

1 Positive interactions support the formation of complex 2 spatial networks

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17 provided new analytical methods, all authors discussed data analysis, commented the results
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19

Abstract

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

32 INTRODUCTION

33 The nature of biodiversity continues to intrigue biologists because of the complexity of inter-
34 actions among species in ecosystems. Due to this complexity, success to build a unified theory
35 of biodiversity has been poor (McGill, 2010). Standard ecological theory assumes as a central
36 pillar that negative interactions between species (e.g. competition) are essential to promote
37 stable species coexistence (Tilman, 1994; Chesson, 2000; Allesina & Levine, 2011; Kraft *et al.*,
38 2014). More recently, the re-discovery of positive interactions emphasised the importance of
39 mutualism and facilitation for biodiversity maintenance and ecosystem stability (Bruno *et al.*,
40 2003; Verdú & Valiente-Banuet, 2008; Bastolla *et al.*, 2009; Schöb *et al.*, 2012; Cavieres *et al.*,
41 2014; Isbell *et al.*, 2015).

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

54 In summary, the potential existence of interaction networks among multiple plant species is
55 often neglected. However, recent studies suggest that such networks are widespread in several
56 vegetation types (Verdú & Valiente-Banuet, 2008; Allesina & Levine, 2011; Saiz *et al.*, 2014;
57 Losapio & Schöb, 2017). The network approach to analyse plant interactions has proved useful
58 for exploring how intransitive competition influences species coexistence (Laird & Schamp,
59 2006; Allesina & Levine, 2011), to better understand the role of facilitation for biodiversity
60 maintenance under global change (Losapio & Schöb, 2017) and to increase prediction accuracy
61 of ecosystem dynamics (Poisot *et al.*, 2016).

62 By considering spatially explicit models, recent studies suggest that the outcome of posi-
63 tive plant interactions may be diffuse, involving many species and varying with spatial scale
64 (Pescador *et al.*, 2014; Chacón-Labela *et al.*, 2016). For plants, and other organisms such
65 as termites and mussels, it has been shown that the emergence of regular spatial patterns is
66 the consequence of scale-dependent feedbacks (Rietkerk *et al.*, 2004; Solé & Bascompte, 2006;
67 Meron, 2012; Tarnita *et al.*, 2017), in which competitive (Tilman, 1994; Durrett & Levin, 1998)
68 and facilitative (Kéfi *et al.*, 2007; Meron, 2012) interactions between species are pivotal. These
69 interaction processes may produce a spatial signal in the component populations and in the
70 whole community and ecosystem, resulting in self-organised patch patterns (Solé & Bascompte,
71 2006). Particularly, competition with distant individuals may allow larger scale species coex-
72 istence in heterogeneous environments (Chesson, 2000; Allesina & Levine, 2011; Tarnita *et al.*,
73 2017), whereas fine scale facilitation between neighbours may promote multi-species clustering
74 (Meron, 2012; Pescador *et al.*, 2014; Chacón-Labela *et al.*, 2016).

75 Here, we wonder how plant interaction networks are structured, how network assembly
76 mechanisms maintain species richness and this changes across spatial scales. To do so, we
77 combined research on the ecology of plant interactions with ecological network models. Specif-
78 ically, we mapped a plant community at the individual level in a sparsely vegetated alpine
79 tundra ecosystem and inferred plant interactions from spatial point pattern analysis (Wiegand
80 & Moloney, 2014; Velázquez *et al.*, 2016). Then, we built plant interaction networks and stud-
81 ied how interaction types change network structure across spatial scales. Because facilitation
82 is known to be a relevant driver in the examined ecosystem (Callaway *et al.*, 2002; Schöb *et al.*,
83 2008; Kikvidze *et al.*, 2015), we tested the hypothesis that facilitation would support the for-
84 mation of complex spatial networks and maintain high species richness at small spatial scale,
85 while competition would lead to network breakdown at larger spatial scales.

86

87 MATERIALS AND METHODS

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

91 Study site

92 An observational study was performed in a sparsely-vegetated alpine tundra ecosystem (Swiss
93 Alps, 2300 m a.s.l., Lat 46.39995°N, Long 7.58224°E, Fig. S1) characterised by patches of the
94 prostate dwarf-shrub *Dryas octopetala* L. (Rosaceae). The plant community was fully mapped
95 with a 1 cm accuracy during August 2015 within a 9 x 3 m rectangular grid (Fig. S2). For each
96 individual plant (i.e. ramet) we recorded: species identity, coordinates of rooting point (x and
97 y) and a set of functional traits (width, height, number of leaves, leaf dry mass) relevant for
98 resource use and competitive ability (Díaz *et al.*, 2016). In total, 2154 individuals belonging to
99 29 species were recorded (Tab. S1). Species richness reached an asymptote in the accumulation
100 curve (Fig. S3), suggesting that a representative area with the entire species pool of this plant
101 community type was sampled. We focused on the 19 species that had more than 10 individuals
102 in order to minimise analytical bias. Small-scale spatial heterogeneity of soil properties was
103 quantified by determining soil gravel content, soil water content and soil C/N ratio with one
104 composite sample in each 1 m² and beneath each *Dryas* patch (see Appendix S1 for details).

105 **Spatial pattern analysis and plant interactions**

106 To detect the statistical association between species we employed spatial point pattern analysis
107 based on second-order statistics (Ripley, 1981; Diggle, 2003; Wiegand & Moloney, 2014; Bad-
108 deley *et al.*, 2015) assuming that plant interaction processes lead to detectable spatial patterns
109 (Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007; Solé & Bascompte, 2006; Verdú & Valiente-Banuet,
110 2008; Schöb *et al.*, 2008; Meron, 2012; Saiz *et al.*, 2014). The scale of analysis was varied from
111 1 cm to 75 cm.

112 Univariate analyses were used to describe the distribution of each species and to identify
113 the effects of environmental heterogeneity on the occurrence probability of the different species
114 (see Appendix S1 for details). Then, to determine interspecific spatial associations we carried
115 out bivariate analyses among all species pairs, determining the probability that species will
116 be more or less associated than expected at random and after controlling for each species'
117 occurrence probability based on each species niche and environmental heterogeneity. Species
118 association was determined using the inhomogeneous cross-type pair correlation function $g_{ij}(r)$
119 (Wiegand & Moloney, 2014). Given the expected number of points of species j around a ring
120 at a distance r from an arbitrary point of species i (Fig. S4b), the probability $p(r)$ of finding
121 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

122 $\lambda_j(j)$ are the estimated intensity functions of the two species (i.e. the λ function that produced
123 the best univariate model fit, see Tab. S2). Values of $g_{ij}(r) > 1$ indicate that there are, on
124 average, more individuals of species j at a distance r from species i than expected by chance.
125 Conversely, values of $g_{ij}(r) < 1$ indicate that the species j is more segregated from species i
126 than expected by chance. When $g_{ij} \approx 1$ the spatial dependency of species j on species i cannot
127 explain more than what we would expect by chance, i.e. given each species' distribution.

128 In order to statistically determine whether an observed pattern was significantly different
129 from what could be expected by chance, Monte Carlo simulation of a realisation of the $g_{ij}(r)$
130 function at each scale (from 1–75 cm with 1 cm steps) was used to generate simulated dis-
131 tributions from the null hypothesis of independence of species j with respect to species i . A
132 total of 199 MC simulations were performed at each scale. The fifth-lowest and the fifth-
133 highest simulated values at each r were used to build 95% confidence envelopes around the
134 mean predictions (Diggle, 2003; Baddeley *et al.*, 2015). Thus, at a given scale r , an empirical
135 $\hat{g}_{ij}(r)$ function higher than the confidence envelope indicates significant positive dependence of
136 species j on species i , while the converse indicates significant negative dependence (Fig. S8,
137 Fig. S9). When $\hat{g}_{ij}(r)$ lies within the MC confidence envelope, neutral association cannot be
138 rejected. Because first order constraints on the distributions of each species are controlled (i.e.
139 microsite heterogeneity, niche and stochastic determinants, see Appendix S1), the obtained pos-
140 itive and negative dependences must result from non-random plant–plant interactions (Tilman,
141 1994; Rietkerk *et al.*, 2004; Kéfi *et al.*, 2007; Wiegand & Moloney, 2014). Because competitive
142 interactions promote fine-scale species segregation (Macarthur & Levins, 1967; Tilman, 1994;
143 Durrett & Levin, 1998; Pescador *et al.*, 2014), while facilitative interactions promote fine-scale
144 species aggregation (Bruno *et al.*, 2003; Schöb *et al.*, 2008; Meron, 2012; Chacón-Labelle *et al.*,
145 2016), we consider spatial aggregation (significantly positive associations) as indicator of facil-
146 itative interactions, and spatial exclusion (significantly negative associations) as indicator of
147 competitive interactions and non significant spatial dependency as indicator of neutral interac-
148 tions. Finally, with this approach we could detect the spatial scales at which such interactions
149 are operating according to the corresponding spatial signals.

150 **Network analysis**

151 Network analysis was employed to identify the web of plant–plant interactions and to assess

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

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

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

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

165 Network structure was analysed using network transitivity C as a clustering coefficient
166 (Watts & Strogatz, 1998). Transitivity tests if two or more species linked to another species
167 are also interacting with each other, measures the local cohesiveness of a group of species and
168 indicates the neighbourhood interaction density as well as the hierarchy and interconnection
169 of a community (Fig. S11). The measure C is defined as the probability that neighbouring
170 nodes (i.e. all plant species connected to a plant species i) of a plant species i are linked to
171 each other. In other words, C for any node i is the fraction of linked neighbours of i , such that
172 $C = N^{-1} \sum_1 (s_i(k_i - 1))^{-1}$, where s_i is the sum of links present among neighbouring nodes for
173 each node i , and k_i is the degree (i.e. the number of neighbours) of node i . Thus, the higher the
174 transitivity, the more the neighbours are connected to each other, the higher the cohesiveness.

175 To reveal network growth and collapse across spatial scales, we calculated the size of the
176 largest connected component R . A connected component of a network is a subset of nodes
177 reachable from every node within it (Molloy & Reed, 1995). In other words, the size of R is

178 equal to the maximum number of species consecutively linked within a network (Fig. S11). The
179 change in the size of R provides basic information about network development and collapse.
180 Hence, the presence of connected components and the change in their size R can be used to
181 characterise the robustness of ecological communities.

182 **Statistical analysis**

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

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

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

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

204 All analyses were done in R 3.3.0 (R Core Team, 2016), using *spatstat* (Baddeley *et al.*,
205 2015) and *ecspa* (De la Cruz, 2008) for spatial pattern analysis, *igraph* (Csárdi & Nepusz,
206 2006) for network analysis and *nmls* (Pinheiro *et al.*, 2016) for statistical analysis.

207

208 RESULTS

209 Local plant interactions

210 The ratio of positive to negative interactions decreased with increasing spatial scale from 1–75
211 cm ($\beta = -10.294$, $\beta^2 = 2.671$, $\beta^3 = -2.417$, $p = 0.0001$, $R^2 = 0.607$; Fig. S12; Tab. S3), along
212 with a decrease of the ratio of mutual to non-mutual interactions ($\beta = -10.328$, $\beta^2 = 6.656$,
213 $\beta^3 = 3.606$, $p = 0.0005$; $R^2 = 0.590$; Fig. S13; Tab. S3).

214 Positive and mutual interactions had a positive effect on the total number of interactions
215 E ($p = 0.0006$, $R^2 = 0.665$; Tab. S3), while only positive, but not negative, interactions had
216 a positive effect on interacting species richness S ($p = 0.0004$, $R^2 = 0.630$). Thus, there was a
217 decrease in the number of interactions associated with a shift in the predominant interaction
218 type from mutual and positive to non-mutual and negative with increasing spatial scale (Fig.
219 2, Tab. S3).

220 Global network structure

221 Network transitivity gradually decreased within the first 30 cm and then abruptly shifted to
222 0 with further distance ($\beta = -0.970$, $\beta^2 = 0.348$, $\beta^3 = -0.062$, $p < 0.0001$, $R^2 = 0.558$; Fig.
223 3a). All interaction-type combinations had significant effects on network transitivity (Tab. S4).
224 However, considering their effect size, positive mutual interactions best explained transitivity
225 ($\beta = 0.044$, $r^2 = 0.361$, $p < 0.0001$), followed by positive non-mutual interactions ($\beta = 0.065$,
226 $r^2 = 0.225$, $p = 0.0018$), whereas negative mutual ($\beta = 0.026$, $r^2 = 0.096$, $p = 0.0247$) and non-
227 mutual ($\beta = -0.089$, $r^2 = 0.117$, $p = 0.0139$) interactions had weaker effects. This suggests that
228 positive mutual interactions among plants increased interactions among neighbouring plants.

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

236

237 DISCUSSION

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

253 **The spatial scale of plant interactions**

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

268 Theoretical and empirical studies in dryland ecosystems indicate that the emergence of spa-
269 tial patterns is due to two main classes of mechanisms of ecological self-organisation (Rietkerk
270 *et al.*, 2004; Solé & Bascompte, 2006; Kéfi *et al.*, 2007; Meron, 2012; Tarnita *et al.*, 2017).
271 The first process considers the role of positive scale-dependent feedbacks between biomass and
272 resources. Water transport within a patch increases its growth while it inhibits the growth
273 of neighbouring patches. Hence within-patch facilitation depends on the possibility to exploit
274 resources within and around the patch, thereby leading to between-patch competition (Meron,
275 2012). The second process recognises the role of species as ecosystem engineers and their in-
276 traspecific competition. Plants and animals can create and modify microhabitats conditions,
277 whose outcome can result in direct interference and avoidance (Tarnita *et al.*, 2017). In ad-
278 dition to these two processes, we postulate here a network mechanism that grants the role of
279 interspecific interactions, both facilitation and competition, in structuring spatial networks of
280 species-rich communities in an alpine ecosystem, which was previously undocumented. Par-
281 ticularly, our results suggest that mutual facilitation could increase the richness of species
282 participating in the interaction networks, where species interact mainly via facilitation. This
283 means that positive mutual interactions promoted the establishment of more positive inter-
284 actions among neighbours, thanks to a mechanism we call 'spread of facilitation'. In such
285 a cooperative network, the establishment of positive mutual interaction among neighbouring
286 plants was promoted by the prevalence of the same positive interactions in the network, accord-
287 ing to an autocatalytic process (Rietkerk *et al.*, 2004; Solé & Bascompte, 2006; Meron, 2012).
288 Conversely, the prevalence of negative non-mutual interactions could reduce the likelihood of
289 interactions and of species occurring in the network. Furthermore, this novel role of facilitation
290 in plant spatial networks is in support of the importance of facilitation for biodiversity and
291 ecosystem functioning (Bruno *et al.*, 2003; Cavieres *et al.*, 2014; Kikvidze *et al.*, 2015; Isbell
292 *et al.*, 2015).

293 **The structure of plant interaction networks**

294 Networks show a high transitivity when the number of interactions among neighbours is large
295 relative to the number of species (Watts & Strogatz, 1998). The decreasing transitivity with in-
296 creasing scale implies that a transition from a cohesive to a hierarchical organisation of networks
297 occurred. This shift was not linear, but gradual until reaching a threshold at 30 cm, beyond

298 which a sudden, critical transition occurred and transitivity rapidly approached zero. This pat-
299 tern concurs with expectations of the behaviour of an (eco)system approaching a tipping point
300 (Solé & Bascompte, 2006), highlighting the presence of an imminent collapse of the structure
301 of plant interaction networks. This collapse could be coupled with the facilitation–competition
302 shift observed across spatial scale in this fragmented ecosystem. Potential mechanisms leading
303 to such a shift can be related to previously described positive scale-dependent feedbacks, where
304 positive interactions prevail at fine scale within patches and negative interactions at larger scale
305 between patches (Meron, 2012). Coupled to this process there is the positive effects that ecosys-
306 tem engineers, like *Dryas octopetala* in our system, have on other species (Tarnita *et al.*, 2017),
307 mainly through the decrease of stress and the amelioration of growth conditions (Klanderud,
308 2005). Finally, the existence of interaction networks with a complex structure can promote or
309 reduce the ‘spread’ of facilitative or competitive interactions, respectively, among diverse plant
310 species.

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

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

324 Our study is one of the first attempts to analyse plant–plant interactions with a network
325 approach and to explore the variation in network structure as a function of spatial scale. We are
326 aware that new questions are now arising. Observational studies such as the present one can only
327 tentatively describe potential mechanisms underpinning spatial signals in patterns of species co-

328 occurrences at different spatial scales. Nevertheless, with our approach we were able to isolate
329 the effect of plant interactions after controlling for other sources of variation affecting local
330 species distributions (Wiegand & Moloney, 2014; Pescador *et al.*, 2014; Chacón-Labela *et al.*,
331 2016). Future experimental studies controlling for differences in demographic stochasticity
332 (e.g. dispersal limitation) and niche processes (e.g. species-specific resource limitation) would
333 be necessary to test the causality of the observed correlations between positive plant–plant
334 interactions and network structure and to understand their role in community assembly. At
335 the same time, further theoretical research should accompany such experimental work to better
336 predict community structure and ecosystem functioning and stability resulting from it under
337 different environmental conditions.

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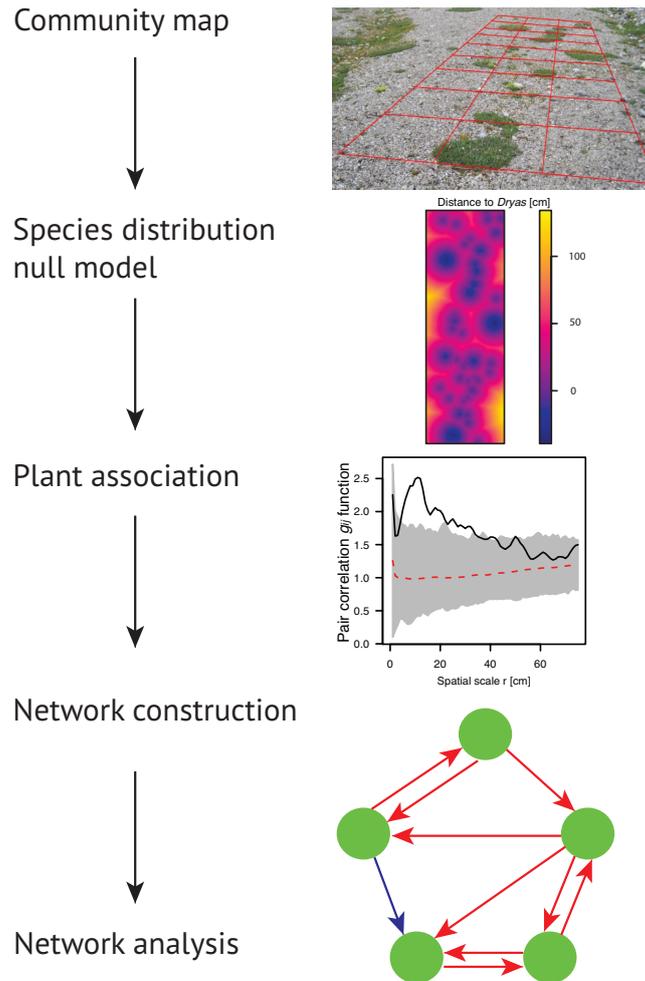
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473 **SUPPORTING INFORMATION**

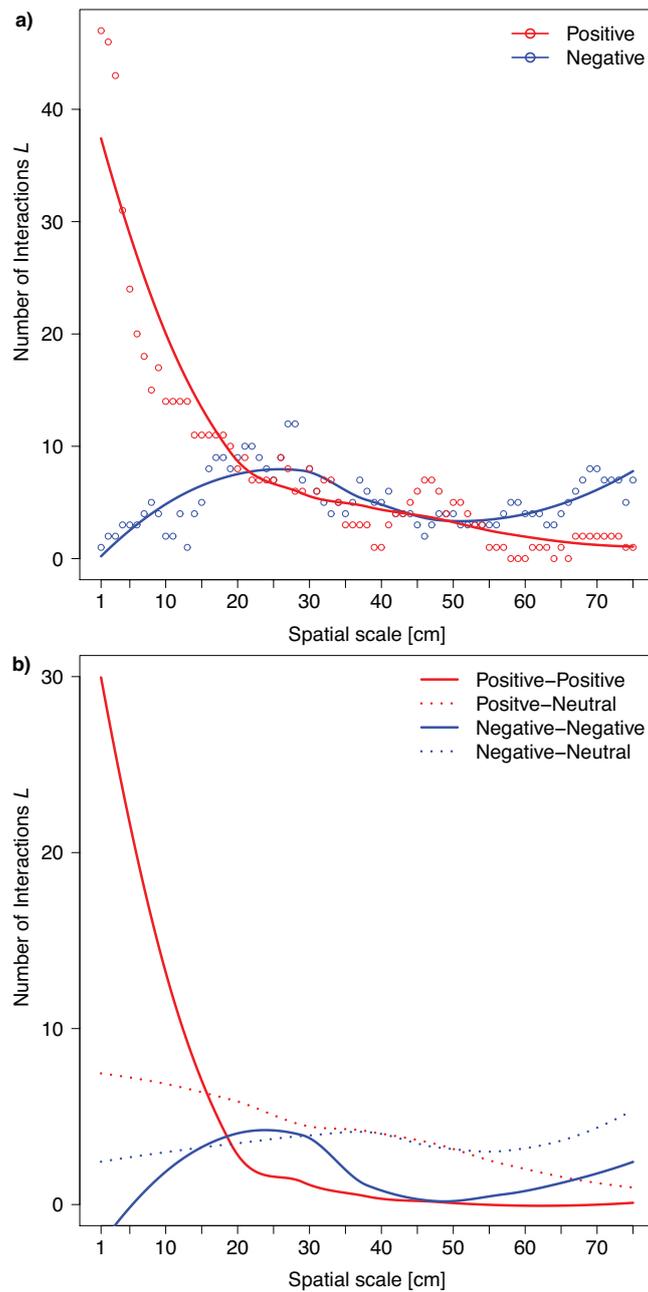
474 Additional Supporting Information may be found online in the supporting information tab for
475 this article.

476 **FIGURES**



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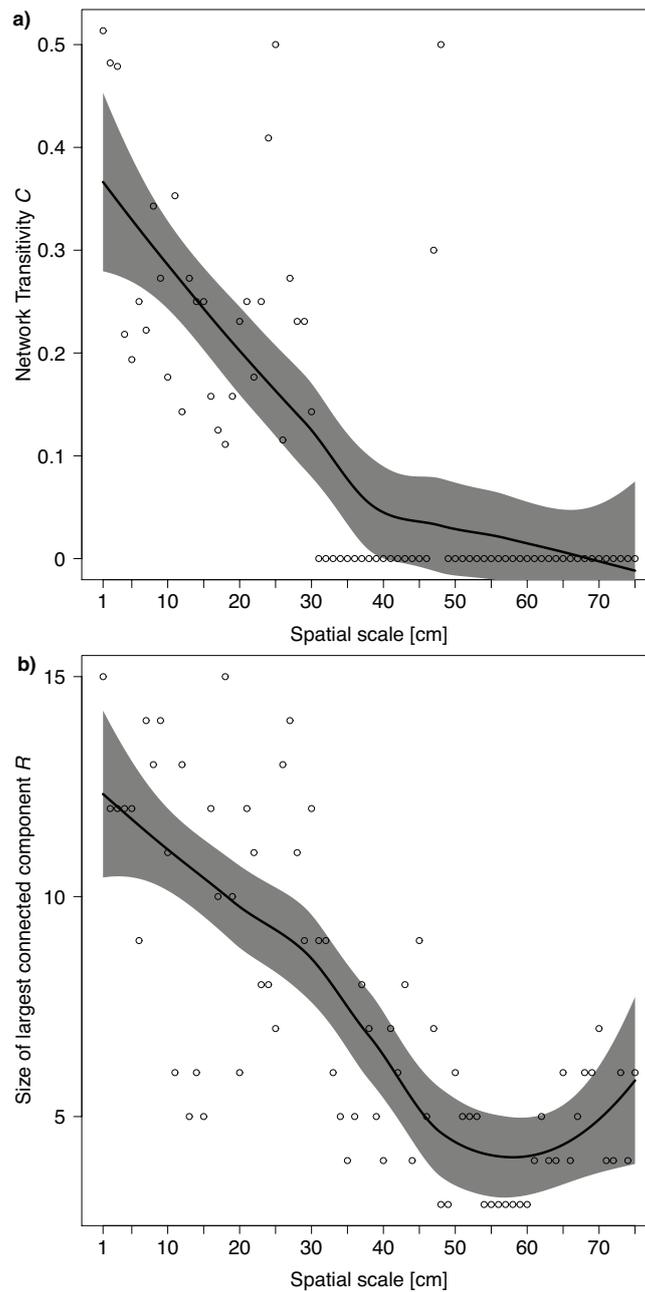
478 **Figure 1** Analytical framework for studying plant interaction networks on the basis of spatial
479 point patterns. A plant community is fully-mapped: for each individual plant, species identity
480 and coordinates are recorded within a spatial grid with a 1 cm accuracy. Spatial point pattern
481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



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492 **Figure 2** Number of positive and negative interactions **(a)** and number of mutual and non-
493 mutual interactions **(b)** across spatial scales. Total number of interactions is 983. Total number
494 of positive interactions is 592 (60.2%), of which 282 (47.6%) are mutual and 310 (52.4%) are
495 non-mutual. Total number of negative interactions is 391 (39.8%), of which 128 are mutual
496 (32.7%) and 263 are non-mutual (67.3%). No negative–positive interactions were observed.
497 Red and blue lines indicate positive and negative interactions, respectively; in **(b)**, solid and
498 dashed lines indicate mutual and non-mutual interactions, respectively. In **(b)**, data points
499 were omitted for clarity. Lines were fitted with a local polynomial surface determined by
500 spatial scale.



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

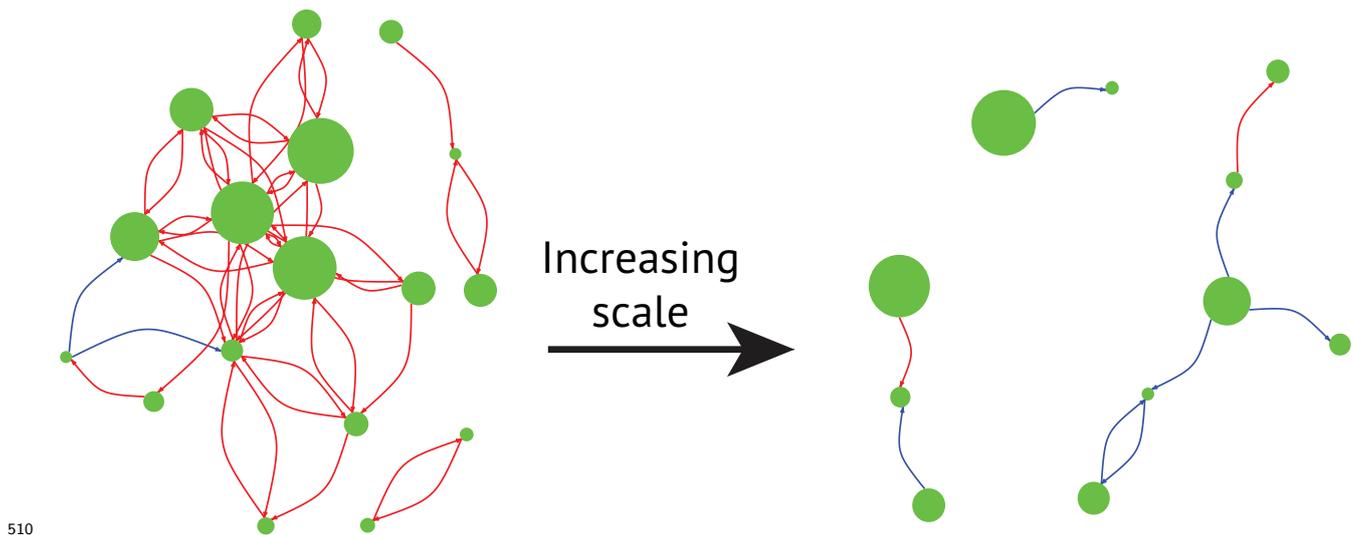


Figure 4 At small spatial scale (left, e.g. 5 cm) positive facilitative interactions (red arrows) build up a network with high transitivity, i.e. high cohesiveness. With increasing scale (right, e.g. 50 cm), negative competitive interactions (blue arrows) predominate and the network becomes more disconnected. 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).