

1 **Title: The assembly of a plant network in alpine vegetation**

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3 **Running head: Network-wide plant associations**

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24 **Abstract**

25 **Questions:** Positive and negative associations among species influence the structure of  
26 plant communities. Yet, how these plant associations are assembled at the community level  
27 is poorly understood. We propose a new approach that combines spatial ecology, network  
28 theory and functional traits to examine the assembly of plant–plant associations at the  
29 community level.

30

31 **Location:** Gemmipass, Swiss Alps.

32

33 **Methods:** We fully mapped a plant community at the individual-plant, recording both plant  
34 coordinates and functional traits for each individual. We identified non-random species  
35 associations using spatial point-pattern analysis and partialled out the effect of abiotic  
36 heterogeneity. We then analyzed the plant network structure and used plant traits to  
37 predict species associations.

38

39 **Results:** We identified 36 significant spatial associations between plant species, 34 positive  
40 and 2 negatives. Dominant, stress-tolerant species such as *Dryas octopetala*, *Linaria alpina*  
41 and *Leontodon montanus* were highly connected in the network whereas rare, water- and  
42 nutrient-demanding species such as *Saxifraga aizoides*, *Galium anisophyllum* and *Thymus*  
43 *praecox* were less connected compared to random expectation. The plant network was  
44 clustered, meaning that species were overall more connected among each other than  
45 expected by chance.

46

47 **Conclusions:** Positive associations among species characterized the studied plant  
48 community. Besides the primary effect of associations of the “foundation” species *D.*  
49 *octopetala* with other species, these “subordinate” plants were also associated with each  
50 other. Our study reveals the assembly of plant communities as driven by positive  
51 associations among stress-tolerant pioneer species, highlighting their role in supporting the  
52 cohesiveness of alpine plant communities.

53

54 **Key-words:** Alpine tundra, biodiversity, community ecology, competition, ecological  
55 networks, facilitation, functional traits, spatial patterns, Swiss Alps

56

## 57 **Introduction**

58 Biological diversity is determined by ecological processes that take place in space and time  
59 (McGill 2010). Environmental heterogeneity, dispersal and biotic interactions can shape the  
60 fine-scale distribution of organisms and affect the spatial structure of populations,  
61 communities and ecosystems (Rietkerk et al. 2004; Kefi et al. 2007; Meron 2012). For  
62 instance, facilitation can induce fine-scale associations (Bruno et al. 2003; Schöb et al. 2008;  
63 Chacon-Labela et al. 2016), while competition can reduce them (MacArthur and Levins  
64 1967; Tilman 1994; Durrett and Levin 1998; Pescador et al. 2014). The structure of plant  
65 communities can therefore be characterised by a network of positive and negative  
66 interactions among species (Verdù and Valiente-Banuet 2008; Levine et al. 2017; Losapio et  
67 al. 2018; Saiz et al. 2018). Although this perspective could shed light on the assembly of  
68 plant communities, the ecological factors contributing to the formation of these plant  
69 networks are poorly understood.

70 Plant networks depend on the method of how interactions are determined. Many  
71 studies rely on the simplistic approach that fine-scale co-occurrence patterns would reflect  
72 species interactions (Delalandre and Montesinos-Navarro 2018). However, several other  
73 processes besides species interactions, such as environmental heterogeneity, species  
74 microhabitat preferences and dispersal limitation, can influence species distribution and  
75 resulting spatial patterns (Condit et al. 2000; McGill 2010; Wiegand and Moloney 2014).  
76 Consequently, these other processes should be taken into account when inferring  
77 interactions from co-occurrence patterns.

78 The use of spatial point-pattern analysis can provide a more appropriate way of  
79 inferring species associations than other co-occurrence statistics (Baddeley, Rubak, &  
80 Turner, 2015). For example, using spatial point-pattern analysis (Diggle 2003; Wiegand and  
81 Moloney 2014; Baddeley et al. 2015) it is possible to infer plant interactions besides the  
82 effects of several other factors responsible for plant distribution, such as environmental  
83 heterogeneity, limited dispersal and shared microhabitat preferences (Chacon-Labela et al.,  
84 2016; Jara-Guerrero, De la Cruz, Espinosa, Méndez, & Escudero, 2015; Pescador et al., 2014;  
85 Wiegand et al., 2012).

86 By capturing essential aspects of the ecophysiology and life-history strategy of species,  
87 functional traits can help to better understand processes responsible for ecological patterns  
88 (McGill et al. 2006, Weiher, & Westoby, 2006). Thus, traits can indicate how the outcome of  
89 species interactions influences community structure (Gross et al. 2009) and how species-  
90 specific plant interactions affect biodiversity (Schöb et al. 2017). Plant traits such as leaf  
91 mass per area, height and diameter reflect species competitive ability (Gross et al. 2009)  
92 and are therefore related to the assembly of plant communities (Schöb et al. 2012). The  
93 sensitivity of plant traits to environmental conditions further allows prediction of the effects

94 of environmental change on plant communities (Losapio & Schöb 2017). Plant traits may  
95 therefore be a suitable tool when it comes to assess the dependence of plant association  
96 networks of a plant community on environmental conditions.

97 In this study, we combine spatial ecology, network theory and functional traits to  
98 reveal the assembly of plant communities. Since facilitation is assumed to be strong in  
99 stressful habitats such as alpine vegetation (Callaway et al. 2002; Schöb et al. 2008; Kikvidze  
100 et al. 2015) and as it is linked to plant community structure and plant functional traits (Gross  
101 et al. 2009; Schöb et al. 2012), we tested the hypothesis that (a) positive associations  
102 characterize a cohesive plant network and (b) functional traits can explain the degree of  
103 network-wide species associations.

104

## 105 **Methods**

### 106 *Study area and sampling design*

107 The study was done in an alpine vegetation (Swiss Alps, 2300 m a.s.l., 46.39995°N,  
108 7.58224°E, Supporting Information Fig. S1) dominated by patches of the prostrate dwarf-  
109 shrub *Dryas octopetala* L. (Rosaceae). This plant forms vegetation patches and has  
110 facilitative sheltering effects on other plant species in tundra ecosystems (Klanderud and  
111 Totland 2005). The plant community was fully mapped with 1 cm accuracy during August  
112 2015 within a 9 x 3 m rectangular grid (Fig. 1, Supporting Information Fig. S2). For each  
113 individual plant (i.e., ramet for clonal plants) we recorded species identity, coordinates of  
114 the rooting point (x and y) and a set of following functional traits: diameter, height, number  
115 of leaves and leaf mass per area (Supporting Information Methods S1). In total, 2154  
116 individuals belonging to 29 species were recorded (Supporting Information Fig. S3). Fine-  
117 scale spatial heterogeneity of soil properties was quantified by determining soil gravel

118 content, soil water content and soil C : N ratio with one composite sample in each 1 m<sup>2</sup> and  
119 beneath each *Dryas* patch ( $n = 27$ , total = 54; see Supporting Information Methods S1 for  
120 more details).

121

## 122 *Spatial analysis and plant–plant associations*

123 To detect the statistical association between plant species, we employed spatial point-  
124 pattern analysis (Ripley 1981; Diggle 2003; McGill 2010; Wiegand and Moloney 2014;  
125 Baddeley et al. 2015).

126 First, for each specie' spatial pattern, we fitted models of fine-scale spatial distribution  
127 that accounted for the effects of environmental heterogeneity and limited dispersal  
128 (Pescador et al., 2014; Jara-Guerrero et al., 2015; Chacon-Labela et al., 2016; see  
129 Supporting Information Methods S2 for details). Then, we assessed interspecific spatial  
130 associations using bivariate point-pattern analysis (Baddeley et al. 2015). Species  
131 associations were estimated using the inhomogeneous cross-type pair correlation function  
132  $g(r)$  (Baddeley et al. 2015). This function looks at the proportion of individuals of species  $j$   
133 occurring within a neighborhood of distance  $r$  of the individuals of species  $i$ . The probability  
134  $p(r)$  of finding two plants of species  $i$  and  $j$  at two localities  $x$  and  $y$  separated by a distance  $r$   
135 is  $p(r) = \lambda_i(x)\lambda_j(y)g_{ij}(r) dx dy$ , where  $\lambda_i(x)$  and  $\lambda_j(y)$  are the densities of the two  
136 species at localities  $x$  and  $y$  estimated for each individual in inhomogeneous space  $dx$  and  
137  $dy$ , respectively (Supporting Information Fig. S6, Table S1).

138 For each species pair, we assessed the deviation of the observed bivariate function  
139 from the expected null model of species independence (i.e., from a distribution of each  
140 species based exclusively on their environmental preferences and dispersal characteristics  
141 and independent of other species). Using this approach, we accounted for spatial

142 environmental heterogeneity, shared microhabitat preferences and random dispersal as  
143 drivers of species associations (Chacon-Labelle et al., 2016; Condit et al., 2000; Pescador et  
144 al., 2014; Wiegand et al. 2012).

145 In order to statistically determine whether observed associations  $\hat{g}_{ij}(r)$  ( $n = 342$ )  
146 were significantly different from expectation of species independence, we used a goodness-  
147 of-fit (GoF) test based on the Diggle-Cressie-Loosmore-Ford (DCLF) test statistic (Diggle  
148 2003; Loosmore and Ford 2006; Baddeley et al. 2014). This is a Monte Carlo test based on  
149 the test statistic  $u = \int_0^R (g(r) - g_{theo}(r))^2 dr$ , which considers the integral of squared  
150 absolute deviation between the  $g(r)$  function and its theoretical value  $g_{theo}(r)$  between  $r =$   
151  $1$  and  $r = R$ . As  $g(r)$  we considered the empirical, observed pattern  $\hat{g}_{ij}(r)$ , and as  $g_{theo}(r)$   
152 the average of the theoretical, computed  $\bar{g}_{ij}(r)$  function (Baddeley et al. 2014). The  
153 maximum spatial distance  $R = 75$  cm was considered because it is one fourth of the shortest  
154 side of the sampling plot (3 m). Monte Carlo (MC) simulations were used to generate  
155  $g_{theo}(r)$  distributions under the null hypothesis of independence of species  $j$  with respect  
156 to species  $i$ . MC simulations consisted in shuffling individuals of species  $i$  according to their  
157 null-model distribution (i.e., the models fitted previously) while keeping the individuals of  
158 species  $j$  at their observed coordinates (Wiegand and Moloney 2014). This process  
159 randomizes the spatial association between species while holding all other processes  
160 constant. A total of 199 MC simulations were performed using the *envelope* function and  
161 tested using the *dclf.test* function in the R package *spatstat* (Baddeley et al. 2015). Note that  
162 statistical artefacts due to different sample sizes to fit species model or random noise in the  
163 MC null model may affect the quality and detectability of species associations (Wiegand and  
164 Moloney 2014; Baddeley et al. 2015).

165

166 *Network analysis*

167 Network models were used to map and analyze plant associations at the community level.  
168 We built a directed network (Kolaczyk and Csárdi 2014)  $G = (V, E)$  composed of  $V$  plant  
169 species and  $E \subseteq V_i \times V_j$  species links. We considered as species links  $E_{ij}$  the significant  
170 spatial associations  $u$  between plant species  $i$  and  $j$  ( $\alpha = 0.05$ ). In other words, we  
171 considered that a link existed between two plant species when the observed  $p$ -value of the  
172 GoF DCLF statistic test was lower than 0.05.

173 To reveal network-wide organization of the plant community, we measured: (a) the  
174 number of connections  $k$  of each plant species. This is the most basic species-level network  
175 property indicating the degree of interconnection of a species within a community. It was  
176 calculated using the *degree* function in igraph (Csárdi and Nepusz 2006). (b) the overall  
177 network structure as clustering or transitivity (Watts and Strogatz 1998; Kolaczyk and Csárdi  
178 2014), which is defined as the probability that two or more species associated to the same  
179 species are also associated with each other (as if friends of mine are also each other's  
180 friends). We calculated transitivity using the clustering coefficient  $c = N^{-1} \sum_{i=1}^N (s_i (k_i -$   
181  $1))^{-1}$ , where  $k_i$  is the number of species associated to species  $i$  and  $s_i$  is the number of  
182 associations among species associated to species  $i$  (Watts and Strogatz 1998). Clustering  $c$   
183 measures the local cohesiveness of a group of species and the degree of interconnections of  
184 a community. We computed clustering using the *transitivity* function in igraph R package  
185 (Csárdi and Nepusz 2006).

186 In order to assess the deviation of observed network properties from random  
187 expectation, we built random networks according to the  $G(n, m)$  Erdős–Rényi model  
188 (Kolaczyk and Csárdi 2014). This null model builds networks by assigning associations  
189 randomly to each pair of species on the basis of independent and identically distributed



190 binomial trials. We built 999 random networks with the same number of species and  
191 associations as the observed network. We used the *sample\_gnm* function in igraph (Csárdi  
192 and Nepusz 2006).

193

#### 194 *Statistical analysis*

195 To test the significance of observed network properties (i.e., species connections and  
196 clustering), we calculated the  $p$ -value as  $\hat{P} = 1 - \sum_i^S I[H_{obs} > H_j]/s$ , where  $I[H_{obs} > H_j]$  is an  
197 indicator function that equals 1 if the observed network property was greater (or smaller)  
198 than the random value and 0 otherwise, across  $s = 999$  simulations. Species connections  
199 were standardized with the  $z$ -score as  $z(k) = \hat{k}_i - \bar{k}_i / sd(k_i)$ , which indicates the relative  
200 deviation of observed number of connections  $k$  of each plant species  $i$  from random mean  
201 expectation  $\bar{k}_i$ .

202 Then, we tested whether species traits predicted species connections. We used  
203 Principal Component Analysis (Le et al. 2008) to reduce the dimensionality of trait space  
204 using the following variables: plant diameter, height, leaf mass per area (LMA), number of  
205 leaves, abundance and cover (Supporting Information Table S2). Variables were  
206 standardized; moss was excluded as lacking leaf traits. We extracted species scores for the  
207 first two principal components (PCs). We used linear models with these two PCs scores as  
208 predictors and species connections as response. We used the *PCA* function in FactoMineR  
209 (Le et al. 2008) and *lm* and *anova* in R (R Core Team 2018).

210

## 211 **Results**

212 We detected a total of 36 significant spatial associations. We found that positive  
213 associations ( $n = 34$ ) but not negative associations ( $n = 2$ ) between species characterized our

214 alpine plant community (Fig. 2). Our plant–plant association network was therefore  
215 composed by  $V = 19$  plant species and  $E = 36$  links (Fig. 3). Three plant species – *Dryas*  
216 *octopetala*, *Linaria alpina* and *Leontodon montanus* – were significantly more connected to  
217 other species than expected by chance ( $P = 0.003$ ,  $P = 0.003$ ,  $P = 0.060$ , respectively; Fig. 4a).  
218 Three plant species – *Galium anisophyllum*, *Saxifraga aizoides* and *Thymus praecox* – were  
219 significantly less connected to other species than expected by chance ( $p = 0.011$ ,  $p = 0.086$ ,  $p$   
220  $= 0.090$ , respectively; Figure 4a).

221 The first PC was composed of species diameter ( $r = 0.952$ ,  $P < 0.001$ ), cover ( $r = 0.872$ ,  
222  $P < 0.001$ ), number of leaves ( $r = 0.846$ ,  $P < 0.001$ ), LMA ( $r = 0.602$ ,  $P < 0.001$ ) and plant  
223 height ( $r = 0.506$ ,  $P = 0.003$ ). This PC1 marginally explained species connections ( $\beta = 0.380 \pm$   
224  $0.178$  SE,  $F_{1,15} = 4.53$ ,  $P = 0.050$ ). The second PC was composed of abundance ( $r = 0.780$ ,  $P =$   
225  $0.001$ ), LMA ( $r = 0.506$ ,  $P = 0.032$ ) and plant height ( $r = -0.576$ ,  $P = 0.012$ ). This PC2  
226 significantly explained species connections ( $\beta = 0.792 \pm 0.273$  SE,  $F_{1,15} = 8.1$ ,  $P = 0.011$ ; Fig.  
227 S7; Tab. S3). Over-connected plant species *D. octopetala*, *L. alpina* and *L. montanus* were  
228 dominant, stress-tolerant with high LMA and small stature. Less-connected plant species *G.*  
229 *anisophyllum*, *S. aizoides* and *T. praecox* were rare, water- and nutrient-demanding species  
230 with low LMA (Fig. S7).

231 The plant interaction network was overall organized in a transitive, cohesive manner.  
232 Indeed, the overall degree of clustering of the plant network was significantly higher  
233 compared with random networks ( $c = 0.33$ ,  $P = 0.001$ , Fig. 4c).

234

235

236 **Discussion**

237 Our new approach combining spatial ecology with network theory and functional traits  
238 provided new insights on assembly process of plant communities. On the one hand, with  
239 spatial point-pattern analysis we could identify and isolate species associations by  
240 considering relevant confounding factors such as environmental heterogeneity and species  
241 microhabitat preferences (Diggle 2003; McGill 2010; Wiegand and Moloney 2014; Baddeley  
242 et al. 2015). On the other hand, with network models we could analyze a complex and  
243 complete set of species associations beyond pairwise interactions (Verdù and Valiente-  
244 Banuet 2008; Levine et al. 2017; Losapio et al. 2018; Delalandre and Montesinos-Navarro  
245 2018). Integrating spatial analysis within network analysis therefore helped us to better  
246 reveal and model the structure of plant communities. In addition, the use of functional traits  
247 could provide a mechanistic, process-oriented view of the assembly of the plant interaction  
248 network.

249 Our findings support the hypothesis that positive associations through stress-tolerant  
250 species can support the cohesiveness of plant networks in this alpine community, with  
251 functional traits explaining the assembly. Our observed network was composed of 19 plant  
252 species linked by 36 associations. This yields a level of connectivity equal to 11%, which is  
253 similar to other plant networks, for instance in deserts (Verdù and Valiente-Banuet 2008;  
254 Losapio et al. 2018) and drylands (Saiz et al. 2018) or even similar compared to aquatic food  
255 webs (Dunne et al. 2002). Only one plant species was completely isolated from the network  
256 whereas three species were significantly more connected to other plant species than  
257 expected by chance. Isolated species were more competitive and nutrient-demanding  
258 plants, as indicated by their lower LMA and taller stature. Highly connected species were  
259 stress-tolerant plants, as indicated by high LMA, that dominate the vegetation. Several  
260 subordinate and less-connected plant species were positively associated with them.

261 In line with experimental evidence of facilitation by *Dryas octopetala* (Klanderud and  
262 Totland 2005), our results indicate that this dwarf shrub can act as “foundation” species.  
263 This highlight that foundation species such as *D. octopetala* can have a pivotal role in the  
264 cohesiveness of plant networks and organization of plant communities. Furthermore, this is  
265 consistent with the idea that facilitation is more common in stressful alpine environments  
266 then elsewhere in grassland (Callaway et al. 2002; Cavieres et al. 2014) and suggests that  
267 species with positive effects on the community are the highly connected, stress-tolerant  
268 species up in the hierarchy, while the potential “beneficiaries” are the less connected,  
269 subordinate species (Brooker et al. 2008).

270 The plant network had a clustering structure, with species significantly interconnected  
271 among each other than expected by chance. This means that, on average, two or more plant  
272 species associated to a common species were likely associated to each other. This indicates  
273 that besides the primary effect of foundation species also subordinate species are in turn  
274 associated with each other. This supports the call to move beyond pair-wise competition in  
275 plant communities (Levine et al. 2017) and considering interactions among plants at the  
276 level of the entire network. Finally, these results might explain the patchy structure of the  
277 examined alpine tundra vegetation because several plant species tended to aggregate more  
278 often than expected by chance. Potential underlying mechanisms might be positive  
279 feedbacks or facilitation cascades among plant species (Bruno et al. 2003; Meron 2012) as  
280 well as increasing pollinator availability among facilitating plants (Losapio et al., 2017).

281 Taken together, our results reveal a network of mostly positively interacting plant  
282 species in an alpine plant community. Few stress-tolerant species are central in supporting  
283 network structure, facilitating the formation of a patchy tundra community. Despite the  
284 lower proportion of species associations compared to neutral associations, the plant

285 community showed a well-structured and cohesive web of interdependencies among plant  
286 species.

287 In conclusion, we have shown that combining spatial patterns with network theory  
288 and functional traits can advance our understanding of the assembly of plant communities.  
289 It is, however, important to bear in mind though that observational studies such as the  
290 present one may only suggest potential mechanisms underpinning observed patterns.  
291 However, since the number of co-occurring species in natural communities can be high,  
292 manipulative experiments used to infer species dependencies are often restricted to a  
293 limited number of pair-wise species combinations. To overcome this limitation including as  
294 many species as possible, this analytical framework can be efficient in revealing the  
295 assembly of plant communities.

296

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303

## 304 **References**

305 Baddeley, A., Diggle, P.J., Hardegen, A., Lawrence, T., Milne, R.K. & Nair, G. (2014) On tests  
306 of spatial pattern based on simulation envelopes. *Ecological Monographs*, 84, 477–489.  
307 Baddeley, A., Rubak, E. & Turner, R. (2015) *Spatial Point Patterns: Methodology and Appli-*  
308 *cations*. USA: CRC Press.

309 Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., ...,  
310 Michalet, R. (2008) Facilitation in plant communities: the past, the present, and the future.  
311 *Journal of Ecology*, 96, 18–34.

312 Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into ecological  
313 theory. *Trends in Ecology & Evolution*, 18, 119–125.

314 Callaway, R.M., Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, ... Cook, B.J. (2002)  
315 Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–848.

316 Cavieres, L.A., Brooker, R.W., Butterfield, B.J., Cook, B.J., Kikvidze, Z., Lortie, C.J., ... Callaway,  
317 R.M. (2014) Facilitative plant interactions and climate simultaneously drive alpine plant  
318 diversity. *Ecology Letters*, 17, 193–202.

319 Chacon-Labela, J., de la Cruz, M. & Escudero, A. (2016) Beyond the classical nurse species  
320 effect: diversity assembly in a mediterranean semi-arid dwarf shrubland. *Journal of*  
321 *Vegetation Science*, 27, 80–88.

322 Chacon-Labela, J., de la Cruz, M. & Escudero, A. (2017) Evidence for a stochastic geometry  
323 of biodiversity: the effects of species abundance, richness and intraspecific clustering.  
324 *Journal of Ecology*, 105, 382-390.

325 Condit, R., Asthon, P. S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., ...  
326 Yamakura, T. (2000) Spatial patterns in the distribution of tropical tree species. *Science*, 288,  
327 1414–1418.

328 Csardi, G. & Nepusz, T. (2006) The igraph software package for complex network research.  
329 *InterJournal Complex Systems*, 1695.

330 Delalandre, L. & Montesinos-Navarro, A. (2018) Can co-occurrence networks predict plant–  
331 plant interactions in a semi-arid gypsum community? *Perspectives in Plant Ecology,*  
332 *Evolution and Systematics*, 31, 36–43.

333 Diggle, P.J. (2003) *Statistical analysis of spatial point patterns*. UK: Edward Arnold.

334 Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Food-web structure and network theory:  
335 The role of connectance and size. *Proceedings of the National Academy of Sciences of the*  
336 *United States of America*, 99, 12917–12922.

337 Durrett, R. & Levin, S. (1998) Spatial aspects of interspecific competition. *Theoretical*  
338 *Population Biology*, 53, 30–43.

339 Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding K.N. & Lavorel, S. (2009) Linking  
340 individual response to biotic interactions with community structure: a trait-based  
341 framework. *Functional Ecology*, 23, 1167-1178.

342 Jara-Guerrero, A., De la Cruz, M., Espinosa, C.I, Méndez, M., Escudero, A. (2015). Does  
343 spatial heterogeneity blur the signature of dispersal syndromes on spatial patterns of woody  
344 species? A test in a tropical dry forest. *Oikos*, 124, 1360–1366.

345 Kefi, S., Rietkerk, M., van Baalen, M. & Loreau, M. (2007) Local facilitation, bistability and  
346 transitions in arid ecosystems. *Theoretical Population Biology*, 71, 367–379.

347 Kikvidze, Z., Brooker, R.W., Butterfield, B.J., Callaway, R.M., Cavieres, L.A., Cook, B.J., ...  
348 Schöb, C. (2015) The effects of foundation species on community assembly: a global study  
349 on alpine cushion plant communities. *Ecology*, 96, 2064–2069.

350 Klanderud, K. & Totland, O. (2005) The relative importance of neighbours and abiotic  
351 environmental conditions for population dynamic parameters of two alpine plant species.  
352 *Journal of Ecology*, 93, 493501.

353 Kolaczyk, E.D. & Csárdi, G. (2014) *Statistical Analysis of Network Data with R*. Springer-  
354 Verlag.

355 Le, S., Josse, J., Husson, F. (2008) FactoMineR: An R package for Multivariate Analysis.  
356 *Journal of Statistical Software*, 25, 1–18-

357 Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017) Beyond pairwise mechanisms  
358 of species coexistence in complex communities. *Nature*, 546, 56–64.

359 Loosmore, N.B. & Ford, E.D. (2006) Statistical inference using the *G* or *K* point pattern spatial  
360 statistics. *Ecology*, 87, 1925–1931.

361 Losapio, G. & Schöb, C. (2017) Resistance of plant–plant networks to biodiversity loss and  
362 secondary extinctions following simulated environmental changes. *Functional Ecology*, 31,  
363 1145–1152.

364 Losapio, G., Pugnaire F.I., O’Brien, M.J. & Schöb, C. (2018) Plant life history stage and nurse  
365 age change the development of ecological networks in an arid ecosystem. *Oikos*.

366 MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of  
367 coexisting species. *The American Naturalist*, 101, 377–385.

368 McGill, B.J. (2010) Measuring the Spatial Structure of Biodiversity. In: Magurran AE, McGill  
369 B, eds. *Biological Diversity. Frontiers in Measurement and Assessment*. Oxford, UK: Oxford  
370 University Press.

371 Meron, E. (2012) Pattern-formation approach to modelling spatially extended ecosystems.  
372 *Ecological Modelling*, 234, 70–82.

373 Pescador, D.S., Chacon-Labela, J., de la Cruz, M. & Escudero, A. (2014) Maintaining  
374 distances with the engineer: patterns of coexistence in plant communities beyond the  
375 patch-bare dichotomy. *New Phytologist*, 204, 140–148.

376 R Core Team (2018). *R: A Language and Environment for Statistical Computing*.  
377 [<http://www.r-project.org/>].

378 Rietkerk, M., Dekker, S.C., de Ruiter, P.C. & van de Koppel, J. (2004) Self-organized  
379 patchiness and catastrophic shifts in ecosystems. *Science*, 305, 1926–1929.

380 Ripley, B.D. (1981) *Spatial Statistics*. John Wiley & Sons, Inc.



381 Saiz, H., Alados, C.L. & Pueyo, Y. (2014). Plant–plant spatial association networks in  
382 gypsophilous communities: the influence of aridity and grazing and the role of gypsophytes  
383 in its structure. *Web Ecology*, 14, 39–49.

384 Saiz, H., Gomez-Gardeñes, J., Borda J.P. & Maestre, F.T. (2018) The structure of plant spatial  
385 association networks is linked to plant diversity in global drylands. *Journal of Ecology*.

386 Schöb, C., Butterfield, B.J. & Pugnaire, F.I. (2012) Foundation species influence trait-based  
387 community assembly. *New Phytologist*, 196, 824–834.

388 Schöb, C., Kammer, P.M., Kikvidze, Z., Choler, P., Veit, H. (2008) Changes in species  
389 composition in alpine snowbeds with climate change inferred from small-scale spatial  
390 patterns. *Web Ecology*, 8, 142–159.

391 Schöb, C., Macek, P., Piston, N., Kikvidze, Z. & Pugnaire, F.I. (2017) A trait-based approach to  
392 understand the consequences of species plant interactions for community structure. *Journal*  
393 *of Vegetation Science*, 696-704.

394 Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, 75,  
395 2–16.

396 Verdù, M. & Valiente-Banuet, A. (2008) The nested assembly of plant facilitation networks  
397 prevents species extinctions. *The American Naturalist*, 172, 751–760.

398 Watts, D.J. & Strogatz, S.H. (1998) Collective dynamics of ‘small-world’ networks. *Nature*,  
399 393, 440-442.

400 Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Savitri Gunatilleke, C.V., Nimal  
401 Gunatilleke, I.A.U. (2012) Testing the independent species’ arrangement assertion made by  
402 theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society B*, 279,  
403 3312–3320.

404 Wiegand, T. & Moloney, K.A. (2014) *Handbook of spatial point-pattern analysis in ecology*.

405 USA: CRC Press.

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407 **Author contributions**

408 GL and CS designed the study, GL collected data and analyzed them, MC provided new  
409 analytical methods, all authors discussed data analysis, commented the results and edited  
410 the manuscript. All authors are included in the author list and agree with its order and they  
411 are aware the manuscript has been submitted. The authors declare no competing financial  
412 interests.

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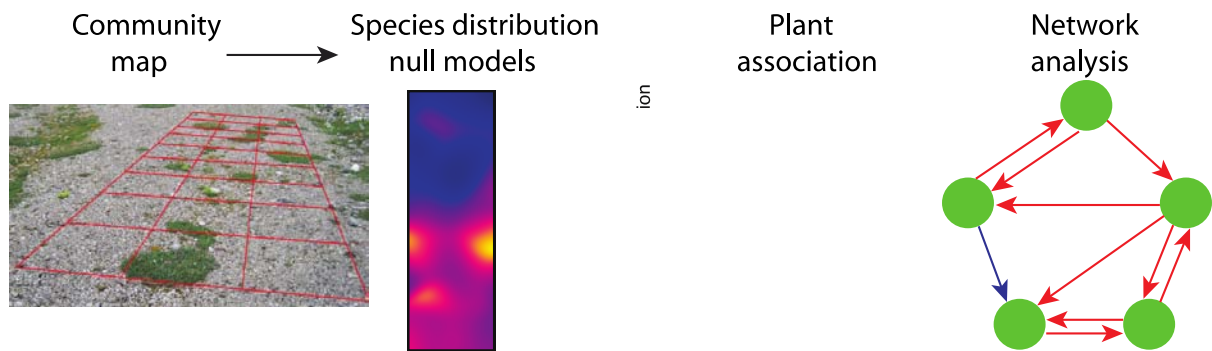
414 **Data accessibility**

415 The raw and analyzed data supporting the findings of this study and R code will be  
416 deposited in ETH Research Collection.

417

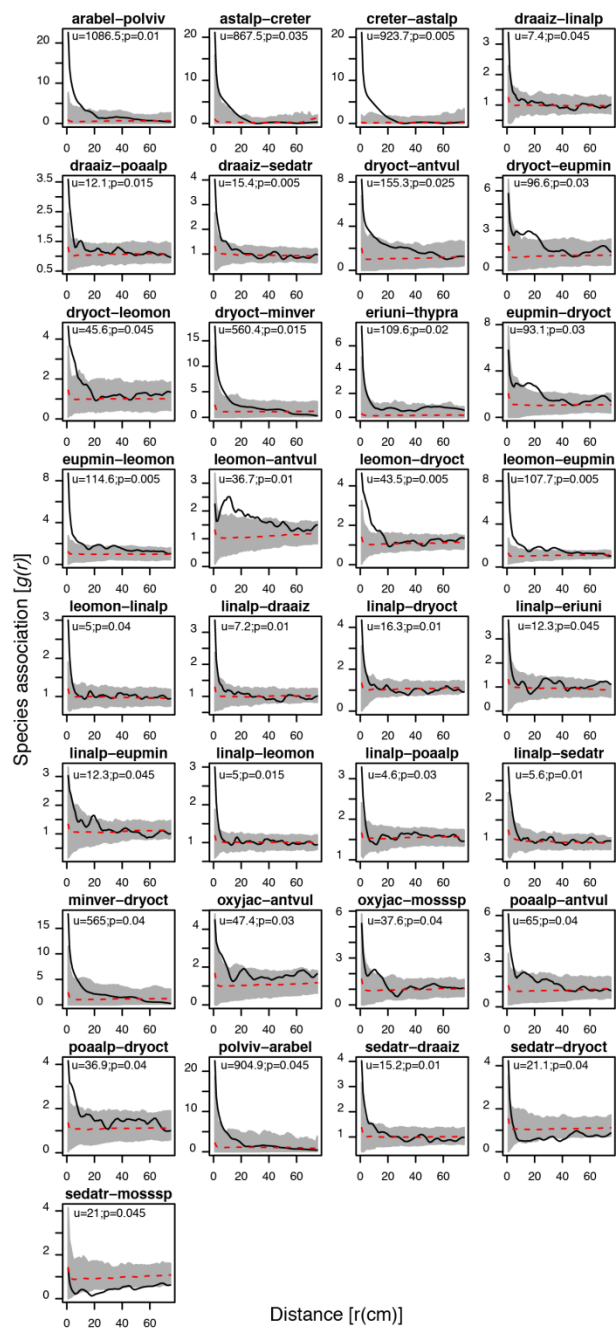
418 **Figures**

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420

421 **Fig. 1** Framework for studying plant networks. A plant community is fully mapped at the  
422 individual level. Spatial point-pattern analysis is then used to identify non-random species  
423 associations. Finally, network analysis is used to reveal structural properties of plant–plant  
424 association networks.



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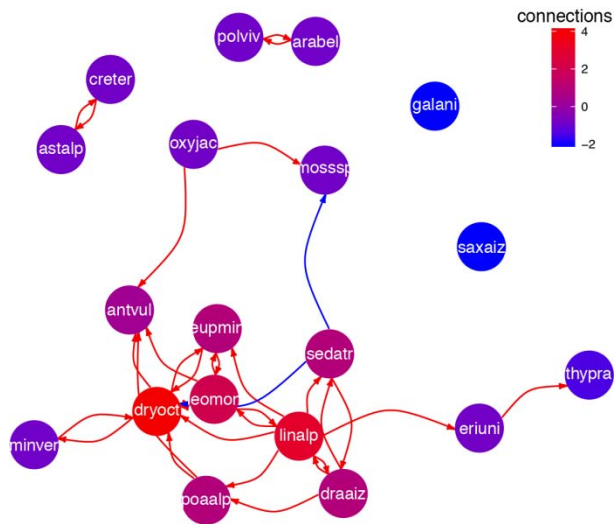
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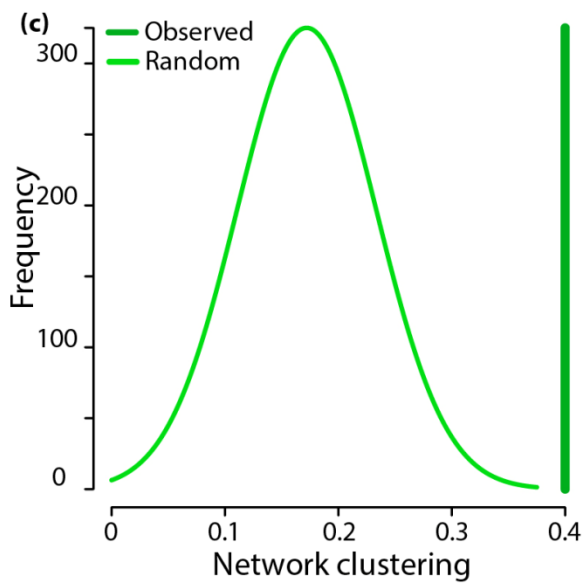
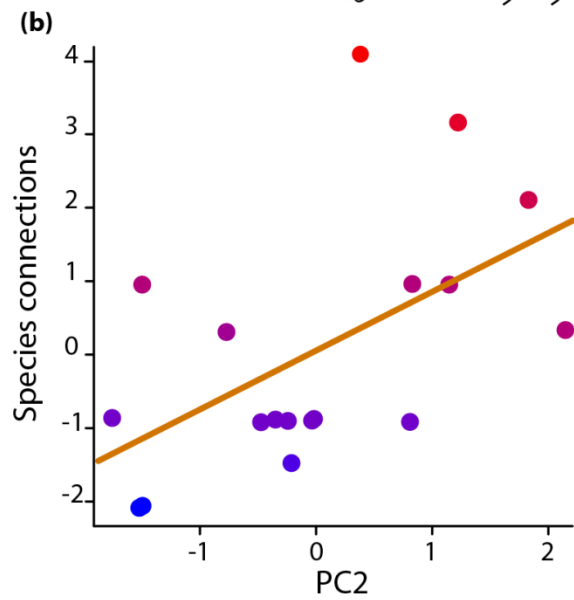
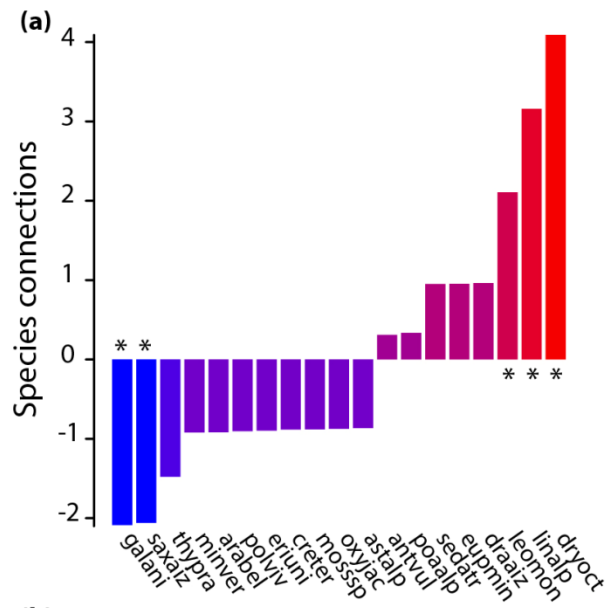
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**Fig. 2** Analysis of spatial patterns using the pair correlation  $g$  function. Panels show significant associations between pairs of plant species (see Tab. S2 for species names). Solid black lines represent the observed pattern  $\hat{g}(r)$ , red dashed lines represent the average of theoretical, simulated patterns  $\bar{g}(r)$ . Shading indicates the pointwise envelope obtained from 199 MC simulations of the  $g$  function. GoF DCLF statistic test  $u$  and relative  $p$  values are reported.



432

433 **Fig. 3.** Plant network in a patchy tundra vegetation dominated by *Dryas octopetala*. Plant  
 434 species are depicted with dots (see Tab. S2 for species names), whose color indicates the  
 435 standardized connections. Positive associations are depicted with red arrows, negative  
 436 associations with blue arrows.



438 **Fig. 4** Analysis of plant networks. **a)** Deviation (z-score) of observed number of connections  
439  $k$  of each plant species from random expectations. **b)** Relationship between PC2 and species  
440 connections. PC2 correlated positively with abundance and LMA and negatively with height  
441 (see also Fig. S7 and Tab. S3). **c)** Observed network clustering  $c$  (line) and distribution of  
442 clustering values from 999 random networks (curve).

443

#### 444 **Supporting Information**

445 Additional Supporting Information may be found in the online version of this article:

446 **Fig. S1** Study area.

447 **Fig. S2** Study site.

448 **Fig. S3** Species accumulation curve.

449 **Fig. S4** Covariate maps.

450 **Fig. S5** Complete spatial randomness (CSR) models.

451 **Fig. S6** Best null models of species independence.

452 **Fig. S7** Factor map of Principal Component Analysis.

453 **Table S1** Best null models of species independence.

454 **Table S2** Summary data of functional traits and species-level network analysis.

455 **Table S3** Summary results of Principal Component Analysis.

456 **Methods S1** Plant functional traits.

457 **Methods S2** Soil analysis.

458 **Methods S3** Spatial point-pattern analysis.