyke 1984). The resulting pattern is an interaction between all these factors (Herrera et al. 2002; Fenster et al. 2004; Dalsgaard et al. 2009; Ibanez et al. 2010).

The simulated networks based on the selected pairs of functional traits presented here predicted only 25–30 % of the species-specific interactions. Future research should, therefore, include other functional traits. The additional functional traits listed above (cognitive abilities, motivation, and strength of the insects; flexibility, hairiness, nectar rewards, color and odor of the flowers) may also explain why as many as 28–34 % of the observed interactions did not respect the optimal thresholds, which suggests that the thresholds rules might be specific to each plant–insect pair. Provided that such traits are similar for species belonging to the same taxon (e.g., to the same family), the threshold values can be defined for each plant and insect family pair.

More interactions could be explained by considering not only additional traits but also functions describing the probability of interaction between plants and insects, instead of a merely simple threshold rule. For example, an asymmetric Gaussian function (Nandi and Mämpel 1995) depending on the trait differences would allow a steep decrease when the proboscis is shorter than the nectar-holder depth, and a slow decrease when the proboscis is much longer than the nectar-holder, reflecting the fact that

it may be difficult for an insect with a long proboscis to probe very short flowers. Three parameters (one for the mean and two for the standard deviations) would be needed for each pair of traits, which would require very large datasets. More generally, instead of an algorithmic approach followed by an analysis with GAMs, it would have also been possible to estimate the model parameters with a maximum likelihood approach, and then to select the best model according to its corrected Akaike's information criteria (AICc). This method has the advantage of taking into account the number of parameters used in each model, whereas the method I used has the advantage of following as closely as possible the sampling method in the field.

The structure of the two alpine pollination webs was strongly influenced by abundance effects together with size thresholds. The effect of the abundance of plant species in shaping the networks can be understood first as a neutral process. If abundances are ignored, all species pairs will have an equal probability of interaction. If abundances are taken into account, the probability of interaction of a pair of species will simply be the product of the relative abundance of both species. However, flowers and insects are different from molecules randomly colliding in a gas. Insects have to actively look for flowers, which mean that they rely on cognitive mechanisms when they perceive the

abundance of plant species. The abundance index ‘logarithm of the number of flowers’ performed better in Guindaine than in Cours, whereas the ‘visibility’ index performed particularly well in Cours. This suggests that, depending on local species assemblages or on the abiotic environment, different cognitive mechanisms may come into play when insects perceive plant abundance. An overall phenological effect for both plants and insects could not be included because there is no independent measure of insect density across the pollination season. Indeed, the apparent insect phenology in the data is entirely dependent on the plant species that were sampled.

Implications for community functioning

Optimal size thresholds at the community level enabled us to predict the distribution of trait differences in a community (Fig. 3). Provided that trait differences are linked with pollination efficiency, the use of optimal size thresholds might be a step towards the prediction of pollination efficiency at the community level. Up to now, despite a growing knowledge of how the plant–pollinator webs are structured and what are the mechanisms responsible for the structure, little is known about how the webs’ function, and, in the case of plant–pollinator webs, how the pollination process works. However, given the immense interests, both theoretical and applied, in predicting pollination efficiency at the community level, more research would be worthwhile in these areas. Both species abundances and functional traits (in particular those documented here) are likely to play a decisive role in such predictions because they are simultaneously involved in two processes: (1) which interactions are possible (and hence, what is the web’s structure), and (2) what is the outcome of the interactions in terms of pollination.

Previous studies have tended to use the structure of plant–pollinator webs, including phylogenetic signals (Bascompte et al. 2006; Rezende et al. 2007), to predict extinction cascades. However, if a pollinator loses its usual plant partners, it is unlikely to just give up and die. Instead, it will forage for new species if it can (Beckerman et al. 2010). Similarly, if a plant loses its main pollinators, it will potentially be visited by new pollinators because the competition among insects will be reduced.

The dual role of functional traits is thus apparent in the context of extinction cascades. In the case of plant–pollinator webs, size thresholds can predict to some extent the structure of the new webs occurring after the first extinctions. The trait differences between pairs of interacting plants and insects can predict, at least partly, their pollination outcome and hence the possible propagation of the extinction cascade.

Using functional traits has another advantage because plant–pollinator networks are highly variable at the species level, both in space (Dupont et al. 2009) and time (Alarcón et al. 2008; Petanidou et al. 2008), so that the precise prediction of the networks at the species level makes little biological sense. Moreover, such prediction is difficult. In this study, only 25–30 % of the species-specific interactions were predicted by the full model. In contrast, plant–pollinator networks might be more stable from a functional point of view, in the sense that the different sets of insects visiting a given plant over the years might be morphologically similar (Gong and Huang 2011). Therefore, predicting the functional properties of the networks, like the distribution of trait differences between interacting species, can help to understand the functioning of the networks better than relying on labile species-specific interactions. This might also be true on an evolutionary scale. The co-evolutionary dynamics of pollination networks may well be governed by multi-specific functional characteristics (Fenster et al. 2004; Rodríguez-Gironés and Santamaría 2007), and not simply by species-specific interactions alone. Given that interactions between species are labile in interaction webs, the evolution of generalist species will not depend on a single selection agent. The selective pressures experienced by species will rather be influenced by all their partners, including their variations in space and time, and the resulting selective pressures will depend on the trait differences between species, and the behavioral responses of pollinators to plant traits. For all these reasons, the optimization method of size thresholds described here, and the resulting network and functional patterns, should prove useful in further exploring the ecological and evolutionary dynamics of pollination networks.

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