

1 **Floral resource-landscapes and pollinator-mediated interactions**  
2 **in plant communities**

3 Nottebrock, Henning <sup>1,3,4\*</sup>, Schmid, Baptiste <sup>2,3</sup>, Mayer, Katharina<sup>3</sup>, Devaux, Céline <sup>4</sup>, Esler,  
4 Karen J. <sup>3</sup>, Böhning-Gaese, Katrin <sup>2,5</sup>, Schleuning, Matthias <sup>2</sup>, Pagel, Jörn <sup>1,4</sup> & Schurr, Frank M.  
5 <sup>1,4</sup>

6 <sup>1</sup> Institute of Landscape and Plant Ecology, University of Hohenheim, August-von-Hartmann-  
7 Str. 3, 70599 Stuttgart, Germany

8 <sup>2</sup> Senckenberg Biodiversity and Climate Research Centre (BiK-F) and Senckenberg  
9 Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

10 <sup>3</sup> Department of Conservation Biology and Entomology and Centre for Invasion Biology,  
11 Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

12 <sup>4</sup> Institut des Sciences de l'Evolution, UMR 5554, Université Montpellier 2, Place Eugène  
13 Bataillon, 34095 Montpellier Cedex 05, France

14 <sup>5</sup> Goethe University Frankfurt, Institute for Ecology, Evolution & Diversity, Max-von-Laue-Str.  
15 13, 60439 Frankfurt (Main), Germany

16

17 \* Correspondence: Henning Nottebrock, University of Hohenheim, Institute of Landscape and  
18 Plant Ecology, August-von-Hartmann Str. 3, Stuttgart 70599, Germany. E-mail:  
19 [henning@nottebrock.net](mailto:henning@nottebrock.net), phone: +49 (0)711 459-22330, fax: +49 (0)711 459-22831

20

21 Short running title: Floral resource-landscapes and pollination

22 Keywords: bird foraging behaviour, community ecology, energetics of pollination,  
23 facilitation, indirect interactions among plants, intra- and interspecific competition, nectar  
24 sugar, plant-animal interactions, plant functional traits, species coexistence.

25 Type of article: Letter

26 Word counts: 150 (Abstract), 4933 (main text)

27 Figures and Tables: 4 Figures in the main text and 2 Figures, 1 Table and 1 Video in  
28 Supplementary Information.

29 References: 46 general references, no data-source references

30

31 **Author contributions**

32 HN, BS, KJE, KBG, MS and FMS designed the study, HN, BS and KM collected data, HN, JP and  
33 FMS ran statistical analyses and wrote a first draft, and all authors contributed substantially  
34 to the manuscript.

35 **Abstract**

36 Plant communities provide floral resource-landscapes for pollinators. Yet, it is insufficiently  
37 understood how these landscapes shape pollinator-mediated interactions among multiple  
38 plant species. Here, we study how pollinators and the seed set of plants respond to the  
39 distribution of a floral resource (nectar sugar) in space and across plant species,  
40 inflorescences and flowering phenologies. In a global biodiversity hotspot, we quantified  
41 floral resource-landscapes on 27 sites of 4 ha comprising 127,993 shrubs of 19 species.  
42 Visitation rates of key bird pollinators strongly depended on the phenology of site-scale  
43 resource amounts. Seed set of focal plants increased with resources of conspecific  
44 neighbours and with site-scale resources, notably with heterospecific resources of lower  
45 quality (less sugar per inflorescence). Floral resources are thus a common currency  
46 determining how multiple plant species interact via pollinators. These interactions may alter  
47 conditions for species coexistence in plant communities and cause community-level Allee  
48 effects that promote extinction cascades.

49

## 50 **Introduction**

51 Pollinators mediate indirect interactions between conspecific and heterospecific plants and  
52 can thus shape the dynamics of plant communities (Ghazoul 2005; Sargent & Ackerly 2008;  
53 Pauw 2013). Within plant populations, these pollinator-mediated interactions can be  
54 positive when neighbouring plants attract pollinators and increase visitation rates, or  
55 negative when plants compete for shared pollinators (Rathcke 1983; Ghazoul 2005). At the  
56 level of plant communities, generalist pollinators can mediate both competitive and  
57 facilitative interactions between plant species (Moeller 2004; Sargent & Ackerly 2008;  
58 Mitchell *et al.* 2009). These interspecific interactions depend on the foraging behaviour of  
59 pollinators in multi-species plants communities, and on whether interspecific pollen transfer  
60 reduces plant reproductive success (Waser 1978). Importantly, the relative magnitude of  
61 intra- and interspecific competition mediated by pollinators determines whether pollinators  
62 promote or hinder coexistence of plant species (Pauw 2013).

63 Energetic principles play a key role for pollinator-mediated interactions (Heinrich & Raven  
64 1972; Heinrich 1975; Tomlinson *et al.* 2014): pollinators take up the energy provided by  
65 inflorescences (notably nectar) and partly use it for foraging movements that define the  
66 pollination services they deliver to plants. Consequently, spatial variation in the floral  
67 resource-landscape generated by a plant community should translate into spatial variation in  
68 pollinator foraging behaviour and pollinator-mediated interactions (Ghazoul 2005; Fig. 1a).  
69 Pollinator-mediated interactions also depend on flowering phenology because pollinators  
70 track temporal changes in resource-landscapes (Hegland *et al.* 2009; Fig. 1a). Despite these  
71 simple principles, pollinator-mediated interactions among plant species within communities  
72 can exhibit considerable complexity. This complexity arises from spatial and temporal

73 variation in floral resources and from the partitioning of these resources among plant  
74 species and individual inflorescences (Fig. 1).

75 Pollinators can mediate interactions among plants at several spatial and temporal scales.  
76 Their small-scale foraging behavior affects interactions among inflorescences on the same  
77 plant (Goulson 2000; Devaux *et al.* 2014) while foraging movements determine interactions  
78 and pollen transfer among neighbouring plants (Seifan *et al.* 2014). At large spatial scales,  
79 pollinator abundance and pollination service respond to floral resource amounts provided by  
80 the entire community (Williams *et al.* 2012; Nottebrock *et al.* 2013). Importantly, the sign of  
81 pollinator-mediated interactions can change with spatial scale (Gunton & Kunin 2009).  
82 Overall, the intensity of pollinator-mediated interactions between two plants should  
83 decrease with the spatial and temporal distance between them (Heinrich & Raven 1972,  
84 Elzinga *et al.* 2007; Devaux & Lande 2009, Fig. 1a). Yet, even plants that do not flower  
85 simultaneously may interact via pollinators: early-flowering species can contribute to high  
86 pollinator densities that benefit late-flowering species (Riedinger *et al.* 2014).

87 In behavioural ecology, it is well established that the quality of resources in patches  
88 affects foraging decisions of animals. From the perspective of a foraging pollinator, an  
89 inflorescence is a food patch whose quality can be defined as the amount of floral resources  
90 available in a single visit (Pyke 1978). Hence, plant-pollinator interactions should not only  
91 depend on total resource amounts but also on whether these resources are split into a few  
92 high-quality inflorescences or into many low-quality inflorescences (Fig. 1b). Optimal  
93 foraging theory predicts that pollinators should respond to differences between the quality  
94 of a focal inflorescence and the quality of surrounding inflorescences: pollinators should  
95 prefer higher-quality inflorescences over lower-quality inflorescences (MacArthur & Pianka  
96 1966) and they should spend more time visiting them (Charnov 1976; Pyke 1978). Higher-

97 quality inflorescences can thus exert negative effects on pollinator visitation and  
98 reproductive success of surrounding plants with lower-quality inflorescences (Kandori *et al.*  
99 2009). Conversely, higher-quality inflorescences could attract more pollinators, which then  
100 pollinate neighbouring plants with lower-quality inflorescences (Seifan *et al.* 2014). The net  
101 outcome of these opposite effects of higher-quality inflorescences on their surroundings  
102 remains unclear. Moreover, it is not obvious how quality differences between a focal  
103 inflorescence and other inflorescences should be evaluated, because the set of available  
104 inflorescences depends on the spatial scale at which pollinators take their foraging decision,  
105 which is generally poorly known (Ghazoul 2005).

106 Pollinator-mediated interactions between a focal plant and the surrounding floral  
107 resources can also be affected by the ‘purity’ of these resources, defined as the proportion  
108 of floral resources contributed by conspecifics (Fig. 1c, Ghazoul 2005). Positive effects of  
109 purity on pollinator efficiency and plant reproductive success result from increased  
110 intraspecific pollen transfer and reduced stigma clogging by incompatible heterospecific  
111 pollen (Waser 1978; Shore & Barrett 1984). Additionally, purity may increase reproductive  
112 success via positive effects on pollinator visitation (Ghazoul 2005) because pollinators  
113 preferentially visit common plant species or because they sequentially visit inflorescences of  
114 the same species (Chittka and Thomson 2001). On the other hand, purity can reduce plant  
115 reproductive success if competition for pollinators is more intense among conspecifics than  
116 among heterospecifics (Pauw 2013). Furthermore, heterospecifics can increase pollinator  
117 visitation if different plant species with temporally staggered flowering phenologies facilitate  
118 each other via the maintenance of high pollinator densities (Riedinger *et al.* 2014). Hence,  
119 the purity of floral resources can have either positive or negative effects on plant

120 reproductive success and the balance between these effects most probably varies with the  
121 spatial and temporal scales at which floral resource purity is considered.

122 The spatial distribution, phenology, quality and purity of floral resource-landscapes are thus  
123 expected to strongly shape pollinator-mediated interactions among plants. Previous studies  
124 considered these aspects individually, demonstrated their relevance for plant-pollinator  
125 interactions but also yielded seemingly conflicting results (e.g. Kunin 1997; Ghazoul 2005,  
126 Gunton & Kunin 2009; Williams *et al.* 2012; Carvalheiro *et al.* 2014; Feldman & McGill 2014).

127 We argue that progress in understanding the effects of floral resources on pollination  
128 requires an integrative approach that quantifies the aforementioned aspects of floral  
129 resource-landscapes and analyses their relative importance for pollinator behaviour and  
130 plant reproductive success (Fig. 1). Here, we develop such an approach and apply it to 27  
131 plant communities from the South African Fynbos biome, a global biodiversity hotspot  
132 (Myers *et al.* 2000). Our objectives are to (1) quantify how floral resource-landscapes vary in  
133 space, time, quality and purity, and (2) determine the relevance of these aspects of floral  
134 resource-landscapes for pollinator visitation and seed set. We show that floral resource-  
135 landscapes explain pollinator-mediated interactions within and among plant species.  
136 Importantly, the multi-scale impacts of floral resources on plant communities can alter  
137 conditions for species coexistence and can cause community-level Allee effects that promote  
138 extinction cascades.

139

## 140 **Material and Methods**

### 141 *Study system and study design*

142 We studied shrub communities dominated by the species-rich genus *Protea* that has high  
143 ecological and economic importance in the Fynbos biome (Schurr et al. 2012) and is well  
144 suited for studying plant-pollinator interactions. *Protea* species frequently dominate the  
145 overstorey of Fynbos shrublands and provide copious amounts of nectar accumulated at the  
146 base of their inflorescences (flowerheads) (Collins & Rebelo 1987). These inflorescences bear  
147 many individual florets, each of which contains a single ovule and can thus produce a single  
148 seed (Rebelo 2001). To set seed, *Protea* species require pollinator visits to inflorescences and  
149 many species are strongly dependent on pollination by nectarivorous birds, notably Cape  
150 sugarbirds (*Promerops cafer*) and orange-breasted sunbirds (*Anthobaphes violacea*, Schmid  
151 et al. 2015). Since inflorescences (referred to as cones after flowering) are the functional unit  
152 of plant-pollinator interactions in our study system, we measured standing nectar sugar  
153 crops, pollinator visitation and seed set at the level of inflorescences.

154 Making use of the high beta-diversity of *Protea* meta-communities, we selected 27 study  
155 sites that vary in species composition and density of *Protea* (Fig. 2a). Each site consisted of a  
156 200x200 m<sup>2</sup> plot with a core zone of 120x120 m<sup>2</sup> surrounded by a 40 m wide buffer zone  
157 (Fig. 2b). To analyse the effects of floral resource-landscapes on pollinator-mediated  
158 interactions at these sites, we (1) generated fine-scale maps of all overstorey *Protea*  
159 individuals, (2) quantified sugar amount per inflorescence and phenological variation in the  
160 number of flowering inflorescences to predict floral resource-landscapes (Fig. 2d), (3)  
161 measured both visitation rates of key bird pollinators and seed set at the inflorescence level  
162 for a further subset of plants, and (4) and ran statistical analyses that quantify how pollinator



163 visitation and seed set are shaped by floral resources at the plant, neighbourhood and site  
164 scale, and by the phenology, quality and purity of these floral resources.

165

#### 166 *Fine-scale mapping*

167 We mapped all overstorey *Protea* plants on the study sites using differential GPS (Trimble  
168 GeoXH; median accuracy 20 cm) and recorded their size (canopy height) and species  
169 identity. In very dense monospecific stands (>6 individuals per 2 m<sup>2</sup>), we mapped the stand  
170 outline, recorded plant density and then simulated plant locations within the stand  
171 according to a complete spatial random distribution with the observed density. The sizes of  
172 these simulated plants were drawn from a stand-specific gamma distribution estimated by a  
173 maximum likelihood fit to the sizes of 30 plants measured per stand. In total, the fine-scale  
174 maps comprise 127,993 individuals of 19 *Protea* species, with 318 to 48,602 individuals per  
175 species, 83 to 37,253 individuals per site, and 3 to 9 species per site.

176

#### 177 *Trait-based prediction of floral resource-landscapes*

178 We monitored individual flowering phenologies for a subsample of 6,943 plants (51 to 1245  
179 plants per species) by counting flowering inflorescences at up to three visits during the  
180 flowering seasons in 2011 (March to December) or 2012 (March to August). For a subsample  
181 of 850 plants in the core zones, (4 to 80 plants per species) we harvested two inflorescences,  
182 measured their size and the proportion of open florets, and extracted their nectar by  
183 centrifugation (Armstrong & Paton 1990). We measured nectar volume with microsyringes  
184 (0.05 mL precision) and nectar concentration with a hand refractometer (Bellingham and  
185 Stanley, reading range: 0-50 Brix). Nectar concentration in Brix was then converted into

186 grams of sugar per litre and multiplied with nectar volume to obtain sugar amount per  
187 inflorescence.

188 To predict floral resource landscapes, we fitted trait-based models of sugar amount per  
189 inflorescence and number of inflorescences per plant. As predictors for these trait-based  
190 models, we measured inflorescence size, cone mass, specific leaf area (SLA), and trunk  
191 length from the ground to the first branch for a subsample of 2,580 plants in the core zone  
192 (25 to 502 plants per species). Additionally, the models included resprouting ability as a  
193 species-level trait (Rebello 2001). The model for inflorescence number also included a date-  
194 derived covariate to describe species-specific flowering phenologies. With these trait-based  
195 models we then predicted phenological variation in inflorescence number, sugar amount per  
196 inflorescence and their product, sugar amount per plant, for all 127,993 mapped plants (for  
197 details see Appendix S1 in Supporting Information).

198 From these spatially explicit predictions, we derived the amount, quality and purity of  
199 floral resources at the neighbourhood and site scales. At the neighbourhood scale (within  
200 40 m radius around each focal plant), we calculated sugar amounts using a neighbourhood  
201 index that accounts for the decline of neighbour effects with distance  $d$  from the focal plant  
202 (Uriarte et al. 2010): we summed the sugar amounts of all neighbours within 40 m weighted  
203 by  $1/(1+d)$ . At the site scale, we calculated the total sugar amount of all plants on the site (in  
204 g/ha). At both the neighbourhood and site scales, we also calculated purity and resource  
205 quality. Purity was calculated as the proportion of the sugar amount at the respective scale  
206 that is contributed by conspecifics of the focal plant. As a relative measure of resource  
207 quality at the neighbourhood and site scale, we subtracted the focal plant's sugar per  
208 inflorescence from the mean sugar per inflorescence at the respective scale.

209 Phenology was treated differently when characterizing floral resource-landscapes for  
210 analyses of pollinator visits and seed set, respectively (see below). For pollinator visits, we  
211 considered floral resource-landscapes at the respective day of observation. In contrast, seed  
212 set integrates over the entire flowering period of an inflorescence and seed set analyses thus  
213 included temporally averaged resource variables that were weighted by the phenology of  
214 the focal plant (Appendix S1).

215

#### 216 *Pollinator observations and seed set measurements*

217 Pollinator visitation and seed set were measured on plants located within the core zones of  
218 the study sites. On up to three visits per site we counted legitimate inflorescence visits by  
219 nectarivorous Cape sugarbirds (*Promerops cafer*) and orange-breasted sunbirds  
220 (*Anthobaphes violacea*). We recorded the number of inflorescences probed by birds for  
221 1,333 plants (1 to 346 plants per species) during 45 min sessions in the morning (8am –  
222 10am, up to 10 plant-level observations per session). We only considered legitimate probing  
223 events, in which birds had contact with stigmas and thus potentially transferred pollen.

224 Seed set was measured for 1,717 plants (22 to 378 plants per species) by counting the  
225 number of fertile seeds ( $W_{\text{fertile}}$ ) in up to five randomly harvested mature cones (Nottebrock  
226 *et al.* 2013). The seeds were cross-cut and then probed with a needle to identify fertile seeds  
227 containing a soft endosperm. Pre-dispersal seed predation rate was estimated as the  
228 proportion of the cross-sectional cone area consumed by predators. The total number of  
229 ovules per plant that could potentially set seed was calculated as  $W_{\text{potential}} = (1 - \pi_p) A_c / A_s$ ,  
230 where  $\pi_p$  is the estimated predation rate,  $A_c$  and  $A_s$  are the cross-sectional areas of cones

231 and seeds ( $A_c$  was measured for each cone,  $A_s$  was determined as the mean of up to 50 seeds  
232 per population).

233

#### 234 *Analysing effects of floral resource-landscapes on pollinator-mediated interactions*

235 To analyse how pollinator visits and seed set respond to different aspects of floral resource-  
236 landscapes, we used generalised linear mixed models (GLMMs, package lme4, Bates *et al.*  
237 2014) in R 3.1.1 (R Core Team 2013). We used Poisson errors for the number of pollinator  
238 visitations and binomial errors for seed set expressed as the ratio of fertile seeds to potential  
239 seeds ( $W_{\text{fertile}}/W_{\text{potential}}$ ). The model for pollinator visitation controlled for the number of  
240 visible inflorescences per plant (included as an offset) in order to describe pollinator  
241 visitation rate per inflorescence.

242 As explanatory variables, the models for both response variables included measures of  
243 floral resources at three spatial scales: the number of inflorescences and sugar per  
244 inflorescence at the focal plant scale, and sugar amount at the neighbourhood and site  
245 scales. To describe how resource purity and quality modify the effects of sugar amount at  
246 the neighbourhood and site scale, we included interactions of purity and quality with sugar  
247 amounts at the respective scale. We did not include main effects of purity and quality since  
248 this would imply that purity and quality play a role when sugar amounts are zero. To  
249 facilitate the interpretation of purity effects, we used impurity (1-purity), which is zero for a  
250 purely conspecific neighbourhood. Hence, the main effects of sugar amounts describe  
251 effects of 'pure' resource-landscapes in which all sugar is provided by conspecifics. By adding  
252 the impurity-interaction term to the corresponding main effect of sugar amount, one obtains  
253 the effect of sugar provided exclusively by heterospecifics with identical resource quality.

254 The further addition of the quality-interaction term describes the effect of sugar provided by  
255 heterospecifics with higher resource quality.

256 Analyses of both pollinator visitation and seed set corrected for focal plant size and the  
257 seed set analysis additionally controlled for direct plant-plant interactions (such as  
258 competition for nutrients) by including the density of con- and heterospecific neighbours  
259 (using again the  $1/(1+d)$  distance-weighting index). Lastly, we accounted for random  
260 variation in space, time and among species: for pollinator visits we included random effects  
261 of plant species and observation session (which encompasses site and day effects) and for  
262 seed set we included random effects of plant species and site.

263 To quantify the relevance of different aspects of floral resource-landscapes for pollinator  
264 visitation and seed set, we calculated the AIC difference between the full models (see above)  
265 and control models without the respective aspect. Control models for different spatial scales  
266 were obtained by dropping all resource variables at the respective scale, whereas control  
267 models for resource quality and purity omitted the respective interaction terms. In the  
268 control model for phenology, we replaced all phenology-weighted resource variables by the  
269 respective annual mean.

270 Finally, we examined the relationship between seed set (response variable) and pollinator  
271 visitation (explanatory variable) for the 279 plants for which both data were available. We  
272 used a binomial GLMM with a fixed effect of visitation per inflorescence and random effects  
273 of species identity and site. Note that pollinator observations were conducted on single  
274 dates within the flowering season, but not necessarily at the plant's peak flowering time.  
275 Pollinator visitation rates that were observed close to a plant's peak flowering time can be  
276 expected to be more representative for the entire flowering period and thus more closely

277 related to seed set than visitation rates observed towards the limits of the plant's flowering  
278 period. We therefore weighted each data point by  $\exp(-\Delta t^2/\sigma)$ , where  $\Delta t$  is the time  
279 difference between the pollinator observation and the plant's peak flowering time and  $\sigma$  is  
280 the standard deviation of the plant's flowering phenology (Appendix S1).

## 281 **Results**

### 282 *Spatiotemporal variation of floral resource-landscapes*

283 Trait-based models of flowering phenology and sugar amount per inflorescence quantify the  
284 spatiotemporal dynamics of floral resource-landscapes in the 27 study communities (Fig. 2,  
285 Video S1). At the plant scale, sugar per inflorescence varied between 0.01 g and 1.94 g, and  
286 the annual maximum of co-flowering inflorescences per plant varied between 0 and 44. The  
287 19 study species showed considerable differences in flowering phenology: their peak  
288 flowering time varied from March to October and they ranged from temporally-peaked to  
289 year-round flowering (Fig. 2c, Table S1). We calculated the average floral resource-landscape  
290 experienced by a flowering inflorescence by integrating sugar amounts and inflorescences  
291 over these flowering phenologies (see Appendix S1). At the site scale, this phenology-  
292 integrated sugar amount was on average 388.9 g/ha (95% interquartile range: 11.1 – 1414.9  
293 g/ha) with a mean purity of 52% (0 – 99%). The mean sugar amount of co-flowering  
294 inflorescences on the same site differed from an inflorescence's own sugar amount by an  
295 average quality difference of +0.008 g (-0.7 – +0.8 g). The summed sugar amount in the  
296 neighbourhood of flowering inflorescences (weighted by  $1/(1+d)$ ) was on average 18.3 g (0.4  
297 – 103.3 g) with a mean purity of 63% (0 – 100%) and a mean quality difference of -0.003 g (-  
298 0.6 – +0.7 g).

299

### 300 *Effects of floral resource-landscapes on pollinator visits and seed set*

301 The spatial structure, quality, purity and phenology of floral resource-landscapes were of  
302 different relevance for pollinator visitation and seed set (Fig. 3). For pollinator visitation, the  
303 relevance of floral resources at different spatial scales increased from the plant over the

304 neighbourhood to the site scale (Fig. 3a). Visitation rates depended strongly on the  
305 phenology of floral resources, and to a lesser extent on resource quality, but resource purity  
306 was of minor relevance for pollinator visitation (Fig. 3a). In contrast, seed set was mostly  
307 driven by floral resources at the neighbourhood scale (Fig. 3b). Moreover, seed set was  
308 strongly affected by the purity of floral resource-landscapes, whereas resource quality had  
309 intermediate relevance and phenology had relatively minor relevance for seed set (Fig. 3b).

310 Significant effects of floral resource-landscapes on pollinator visitation were only found at  
311 the neighbourhood and site scales, where the main effects of sugar amount were modified  
312 by interactions with resource quality (Fig. 4a). Pollinator visitation increased with sugar  
313 amount at the neighbourhood scale if neighbouring inflorescences had higher resource  
314 quality than the focal inflorescence (positive quality-resource interaction,  $\chi^2_{1 \text{ df}} = 4.33$ ,  $P <$   
315  $0.05$ , Fig. 4a). Site-scale sugar amounts had a strong negative effect on pollinator visitation,  
316 which was particularly pronounced if site-scale sugar amounts were composed of higher-  
317 quality inflorescences (negative quality-resource interaction,  $\chi^2_{1 \text{ df}} = 6.93$ ,  $P < 0.01$ , Fig. 4a).  
318 In contrast, the purity of floral resources did not alter the effect of sugar amount on  
319 pollinator visitation at either scale ( $P > 0.05$ ).

320 Seed set showed significant responses to all aspects of floral resource-landscapes at all  
321 spatial scales (Fig. 4b). At the plant scale, seed set increased with sugar amount per  
322 inflorescence ( $\chi^2_{1 \text{ df}} = 22.6$ ,  $P < 0.001$ , Fig. 4b) and decreased with the number of  
323 inflorescences on the focal plant ( $\chi^2_{1 \text{ df}} = 96.7$ ,  $P < 0.001$ , Fig. 4b). At the neighbourhood  
324 scale, seed set increased with floral resource amounts consisting entirely of conspecific  
325 sugar (positive main effect of neighbour sugar amount), but slightly decreased with resource  
326 amounts consisting entirely of heterospecific sugar (the positive main effect of neighbour  
327 sugar amount was outweighed by the negative impurity-resource interaction,  $\chi^2_{1 \text{ df}} = 262.0$ ,



328  $P < 0.001$ , Fig. 4b). This negative effect was particularly pronounced if neighbouring  
329 inflorescences had lower quality than the focal inflorescence (positive quality-resource  
330 interaction,  $\chi^2_{1 \text{ df}} = 117.3$ ,  $P < 0.001$ , Fig. 4b). While floral resource neighbourhoods had  
331 either positive or negative effects on seed set (depending on resource purity and quality),  
332 the effects of neighbour plant density were consistently negative. The negative intraspecific  
333 density dependence of seed set was stronger than the negative interspecific density  
334 dependence ( $\chi^2_{1 \text{ df}} = 57.8$ ,  $P < 0.001$ ). This negative effect of conspecific density was almost  
335 exactly compensated by the positive effect of conspecific sugar amounts (standardized  
336 regression coefficients for conspecific density and sugar amount were -0.33 and +0.33,  
337 respectively, Fig. 4b). At the site scale, we found a strong positive effect of sugar amounts,  
338 which was more positive if site-scale sugar resources were provided by heterospecific plants  
339 (positive impurity-resource interaction,  $\chi^2_{1 \text{ df}} = 100.3$ ,  $P < 0.001$ ) and by lower-quality  
340 inflorescences (negative quality-resource interaction,  $\chi^2_{1 \text{ df}} = 165.4$ ,  $P < 0.001$ , Fig. 4b). A  
341 positive relationship between pollinator visitation and seed set was found for the 279 focal  
342 plants on which we had measured both variables. The seed set of these plants showed a  
343 logistic response to pollinator visitation rate ( $\chi^2_{1 \text{ df}} = 9.7$ ,  $P < 0.01$ ).

344

## 345 **Discussion**

346 The high-resolution description of floral resource-landscapes for 27 plant communities  
347 enabled us to quantify how floral resources (nectar sugar amounts) vary in space and time,  
348 and how their partitioning among plant species and inflorescences causes differences in  
349 resource purity and quality. The relevance of these aspects of floral resource-landscapes  
350 differed between pollinator visitation and seed set: pollinator visitation largely depended on  
351 site-scale floral resources, whereas seed set was determined jointly by floral resources at the  
352 plant, neighbourhood and site scales (Figs. 3 and 4). Here we discuss the mechanisms  
353 causing these floral resource effects and their consequences for the dynamics of plant  
354 communities.

355

### 356 *Floral resource effects on pollination and seed set*

357 Floral resource amounts at the site scale had a strong negative effect on pollinator visitation  
358 per inflorescence but a strong positive effect on seed set (Fig. 4). While the negative  
359 response of pollinator visitation may seem surprising, it can be explained by the behaviour of  
360 bird pollinators. On the same study sites, bird pollinator abundance increases less than  
361 proportional with site-scale resources (B. Schmid, *personal communication*), possibly due to  
362 territoriality of bird pollinators. This negative effect does, however, not propagate into seed  
363 set (Fig. 4b). The opposite response of seed set to site-scale floral resources could result  
364 from saturation of stigmas at relatively low levels of pollinator visits, above which more visits  
365 do not translate into higher seed set. We observed such a saturating effect in the logistic  
366 relationship between seed set and pollinator visitation. Importantly, any interpretation of  
367 the differential responses of pollinator visitation and seed set to site-scale resource amounts

368 must consider the different temporal scales at which pollinator-mediated interactions act:  
369 competition for pollination results mainly from the behavioural response of pollinators to  
370 instantaneous resource offers, whereas facilitation mainly results from the numerical  
371 response of pollinators to long-term resource availability (Gahzoul 2005; Riedinger *et al.*  
372 2014). Facilitative effects caused by increased pollinator abundance thus likely dominate the  
373 positive effect of phenology-integrated resource variables on seed set. In contrast, pollinator  
374 visitation was negatively related to floral resource availability on the same day, which likely  
375 results from short-term competition for pollinator visits.

376 The purity of floral resources had weak effects on visitation (Figs. 3a and 4a), which is  
377 consistent with the finding that the bird pollinators of our study species are generalists that  
378 visit all available study species (B. Schmid, *personal communication*). In contrast, seed set  
379 increased with the purity of floral resources in the neighbourhood and decreased with the  
380 number of inflorescences on the focal plant (Fig. 4b), which is expected if seed set is limited  
381 by the availability of outcrossed conspecific pollen. The larger importance of phenology for  
382 pollinator visitation rather than seed set could arise because pollinator visitation depends on  
383 instantaneous resource-landscapes at the day of pollinator observation, whereas seed set  
384 integrates over phenological variation throughout the season. These different temporal  
385 scales could also explain why the positive effect of the site-scale floral resources on seed set  
386 increased with impurity (Fig. 4b) so that heterospecific floral resources had a stronger  
387 facilitative effect than conspecific resources. The flowering phenologies of our study species  
388 are displaced (Fig. 2b), which should reduce interspecific competition for shared pollinators  
389 (Devaux & Lande 2009). On the other hand, facilitative effects via the maintenance of high  
390 pollinator populations through the season are enhanced by the staggering of flowering  
391 phenologies among species (Moeller 2004; Riedinger *et al.* 2014). Overall, the balance

392 between competitive and facilitative effects on pollination visitation and seed set can thus  
393 be more positive for heterospecific than for conspecific floral resources.

394 The resource quality (sugar per inflorescence) of focal plants had a positive effect on their  
395 seed set (Fig. 4). Moreover, pollinator visitation and seed set of plants with lower-quality  
396 resources benefitted from higher-quality neighbours, which suggests that these neighbours  
397 attract pollinators and exert a 'magnet effect' (Moeller 2004; Seifan et al. 2014). In contrast,  
398 it is disadvantageous for a plant to offer resources of lower quality than the site-scale  
399 average. This possibly arises because the large-scale foraging decisions of pollinators induce  
400 site-scale competition for pollination.

401

#### 402 *Floral resources and plant community dynamics*

403 The role of floral resources and pollinator-mediated interactions for the dynamics of plant  
404 communities has received increasing attention in recent years (Sargent & Ackerly 2008;  
405 Pauw 2013; Greenspoon & M'Gonigle 2013). We found that both intra- and interspecific  
406 floral resources at the site scale have strong positive effects on plant reproductive success.  
407 Previously, Nottebrock *et al.* (2013) found positive effects of large-scale community density  
408 on seed set and lifetime fecundity of *Protea repens*. The present study of 19 *Protea* species  
409 in 27 communities suggests that such community-level Allee effects are a general feature of  
410 *Protea* communities and that they are mediated by floral resources. Community-level Allee  
411 effects can have profound consequences for plant population and community dynamics:  
412 decreased floral resources of certain plant species can increase the extinction risk of other  
413 plant species, thus increasing the susceptibility of communities to extinction cascades  
414 (Colwell et al. 2012).

415 Our findings also have interesting implications for species coexistence and the structure  
416 of diverse plant communities. We found that seed set in *Protea* communities is affected by  
417 negative direct effects of plant density and by predominantly positive effects of floral  
418 resources (Fig. 4b). The direct density effects reveal that intraspecific density-dependence is  
419 more negative than interspecific density-dependence, which should cause rare species to  
420 experience less competition than common species and should therefore stabilize  
421 coexistence (Chesson 2000). These stabilizing density effects are, however, counteracted by  
422 pollinator-mediated effects at the neighbourhood scale: conspecific floral resources increase  
423 seed set whereas heterospecific resources have much weaker effects (Fig. 4b). These  
424 resource-based effects thus tend to neutralize intraspecific competition while leaving  
425 interspecific competition unaffected. Hence, an individual plant immigrating into a  
426 neighbourhood dominated by another species will have strongly reduced seed set compared  
427 to a member of the dominant species. This ‘priority effect’ should promote the formation of  
428 monospecific stands (M’Gonigle & Greenspoon 2014) that are a prominent feature of *Protea*  
429 communities (cf. Fig. 2a). The emergence of such monospecific stands reduces  
430 neighbourhood-scale coexistence but can facilitate larger-scale coexistence. This is because  
431 stable stand boundaries slow down large-scale competitive exclusion which led M’Gonigle &  
432 Greenspoon (2014) to state that it ‘stabilizes coexistence’. In the classification of Chesson  
433 (2000), however, this effect is equalizing (reducing fitness differences between species)  
434 rather than stabilizing (favouring rare species). In contrast, the positive effects of site-scale  
435 floral resources on seed set (Fig. 4b) are stabilizing *sensu* Chesson (2000): site-scale  
436 facilitation is stronger between than within species, which favours species that are rare at  
437 the site scale.

438 Our results suggest that pollinator-mediated interactions contribute to the formation of  
439 monospecific stands, but cause interspecific facilitation across stand boundaries, which  
440 stabilizes site-scale coexistence. These effects can help to explain the typical spatial structure  
441 of plant communities in the biodiversity hotspot studied here, which differs from other  
442 megadiverse systems (such as tropical forests) through the existence of monospecific stands  
443 at small scales, but high species richness at larger scales and thus high beta-diversity  
444 (Goldblatt & Manning 2002). Such multi-scale impacts of pollinator-mediated interactions on  
445 plant communities are not fully covered by existing single-scale theories (Sargent & Ackerly  
446 2008; Pauw 2013; Greenspoon & M'Gonigle 2013).

447

#### 448 *Conclusions and Outlook*

449 This study shows that floral resources are a common 'interaction currency' (Kissling *et al.*  
450 2012) that determines how multiple plant species interact via their shared generalist  
451 pollinators. It identifies inflorescence number and sugar amount per inflorescence as key  
452 quantities that convert the spatial structure and phenology of individual plant species into  
453 the spatiotemporal dynamics, purity and quality of this common currency at the community  
454 level. Pollinator visitation and seed set respond to these multiple aspects of the floral  
455 resource currency, with potentially important consequences for the dynamics and  
456 coexistence of plant species within communities. The identification of such interaction  
457 currencies is crucial for both developing a more general understanding of community  
458 dynamics and predicting community dynamics in changing environments (McGill *et al.* 2006;  
459 Kissling *et al.* 2012). It is timely to test whether resource-landscapes play similar roles in

460 other pollination systems and for other types of generalized trophic interactions, such as  
461 plant-herbivore and plant-frugivore networks.

462

### 463 **Acknowledgements**

464 This paper is dedicated to the memory of the late Brummer Olivier without whom this study  
465 would not have been possible. For discussion and input we are grateful to Anton Pauw,  
466 Phoebe Barnard and Tony Rebelo. We also thank a large number of field and lab assistants.  
467 We were able to accomplish our study thanks to the support of private land-owners (Giel  
468 von Deventes, Flower Valley Conservation Trust; Mathia, Nayna and Walter Heidehof,  
469 Gansbaai; Bairie and Peter Gibson, Macially High Noon Farm G. and S. Moskovitz) and nature  
470 reserves (Grootbos, Fernkloof, Helderberg, Hottentots-Holland, Jonaskop, Limietberg, Mont-  
471 Rochelle). Field work was conducted under Cape Nature permit AAA005-00213-0028. This  
472 work was supported by the German Research Foundation (grant numbers SCHU 2259/3-1,  
473 SCHL 1934/1-1). This is publication number ISEM X-X.

474

475 **References**

476 1.

477 Armstrong, D.P., & Paton, D.C. (1990). Methods for measuring amounts of energy available  
478 from Banksia inflorescences. *Austral. Ecol.*, 15, 291–297.

479 2.

480 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models  
481 using Eigen and S4. R package version 1.1-7, URL: <http://CRAN.R-project.org/package=lme4>.  
482 Last accessed 31. March 2015

483 3.

484 Brown, B.J., & Mitchell, R.J. (2001). Competition for pollination: effects of pollen of an  
485 invasive plant on seed set of a native congener. *Oecologia*, 129, 43–49.

486 4.

487 Carvalheiro, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M., Bartomeus, I., *et al.* (2014).  
488 The potential for indirect effects between co-flowering plants via shared pollinators depends  
489 on resource abundance, accessibility and relatedness. *Ecol. Lett.*, 17, 1389-1399.

490 5.

491 Charnov, E. (1976). Optimal foraging: The marginal value theorem. *Theor. Popul., Biol.* 9,  
492 129–136.

493 6.

494 Chesson, P. (2000). General theory of competitive coexistence in spatially-varying  
495 environments. *Theor. Popul. Biol.*, 58, 211–237.

496 7.

497 Chittka, L. & Thomson, J.D. (eds.) (2001). *Cognitive ecology of pollination - animal behavior*  
498 *and floral evolution*. Cambridge University Press, 423pp.



499 8.

500 Collins, B.G. & Rebelo, T. (1987). Pollination biology of the Proteaceae in Australia and  
501 southern Africa. *Austral. Ecol.*, 12, 387–421.

502 9.

503 Colwell, R. K., Dunn, R. R. & Harris, N. C. (2012). Coextinction and persistence of dependent  
504 species in a changing world. *Annu. Rev. Ecol. Evol. Syst.* 43, 183–203.

505 10.

506 Devaux, C. & Lande, R. (2009). Displacement of flowering phenologies among plant species  
507 by competition for generalist pollinators *J. Evol. Biol.*, 22, 1460–1470.

508 11.

509 Devaux, C., Lepers, C. & Porcher, E. (2014). Constraints imposed by pollinator behaviour on  
510 the ecology and evolution of plant mating systems. *J. Evol. Biol.*, 27, 1413–1430.

511 12.

512 Elzinga, J.A., Atlan, A., Biere, A., Gigord, L.D.B., Weis, A. & Bernasconi, G. (2007). Time after  
513 time: flowering phenology and biotic interactions. *Trends Ecol. Evol.*, 22, 432–439.

514 13.

515 Feldman, R.E. & McGill, B.J. (2014). How important is nectar in shaping spatial variation in  
516 the abundance of temperate breeding hummingbirds? *J. Biogeogr.*, 41, 489–500.

517 14.

518 Ghazoul, J. (2005). Pollen and seed dispersal among dispersed plants. *Biol. Rev.*, 80, 413–  
519 443.

520 15.

521 Goldblatt, P. & Manning, J.C. (1999). The long-proboscid fly pollination system in *Gladiolus*  
522 (*Iridaceae*). *Ann. Missouri Bot. Gard.*, 86, 758–774.

- 523 16.
- 524 Goulson, D. (2000). Why do pollinators visit proportionally fewer flowers in large patches?
- 525 *Oikos*, 91, 485–492.
- 526 17.
- 527 Greenspoon, P.B. & M'Gonigle, L.K. (2013). Can positive frequency-dependence facilitate
- 528 plant coexistence? *Trends Ecol. Evol.*, 28,317-318.
- 529 18.
- 530 Gunton, R.M. & Kunin, W.E. (2009). Density-dependence at multiple scales in experimental
- 531 and natural plant populations. *J. Ecol.*, 97, 567–580.
- 532 19.
- 533 Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L. & Totland, Ø. (2009). How does climate
- 534 warming affect plant–pollinator interactions? *Ecol. Lett.*, 12, 184-195.
- 535 20.
- 536 Heinrich, B. & Raven, P.H. (1972). Energetics and pollination ecology. *Science*, 176, 597–602.
- 537 21.
- 538 Heinrich, B. (1975). Energetics of Pollination. *Annu. Rev. Ecol.*, 6, 139–170.
- 539 22.
- 540 Kandori, I., Hirao, T., Matsunaga, S. & Kurosaki, T. (2009). An invasive dandelion unilaterally
- 541 reduces the reproduction of a native congener through competition for pollination.
- 542 *Oecologia*, 159, 559–569.
- 543 23.
- 544 Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerney, G.J., *et al.*
- 545 (2012). Towards novel approaches to modelling biotic interactions in multispecies
- 546 assemblages at large spatial extents. *J. Biogeogr.*, 39, 2163–2178.

547 24.

548 Kunin, W.E. (1997). Population size and density effects in pollination: pollinator foraging and  
549 plant reproductive success in experimental arrays of *Brassica kaber*. *J. Ecol.*, 85, 225–234.

550 25.

551 MacArthur, R. H. & Pianka, E. R. (1966). On optimal use of a patchy environment. *Amer. Nat.*,  
552 100, 603-609.

553 26.

554 McGill, B.J., Enquist, B.J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology  
555 from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

556 27.

557 M'Gonigle, L.K. & Greenspoon, P.B. (2014). Allee effects and species coexistence in an  
558 environment where resource abundance varies. *J. Theor. Biol.*, 361, 61-68.

559 28.

560 Mitchell, R.J., Irwin, R.E., Flanagan, R.J. & Karron, J.D. (2009). Ecology and evolution of plant–  
561 pollinator interactions. *Ann. Bot.*, 103, 1355–1363.

562 29.

563 Moeller, D.A. (2004). Facilitative interactions among plants via shared pollinators. *Ecology*,  
564 85, 3289–3301.

565 30.

566 Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000).  
567 Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

568 31.

569 Nottebrock, H., Esler, K.J. & Schurr, F.M. (2013). Effects of intraspecific and community  
570 density on the lifetime fecundity of long-lived shrubs. *Perspect. Plant Ecol. Evol. Syst.*, 15,  
571 150–161.  
572 32.

573 Pauw, A. (2013). Can pollination niches facilitate plant coexistence? *Trends Ecol. Evol.*, 28,  
574 30–37.  
575 33.

576 Pyke, G.H. (1978). Optimal foraging in hummingbirds: testing the maginal value theorem.  
577 *Amer. Zool.*, 18 (4), 739-752.  
578 34.

579 R Core Team. (2015). R: A language and environment for statistical computing. R Foundation  
580 for statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.  
581 35.

582 Rathcke, B. (1983) Competition and facilitation among plants for pollination. In: (*Pollination*  
583 *Biology*), [ed. Real, L.]. Academic Press, London (UK), pp. 305–329.  
584 36.

585 Rebelo, T. (2001). *Proteas: field guide to the proteas of South Africa*. Fernwood; Global,  
586 Vlaeberg; London.  
587 37.

588 Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I. & Holzschuh, A. (2014). Early  
589 mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape. Ecol.*,  
590 29, 425–435.  
591 38.

592 Sargent, R.D. & Ackerly, D.D. (2008). Plant–pollinator interactions and the assembly of plant  
593 communities. *Trends Ecol. Evol.*, 23, 123–130.  
594 39.

595 Schmid, B., Nottebrock, H., Esler, K.J., Pagel, J., Pauw, A., Böhning-Gaese, K., *et al.* (2015).  
596 Reward quality predicts effects of bird-pollinators on plant reproduction in African *Protea*  
597 spp. *Perspect. Plant Ecol. Evol. Syst.*, 17, 209-217.  
598 40.

599 Schurr, F.M., Esler, K.J., Slingsby, J.A. & Allsopp, N. (2012). Fynbos Proteaceae as model  
600 organisms for biodiversity research and conservation. *S. Afr. J. Sci.*, 108, 11-12.  
601 41.

602 Seifan, M., Hoch, E.-M., Hanoteaux, S. & Tielbörger, K. (2014). The outcome of shared  
603 pollination services is affected by the density and spatial pattern of an attractive neighbour.  
604 *J. Ecol.*, 102, 953–962.  
605 42.

606 Shore, J.S. & Barrett, S.C.H. (1984). The effect of pollination intensity and incompatible  
607 pollen on seed set in *Turnera ulmifolia* (Turneraceae). *Can. J. Bot.*, 62, 1298–1303.  
608 43.

609 Tomlinson, S., Arnall, S.G., Munn, A., Bradshaw, S.D., Maloney, S.K., Dixon, K.W., *et al.*  
610 (2014). Applications and implications of ecological energetics. *Trends Ecol. Evol.*, 29, 280–  
611 290.  
612 44.

613 Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., John Kress, W., Erickson, D., *et al.*  
614 (2010). Trait similarity, shared ancestry and the structure of neighbourhood interactions in a  
615 subtropical wet forest: implications for community assembly. *Ecol. Lett.*, 13, 1503–1514.

616 45.

617 Waser, N.M. (1978). Competition for hummingbird pollination and sequential flowering in  
618 two Colorado wildflowers. *Ecology*, 59, 934–944.

619 46.

620 Williams, N.M., Regetz, J. & Kremen, C. (2012). Landscape-scale resources promote colony  
621 growth but not reproductive performance of bumble bees. *Ecology*, 93, 1049–1058.

622

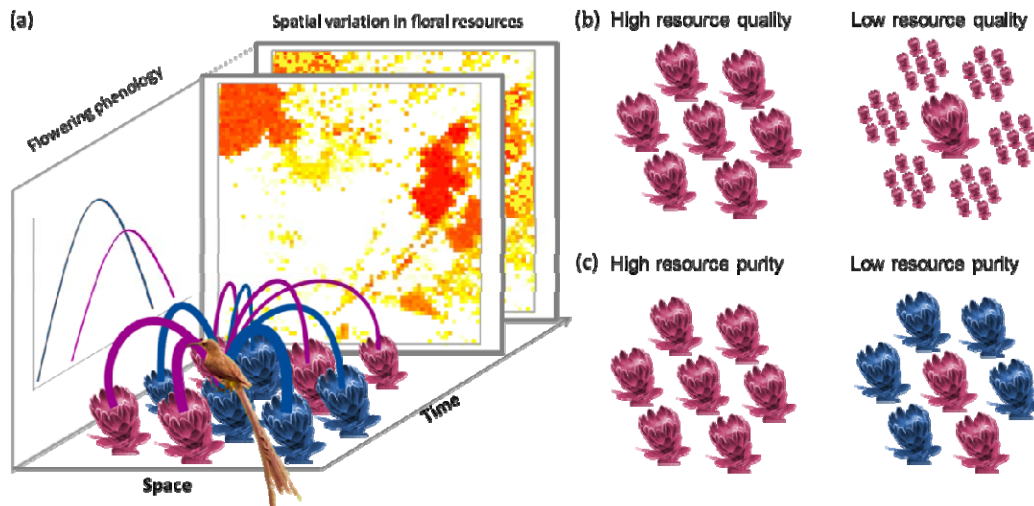
### 623 **Supporting Information**

624 Additional Supporting Information may be downloaded via the online version of this article  
625 at Wiley Online Library ([www.ecologyletters.com](http://www.ecologyletters.com)).

626 As a service to our authors and readers, this journal provides supporting information  
627 supplied by the authors. Such materials are peer-reviewed and may be re-organized for  
628 online delivery, but are not copy-edited or typeset. Technical support issues arising from  
629 supporting information (other than missing files) should be addressed to the authors.

630 **Figures**

631



632

633

634 Figure 1: A conceptual framework for studying effects of floral resource-landscapes on

635 pollinator-mediated interactions among plants. (a) Effects of spatial and phenological

636 variation in floral resource amounts: the strength of pollinator-mediated interactions

637 experienced by a focal inflorescence depends on the resource amount, spatial and

638 phenological proximity of other inflorescences (interaction strength indicated by line

639 widths). (b) Effects of floral resource quality: pollinator-mediated interactions depend on

640 whether a given floral resource amount is split into a few high-quality inflorescences or into

641 many low-quality inflorescences. In the example figures, the central inflorescence is either

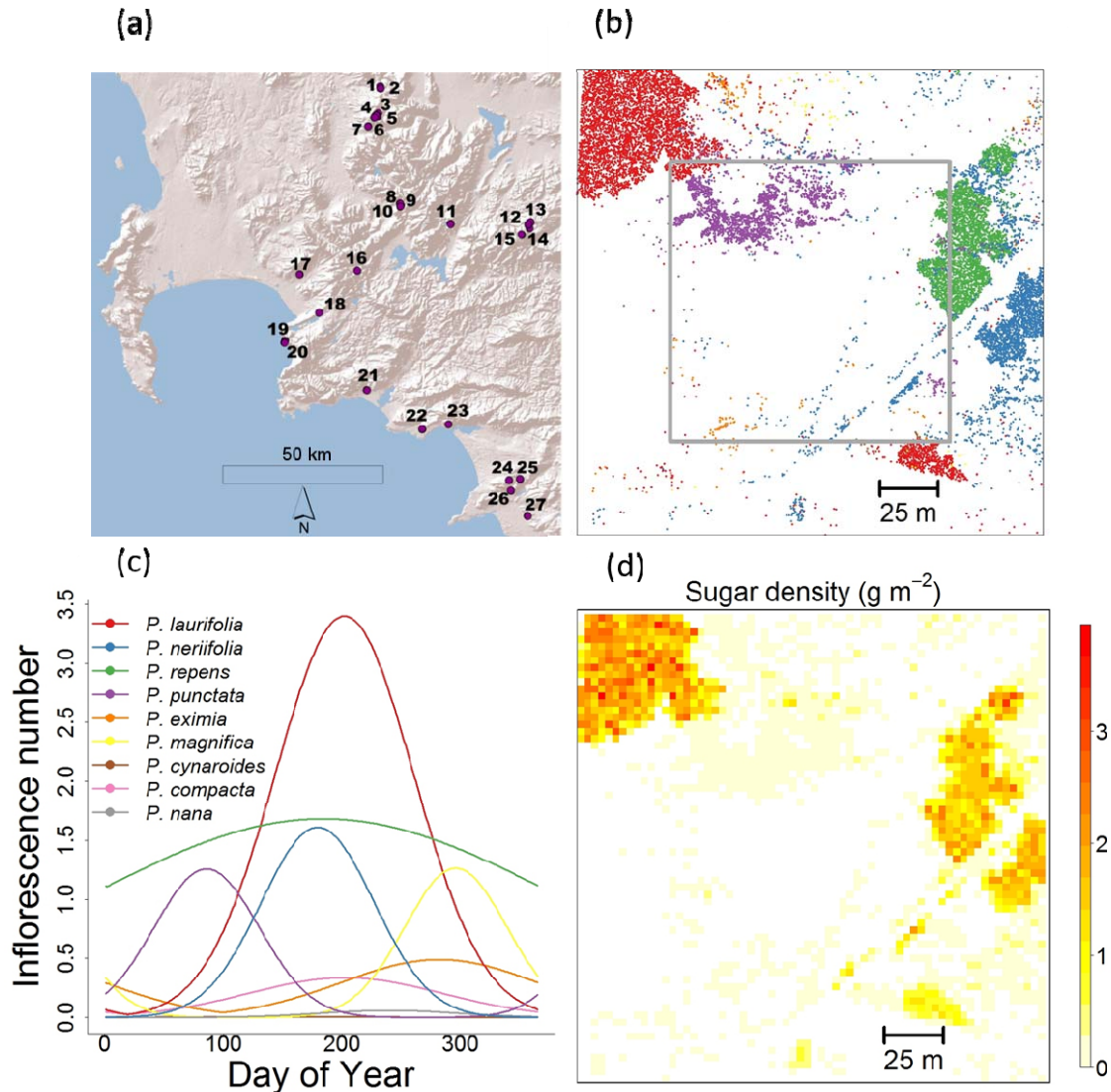
642 surrounded by inflorescences of equal quality (left) or lower quality (right). (c) Effects of

643 floral resource purity: pollinator-mediated interactions depend on the proportion of

644 conspecific floral resources. The example figures show cases of high purity (left) and low

645 purity (right).

646



647

648

649 Figure 2: Quantifying the spatiotemporal dynamics of floral resource-landscapes. (a)

650 Location of 27 study sites in the Fynbos biome, South Africa. (b) Map of 16,948 shrub

651 individuals on study site 4 with colours indicating different *Protea* species (see legend in (c)).

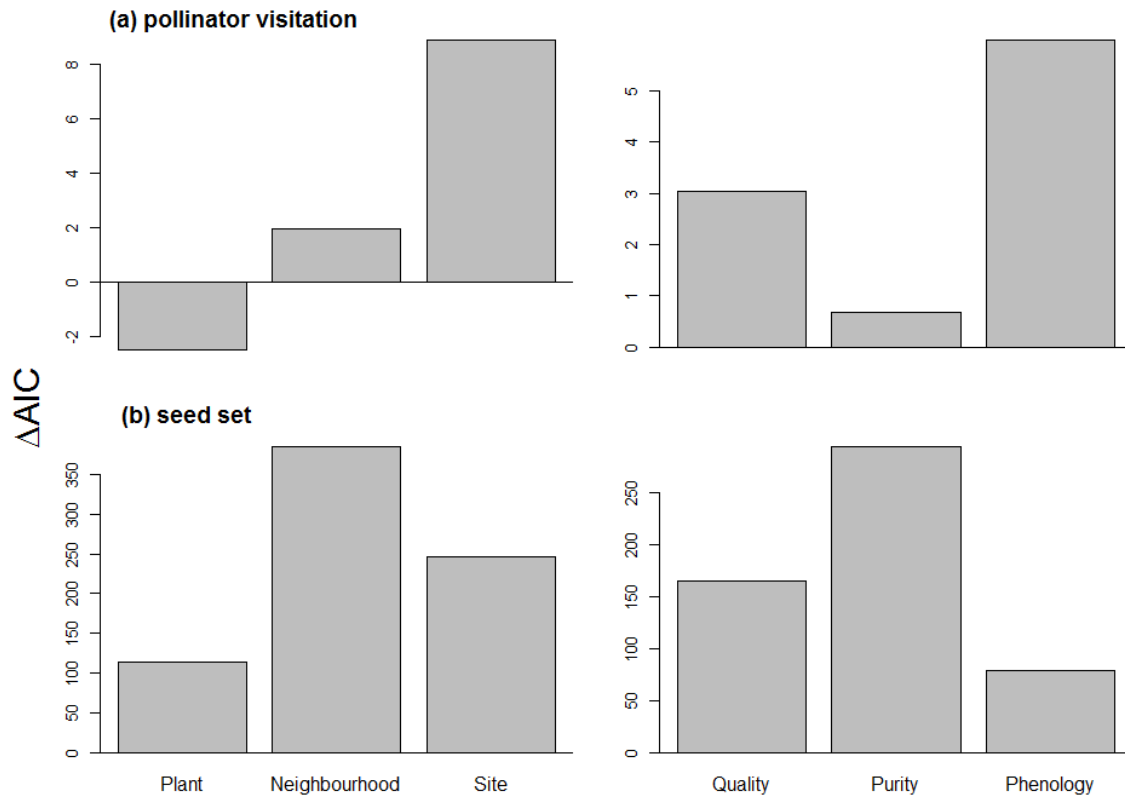
652 (c) Flowering phenologies of the nine *Protea* species on this site (shown as the number of

653 flowering inflorescences of a median-sized plant). (d) Spatial distribution of nectar sugar on

654 the site predicted for a given day (4 July).

655

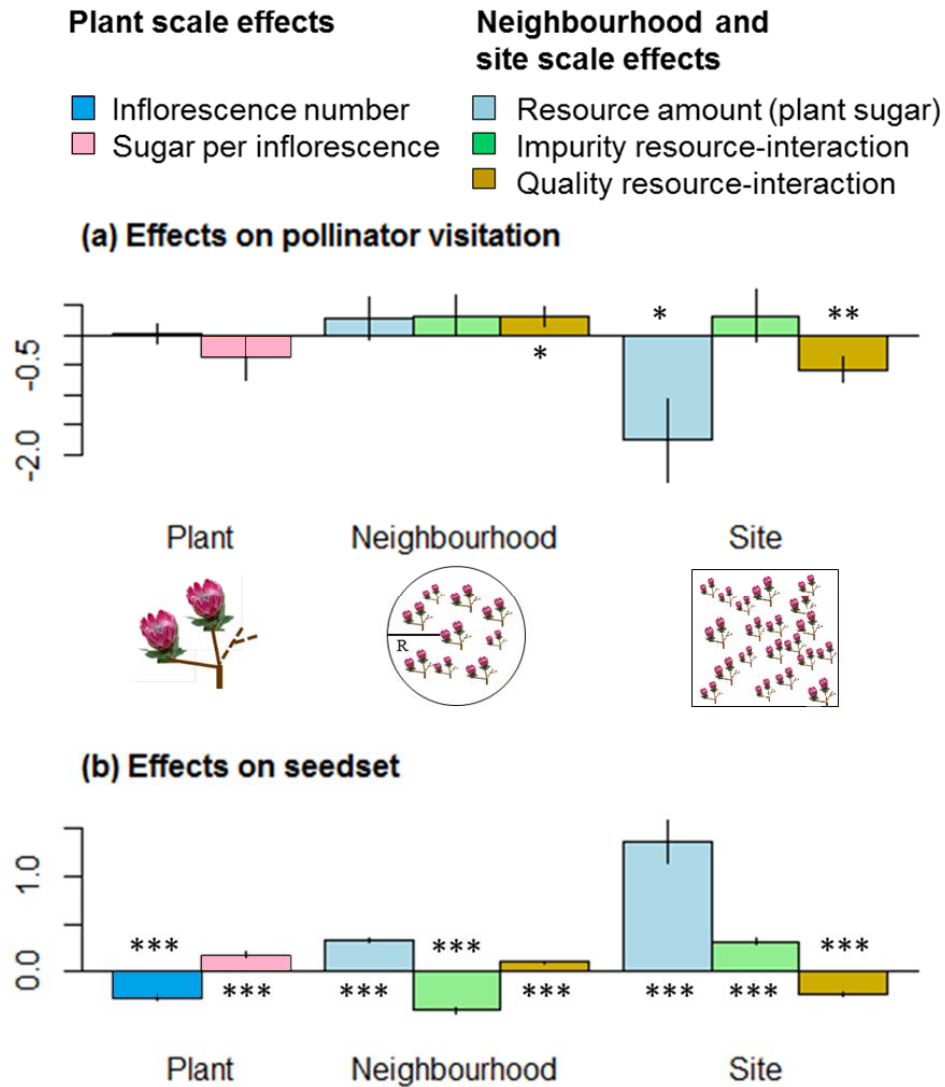




656

657 Figure 3: Relevance of different aspects of floral resource-landscapes for (a) pollinator  
658 visitation per inflorescence and (b) seed set per inflorescence. The left panels show the  
659 relevance of floral resources at three spatial scales, the right panels show the relevance of  
660 floral resource quality, purity, and phenology. The relevance of a given aspect of resource-  
661 landscapes is measured as the AIC difference difference between a control model model  
662 without the respective aspect and the full model (a positive value indicates better  
663 performance of the full model).

664



665

666

667 Figure 4: Effects of floral resource-landscapes at the plant, neighbourhood and site scale on  
 668 (a) pollinator visitation and (b) seed set per inflorescence. Bars indicate standardized  
 669 regression coefficients, whiskers the corresponding standard errors and stars the  
 670 significance of effects (\*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ). At the plant scale, bars show  
 671 the effect of inflorescence number (dark blue) and sugar amount per inflorescence (pink). At  
 672 the neighbourhood and site scale, light blue bars show main effects of sugar amount, green

673 bars show interactions between impurity (proportion of heterospecific sugar) and sugar  
674 amount, and brown bars show interactions between relative resource quality (difference in  
675 sugar per inflorescence) and sugar amount. Light blue bars at the neighbourhood and site  
676 scale thus represent effects of purely conspecific sugar amounts, the addition of the  
677 corresponding green bars yields the effect of heterospecific sugar amounts with identical  
678 quality, and the addition of the corresponding brown bars shows how resource effects are  
679 altered for heterospecifics with higher resource quality.

680

681