

## LETTER

## Spatial mating networks in insect-pollinated plants

Miguel A. Fortuna,<sup>1\*</sup> Cristina García,<sup>1</sup> Paulo R. Guimarães Jr.<sup>1,2</sup> and Jordi Bascompte<sup>1</sup>

<sup>1</sup>Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain

<sup>2</sup>Departamento de Física da Matéria Condensada, Instituto de Física Gleb Wataghin, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970 Campinas, São Paulo, Brazil

\*Correspondence: E-mail: fortuna@ebd.csic.es

## Abstract

Gene flow in plant populations is largely determined by landscape heterogeneity. Both the shape of the pollination kernel and the spatial distribution of trees affect the distribution of pollen grains and the genotypes they harbour, but little is known about the relative contribution of each of these two factors. Using genetic markers we build a spatial network of pollination events between any two trees in a population of *Prunus mahaleb*, an insect-pollinated plant. Then, we apply tools from the science of complex networks to characterize the structure of such a mating network. Although the distribution of the number of pollen donors per tree is quite homogeneous, the identity of donors is distributed heterogeneously across the population. This results in a population structured in well-defined modules or compartments, formed by a group of mother trees and their shared pollen donors. Long-distance pollination events decrease the modular structure by favouring mating among all available mates. This increases gene flow across the entire population, reducing its genetic structure, and potentially decreasing the role of genetic drift.

## Keywords

Complex networks, dispersal kernel, gene flow, mating system, pollination, *Prunus mahaleb*, spatial networks.

*Ecology Letters* (2008) 11: 490–498

## INTRODUCTION

Pollen dispersal is a key demographic process with relevant ecological and genetic consequences for plant populations (Barrett & Harder 1996). Pollen movement determines mating patterns (i.e. who mates whom) and the extent of gene flow within and among populations (Sork *et al.* 1999; Liepelt *et al.* 2002). Molecular markers have shown a non-random spatial assortment of mating events among conspecifics mediated by pollinators (Gérard *et al.* 2006). As a consequence, pollen donors do not distribute their pollen evenly among mother trees, but rather among a non-random subset of available mother trees. Recent literature documents the strong interaction between the dispersal mode and the spatial arrangement of the adult trees in determining these non-random mating patterns (Meagher & Vassiliadis 2003). One remaining issue lies on elucidating the structure of such heterogeneous mating patterns and its consequences to gene flow within populations. This has been elusive because we were missing appropriate tools to address the structure of complex spatial patterns. Here we use the framework of complex networks (Urban & Keitt 2001; Proulx *et al.* 2005;

Fortuna *et al.* 2006; May 2006; Bascompte 2007) to quantify the level of heterogeneity of spatial mating patterns, and to explore how such a structure varies with the shape of the dispersal kernel and the spatial distribution of parent trees.

The interplay between the overall distances reached by dispersed propagules (i.e. the dispersal kernel) and the arrangement of the adult trees determines the distribution of the genetic diversity among isolated populations (Sork *et al.* 1999; Liepelt *et al.* 2002). At the population level, the bulk of pollen dispersal events reach short distances from the source tree, and thus, maternal pollen pools tend to be dominated by nearby trees or by selfing events in autocompatible species (Robledo-Arnuncio *et al.* 2004; García *et al.* 2005). Furthermore, the genetic composition of the pollen pool is dramatically influenced by the shape of the tail of the dispersal kernel (Klein *et al.* 2006).

Here we analyse the interplay between the movement of pollinators and the spatial distribution of trees within a population in determining the structure of the spatial mating network of a *Prunus mahaleb* isolated population pollinated by insects. First, we used a previous data set based on highly polymorphic DNA markers that allowed the identification

of all adult trees in the population and the tracking of pollen dispersal events (Godoy & Jordano 2001; García *et al.* 2007). This information was used to build the spatial mating network. This network represents adult trees as nodes and mating events as links among interacting nodes (siring trees and mother trees). This simplified description of the system allows us to establish a powerful framework to study the relationship between the structure of the mating network and the processes occurring in such a network (Urban & Keitt 2001; Dyer & Nason 2004; Proulx *et al.* 2005; Fortuna *et al.* 2006; May 2006; Bascompte 2007). Second, once the mating network is built, we characterized its structure using both the frequency distribution of the number of links per tree and modularity analysis, i.e. a description of non-random mating associations among groups of trees. Third, using simulated spatial scenarios and a thin-tailed version of the pollination kernel, we investigate to what extent the spatial distribution of the trees in the population interacts with the form of the pollen dispersal kernel to shape the structure of the spatial mating network.

## MATERIALS AND METHODS

### Building the mating network

#### *Study site and species characteristics*

We focus on *P. mabaleb*, a gynodioecious species, i.e. populations are composed by hermaphrodite and female individual trees. The study population consists of 131 hermaphrodite and 64 female trees with most trees patchily distributed and some individuals isolated from patches. It is located in Nava de las Correhuellas (Parque Natural de las Sierras de Cazorla, Segura y las Villas, Jaen province, Southeastern Spain), at an elevation of 1615 m. The site is dominated by grasslands with scattered patches of deciduous vegetation, gravelly soil or rock outcrops covered with shrubs or small isolated trees. The rocky slopes are dominated by open pine forest (*Pinus nigra* ssp. *salzmannii*). Populations of *P. mabaleb* are found in this region as small, isolated patches of trees, frequently with < 100 trees. The nearest *P. mabaleb* population to our isolated study population is located at 1.5 km.

This species flowers between mid-May and mid-June at high elevations (over 1300 m), and is pollinated by insects, mainly bees (Hymenoptera: Andrenidae, Apidae) and flies (Diptera: Calliphoridae, Syrphidae) (see Jordano 1993 for a more detailed description).

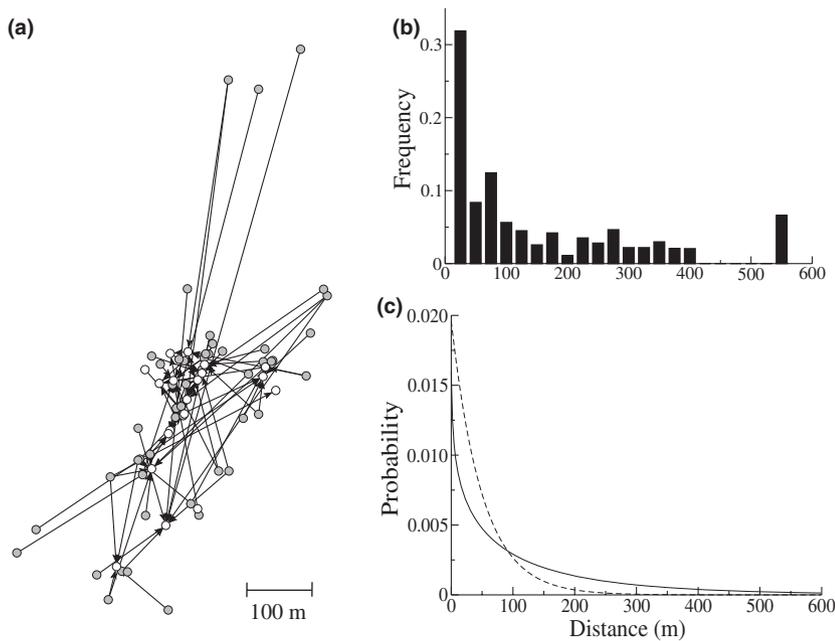
#### *Sampling design and paternity analysis*

In a previous study, García *et al.* (2005) randomly selected 20 mother trees stratified by gender type (hermaphrodite and female mother trees) and local density (high and low density of conspecifics). Ten fruits per mother tree were

collected from the canopy and the embryo of each fruit was genotyped for 10 microsatellite loci. Paternity analysis was used to assign the most likely father to each mother-offspring pair on the basis of the multilocus genotypes of the mother, the embryo, and all the candidate fathers. A single most likely father was assigned to 99 embryos with a confidence level of 95%. For the remainder embryos, more than one most likely father was found for 58 embryos, no compatible father was found for 13 embryos (implying that the pollen donor was located outside the population), 3 embryos were discarded due to amplification failures for several markers, and 27 embryos were a consequence of selfing. Unassigned seeds reduced our sample size. However, we do not expect that this reduction will affect the shape of intrapopulation dispersal kernel because unassigned seeds may be a random sample of all the seeds analysed. Based on the identity and location of the mating trees, we obtained the frequency distribution of pollen dispersal distances (pollen dispersal kernel, Fig. 1). In this study, we focus exclusively in inter-individual pollination events. Subsequently, the spatial mating network of the studied population was built based on this pollen dispersal kernel.

#### *Design of the spatial mating networks*

We generated spatial mating networks following a factorial design among two pollen dispersal kernels and different spatial scenarios. Hermaphrodite trees have perfect flowers, with functional male and female roles. Female trees have male-sterile flowers and thus have only a female function. Thus, for each pair of nodes hermaphrodite–female and hermaphrodite–hermaphrodite we calculated the distance among them, and a probability of mating (occurrence of a pollination event) was assigned as a function of the dispersal kernel (we used both the observed dispersal kernel with fat tails and an alternative kernel with thin tails; see next section). If that probability was higher than a uniformly distributed random number between 0 and 1, we created a link between both nodes. This procedure was repeated for all these pairs of nodes 20 times to ensure that each node had at least one link. In such a way, the number of links (pollination events) per node (tree), i.e. its degree, was > 0. We have repeated the same number of potential pollination events to generate the networks using both types of pollen dispersal kernels (fat-tailed and thin-tailed) for all spatial scenarios (real, clumped, exponential-density gradient, random and uniform). The different shape of the kernels will be translated in a different density of links. If the same number of links was kept fixed for both kernels (the same network connectance), we would be masking a biological difference between kernels by eliminating the effect of therein different probabilities of pollination as a function of distance for both pollen dispersal kernels. The



**Figure 1** (a) Subnetwork of the *Prunus mahaleb* population representing the fraction of sampled offspring assigned to a putative donor tree ( $n = 99$ ). Gray nodes represent donor trees (hermaphrodites) and white nodes represent mother trees (hermaphrodites and females). Arrows indicate observed pollination events (from donor to mother trees) mediated by insects. (b) The relative frequency of pollen dispersal distances corrected by the heterogeneous spatial distribution of the population. (c) The two pollen dispersal kernels considered here. The continuous line represents data fitted to a Weibull probability density function (scale parameter  $\alpha = 125.7$  and shape parameter  $\beta = 0.821$ ). The dashed line represents an exponential probability density function ( $\beta = 50$ ).

network structure will change as a consequence of the shape of the pollen dispersal kernels. Increasing the number of potential pollination events could lead to a fully-connected network in which all mother trees could be pollinated by all donor trees in the population. For each combination of factors (dispersal kernel and spatial scenario), we built 1000 replicates. Although selfing events may have relevant consequences for pollination dynamics in *P. mahaleb*, here we focus in interindividual interactions and therefore our networks show no link connecting an individual to itself.

#### Fitting the pollen dispersal kernel

In the studied population, the probability of a mother tree being pollinated by a nearby father is higher than expected based just on the distance because the number of potential fathers in the vicinity is higher than far away. Hence, the observed distribution of the pollen dispersal distances is not independent of the population spatial distribution. This heterogeneous spatial configuration must be taken into account before fitting the pollen dispersal kernel to the data.

By setting circular bands at constant distances from the mother trees and calculating the ratio between the number of total potential and realized father trees within them, we removed the effect of the spatial heterogeneity on pollen dispersal. We chose bands of 25 m from each mother tree. We considered the resulting intervals (from 25 to 550 m) small enough to capture the spatial heterogeneity in the distribution of the subset of trees. The relative frequency of

these rates for each distance band (see Fig. 1b) was used to obtain randomly 1000 dispersal distance values according to its frequency on each of them. We fitted a Weibull distribution to these values because its very flexible shape allows us to take into account the observed few long-distance dispersal events (see Fig. 1c). The Weibull probability density function is described by:

$$y = \left(\frac{\beta}{\alpha}\right) \left(\frac{x}{\alpha}\right)^{\beta-1} e^{-(x/\alpha)^\beta}$$

where  $\alpha$  is the scale parameter and  $\beta$  is the shape (or slope) parameter. This is the observed, fat-tailed pollination kernel.

#### Measures of network topology

##### Connectance

One of the simplest measures of network structure is connectance ( $C$ ) defined as the ratio of the number of realized links to the number of possible links. In our case, connectance is defined as:

$$C = \frac{p}{b(b-1)/2 + bf}$$

where  $p$  is the realized number of links,  $b$  is the number of hermaphrodite trees and  $f$  is the number of female trees. In the context of the pollination mating network, connectance should be interpreted as the probability of interaction between two randomly selected individuals.

### Modularity analysis

There are several algorithms to detect modules (also known as communities) in networks (see Newman & Girvan 2004; Guimerà & Amaral 2005; Newman 2006; Rosvall & Bergstrom 2007). In this study we used the Guimerà & Amaral's (2005) algorithm based on simulated annealing (Kirkpatrick *et al.* 1983). Basically, the program uses a heuristic procedure to find an optimal solution (i.e. the maximization of a function called modularity) when the number of combinatorial states is intractable. The simulated annealing method uses the physical concept of temperature to indicate to what extent the state of the system is close to the optimal solution. The modularity function  $M$  determines the tendency of the network to be organized in well-defined, disjoint modules. The higher  $M$ , the higher the density of links inside each module as compared to the expectation based on the total density of links. The modularity is given by (Newman & Girvan 2004):

$$M = \sum_{s=1}^{N_M} \left[ \frac{l_s}{L} - \left( \frac{d_s}{2L} \right)^2 \right],$$

where  $N_M$  is the number of modules,  $L$  is the number of links in the network,  $l_s$  is the number of links between nodes in module  $s$  and  $d_s$  is the sum of the degrees of the nodes in module  $s$ . We analysed 100 replicates for each spatial scenario, allowing us to estimate the confidence interval for the level of modularity. The significance of modularity is established by comparing the observed  $M$  value with the values for 100 randomizations of the network keeping the same connectance (see Guimerà & Amaral 2005). Networks created with the two dispersal kernels have a different connectance. To control for this difference when comparing the modularity, we calculated the relative modularity defined as:

$$M^* = \frac{M_{\text{real}} - \bar{M}_{\text{random}}}{\bar{M}_{\text{random}}}$$

Once we have detected a significant modular organization, we want to look at how many distinct modules are there, and how are they distributed in space. This algorithm also provides these distinct modules.

The Wilcoxon rank sum test was used for comparing the relative modularity between different dispersal kernels from the same spatial scenario, and each scenario with random networks.

### Spatial distribution and shape of the dispersal kernel

In order to explore the role of the spatial distribution of the tree population on the relevance of the dispersal kernel, we created some alternative spatial scenarios: clumped (Fig. 3a,e), exponential-density gradient (Fig. 3b,f), random

(Fig. 3c,g) and uniform (Fig. 3d,h). We built these spatial configurations by distributing randomly the same number of female and hermaphrodite trees as in the real population inside the area delimited by the real population. For the clumped and the exponential-density gradient distributions, we have used the centre of the study area as a fixed point from which we have randomly distributed the trees as a function of a beta and exponential probability density functions, respectively.

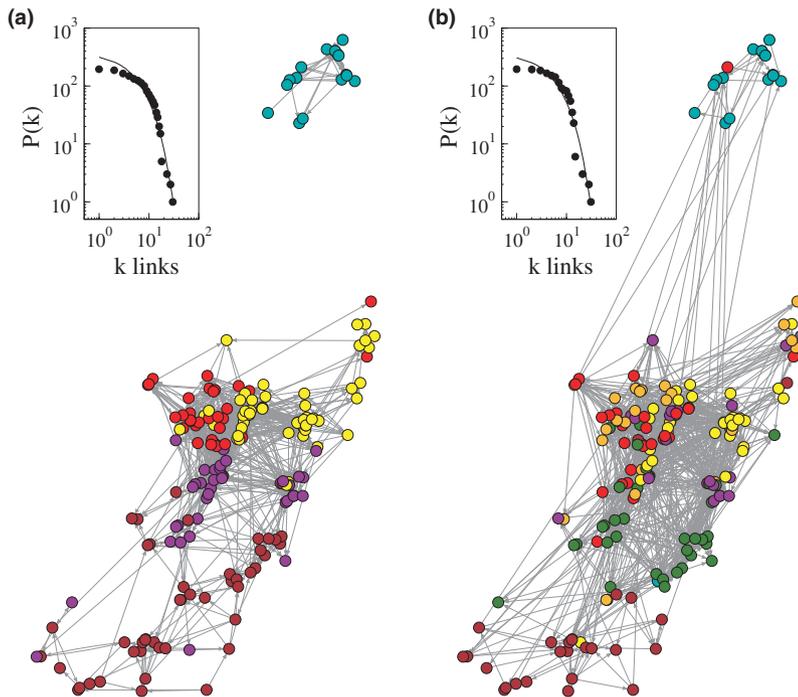
Our aim is not to obtain a precise fit of our data to the most appropriate pollen dispersal kernel (see Austerlitz & Smouse 2001), but to compare the effect of the observed fat-tailed kernel in relation to a thin-tailed one. For this reason, we compared the fitted dispersal kernel to an exponential one (thin-tailed dispersal kernel) with a scale parameter  $\beta = 50$  (Fig. 1c). The exponential probability density function is given by:

$$y = \frac{1}{\beta} e^{(-x/\beta)}$$

### RESULTS

Figure 1a represents the observed subnetwork of mating events in our population. From this network we obtained the relative frequency of pollen dispersal distances corrected by the non-homogeneous spatial distribution of trees (Fig. 1b). We find the best fit to this observed distance frequency distribution (Fig. 1c). This constitutes the observed pollination kernel that is used to build replicates of the entire network ( $\alpha = 125.696$  and  $\beta = 0.821$ ; slope and shape parameters, respectively, of the fit to a Weibull distribution). We used an artificial thin-tailed exponential kernel with a scale parameter  $\beta = 50$ . Comparing networks built from the two dispersal kernels will allow us to characterize the effect of long-distance pollination events on structuring the mating network. Not surprisingly, the fat-tailed dispersal kernel allows the existence of a higher number of mating events than the thin-tailed kernel. This fact leads to a significantly higher connectance ( $P < 0.001$ ) when creating networks using the Weibull pollen dispersal kernel ( $C = 0.062 \pm 0.001$ , from 1000 replicates) than when using the exponential one ( $C = 0.057 \pm 0.001$ , from 1000 replicates).

Once we have built the mating networks by using two distinct dispersal kernels, let us now characterize their structure. If we look at the distribution of the number of links per mother tree, that is, how many donor trees can pollinate a particular mother tree, we see no differences in the shape of the distribution for the two types of dispersal kernels. Insets on Fig. 2 show the exponential fitting to the cumulative degree distribution ( $P < 0.001$  for both the Weibull and exponential kernels). This result indicates that



**Figure 2** Modular organization of the spatial mating network of the *Prunus mabaleb* population. Nodes ( $n = 195$ ) represent trees (hermaphrodites and females) and lines indicate pollination events mediated by insects. Each colour represents a module, i.e. a group of non-overlapping highly connected trees, detected by the algorithm. (a) Network created using the exponential dispersal kernel. In this case the algorithm detects seven modules. (b) One replicate of the networks created using the Weibull dispersal kernel. In this case the algorithm detects five modules. Insets show the cumulative degree distribution of the mother trees using the exponential (a) and the Weibull dispersal kernel (b).

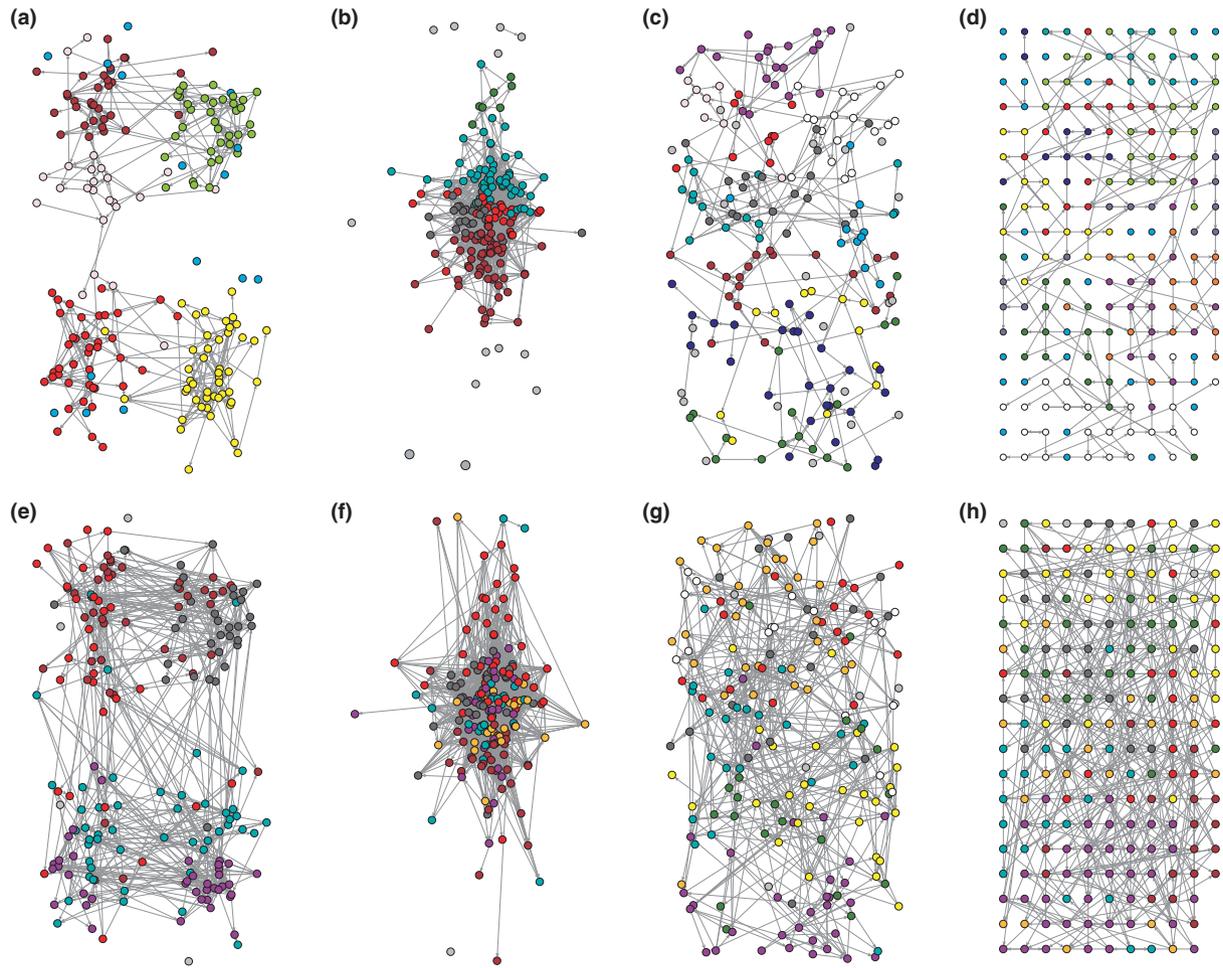
the mating network is quite homogeneous: the bulk of trees have a similar number of donor trees. However, if we look at a deeper level of structure, focusing now on the identity of the donor trees that pollinate a given mother tree, results are quite different. The modularity analysis reveals a significant value of modularity in our population, that is, a significant tendency of the network to be organized in well-defined, disjoint modules. The mean modularity and standard deviation for randomizations is  $M = 0.293 \pm 0.003$  and  $M = 0.298 \pm 0.002$  for the observed fat-tailed and the exponential dispersal kernels, respectively. This is the modular structure of the null model corresponding to each pollen dispersal kernel. The values of modularity for the fitted dispersal kernels are  $M = 0.382 \pm 0.01$  and  $M = 0.321 \pm 0.01$  (for thin-tailed and fat-tailed pollen dispersal kernels, respectively). Networks created using the observed fat-tailed pollen dispersal kernel are significantly more modular than expected by chance ( $P < 0.001$ ). This means that mother trees do not sample pollen randomly from the donor trees in the population, but that there is a tendency for groups of mother trees to receive pollen from the same donors.

Having characterized the modular organization of the mating network, we next consider how long-distance pollination events contribute to such modularity. Modularity is significantly lower ( $P < 0.001$ ) when using the fat-tailed pollination kernel than when using the thin-tailed kernel. This means that the observed long-distance pollination events reduce the modular structure of the mating network

in our population. The reduction is even higher when we take into account the different values of connectance for networks created using both types of kernels. The relative modularity for networks created using the observed fat-tailed pollen dispersal kernel is much lower ( $M^* = 0.095$ ) than that resulting from create networks using the thin-tailed one ( $M^* = 0.281$ ).

Let us turn now to the identification of the different modules that create the overall modular structure noted above. The modularity analysis detects several distinct compartments formed by a group of mother trees and their shared pollen donors. The number of modules is  $6.9 \pm 0.658$  (mean and standard deviation; Fig. 2b) when the networks are created using the observed, fat-tailed pollen dispersal kernel. The number of modules is significantly reduced to  $5.1 \pm 0.551$  ( $P < 0.001$ ; Fig. 2a) when using the exponential thin-tailed pollination kernel. Thus, long-distance pollen dispersal events seem to contribute not only to create a larger number of compartments, but also to an increase on pollen flow among them by reducing modularity, as we have shown above (see Fig. 2).

Regarding the effect of the spatial distribution of trees, different results are obtained when we distribute the same number of trees but in different spatial configurations (see Fig. 3), and use again the two pollen dispersal kernels. The number of links created is significantly higher for the Weibull dispersal kernel (Fig. 3e–h) than for the exponential one (Fig. 3a–d) for all spatial scenarios ( $P < 0.001$  for



**Figure 3** Different simulated tree spatial distributions. Nodes ( $n = 195$ ) represent trees and lines indicate simulated pollination events mediated by insects. Each colour represents a module, i.e. a group of non-overlapping, highly connected trees, detected by the algorithm. Spatial distributions are clumped (a, e), exponential (b, f), random (c, g) and uniform (d, h). Networks were created using the exponential (a–d) and Weibull (e–h) dispersal kernels.

connectance). In relation to modularity analysis, there are three main results. First, all simulated spatial scenarios show a higher significant modular structure than expected by chance ( $P < 0.001$  in all cases). The values of modularity for randomizations are  $M = 0.441 \pm 0.004$ ,  $M = 0.438 \pm 0.008$ ,  $M = 0.225 \pm 0.004$  and  $M = 0.409 \pm 0.004$  for networks created using the Weibull pollen dispersal kernel and under random, uniform, exponential and clumped spatial scenarios, respectively. For networks created using the exponential kernel, the values of modularity are  $M = 0.608 \pm 0.010$ ,  $M = 0.628 \pm 0.011$ ,  $M = 0.224 \pm 0.004$  and  $M = 0.473 \pm 0.005$ , under random, uniform, exponential and clumped spatial scenarios, respectively. Second, all these modular spatial distributions but the exponential ( $M = 0.291 \pm 0.008$  and  $M = 0.235 \pm 0.003$  for the Weibull and the exponential kernels) lead to similar

modularity for both dispersal kernels ( $M = 0.459 \pm 0.007$ ,  $M = 0.474 \pm 0.009$ ,  $M = 0.471 \pm 0.012$  and  $M = 0.661 \pm 0.012$ ,  $M = 0.711 \pm 0.008$ ,  $M = 0.685 \pm 0.010$ , respectively). Note that the real spatial distribution leads to intermediate values of modularity, in-between no modular (as in the exponential spatial distribution) and the highly structured patterns observed in the other simulated spatial scenarios. Third, Weibull pollen dispersal kernels lead to a significantly lower average modularity than exponential pollination kernels within the same spatial distribution ( $P < 0.001$  in all cases).

The number of modules detected by the algorithm in the simulations depends on the spatial scenario considered (Fig. 3). For aggregated spatial distributions (exponential and clumped), the number of modules is significantly lower ( $P < 0.01$ ) or similar ( $P = 0.744$ ), respectively, when using

the exponential kernel (Fig. 3b,  $4.5 \pm 0.612$ ; Fig. 3a,  $5.1 \pm 0.398$ ) than when using the fat-tailed one (Fig. 3f,  $5.8 \pm 0.491$ ; Fig. 3e,  $5.2 \pm 0.683$ ). On the contrary, for the other spatial scenarios (random and uniform) the number of modules is significantly higher ( $P < 0.05$  and  $P < 0.001$ ) when creating networks using the thin-tailed pollen dispersal kernel (Fig. 3c,  $8.7 \pm 0.913$ ; Fig. 3d,  $9.2 \pm 0.755$ ) than when using the fat-tailed one (Fig. 3g,  $7.5 \pm 0.541$ ; Fig. 3h,  $6.7 \pm 0.811$ ).

## DISCUSSION

This study aimed at exploring intrapopulation mating patterns resulting from non-random pollen dispersal movement in spatially structured plant populations. We built the spatial mating network based on direct tracking of pollen dispersal events that provide the composition of the maternal pollen clouds. Then, we characterized the structure of the mating network and quantified its dependence on the pollen dispersal kernel and the spatial distribution of trees. We found that the non-random pollen dispersal patterns resulted in a compartmentalized mating network structured in modules. Each one of these modules is formed by a group of mother trees and their shared pollen donors. More specifically, the modular organization of the mating networks was mainly determined by the spatial distribution of the adult trees. Changes in this modular organization varied when applying different dispersal kernels in distinctive spatial scenarios. Previous studies analytically showed pervasive effects of the interaction between spatial arrangement of the adult trees and the shape of the dispersal kernel in determining the genetic diversity of the propagules reaching a distant point in the population (Klein *et al.* 2006). Our work extends the influence of this interaction in generating a spatial assortment of the mating events resulting in a significant modular structure of the mating networks in plant populations.

The shape of the dispersal kernel is recognized to determine to what extent pollen flows among populations or patches (Sork *et al.* 1999; Austerlitz *et al.* 2004). However, fat-tailed kernels also affect gene movement within populations. The connectivity of the mating network increased 10% when long distance dispersal was allowed by incorporating isolated trees. An increase in the connectivity of the network involves that new genotypes are available to be dispersed as seeds. This potentially leads to a higher genetic diversity in the population. Long distant pollen dispersal events have been largely recognized to prevent genetic isolation and counterbalance genetic drift by connecting distant populations (Sork *et al.* 1999; Liepelt *et al.* 2002). Our results, additionally, show that fat-tailed kernels decrease the modularity of the mating network by favouring mating

among all available mates. This increases gene flow across the entire population, reducing its genetic structure, and potentially decreasing the role of genetic drift.

Furthermore, our results show that the interaction between the spatial distribution of trees and the shape of the dispersal kernel is complex. When the plant population is highly aggregated following an exponential density gradient, mother trees receive a similar combination of pollen genotypes, as indicated by the low modularity values (i.e. close to a panmictic situation). Thus, this large central core works as a large genetic neighbourhood where the pollen pools of the maternal trees overlap. As trees tended to spread over the landscape occupying a larger area (as in the clumped, random and uniform distribution) modularity increased involving a significant genetic structure among pollen clouds. The intermediate values yielded by the actual distribution of adult trees suggest that natural populations, in fact, present a mixed distribution with high levels of aggregation (as in the simulated exponential distribution) and scattered trees occupying the whole population area. Modular structure, additionally, offers us a visual picture of the groups of mother trees sharing pollen donors. The spatial distribution of modules resembled the spatial aggregation of the trees for clumped distributions, whereas non-aggregated distributions did not strongly retain the spatial distribution of the adult trees, especially for fat-tailed kernels.

Compared to previous statistical methods, our network approach provides a powerful tool to study intrapopulation mating patterns in plant populations. For example, classical genetic/demographic parameters such as  $N_{ep}$  (effective number of pollen donors) ignores the identity of such pollen donors and their spatial location. Similarly, paternity analyses identify pairwise, mother–father interactions, but do not allow to scale-up the entire mating network. Our network approach quantifies the spatial structure of the overall set of mating events taking into account not only mother–father interactions, but also the resemblance among maternal pollen clouds. Additionally, it yields a straightforward visualization of the mating network and a meaningful statistical evaluation of the factors shaping such a network.

Complex networks are a powerful tool to characterize heterogeneity in a wide range of systems that can be described as a collection of nodes connected by links (Albert *et al.* 2000; Liljeros *et al.* 2001; Newman 2001; Proulx *et al.* 2005). Spatial networks have been recently used to describe dispersal in heterogeneous environments and robustness to patch removal (Urban & Keitt 2001; Fortuna *et al.* 2006; Campbell Grant *et al.* 2007; Schick & Lindley 2007). Here we use spatial networks to quantify the amount of spatial heterogeneity in mating traits. We have reported a pattern of assortative mating, where

certain mother trees share pollen donors. This network structure might set the first genetic template on top of which the adult spatial genetic structure would emerge. This would contribute to explain why most plant populations show higher levels of genetic structure and diversity within populations than among populations (Hamrick *et al.* 1993; Epperson 2003). As for example, the study population of *P. mabaleb* presents a fine-scale spatial genetic structure (reaching 30 m, Jordano & Godoy 2002). This is congruent with the seed dispersal pattern observed with the bulk of dispersal events occurring within this distance from the mother tree (Godoy & Jordano 2001; García *et al.* 2005). However, the genetic composition of the dispersed seeds is set during the mating stage, where most maternal trees sharing pollen donors are located within this distance. Thus, regardless of the pollen dispersal distances (up to 548 m for this *P. mabaleb* population) the modular arrangement of the maternal pollen clouds promotes the emergence of a fine genetic structure in the population as the pool of dispersed seeds from a module tend to be half-sibs or genetically closely related. The evolutionary consequences of these mating patterns are potentially pervasive. For example, these high levels of spatial structure would favour local selection in response to local changes in plant resources, This would provide chances for local variation and adaptation (Savolainen *et al.* 2007). However, the long-term consequences of the spatially compartmentalized mating networks would finally depend on whether postdispersal processes enhance or erase this genetic signal first originated through non-random pollen dispersal patterns in spatially structured populations.

#### ACKNOWLEDGEMENTS

Roger Guimerà kindly sent us the algorithm to detect modules. We thank P. Jordano, O. Ovaskainen, I. Hanski, and E. L. Rezende for helpful discussions, and J. M. Arroyo and J. A. Godoy for their work in the lab. P. Guimarães helped in preliminary modularity analysis. Previous work on the molecular markers was funded by Grants REN-2003-00273 and CGL2006-00373 from the Spanish Ministry of Education and Science. During this work M.A.F. was funded by the Spanish Ministry of Education and Science (Fellowship BES-2004-6682). C.G. was supported by the Spanish Ministry of Education and Science (Fellowship FP-2002-5627) and ConGen Exchange (Grant-1377) funded by the European Science Foundation. P.R.G. was supported by FAPESP. This work was also funded by the European Heads of Research Councils, the European Science Foundation and EC Sixth Framework Programme through a EURYI (European Young Investigator) Award (to J.B.).

#### REFERENCES

- Albert, R., Barabási, A.-L. & Jeong, H. (2000). Error and attack tolerance in complex networks. *Nature*, 406, 378–382.
- Austerlitz, F. & Smouse, P.E. (2001). Two-generation analysis of pollen flow across a landscape. II. Relation between  $\Phi_i(f)$ , pollen dispersal and interfemale distance. *Genetics*, 157, 851–857.
- Austerlitz, F., Dick, C.W., Dutech, C., Klein, E.K., Oddou-Muratario, S., Smouse, P.E. *et al.* (2004). Using genetic markers to estimate the pollen dispersal curve. *Mol. Ecol.*, 13, 937–954.
- Barrett, S.C.H. & Harder, L.D. (1996). Ecology and evolution of plant mating. *Trends Ecol. Evol.*, 11, A73–A79.
- Bascompte, J. (2007). Networks in ecology. *Basic Appl. Ecol.*, 8, 485–490.
- Campbell Grant, E.H., Lowe, W.H. & Fagan, W.F. (2007). Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecol. Lett.*, 10, 165–175.
- Dyer, R.J. & Nason, J. (2004). Population graphs: the graph theoretic shape of genetic structure. *Mol. Ecol.*, 13, 1713–1727.
- Epperson, B.K. (2003). *Geographical Genetics*. Princeton University Press, Princeton.
- Fortuna, M.A., Gómez-Rodríguez, C. & Bascompte, J. (2006). Spatial network structure and amphibian persistence in stochastic environments. *Proc. R. Soc. Lond. B*, 273, 1429–1434.
- García, C., Arroyo, J.M., Godoy, J.A. & Jordano, P. (2005). Mating patterns, pollen dispersal, and the ecological maternal neighbourhood in a *Prunus mabaleb* population. *Mol. Ecol.*, 14, 1821–1830.
- García, C., Jordano, P. & Godoy, J.A. (2007). Contemporary pollen and seed dispersal patterns and the spatial genetic structure in a *Prunus mabaleb* population. *Mol. Ecol.*, 16, 1947–1955.
- Gérard P.R., Klein, E.K., Austerlitz, F., Fernández-Manjarrés, J.F., Frascaria-Lacoste, N. (2006). Assortative mating and differential male mating success in an ash hybrid zone population. *BMC Evol. Biol.*, 6, 96.
- Godoy, J.A. & Jordano, P. (2001). Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Mol. Ecol.*, 10, 2275–2283.
- Guimerà, R. & Amaral, L.A.N. (2005). Functional cartography of complex metabolic networks. *Nature*, 433, 895–900.
- Hamrick, J.L., Murawski, D.A. & Nason, J.D. (1993). The influence of seed dispersal mechanisms on the genetic structure of tropical tree populations. *Vegetatio*, 107/108, 281–297.
- Jordano, P. (1993). Pollination biology of *Prunus mabaleb* deferred consequences of gender variation for fecundity and seed size. *Biol. J. Linnean Soc.*, 50, 65–84.
- Jordano, P. & Godoy, J.A. (2002). Frugivore-generated seed shadows: a landscape view of the demographic and genetic effects. In: *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation* (eds Levey, D.J., Silva, W.R. & Galetti, M.). CABI Publishing, Wallingford, UK, pp. 305–321.
- Kirkpatrick, S., Gelatt, C.D., Jr & Vecchi, M.P. (1983). Optimization by simulated annealing. *Science*, 220, 671–680.
- Klein, E.K., Lavinge, C. & Gouyan, P.-H. (2006). Mixing of propagules from discrete sources at long distances: comparing a dispersal tail to an exponential. *BMC Ecol.*, 6, 3.
- Liepelt, S., Bialozyt, R. & Ziegenhagen, B. (2002). Wind-dispersed pollen mediates postglacial gene flow among refugia. *Proc. Natl. Acad. Sci. USA*, 99, 14590–14594.

- Liljeros, F., Edling, C.R., Amaral, L.A.N., Stanley, H.E. & Aberg, Y. (2001). The web of human sexual contacts. *Nature*, 411, 907–908.
- May, R.M. (2006). Network structure and the biology of populations. *Trends Ecol. Evol.*, 21, 394–399.
- Meagher, T.R. & Vassiliadis, C. (2003). Spatial geometry determines gene flow in plant populations. In: *Genes in Environment: 15th Special Symposium of the British Ecological Society* (eds Hails, R., Beringer, J. & Godfray, H.C.). British Ecological Society, London, pp. 76–90.
- Newman, M.E.J. (2001). The structure of scientific collaboration networks. *Proc. Natl. Acad. Sci. USA*, 98, 404–409.
- Newman, M.E.J. (2006). Modularity and community structure in networks. *Proc. Natl. Acad. Sci. USA*, 113, 8577–8582.
- Newman, M.E.J. & Girvan, M. (2004). Finding and evaluating community structure in networks. *Phys. Rev. E*, 69, 026113.
- Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). Network thinking in ecology and evolution. *Trends Ecol. Evol.*, 20, 345–353.
- Robledo-Arnuncio, J.J., Alia, R. & Gil, L. (2004). Increased selfing and correlated paternity in a small population of a predominantly outcrossing conifer, *Pinus sylvestris*. *Mol. Ecol.*, 13, 2567–2577.
- Rosvall, M. & Bergstrom, C.T. (2007). An information-theoretic framework for resolving community structure in complex networks. *Proc. Natl. Acad. Sci. USA*, 104, 7327–7331.
- Savolainen, O., Pyhäjärvi, T. & Knürr, T. (2007). Gene flow and local adaptation in trees. *Ann. Rev. Ecol. Syst.*, 38, 595–619.
- Schick, R.S. & Lindley, S. (2007). Directed connectivity among fish populations in a riverine network. *J. Appl. Ecol.*, 44, 1116–1126.
- Sork, V.L., Nason, J., Campbell, D.R. & Fernandez, J.F. (1999). Landscape approaches to historical and contemporary gene flow in plants. *Trends Ecol. Evol.*, 14, 219–224.
- Urban, D. & Keitt, T. (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology*, 82, 1205–1218.

Editor, Jonathan Chase

Manuscript received 10 December 2007

First decision made 11 January 2008

Manuscript accepted 21 January 2008