Positive interactions support the formation of complex spatial networks

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Abstract

Ecosystems are structured by networks of interactions among species, but this hypothesis has rarely been tested in plant communities. Indeed, the structure and functioning of plant interaction networks have remained elusive so far and the mechanisms underlying their origin and maintenance remain unknown. By developing a novel approach that integrates the ecology of plant interactions with network theory and using spatial pattern analysis, we show that plant communities are organised in spatially variable and complex networks. Specifically, we found that positive plant interactions promote the formation and the cohesiveness of large networks. At small spatial scale, where positive mutual interactions prevailed, the network was characterised by a large connected component. With increasing scale, when negative interactions took over, network structure became more hierarchical with many detached components. These findings shade new light on the complex networks of interactions occurring in plant communities.

INTRODUCTION

The nature of biodiversity continues to intrigue biologists because of the complexity of interactions among species in ecosystems. Due to this complexity, success to build a unified theory of biodiversity has been poor (McGill, 2010). Standard ecological theory assumes as a central pillar that negative interactions between species (e.g. competition) are essential to promote stable species coexistence (Tilman, 1994; Chesson, 2000; Allesina & Levine, 2011; Kraft *et al.*, 2014). More recently, the re-discovery of positive interactions emphasised the importance of mutualism and facilitation for biodiversity maintenance and ecosystem stability (Bruno *et al.*, 2003; Verdú & Valiente-Banuet, 2008; Bastolla *et al.*, 2009; Schöb *et al.*, 2012; Cavieres *et al.*, 2014; Isbell *et al.*, 2015).

The study of networks of mutualistic interactions among plants and animals has increased our understanding of ecological and evolutionary processes shaping communities and ecosystems (Bascompte & Jordano, 2014). However, research on plant interactions has historically focused on unidirectional interactions between two species at a time (Mayfield & Stouffer, 2017). This might be due to plants being autotrophic organisms that do not depend on other species as resources. Hence most plant interactions are facultative (Kéfi *et al.*, 2012), can be positive, neutral or negative (Schöb *et al.*, 2014a) and can vary with environmental conditions (Callaway *et al.*, 2002; He *et al.*, 2013). Consequently, these different interaction types are rarely considered jointly (Kéfi *et al.*, 2012; Schöb *et al.*, 2013; Saiz *et al.*, 2014). In particular, plant interactions have often been studied only for one of the interacting partner as an unidirectional interaction, for example looking at the effect of nurse plants on beneficiary species (He *et al.* (2013); Cavieres *et al.* (2014); Losapio & Schöb (2017) but see e.g. Schöb *et al.*, 2014b).

In summary, the potential existence of interaction networks among multiple plant species is often neglected. However, recent studies suggest that such networks are widespread in several vegetation types (Verdú & Valiente-Banuet, 2008; Allesina & Levine, 2011; Saiz *et al.*, 2014; Losapio & Schöb, 2017). The network approach to analyse plant interactions has proved useful for exploring how intransitive competition influences species coexistence (Laird & Schamp, 2006; Allesina & Levine, 2011), to better understand the role of facilitation for biodiversity maintenance under global change (Losapio & Schöb, 2017) and to increase prediction accuracy of ecosystem dynamics (Poisot *et al.*, 2016).

By considering spatially explicit models, recent studies suggest that the outcome of positive plant interactions may be diffuse, involving many species and varying with spatial scale (Pescador *et al.*, 2014; Chacón-Labella *et al.*, 2016). For plants, and other organisms such as termites and mussels, it has been shown that the emergence of regular spatial patterns is the consequence of scale-dependent feedbacks (Rietkerk *et al.*, 2004; Solé & Bascompte, 2006; Meron, 2012; Tarnita *et al.*, 2017), in which competitive (Tilman, 1994; Durrett & Levin, 1998) and facilitative (Kéfi *et al.*, 2007; Meron, 2012) interactions between species are pivotal. These interaction processes may produce a spatial signal in the component populations and in the whole community and ecosystem, resulting in self-organised patch patterns (Solé & Bascompte, 2006). Particularly, competition with distant individuals may allow larger scale species coexistence in heterogeneous environments (Chesson, 2000; Allesina & Levine, 2011; Tarnita *et al.*, 2017), whereas fine scale facilitation between neighbours may promote multi-species clustering (Meron, 2012; Pescador *et al.*, 2014; Chacón-Labella *et al.*, 2016).

Here, we wonder how plant interaction networks are structured, how network assembly mechanisms maintain species richness and this changes across spatial scales. To do so, we combined research on the ecology of plant interactions with ecological network models. Specifically, we mapped a plant community at the individual level in a sparsely vegetated alpine tundra ecosystem and inferred plant interactions from spatial point pattern analysis (Wiegand & Moloney, 2014; Velázquez *et al.*, 2016). Then, we built plant interaction networks and studied how interaction types change network structure across spatial scales. Because facilitation is known to be a relevant driver in the examined ecosystem (Callaway *et al.*, 2002; Schöb *et al.*, 2008; Kikvidze *et al.*, 2015), we tested the hypothesis that facilitation would support the formation of complex spatial networks and maintain high species richness at small spatial scale, while competition would lead to network breakdown at larger spatial scales.

MATERIALS AND METHODS

We have developed a novel analytical framework to analyse the structure of plant interactions networks across spatial scales by combining spatial pattern analysis to estimate plant–plant interactions with network models (Fig. 1).

Study site

An observational study was performed in a sparsely-vegetated alpine tundra ecosystem (Swiss Alps, 2300 m a.s.l., Lat 46.39995°N, Long 7.58224°E, Fig. S1) characterised by patches of the prostate dwarf-shrub *Dryas octopetala* L. (Rosaceae). The plant community was fully mapped with a 1 cm accuracy during August 2015 within a 9 x 3 m rectangular grid (Fig. S2). For each individual plant (i.e. ramet) we recorded: species identity, coordinates of rooting point (x and y) and a set of functional traits (width, height, number of leaves, leaf dry mass) relevant for resource use and competitive ability (Díaz *et al.*, 2016). In total, 2154 individuals belonging to 29 species were recorded (Tab. S1). Species richness reached an asymptote in the accumulation curve (Fig. S3), suggesting that a representative area with the entire species pool of this plant community type was sampled. We focused on the 19 species that had more than 10 individuals in order to minimise analytical bias. Small-scale spatial heterogeneity of soil properties was quantified by determining soil gravel content, soil water content and soil C/N ratio with one composite sample in each 1 m^2 and beneath each *Dryas* patch (see Appendix S1 for details).

Spatial pattern analysis and plant interactions

To detect the statistical association between species we employed spatial point pattern analysis based on second-order statistics (Ripley, 1981; Diggle, 2003; Wiegand & Moloney, 2014; Baddeley *et al.*, 2015) assuming that plant interaction processes lead to detectable spatial patterns (Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007; Solé & Bascompte, 2006; Verdú & Valiente-Banuet, 2008; Schöb *et al.*, 2008; Meron, 2012; Saiz *et al.*, 2014). The scale of analysis was varied from 1 cm to 75 cm.

Univariate analyses were used to describe the distribution of each species and to identify the effects of environmental heterogeneity on the occurrence probability of the different species (see Appendix S1 for details). Then, to determine interspecific spatial associations we carried out bivariate analyses among all species pairs, determining the probability that species will be more or less associated than expected at random and after controlling for each species' occurrence probability based on each species niche and environmental heterogeneity. Species association was determined using the inhomogeneous cross-type pair correlation function $g_{ij}(r)$ (Wiegand & Moloney, 2014). Given the expected number of points of species j around a ring at a distance r from an arbitrary point of species i (Fig. S4b), the probability $p(r)$ of finding two points i and j separated by a distance r is equal to $p(r) = \lambda_i(x)\lambda_j(j)$, where $\lambda_i(x)$ and

$\lambda_j(j)$ are the estimated intensity functions of the two species (i.e. the λ function that produced the best univariate model fit, see Tab. S2). Values of $g_{ij}(r) > 1$ indicate that there are, on average, more individuals of species j at a distance r from species i than expected by chance. Conversely, values of $g_{ij}(r) < 1$ indicate that the species j is more segregated from species i than expected by chance. When $g_{ij} \approx 1$ the spatial dependency of species j on species i cannot explain more than what we would expect by chance, i.e. given each species' distribution.

In order to statistically determine whether an observed pattern was significantly different from what could be expected by chance, Monte Carlo simulation of a realisation of the $g_{ij}(r)$ function at each scale (from 1–75 cm with 1 cm steps) was used to generate simulated distributions from the null hypothesis of independence of species j with respect to species i. A total of 199 MC simulations were performed at each scale. The fifth-lowest and the fifth-highest simulated values at each r were used to build 95% confidence envelopes around the mean predictions (Diggle, 2003; Baddeley *et al.*, 2015). Thus, at a given scale r, an empirical $\hat{g}_{ij}(r)$ function higher than the confidence envelope indicates significant positive dependence of species j on species i, while the converse indicates significant negative dependence (Fig. S8, Fig. S9). When $\hat{g}_{ij}(r)$ lies within the MC confidence envelope, neutral association cannot be rejected. Because first order constraints on the distributions of each species are controlled (i.e. microsite heterogeneity, niche and stochastic determinants, see Appendix S1), the obtained positive and negative dependences must result from non-random plant–plant interactions (Tilman, 1994; Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007; Wiegand & Moloney, 2014). Because competitive interactions promote fine-scale species segregation (Macarthur & Levins, 1967; Tilman, 1994; Durrett & Levin, 1998; Pescador *et al.*, 2014), while facilitative interactions promote fine-scale species aggregation (Bruno *et al.*, 2003; Schöb *et al.*, 2008; Meron, 2012; Chacón-Labella *et al.*, 2016), we consider spatial aggregation (significantly positive associations) as indicator of facilitative interactions, and spatial exclusion (significantly negative associations) as indicator of competitive interactions and non significant spatial dependency as indicator of neutral interactions. Finally, with this approach we could detect the spatial scales at which such interactions are operating according to the corresponding spatial signals.

Network analysis

Network analysis was employed to identify the web of plant–plant interactions and to assess how network structure may promote species coexistence and maintain species richness. At each scale we built a unipartite directed network $G = (V, E)$ composed of $V = 19$ plant species and $E \subseteq V_i \times V_j$ significant directional interactions (i.e. distinguishably E_{ij} and E_{ji}), for a total of 75 networks and 983 species interactions (Fig. S10 and online video). Each network G was represented by an adjacency matrix M composed of 19 rows and 19 columns describing interactions among plant species.

Species interactions E_{ij} are described by directed ternary links such that

$$E_{ij} = \begin{cases} 1 & \text{for facilitation} \quad \text{if } \hat{g}_{ij}(r) > \overline{g}_{theo}(r) + 95\%\ \text{CI} \\ \text{-1} & \text{for competition} \quad \text{if } \hat{g}_{ij}(r) < \overline{g}_{theo}(r) - 95\%\ \text{CI} \\ 0 & \text{for neutral} \qquad \text{else } (i, j) \notin E \end{cases}$$

To reveal changes in local plant–plant interactions across scales, for each network we calculated the total number of interactions E, the number of species S with at least one interaction ($S < V$), and the number of pairwise interactions for each bidirectional interaction type, i.e. positive mutual (facilitation–facilitation), positive non-mutual (facilitation–neutral), negative mutual (competition–competition), negative non-mutual (competition–neutral) and negative–positive (facilitation–competition) (Fig. S11).

Network structure was analysed using network transitivity C as a clustering coefficient (Watts & Strogatz, 1998). Transitivity tests if two or more species linked to another species are also interacting with each other, measures the local cohesiveness of a group of species and indicates the neighbourhood interaction density as well as the hierarchy and interconnection of a community (Fig. S11). The measure C is defined as the probability that neighbouring nodes (i.e. all plant species connected to a plant species i) of a plant species i are linked to each other. In other words, C for any node i is the fraction of linked neighbours of i, such that $C = N^{-1} \sum_1 (s_i(k_i - 1))^{-1}$, where s_i is the sum of links present among neighbouring nodes for each node i, and k_i is the degree (i.e. the number of neighbours) of node i. Thus, the higher the transitivity, the more the neighbours are connected to each other, the higher the cohesiveness.

To reveal network growth and collapse across spatial scales, we calculated the size of the largest connected component R. A connected component of a network is a subset of nodes reachable from every node within it (Molloy & Reed, 1995). In other words, the size of R is equal to the maximum number of species consecutively linked within a network (Fig. S11). The change in the size of R provides basic information about network development and collapse. Hence, the presence of connected components and the change in their size R can be used to characterise the robustness of ecological communities.

Statistical analysis

We first analysed the changes in plant–plant interactions across spatial scales and then we tested the relationships between such changes and network structure.

We used regression models to relate the response of i) the total number of interactions E and ii) the interacting species richness S to the ratio between positive and negative interactions, the ratio between mutual and non-mutual interactions, and their interactions (fixed effects with third degree polynomials for each ratio, i.e. $\mathrm{r} + \mathrm{r}^2 + \mathrm{r}^3$). Besides, we previously tested with the same approach if the ratio between positive and negative interactions and the ratio between mutual and non-mutual interactions changes across scale (i.e. $\mathrm{s} + \mathrm{s}^2 + \mathrm{s}^3$).

Then, to determine bottom-up effects of local plant–plant interactions on network structure, we used regression models to test the effects of pairwise interaction combinations (i.e. number of positive–positive, positive–neutral, negative–negative, negative–neutral, negative–positive interactions as fixed effects) on i) the network transitivity C and on ii) the size of the largest connected component R. By using the absolute number of each interaction-type combination as independent variable we accounted for changes in the total number of interactions across scales. To quantify the importance (i.e. effect size) of the different interaction types and spatial scale, we used the partial r^2, i.e. the proportion of variation that can be explained by each explanatory variable, calculated as $r^2_{y,xi|xk} = \frac{SSE_{(reduced)} - SSE(full)}{SSE(reduced)}$, where the error sum of squares SSE (i.e. residuals) were compared between reduced models excluding only one interaction type x_i and the full model containing all interaction types x_k.

We accounted for spatial autocorrelation across scales by including an autoregressive covariance structure ($AR_{(1)}\sigma_{ij} = \sigma^2\rho^{|i-j|}$) in all models (Pinheiro *et al.*, 2016).

All analyses were done in R 3.3.0 (R Core Team, 2016), using *spatstat* (Baddeley *et al.*, 2015) and *ecespa* (De la Cruz, 2008) for spatial pattern analysis, *igraph* (Csárdi & Nepusz, 2006) for network analysis and *nmle* (Pinheiro *et al.*, 2016) for statistical analysis.

RESULTS

Local plant interactions

The ratio of positive to negative interactions decreased with increasing spatial scale from 1–75 cm ($\beta = -10.294$, $\beta^2 = 2.671$, $\beta^3 = -2.417$, $p = 0.0001$, $R^2 = 0.607$; Fig. S12; Tab. S3), along with a decrease of the ratio of mutual to non-mutual interactions ($\beta = -10.328$, $\beta^2 = 6.656$, $\beta^3 = 3.606$, $p = 0.0005$; $R^2 = 0.590$; Fig. S13; Tab. S3).

Positive and mutual interactions had a positive effect on the total number of interactions E ($p = 0.0006$, $R^2 = 0.665$; Tab. S3), while only positive, but not negative, interactions had a positive effect on interacting species richness S ($p = 0.0004$, $R^2 = 0.630$). Thus, there was a decrease in the number of interactions associated with a shift in the predominant interaction type from mutual and positive to non-mutual and negative with increasing spatial scale (Fig. 2, Tab. S3).

Global network structure

Network transitivity gradually decreased within the first 30 cm and then abruptly shifted to 0 with further distance ($\beta = -0.970$, $\beta^2 = 0.348$, $\beta^3 = -0.062$, $p < 0.0001$, $R^2 = 0.558$; Fig. 3a). All interaction-type combinations had significant effects on network transitivity (Tab. S4). However, considering their effect size, positive mutual interactions best explained transitivity ($\beta = 0.044$, $r^2 = 0.361$, $p < 0.0001$), followed by positive non-mutual interactions ($\beta = 0.065$, $r^2 = 0.225$, $p = 0.0018$), whereas negative mutual ($\beta = 0.026$, $r^2 = 0.096$, $p = 0.0247$) and non-mutual ($\beta = -0.089$, $r^2 = 0.117$, $p = 0.0139$) interactions had weaker effects. This suggests that positive mutual interactions among plants increased interactions among neighbouring plants.

There were connected components across all scales, but their size decreased with increasing scale ($\beta = -22.530$, $\beta^2 = 6.343$, $\beta^3 = 4.270$, $p < 0.0001$, $R^2 = 0.599$) up to about 55 cm (Fig. 3b). Positive mutual and non-mutual interactions and negative non-mutual interactions had significant positive effects on the size of the largest connected component R (Tab. S4). Again, positive mutual interactions ($\beta = 1.189$, $r^2 = 0.504$, $p < 0.001$) and positive non-mutual interactions ($\beta = 2.090$, $r^2 = 0.383$, $p < 0.0001$) best explained variation in R, followed by negative non-mutual interactions ($\beta = 3.810$, $r^2 = 0.249$, $p < 0.0001$).

DISCUSSION

Our study highlights the essential role of facultative positive interactions among plant species for the formation of complex plant–plant interaction networks networks at fine spatial scale. In our alpine ecosystem, we found that facilitation prevailed at spatial scales up to 25 cm, while competition became dominant from spatial scales larger than 50 cm. The shift from facilitation to competition with increasing scales was coupled with a de-structuring of plant–plant networks which resulted in less interacting species. These results suggest that facultative positive plant interactions are the main driver of the network organisation of species-rich patches in this stressful environment. Furthermore, they confirm our hypothesis that plant networks change across spatial scales (Fig. 4). In summary, at small spatial scales positive interactions promoted the development of cohesive networks with high transitivity and large connected components, whereas at larger spatial scales networks became more hierarchical and less cohesive in parallel with a relative increase in competitive interactions. Because network complexity can increase ecosystem stability (Solé & Bascompte, 2006), facultative positive plant interactions may promote plant species richness and ecosystem stability, similar to obligate mutualistic interactions (Bastolla *et al.*, 2009).

The spatial scale of plant interactions

The scale-dependent shift in plant interactions that we observed in our study system, after correcting each species' distribution for environmental heterogeneity and stochasticity, concurs with expectations from Turing's activator-inhibitor principle (Rietkerk *et al.*, 2004; Solé & Bascompte, 2006; Meron, 2012). At short distance, plants increase resource availability for neighbours and then ameliorate growth conditions in environments with high abiotic stress as our alpine system (Schöb *et al.*, 2012; Kikvidze *et al.*, 2015). This means that the more plants the stronger the stress amelioration by facilitation can be. This positive feedback mechanism causes facilitation to prevail at the very close proximity to plants. On the other hand, the importance of competition varied relatively less across scales, with a prevalence of competitive interactions at larger distances where facilitation cannot compensate due to the changed resource dynamics between local patches compared to those with facilitation within patches (Tilman, 1994; Rietkerk *et al.*, 2004; Meron, 2012). In summary, facilitation is strongly scale dependent, whereas competition is more constant along space in the observed fragmented alpine ecosystem.

Theoretical and empirical studies in dryland ecosystems indicate that the emergence of spatial patterns is due to two main classes of mechanisms of ecological self-organisation (Rietkerk *et al.*, 2004; Solé & Bascompte, 2006; Kéfi *et al.*, 2007; Meron, 2012; Tarnita *et al.*, 2017). The first process considers the role of positive scale-dependent feedbacks between biomass and resources. Water transport within a patch increases its growth while it inhibits the growth of neighbouring patches. Hence within-patch facilitation depends on the possibility to exploit resources within and around the patch, thereby leading to between-patch competition (Meron, 2012). The second process recognises the role of species as ecosystem engineers and their intraspecific competition. Plants and animals can create and modify microhabitats conditions, whose outcome can result in direct interference and avoidance (Tarnita *et al.*, 2017). In addition to these two processes, we postulate here a network mechanism that grants the role of interspecific interactions, both facilitation and competition, in structuring spatial networks of species-rich communities in an alpine ecosystem, which was previously undocumented. Particularly, our results suggest that mutual facilitation could increase the richness of species participating in the interaction networks, where species interact mainly via facilitation. This means that positive mutual interactions promoted the establishment of more positive interactions among neighbours, thanks to a mechanism we call 'spread of facilitation'. In such a cooperative network, the establishment of positive mutual interaction among neighbouring plants was promoted by the prevalence of the same positive interactions in the network, according to an autocatalytic process (Rietkerk *et al.*, 2004; Solé & Bascompte, 2006; Meron, 2012). Conversely, the prevalence of negative non-mutual interactions could reduce the likelihood of interactions and of species occurring in the network. Furthermore, this novel role of facilitation in plant spatial networks is in support of the importance of facilitation for biodiversity and ecosystem functioning (Bruno *et al.*, 2003; Cavieres *et al.*, 2014; Kikvidze *et al.*, 2015; Isbell *et al.*, 2015).

The structure of plant interaction networks

Networks show a high transitivity when the number of interactions among neighbours is large relative to the number of species (Watts & Strogatz, 1998). The decreasing transitivity with increasing scale implies that a transition from a cohesive to a hierarchical organisation of networks occurred. This shift was not linear, but gradual until reaching a threshold at 30 cm, beyond which a sudden, critical transition occurred and transitivity rapidly approached zero. This pattern concurs with expectations of the behaviour of an (eco)system approaching a tipping point (Solé & Bascompte, 2006), highlighting the presence of an imminent collapse of the structure of plant interaction networks. This collapse could be coupled with the facilitation–competition shift observed across spatial scale in this fragmented ecosystem. Potential mechanisms leading to such a shift can be related to previously described positive scale-dependent feedbacks, where positive interactions prevail at fine scale within patches and negative interactions at larger scale between patches (Meron, 2012). Coupled to this process there is the positive effects that ecosystem engineers, like *Dryas octopetala* in our system, have on other species (Tarnita *et al.*, 2017), mainly through the decrease of stress and the amelioration of growth conditions (Klanderud, 2005). Finally, the existence of interaction networks with a complex structure can promote or reduce the 'spread' of facilitative or competitive interactions, respectively, among diverse plant species.

The size of the largest connected components in our networks decreased with increasing spatial scale to half the size at 30 cm and to one-fifth at 55 cm. Again, this reduction in component size can be due to a reduction in positive, mutual and non mutual interactions. Indeed, we observed that facilitation could build-up parger, presumably more robust components. In line with this result, we also found a higher number of cliques (i.e. small densely interconnected components, Fig. S15) and a higher species proximity in the network (Fig. S16) at fine spatial scales where positive mutual interactions were predominant. Taken together, these results suggest a breakdown of the largest connected components with increasing spatial scale, as species tend to segregate into many detached components when positive interactions wane.

Finally, it is necessary to take into consideration that the spatial signal left by plant–plant interactions becomes blurred with distance. This decrease indicates that part of this breakdown may be, at least partially, a simple consequence of such a dilution in which positive interactions disappeared whereas competition remained until network collapse.

Our study is one of the first attempts to analyse plant–plant interactions with a network approach and to explore the variation in network structure as a function of spatial scale. We are aware that new questions are now arising. Observational studies such as the present one can only tentatively describe potential mechanisms underpinning spatial signals in patterns of species cooccurrences at different spatial scales. Nevertheless, with our approach we were able to isolate the effect of plant interactions after controlling for other sources of variation affecting local species distributions (Wiegand & Moloney, 2014; Pescador *et al.*, 2014; Chacón-Labella *et al.*, 2016). Future experimental studies controlling for differences in demographic stochasticity (e.g. dispersal limitation) and niche processes (e.g. species-specific resource limitation) would be necessary to test the causality of the observed correlations between positive plant–plant interactions and network structure and to understand their role in community assembly. At the same time, further theoretical research should accompany such experimental work to better predict community structure and ecosystem functioning and stability resulting from it under different environmental conditions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

FIGURES

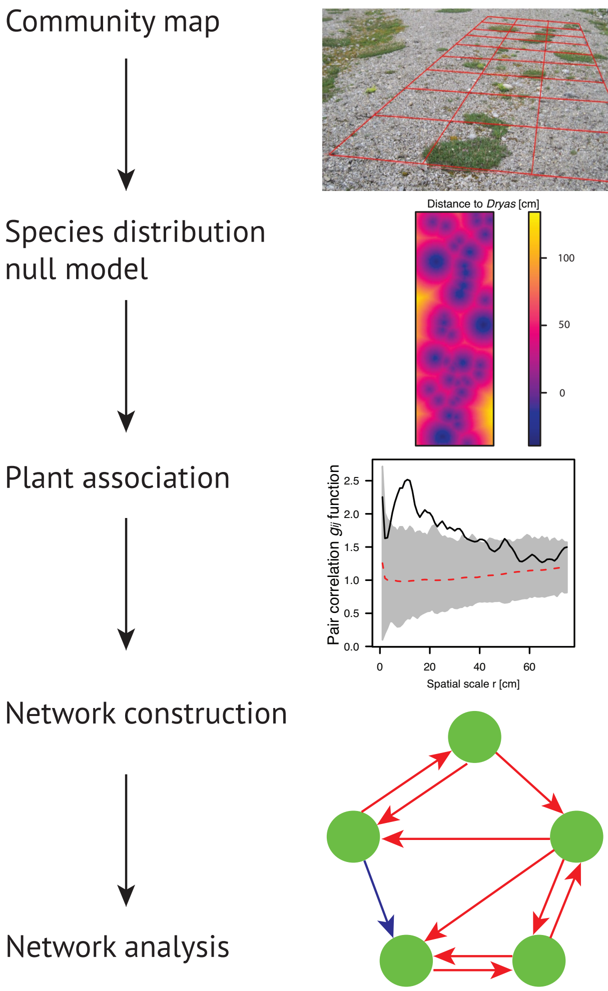

Figure 1 Analytical framework for studying plant interaction networks on the basis of spatial point patterns. A plant community is fully-mapped: for each individual plant, species identity and coordinates are recorded within a spatial grid with a 1 cm accuracy. Spatial point pattern analysis is then employed. First, the distribution of each species is analysed (see Appendix S1 for details). Second, pairwise species associations are estimated after removing the effects of environmental heterogeneity and niche and stochastic processes. Then, species interactions are inferred from spatial association patterns: a positive dependence of species j on species i is assumed to indicate facilitation of species i on species j, a negative dependence is assumed to indicate competition, and no association is assumed to indicate neutral interaction. Hence, interaction types are calculated considering the combination between positive, negative and neutral interactions. Finally, network analysis is used to reveal the structural properties, the growth or the collapse of the interaction networks across spatial scales.

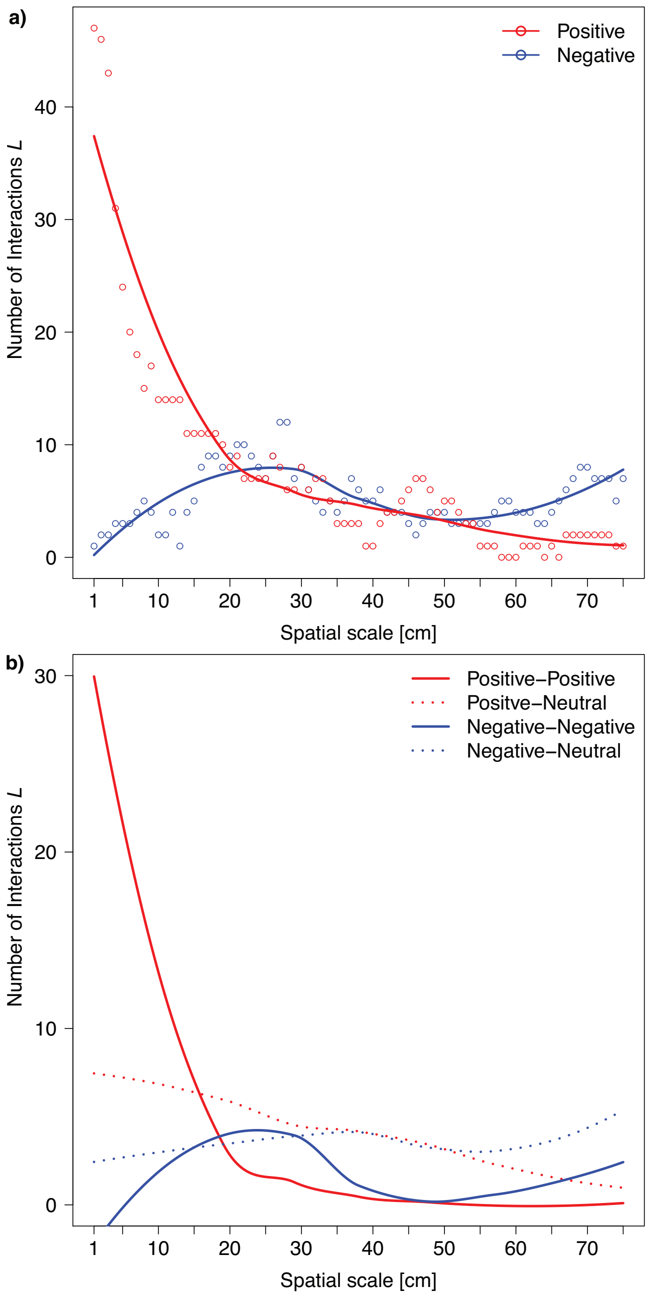

Figure 2 Number of positive and negative interactions **(a)** and number of mutual and non-mutual interactions **(b)** across spatial scales. Total number of interactions is 983. Total number of positive interactions is 592 (60.2%), of which 282 (47.6%) are mutual and 310 (52.4%) are non-mutual. Total number of negative interactions is 391 (39.8%), of which 128 are mutual (32.7%) and 263 are non-mutual (67.3%). No negative–positive interactions were observed. Red and blue lines indicate positive and negative interactions, respectively; in **(b)**, solid and dashed lines indicate mutual and non-mutual interactions, respectively. In **(b)**, data points were omitted for clarity. Lines were fitted with a local polynomial surface determined by spatial scale.

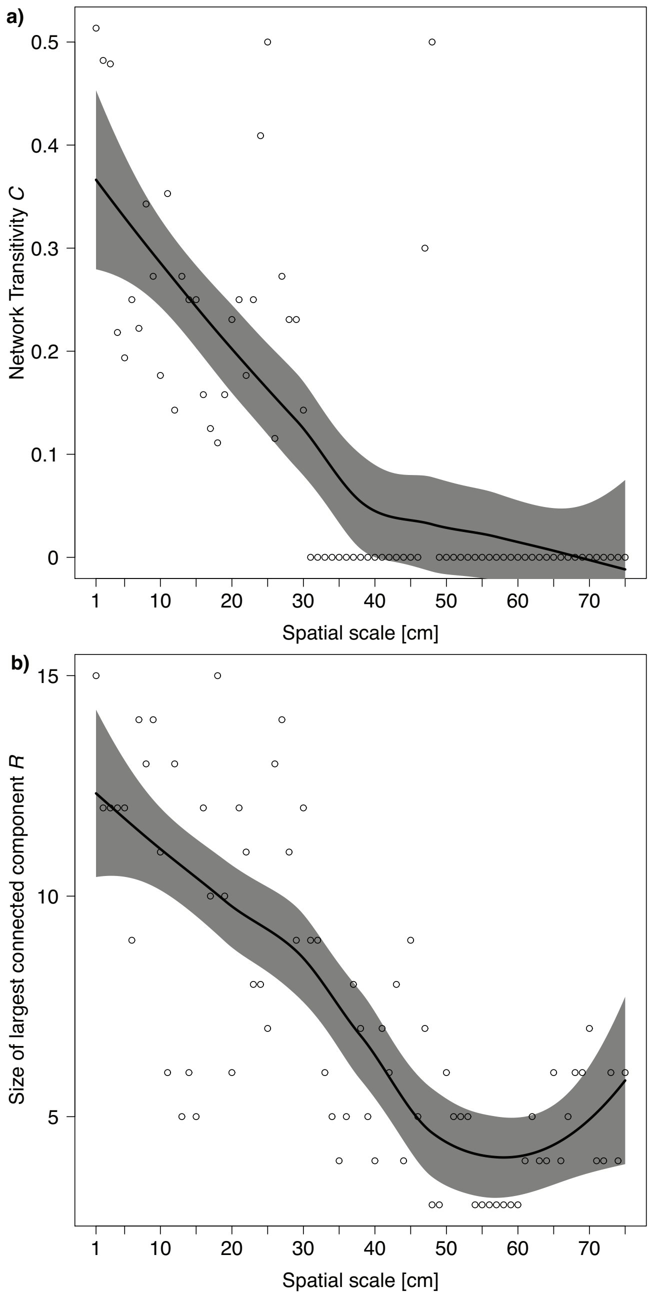

Figure 3 Network transitivity **(a)** and size of the largest connected component R **(b)** across spatial scales. Transitivity measured by the clustering coefficient C (Watts & Strogatz, 1998), see Methods section and Fig. S11, indicates local cohesiveness of a group of nodes (i.e. species). The size of the largest connected component R is the maximum number of interconnected species within a network (Molloy & Reed, 1995). A change in the size of the largest connected component provides basic information about the growth of a network. Fitted lines and 95% CI shown.

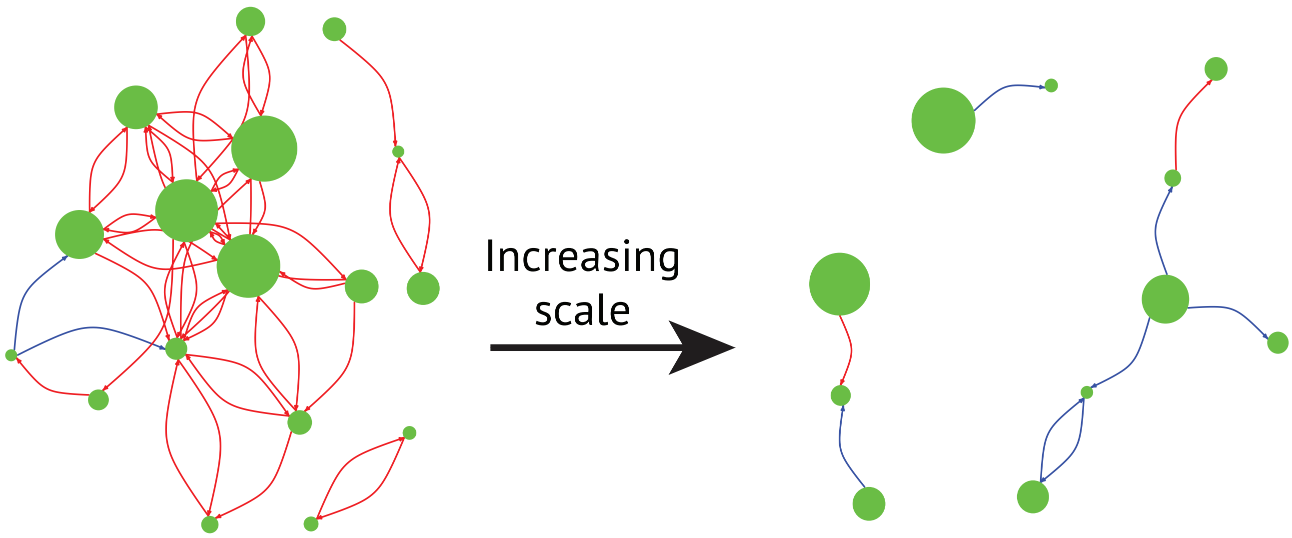

Figure 4 At small spatial scale (left, e.g. 5 cm) positive facilitative interactions (red arrows) build up a network with high transitivity, i.e. high cohesiveness. With increasing scale (right, e.g. 50 cm), negative competitive interactions (blue arrows) predominate and the network becomes more disconnected. The size of the nodes (green dots) is proportional to relative species abundance (See Fig. S10 and the online video for the network at every centimetre).