

# Quantitative predictions of pollinators' abundances from qualitative data on their interactions with plants and evidences of emergent neutrality

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Making quantitative predictions of the effects of human activities on ecological communities is crucial for their management. In the case of plant–pollinator mutualistic networks, despite the great progress in describing the interactions between plants and their pollinators, the capability of making quantitative predictions is still lacking. Here, in order to estimate pollinator species abundances and their niche distribution, I propose a general method to transform a plant–pollinator network into a competition model between pollinator species. Competition matrices were obtained from ‘first principles’ calculations, using qualitative interaction matrices compiled for a set of 38 plant–pollinator networks. This method is able to make accurate quantitative predictions for mutualistic networks spanning a broad geographic range. Specifically, the predicted biodiversity metrics for pollinators – species relative abundances, Shannon equitability and Gini–Simpson indices – agree quite well with those inferred from empirical counts of visits of pollinators to plants. Furthermore, this method allows building a one-dimensional niche axis for pollinators in which clusters of generalists are separated by specialists thus rendering support to the theory of emergent neutrality. The importance of interspecific competition between pollinator species is a controversial and unresolved issue, considerable circumstantial evidence has accrued that competition between insects does occur, but a clear measure of its impact on their species abundances is still lacking. I contributed to fill this gap by quantifying the effect of competition between pollinators. Particular applications of our analysis could be to estimate the quantitative effects of removing a species from a community or to address the fate of populations of native organisms when foreign species are introduced to ecosystems far beyond their home range.

Plant–pollinator mutualistic networks are complex systems that are difficult to analyse because the combination of the heterogeneity of their constituent species (typical size, behavior, fitness, generalism and phenology) and the large number of interactions between them. This results in large sets of parameters for describing their interaction, which are very hard to estimate from the scarcely available empirical data. Therefore, theoretical approaches for plant–pollinator networks unavoidably make drastic simplifying assumptions like for example the fully connected network approximation – all species of plants and animals interacting between each other – and/or the homogeneity approximation – all the interaction coefficients between species equal (Bascompte et al. 2006, Holland et al. 2006, Bastolla et al. 2009). Some general findings of these simplified mutualistic interaction models provide useful insight into the relationship between community structure and biodiversity, e.g. the fact that nestedness enhances the number of coexisting species (Bastolla et al. 2009) or the strong relationships found among species abundances, nested architecture and community stability (Fontaine 2013, Suweis et al. 2013). However, a more accurate and realistic understanding of these plant–pollinator

interactions is required when assessing the impact of management decisions on communities after the loss or gains of species. That is, we would need to go beyond the qualitative biodiversity analysis of general and abstract communities and be able to make ‘quantitative’ predictions for ‘real’ and ‘specific’ communities found in nature.

A considerable amount of evidence suggests that competition for floral resources between pollinators is important and widespread (Waser and Real 1979, Kevan and Baker 1983, Willmer 2011) because the availability of partner plants represents a limiting resource (Palmer et al. 2003). The shared use of common resources results in interference and exploitative competition among pollinators that not only reduces foraging efficiency at feeding patches (Johnson and Hubbell 1974, Roubik 1980) but also pollen and nectar harvest of colonies (Roubik et al. 1986, Wilms and Wiechers 1997). Availability of either foods or nest sites is thus likely to limit population density of some pollinator species (Hubbell and Johnson 1977, Inoue et al. 1993). However, little is known about direct consequences of competition for the abundance and community structure of insect pollinators (Steffan-Dewenter and Tscharnkte 2000, Goulson 2003, Palmer et al. 2003).

Thus, here I propose to focus only on pollinator populations and consider plants just as the resource they consume and for which they compete, rather than to explicitly consider the mutualistic interactions of plants and pollinators. This provides a general method to transform qualitative data for a mutualistic plant–pollinator network, denoting the insect species visiting each plant species, into a unipartite resource-utilization system from which one can predict the relative abundances of pollinator species (RAPS). That is, a method that allows the estimation of biodiversity metrics (relative abundances, Shannon equitability and Gini–Simpson index) only from the knowledge of the links that make the mutualistic network.

The data set of plant–pollinator interactions was compiled using the data of Rezende et al. (2007) plus data from the National Center for Ecological Analysis and Synthesis (NCEAS 2014) and comprises 38 networks spanning a broad geographic range, providing an ideal opportunity to test this method. For each of these networks the interactions between the  $S_A$  animal species and  $S_P$  plant species are summarized in the  $S_A \times S_P$  adjacency matrices of the mutualistic networks  $g_{ap}$  (Rezende et al. 2007, Bastolla et al. 2009, NCEAS 2014). Each matrix has rows and columns corresponding to the animal and plant species of the system respectively and 1's and 0's in the row–column intersections represent interactions or their absence, respectively. The number of plant species with which the animal species  $a$  interacts, i.e. the number of 1's in a row of  $g_{ap}$  for a given animal species, is called its degree  $D_a$  (Jordano et al. 2003). The higher (lower) this index is, the more generalist (specialist) the pollinator species is. For 13 of the 38 animal–plant networks, in addition to the qualitative information provided by  $g_{ap}$ , there is also a quantitative interaction matrix,  $q_{ap}$ , that specifies the number of observed visits of each animal species  $a$  (row) to each plant species  $p$  (column) (Rezende et al. 2007, NCEAS 2014). In these cases, for a given pollinator species  $a$ , one can estimate from  $q_{ap}$  its relative abundance,  $n_a$ , simply as proportional to the sum of the matrix elements over the corresponding row  $a$  i.e. all the recorded visits of this animal species to the different species of plants (Willmer 2011). It turns out that the predicted RAPS, the Shannon equitability and the Simpson–Gini index agree quite well with those inferred from the  $q_{ap}$  matrices. The good matching for the 13 networks for which there is quantitative data on plant–pollinator interactions suggests that the proposed approach could reliably predict biodiversity metrics for the remaining 25 mutualistic networks for which these quantitative interaction matrices were not available. Most of the analyses, and especially the validation of the method, lie on the 13 datasets with quantified interaction strengths.

I also discuss how the proposed method allows to build a one-dimensional resource utilization niche axis  $x$  for pollinator species. This concept of resource utilization niche (MacArthur and Levins 1967) focuses on how species use consumable resources. Niche theory was essentially a group of theoretical models designed to address the problem of how many and how similar coexisting species could be within a given community (MacArthur and Levins 1967, May and MacArthur 1972). The relative utilization of resources along a resource spectrum or niche axis can be described as a frequency distribution. Species are thus characterized in

terms of their similarity in resource use or their niche overlap. The basic idea is that there is a strong correspondence between the degree of niche overlap between two species and the intensity of their competition by shared resources (Morin 2011). A remarkable finding is that RAPS along  $x$  for all the 38 plant–pollinator networks exhibit a lumpy pattern of – humps separated by gaps – thus rendering support to the theory of emergent neutrality (Vergnon et al. 2012). This phenomenon of spontaneous emergence of self-organized coexistence in clusters of look-alikes separated along  $x$  by gaps with no survivors is supported by empirical evidence from other communities ranging from mammals (Siemann and Brown 1999) and birds (Holling 1992) to plankton (Segura et al. 2011, 2013). Interestingly, we found that abundant pollinator species, at the humps, tend to be generalists while rare pollinator species, at the gaps, tend to be specialists.

## Methods

I assumed that the dynamic is governed by the simple linear Lotka–Volterra competition equations (without density-dependent terms regulating the growth of species) for the abundances  $N_a$  of the  $S_A$  animal species:

$$\frac{dN_a}{dt} = r_a N_a \left( 1 - \sum_{a'=1}^{S_A} \alpha_{aa'} \frac{N_{a'}}{K_a} \right), \quad a = 1, \dots, S_A \quad (1)$$

where  $r_a$  and  $K_a$  denote the logistic coefficients, respectively the maximum growth rate and the carrying capacity, and  $\alpha_{aa'}$ , the competition coefficient between animal species  $a$  and  $a'$ . Since we are interested in the stationary behaviour we took  $r_a = 1$  for all the animal species. Additionally notice that in order to predict the RAPS only the relative values of their carrying capacities,  $k_a = K_a/K_{\min}$ , are required rather than the values of the carrying capacities themselves. So Eq. 1 in terms of relative quantities becomes

$$\frac{dn_a}{dt} = n_a \left( 1 - \sum_{a'=1}^{S_A} \alpha_{aa'} \frac{n_{a'}}{k_a} \right), \quad a = 1, \dots, S_A \quad (2)$$

An advantage of the approach I am proposing for modelling the pollinator population dynamics is that it is straightforward to estimate the required parameters from the qualitative information on the plant–pollinator interactions. In fact, in principle, only two sets of parameters have to be estimated:  $\{k_a\}$  and  $\{\alpha_{aa'}\}$  and actually we will see that the choice  $k_a = D_a$  works pretty well and so only the competition coefficients have to be estimated.

## Estimation of parameters

According to MacArthur and Levins 1967, the interspecific competition coefficient  $\alpha_{aa'}$  between animal species  $a$  and  $a'$  is proportional to the number of shared resources (plants) or their resource overlap (Fig. 1). The resource overlap between species  $a$  and  $a'$  is quantified by the Jaccard similarity index (Jaccard 1901)  $J_{aa'}$ , which can be easily obtained from  $g_{ap}$  and is given by (Jaccard 1901)

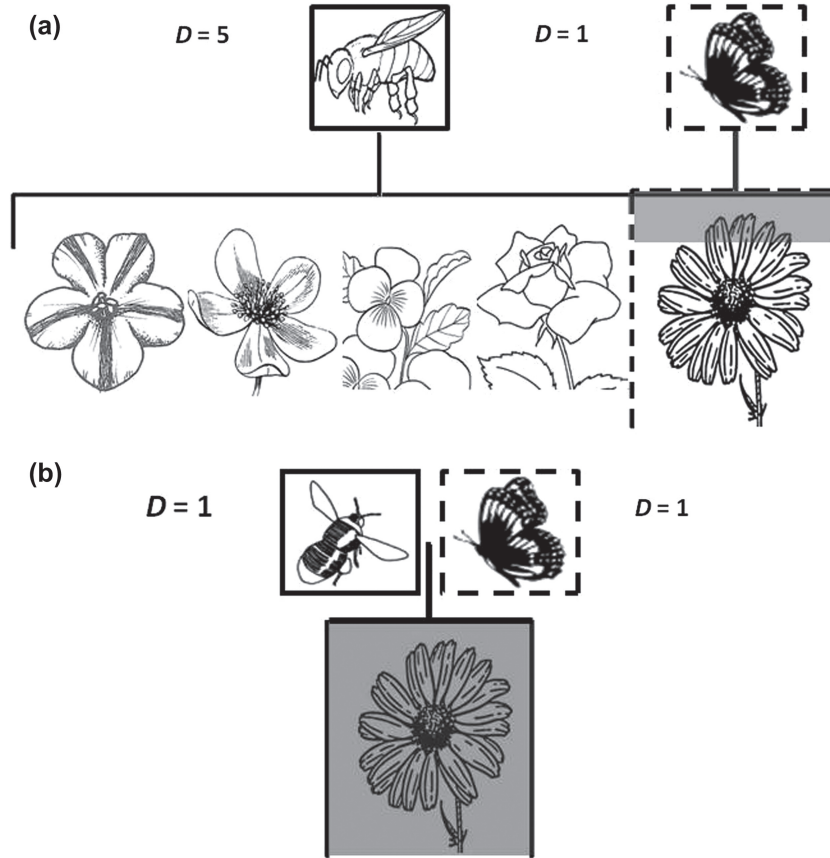


Figure 1. The intensity of competition between pollinator species depends on the number of plants they share. The resource utilization function for each pollinator species is represented by a horizontal bracket, the higher the pollinator degree  $D$ , the wider this bracket (and the shorter, in order to preserve the area below the bracket = 1). (a) Interaction between a pollinator  $a$  with  $D_a = 5$  (filled line) with another  $a'$  with  $D_{a'} = 1$  (dashed line), that share one plant species i.e. their niche overlap consists of just one plant species and is represented by a short gray rectangle of area  $< 1$ . That is, the Jaccard coefficient  $J_{aa'}$  is relatively small. (b) Interaction between two pollinators with  $D_a = D_{a'} = 1$ , that share the plant species which both interact i.e. they have full niche overlap represented by a gray rectangle of maximum area = 1. Therefore their Jaccard coefficient is maximum,  $J_{aa'} = 1$ .

$$J_{aa'} = \frac{P_{aa'}^{11}}{P_{aa'}^{01} + P_{aa'}^{10} + P_{aa'}^{11}} \quad (3)$$

where  $P_{aa'}^{11}$  represents the number of species of plants visited by both species of animals and  $P_{aa'}^{10}$ , ( $P_{aa'}^{01}$ ) the number of species of plants which are visited only by  $a$  ( $a'$ ). Notice that if the two pollinator species share all the plants, i.e.  $P_{aa'}^{10} = 0 = P_{aa'}^{01}$ , then  $J_{aa'} = 1$ . This situation of full overlap in general occurs between maximum specialists with  $D = 1$  (as illustrated in Fig.1b). Therefore,

$$\alpha_{aa'} = N_{aa'} J_{aa'} \quad (4)$$

where the factors  $N_{aa'}$  are equal to 1 for  $a = a'$  in such a way that intraspecific competition coefficients  $\alpha_{aa'} = J_{aa}$  become 1. The non diagonal factors  $N_{aa'}$  were chosen as random numbers from a uniform distribution and serve two different purposes. First, to include the fact that interspecific competition between pollinators is in general highly asymmetrical (Kaplan and Denno 2007). This asymmetry is known to be particularly important in the case of interference competition i.e. when each species harm the other directly (Keddy 2001). Nevertheless, here I did not distinguish between interference

competition and exploitative competition (when each species alter the abundance of some shared resource to the other). Second, to take into account different mechanisms that tend to weaken interspecific competition between animals, such as facilitation between them (Kaplan and Denno 2007, Denno and Kaplan 2007) or resource partitioning (Lande 1996, Denno and Kaplan 2007), these  $N_{aa'}$  must be smaller than 1 (I checked that if one chooses simply all  $N_{aa'} = 1$  for  $a \neq a'$ , the interspecific competition seems to be too strong and the model fails to reproduce the abundance of rare species i.e. it just yields relative abundance  $n_a = 0$  for them).

Before discussing how I obtain the  $\{k_a\}$  we need to explain how the relative abundances  $\{n_a\}$  were estimated for the 13 networks for which quantitative interaction matrices  $\{q_{ap}\}$  were available (Rezende et al. 2007, NCEAS 2014). Since  $q_{ap}$  specifies the number of observed visits of animal species  $a$  to plant species  $p$ , the  $n_a$  can be obtained as

$$n_a = \frac{\sum_{p=1}^{S_p} q_{ap}}{\sum_{a=1}^{S_A} \sum_{p=1}^{S_p} q_{ap}} \quad a=1, \dots, S_A \quad (5)$$

such that  $\sum_{p=1}^{S_A} n_a = 1$ .

The  $\{k_a\}$  in turn were obtained from an empiric fact: the correlation between the observed empiric relative abundances and degree were large and significant (Supplementary material Appendix 1 Fig. S1). This same correlation was found by Suweis et al. (2013). Indeed MacArthur (1972) and later Brown (1984) suggested that species with a broad ecological niche would, as a consequence, be able to reach higher abundances than species with a narrow niche breadth. Such a positive relationship between niche width or generalization level in resource use and relative abundance of individual species suggested that we can take  $k_a$  just identical to the degree  $D_a$ , an assumption that turned out to work pretty well. Moreover, I checked whether the simplest choice of assuming  $k_a$  the same value  $k$  for all species did not work because it led to a negative correlation between  $\{n_a\}$  and  $\{D_a\}$ . Another possibility would have been to use  $n_a$  to estimate the  $k_a$  as a function of it. However, since the  $\{n_a\}$  are precisely the quantities to be predicted, I preferred to rule out the possibility of circularity.

A more accurate estimation of the competition coefficients was also possible from the  $\{n_a\}$  (for details see Supplementary material Appendix 1).

## Simulations

For each network 200 simulations were run for computing the mean abundances of each pollinator species and their standard deviations. There were two sources of stochasticity: firstly, in the initial conditions, each simulation starts from a random abundance for each animal species. In each simulation a rapid convergence (in less than 100 temporal steps) to the equilibrium abundances was observed. Secondly, the non diagonal random normalizing factors  $N_{aa'}$  were drawn at the beginning of each simulation.

## Comparison between empirical and theoretical RAPS

To measure the agreement between empirical and theoretical RAPS I used two indices between 0 and 1 (1 indicating perfect agreement between predicted and observed data and 0 indicating complete disagreement.). First, the Willmott index of agreement  $d_{emp-theo}$  (1981):

$$d_{emp-theo} = \frac{\sum_{a=1}^{S_A} (n_a^{theo} - n_a^{emp})^2}{\sum_{a=1}^{S_A} \left( \left| n_a^{theo} - \overline{n_a^{theo}} \right| + \left| n_a^{emp} - \overline{n_a^{emp}} \right| \right)^2} \quad (6)$$

(notice that the expected value of  $d$  for two independent random variables is  $d_{random} = 3/7 \approx 0.429$ ). Second, the Pearson correlation coefficient  $r$ .

## Biodiversity indices

Other biodiversity metrics that can be built from the  $\{n_a\}$  are the Shannon equitability and the Simpson–Gini index defined, respectively, by  $H = \sum_a^S n_a \ln n_a / S_A$  and  $SG = 1 - \sum_a^S n_a^2$ .

## Construction of the niche axis

It is enlightening to regard plants as a one-dimensional discrete resource spectrum (May and MacArthur 1972) for pollinators being the competition intensity between pairs of pollinator species equal to their niche overlap (MacArthur and Levins 1967). To construct this niche axis, it is necessary to group together all pollinator species that exhibit a large resource overlap, reordering them from degree-order to niche-order, by assigning to each species an integer  $x_a$  between 1 and  $S_A$  that denotes its niche ‘position’. To accomplish this I used a ‘simulating annealing’ algorithm (Kirkpatrick et al. 1983). This algorithm favours the proximity of interacting species by minimizing a cost function or ‘energy’  $E$ , assigned to each ordering, given by (Rybarczyk et al. 2010)

$$E = \sum_{i=1}^{S_A} \sum_{j=1}^{S_A} d_{ij} \{ |\alpha_{ij} - \alpha_{i+1j}| + |\alpha_{ij} - \alpha_{i-1j}| + |\alpha_{ij} - \alpha_{ij+1}| + |\alpha_{ij} - \alpha_{ij-1}| \} \quad (7)$$

where,  $i$  and  $j$  are integers,  $|\dots|$  stands for the positive value of the difference of the competition matrix elements for neighbouring positions and  $d_{ij} = |i - j|$  is the distance from the ‘site’  $(i, j)$  to the diagonal. This cost function penalizes variations of competition coefficients between neighbour species and penalizes further when these variations are far from the diagonal. Starting with a decreasing  $D$ -ordered list of species and its corresponding interaction matrix with energy  $E_0$ , the algorithm proceeds by randomly choosing a pair of species and swapping their positions on the ordering. A new interaction matrix is produced for this new ordering and its cost is recalculated using E. 7. If the cost decreases, the change is accepted. If the cost is increased by  $\Delta E$ , the change is accepted with probability  $\exp[-\Delta E/T]$ , where  $T$  is a virtual temperature. I started with  $T = 5 \times E_0$  and every 50 of these Monte Carlo steps (MCS) the temperature is lowered to 5% of its previous value. A MCS is a number of random choices equal to  $S_A$ . When changes are not accepted, they are discarded and a new pair of species is chosen to repeat the process. This procedure is repeated until the calculated value of cost is stabilized for a configuration in which sites  $(i, j)$  far from the diagonal, which present very different positions along the niche axis, correspond to pairs of species that have a small overlap, implying then weak competition between them.

## Emergent neutrality: testing for multimodality of RAPS

The lumpy structure of RAPS is observable to the naked eye for all the studied mutualistic networks. However this lumpiness or multimodality can be quantitatively assessed. There are few statistical tests for discovering multimodality in a distribution. One of such tests is the DIP test (Hartigan and Hartigan 1985). The dip test measures multimodality in a sample by the maximum difference, over all sample points, between the empirical distribution function, and the unimodal distribution function that minimizes that maximum difference. The uniform distribution is the asymptotically least favorable unimodal distribution, and



the distribution of the test statistic is determined asymptotically and empirically when sampling from the uniform.

## Results

### Predicted versus empirical biodiversity metrics

The predicted RAPS were in general in quite good agreement with the empirical ones (Fig. 2, Table 1). For the 13 networks  $d_{emp-theo} > 0.5$  and in general well above 0.5 (Table 1).

We can see that the best matching between theoretical predictions and empirical data for all the biodiversity metrics RAPS,  $H$ ,  $S\hat{G}$  occurs for the MEMM network (Table 1), while the worst matching occurs for the SMAL network.

The highest concordance between the empirical and theoretical relative abundances occurred either for highly specialised pollinator species (low  $D_a$ ), unless two exceptions. These two exceptions for which the method fails to reproduce the abundance of specialist insect species with relative abundance above 5%, occur one for the INPK network (Fig. 2d) and one for the SMAL network (Fig. 2i). How to fix these significant underestimations of specialist species is treated in the Discussion section.

### Calculations using competition coefficients obtained from quantitative matrices

Using Eq. A2 (Supplementary material Appendix 1) for computing the competition coefficients improved,

Table 1. Empirical and theoretical biodiversity metrics for 13 plant–pollinator networks with quantitative matrices available. These 13 networks, of a total of 38, were those for which there was quantitative information (i.e. quantitative interaction matrices  $q_{ap}$ ). Two measures of agreement between empiric and theoretical RAPS were considered: the ‘index of agreement’ (Willmott 1981)  $d_{emp-theo}$  and the Pearson correlation coefficient  $r_{emp-theo}$ . For all the networks, except for the SMAL network,  $p\text{-value} < 0.01$  and the correlation was significant. (\*): (Rezende et al. 2007, NCEAS 2014).

Network code (*)	Richness $S_A^{(*)}$	Agreement emp. and theo. RAPS		Shannon’s equitability		Simpson–Gini	
		$d_{emp-theo}$	$r_{emp-theo}$	$H_{emp}$	$H_{theo}$	$SG_{emp}$	$SG_{theo}$
BAHE	102	0.74	0.59	0.74	0.69	0.93	0.93
BEZE	13	0.98	0.97	0.79	0.75	0.82	0.82
DIHI	61	0.77	0.67	0.56	0.66	0.80	0.90
DISH	36	0.78	0.78	0.53	0.76	0.68	0.90
INPK	85	0.81	0.72	0.66	0.77	0.90	0.95
KT90	679	0.78	0.70	0.84	0.67	0.99	0.97
MEMM	79	0.96	0.91	0.72	0.71	0.93	0.93
MOMA	18	0.85	0.74	0.79	0.83	0.85	0.87
MOTT	44	0.63	0.54	0.59	0.80	0.80	0.94
OLLE	56	0.89	0.88	0.65	0.77	0.87	0.94
SCHE	32	0.83	0.72	0.73	0.78	0.87	0.91
SMAL	34	0.51	0.28	0.93	0.89	0.95	0.94
VASI	30	0.81	0.79	0.58	0.80	0.78	0.91

although not dramatically, the matching between the theoretical and empirical RAPS (Supplementary material Appendix 1 Fig. S2).

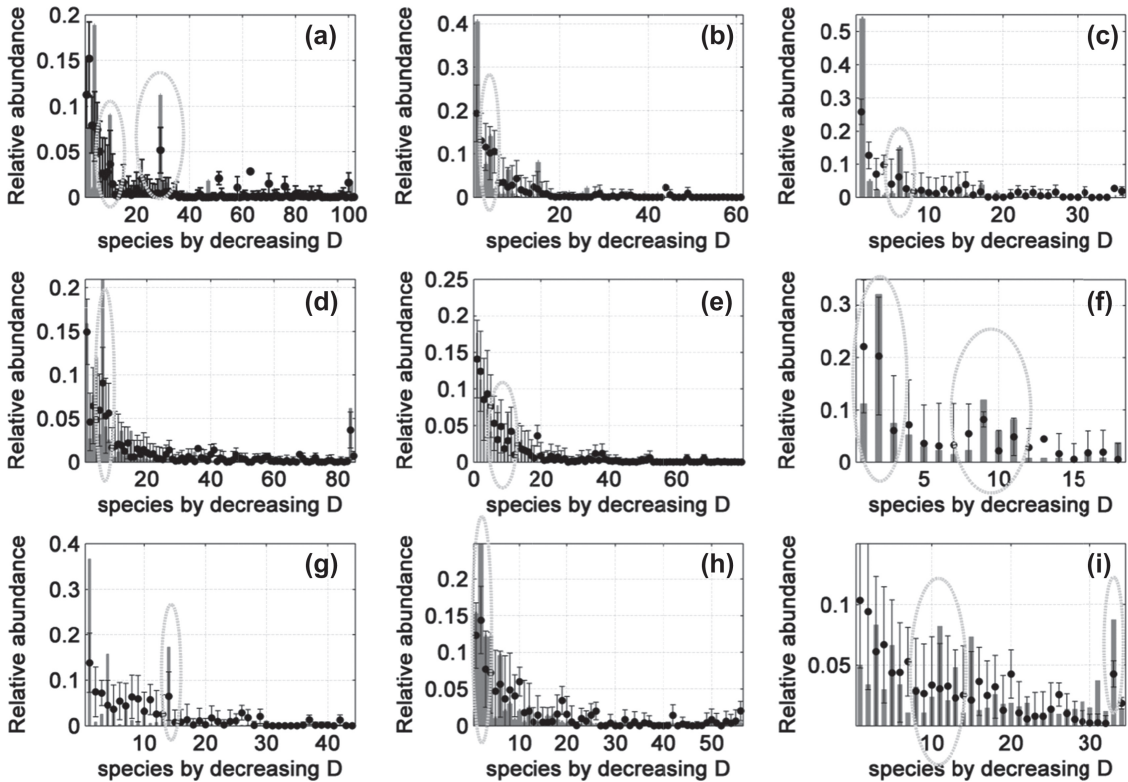


Figure 2. Predicted and observed RAPS. Empiric (gray bars) and theoretical (black with errors = 1 SD for 100 simulations) RAPS for nine of the 13 plant–pollinator networks for which there is quantitative information (Table 1): BAHE (a), DIHI (b), DISH (c), INPK (d), MEMM (e), MOMA (f), MOTT (g), OLLE (h) and SMAL (i) (Rezende et al. 2007). Insect species are numbered according to decreasing degree  $D_a$ . See text in Discussion for the ovals.

## Building the niche ecological axis for each community of pollinators

When reordering the species along the niche axis  $x$ , two structural patterns, i.e. independent of the resulting RAPS, become evident for all analysed plant–pollinator networks. Firstly, the competition matrices display a block structure (blocks of side greater than 1) along the diagonal that now corresponds to the niche axis (Fig. 3b, 4a, Supplementary material Appendix 1 Fig. S4b). Such structure is typical of competition matrices computed using MacArthur and Levins niche overlap (Supplementary material Appendix 1 Fig. S3). These blocks correspond to sectors of strong resource overlap and therefore high interspecific competition.

The blocks of maximum competition,  $J_{ad'} = 1$  (white squares of Fig. 3b, 4a), occur for sets of specialists ( $D_a = 1$  or 2) that all share one or at most two plants as their resource. In fact, when animal species are ordered by decreasing  $D_a$ , the competition matrices show many large elements

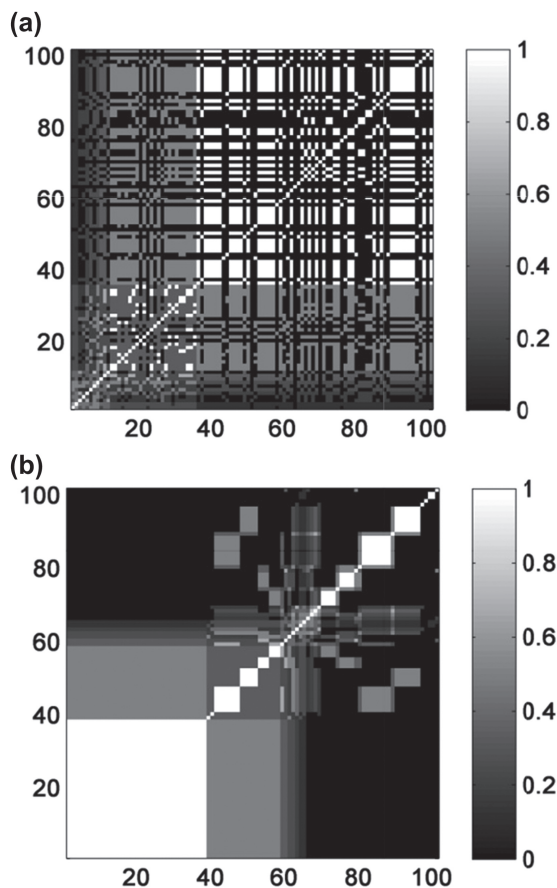


Figure 3. Competition (Jaccard) matrices  $J_{ad'}$  between pollinators for D-order versus niche order. ARR1 network, of  $S_A = 101$  pollinator species. Colour code: white sites correspond to high competition ( $J_{ad'}$  close to 1) while black sites correspond to low competition ( $J_{ad'}$  close to 0). By definition  $\alpha_{aa} = J_{aa} = 1$  corresponding to unit squares at the diagonal. (a) Pollinator species ordered by decreasing degree  $D_a$ . The competition matrix shows many large elements in the upper right quadrant, corresponding to the strong resource overlap between pairs of specialist pollinator species ( $D_a = 1$  or 2). (b) Species ordered according to their niche (integer) 'position'  $x_a$ . Now maximum competition,  $J_{ad'} = 1$ , between specialists appears as white blocks.

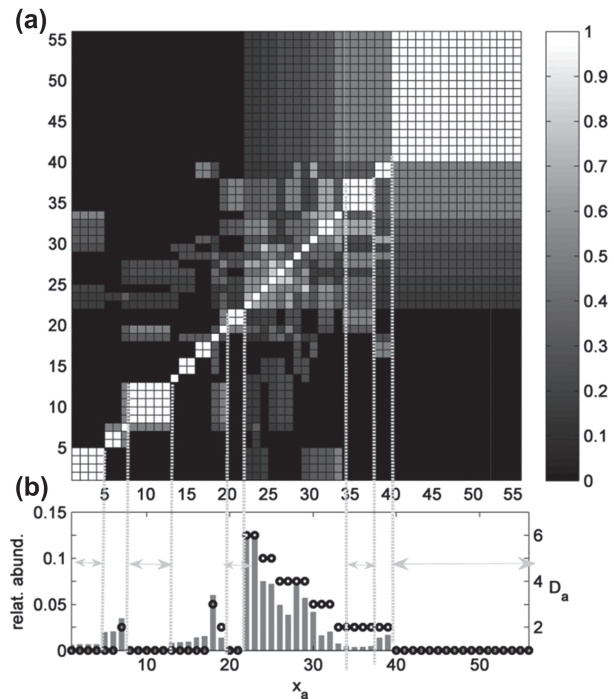


Figure 4. The relationship competition–degree–abundance along the niche axis. OLE network,  $S_A = 56$ . (a) The competition (Jaccard) matrix for species ordered according to their 'niche position'; colour code: black (white) corresponds to  $J_{ad'} = 0$  (1). By definition  $\alpha_{aa} = J_{aa} = 1$  (Methods) corresponding to the unit squares at the diagonal. (b) Degree  $D_a$  and RAPS  $n_a$  versus 'niche position'. The blocks of  $a_{ad'} = 1$  centred at the diagonal (signalled by dashed gray lines and double arrows) correspond to sets of specialist pollinators, with  $D_a = 1$  or 2 (panel b), sharing one or at most two plants. E.g. the block above and at the right in panel a corresponds to a set of specialist pollinators from  $x_a = 40$  to  $x_a = 56$  all sharing the *Xysmalobium gerrardii* as their resource (Rezende et al. 2007). Notice that the abundances are in all the cases very low. By contrast, the block at the centre of the competition matrix, covering a wide range of colours ( $0 < a_{ad'} < 1$ ), corresponds to the lump of generalists with high abundances at the middle of the niche axis in panel (b).

in the upper right quadrant, corresponding to the strong resource overlap between pairs of specialist pollinator species (Fig. 3a, Supplementary material Appendix 1 Fig. S4a). By contrast, generalists give rise to blocks covering a wide range of colours ( $0 < J_{ad'} < 1$ ) since they have smaller overlaps with many species of insects (square at the centre of Fig. 4a).

Secondly, the degree of generalism versus the niche position,  $D(x)$ , exhibits a pattern of 'hills' and shallow 'valleys' corresponding to alternating clusters of generalists and specialists (Fig. 4b, 5).

## Lumpy patterns and multimodal species abundance distributions

In addition, the relative abundances  $\{n_a\}$  plotted versus  $\{x_a\}$  exhibit a lumpy structure of clusters of abundant species at self-organized niches separated by groups of rarer species (Fig. 5), for all the 38 plant–pollinator networks according to the DIP test (p-value  $< 0.01$  always). In particular, the model reproduces very well the empirically observed 'gaps' of species along the niche axis (regions with very low abundances).

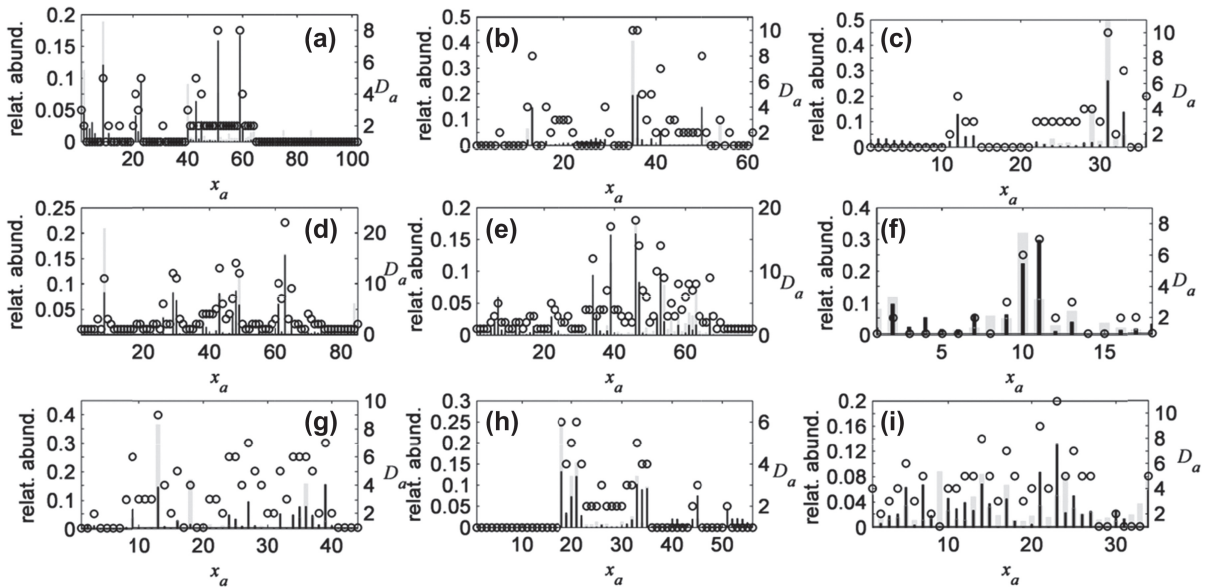


Figure 5. Lumpy patterns for predicted and observed RAPS along the niche axis. Empiric (gray bars) and theoretical (black bars) RAPS (left axis), and their degree  $D_a$  (circles, right axis) for nine of the 13 plant–insect networks for which there is quantitative information: BAHE (a), DIHI (b), DISH (c), INPK (d), MEMM (e), MOMA (f), MOTT (g), OLLE (h) and SMAL (i). The RAPS were computed using the more refined interaction coefficients  $\alpha_{ad}^{quant}$  obtained from the frequencies of animal species  $a$  with plant species  $p$  (Eq. 7). Species are numbered according to their niche (integer) ‘position’  $x_a$ .

When the species abundance distributions (SAD) are represented as histograms of number of species on the ordinate axis against log-transformed abundance on the abscissa axis using base 2, or Preston diagrams (Preston 1962), most of them seem multimodal to the naked eye (Supplementary material Appendix 1 Fig. S5). Indeed, the DIP test (Hartigan and Hartigan 1985) showed that all (but the one for the SMAL mutualistic network) predicted SAD were multimodal (p-value < 0.05).

### Non-linear versus linear Lotka–Volterra competition equations

It was checked that the results don’t change very much if we consider non-linear equations, for example involving quadratic dependencies in the parenthesis of Eq. 2 (Supplementary material Appendix 1 Fig. S6).

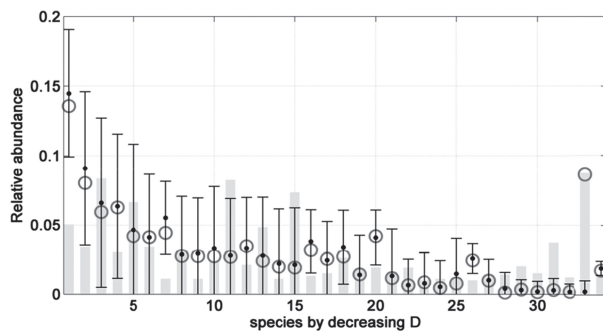


Figure 6. Improvements in the predicted RAPS when changing the carrying capacity of one species. The same RAPS from Fig. 2i: empiric (gray bars), theoretical predictions without change (black dots with errors = 1 SD for 100 simulations); plus the predicted RAPS when changing the relative carrying capacity of *Dilophus caurinus* from  $k_m = 1$  to  $k_m = 5$  (large gray circles).

## Discussion

In order to evaluate the impact of human activities on ecological communities, that lead to the loss or gains of species, and to decide on the most effective actions for nature conservation, we need to develop quantitative prediction tools. In the specific case of plant–pollinator communities predictive capacities are limited to qualitative assessments (Bascompte et al. 2006, Bastolla et al. 2009).

I presented a simple method to obtain quantitative predictions about the animal relative abundances from the qualitative information of their animal–plant mutualistic networks summarized in the adjacency matrices  $g_{ap}$ . Even though the theoretical parameters were estimated from such coarse (binary) data, the predicted RAPS are in general in quite good agreement with the empirical ones – estimated from the quantitative interaction matrices  $q_{ap}$ . The comparison between theoretical and empirical biodiversity indices shows a better agreement for the Simpson–Gini than for the Shannon equitability. This can be easily understood from the fact that the theoretical RAPS are averages over samples of 200 simulations whose rare species have larger coefficients of variation. Therefore, since the Simpson–Gini index responds basically to changes in the most common species, while the Shannon index is more sensible to changes in the abundance of the rarest species (Peet 1974, Supplementary material Appendix 1 Fig. S7). Notice that the proposed method goes far beyond than previous approaches that make the simplest choice for the mutualistic coefficients (Supplementary material in Bascompte et al. 2006, Holland et al. 2006 and Bastolla et al. 2009). Actually the former not only allows testing ‘quantitative’ predictions on biodiversity metrics, there are also important qualitative differences. For example fully connected mutualistic communities yield relative abundances for animals varying in a narrow range



(Supplementary material in Bastolla et al. 2009). By contrast, the present analysis yields RAPS which, like the real ones, are very uneven with few abundant species and many rare species.

A limitation of the proposed method relies on the lack of independence between the estimation of the relative abundance of pollinator species and their degree. Empirical relative abundances are obtained from data not independent from the data used to obtain interactions. This is a quite general problem in the study of mutualistic networks which lack independent estimations of species abundances. Thus a note of caution is in order: as it was pointed out by Blüthgen (2010), observation limitation is ubiquitous in plant–pollinator mutualistic datasets. For example, when interactions are recorded in natural communities, only a small subset of the existing interactions is usually observed and this introduces bias into the analysis. In fact, the ideal way to estimate the carrying capacities  $\{k_a\}$  and the competition coefficients  $\{\alpha_{ad}\}$  would be to measure the abundances of all isolated pollinator species, to obtain  $\{k_a\}$ , and then to measure the abundances of species taken in pairs and isolated from the rest to obtain  $\{\alpha_{ad}\}$ . But this is not practically feasible. For example for a network like INPK – with 85 species of insects – in order to experimentally estimate the competition coefficients,  $85 \times 84 = 7140$  of these ‘experiments’ would be required! Thus here I propose a method that uses the best available data we have (which are far from ideal data).

An important implication of the results I obtained is concerning the importance of interspecific competition between pollinator species. This is a controversial and unresolved issue for plant-insects in general (Kaplan and Denno 2007). Considerable circumstantial evidence has accrued that competition between insects does occur, but a clear measure of its impact on their species abundances is still lacking. I contributed to fill this gap by quantifying the effect of competition between pollinators. That is, competition matrices were obtained from ‘first principles’ calculations, using the available empirical data for the 38 plant–pollinator networks: the number of shared plants between each pair of pollinator species. The higher the fraction of shared plant species by two pollinator species, the stronger their competition. Yet one could wonder to what extent taking into account competition among pollinators really increases the fit of estimated relative densities compared to a neutral model with no interspecific interactions and  $k_a$  identical to the degree  $D_a$  plus some sort of random noise. However, without noise, such a model would predict a monotonic abundance– $D$  functional relationship, which is different from what the empirical data show. That is: 1) species with low  $D$  are frequently more abundant than other with high  $D$ , and 2) species with equal  $D$  sometimes exhibit important differences in their abundances. It turns out that the interspecific competition interactions can explain both 1) and 2). In Fig. 2 the ovals point entire sectors of the RAPS departing from the neutral monotonic behavior that can be reproduced by the proposed competition model. The addition of noise to the neutral model would hardly reproduce these empirical observations.

The proposed model can be regarded as a 0-level approach: competition between pollinators for their resources (plants) is the only determinant of the population dynamics.

Its performance is encouraging, suggesting that taking into account other drivers of pollinator population dynamics beyond pure competition (Vázquez et al. 2009) or using more accurate estimations of the parameters more reliable predictions would be obtained. For instance, I have shown that the use of competition coefficients estimated from quantitative interaction matrices improves the agreement between empirical and theoretical biodiversity metrics. Another example of how the 0-level model can be improved is provided by those particular situations in which, as we have seen, this model fails to reproduce the abundance of an abundant specialist insect species (e.g. for the SMAL network). A simple explanation for this mismatch is that the floral host, *Nemopanthus mucronata*, of this specialist, *Dilophus caurinus* (Rezende et al. 2007), be highly abundant (unfortunately, as far as I know, there is no data on the abundance of plants). So a simple way to improve the model predictions in these cases is to incorporate either plausible or known empirical facts yielding a higher level model. For instance, if the floral resource of a specialist is known to be highly abundant, for this species it is sensible to go beyond the simple rule of taking the carrying capacity as proportional to the species degree and rather take a larger value for its carrying capacity. Figure 6 shows how the predictions of the model for the SMAL network improve by changing the carrying capacity of *Dilophus caurinus*, from  $k_{Dc} = D_{Dc} = 1$  to  $k_{Dc} = 5$  (since no data on this plant abundance was available the value of  $k_{Dc}$  was determined by trial and error to achieve the best agreement with the estimated empirical relative abundance for *Dilophus caurinus*). Notice that, besides the dramatic improvement for the predicted abundance of this particular species, the matching between theoretical and empirical relative abundances of all the other species also improves in some degree.

In order to provide some context concerning the importance of estimations of species abundances, two general comments are in order. The first one is about the important role of species abundances in structuring ecological networks. It was recently discovered that they are positively related to nestedness (Fontaine 2013, Suweis et al. 2013). The second one is methodological. Quantitative analyses reflect properties of interaction networks more appropriately than qualitative attempts, and are more robust against variation in sampling intensity and network size (Blüthgen et al. 2006, Blüthgen 2010).

The other main goal of this work was the construction of the distribution of pollinator niches. It is known that differences among species in their niches are important in determining the outcome of species interactions as might be revealed in their distributions and/or abundances, as well as in their biodiversity and their functional role in ecosystems (Chase and Leibold 2003). Indeed the niche concept is an important element in many aspects of ecological thinking, across levels of organization, from individuals (concerning their behaviour, morphology, and physiology) to ecosystems (to evaluate how species participate in ecosystem functioning) (Chase and Leibold 2003). The niche framework helps to devise each specie’s place and role in the community to which it belong as well as it provides a better understanding of species coexistence, new insights and interpretations about ecological patterns and processes in ecology and how



fluctuating environments might regulate population dynamics and species interactions. From the competition matrices I managed to solve the inverse problem of building the corresponding one-dimensional niche space or niche axis. No assumption on the shape of the resource utilization function, e.g. Gaussian (May 1974), or on the niche variable, e.g. food size (May 1974), was made. Rather the niche axis was constructed by regarding each element of the competition matrix as the overlap of the corresponding pair of pollinator species and then grouping together all the species with large overlaps. The lumpy distribution of species along the niche axis  $x$  together with the multimodality of the Preston histograms, provide strong support to the theory of 'emergent neutrality' (EN) (Vergnon et al. 2012). The theory of EN predicts a competition-driven, self-organized evolutionary emergence of groups of similar species, with clusters where they coexist in essentially the same niche, bridging a link between niche (MacArthur and Levins 1967) and neutral theory (Hubbell 2001). Furthermore, in all the 36 niche axis the same pattern was observed: the abundant pollinator species at the lumps include a large proportion of generalist pollinators with high  $D_a$  while the gaps between them correspond mainly to specialists with low  $D_a$ . This rule of 'lumps of generalist pollinators and specialists at the gaps', can be explained because as generalist pollinators have wider niches, the niche overlap between them tends to be large. It provides further insight into how those groups of ecologically similar species self-organize into niches and are similar in several biological traits including their abundance.

The application of quantitative community ecology to emerging problems in human dominated ecosystems could provide insights to solve important issues concerning the management of natural, altered, or reconstructed plant–pollinator communities. Many attempts to manage wild populations, whether introduced or natural, ignored the many possible interactions of those populations with other species that might play crucial a role for preserving the entire community (Morin 2011). Particular applications of our analysis could be to estimate the quantitative effects of removing a species from a community or to address the fate of populations of native organisms when foreign species are introduced to ecosystems far beyond their home range. The devastating impacts that some invading organisms have caused on native ecosystems (Goulson 2003) should deserve first a careful analysis of the pros and cons of allowing release of alien species. Indeed restoration ecology is an important new field that might benefit from quantitative predictive tools for community ecology, to establish and accelerate the development of communities in degraded or altered ecosystems (Montalvo et al. 1997, Palmer et al. 1997).

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Supplementary material (available online as Appendix oik. 01539 at <[oikosjournal.org/readers/appendix](http://oikosjournal.org/readers/appendix)>). Appendix 1.