

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

3 Nottebrock, Henning ^{1,3,4*}, Schmid, Baptiste ^{2,3}, Mayer, Katharina³, Devaux, Céline ⁴, Esler,
4 Karen J. ³, Böhning-Gaese, Katrin ^{2,5}, Schleuning, Matthias ², Pagel, Jörn ^{1,4} & Schurr, Frank M.
5 ^{1,4}

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

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

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

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

14 ⁵ 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, phone: +49 (0)711 459-22330, fax: +49 (0)711 459-22831

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31 **Author contributions**

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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 m² plot with a core zone of 120x120 m² 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 m²), 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_{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 π_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 Δt is the time
279 difference between the pollinator observation and the plant's peak flowering time and σ 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

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474

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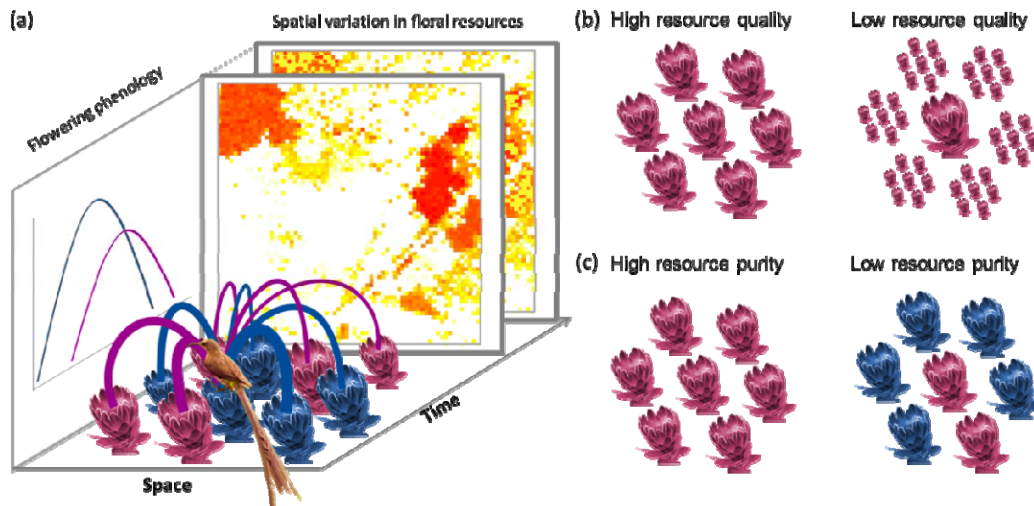
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630 **Figures**

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

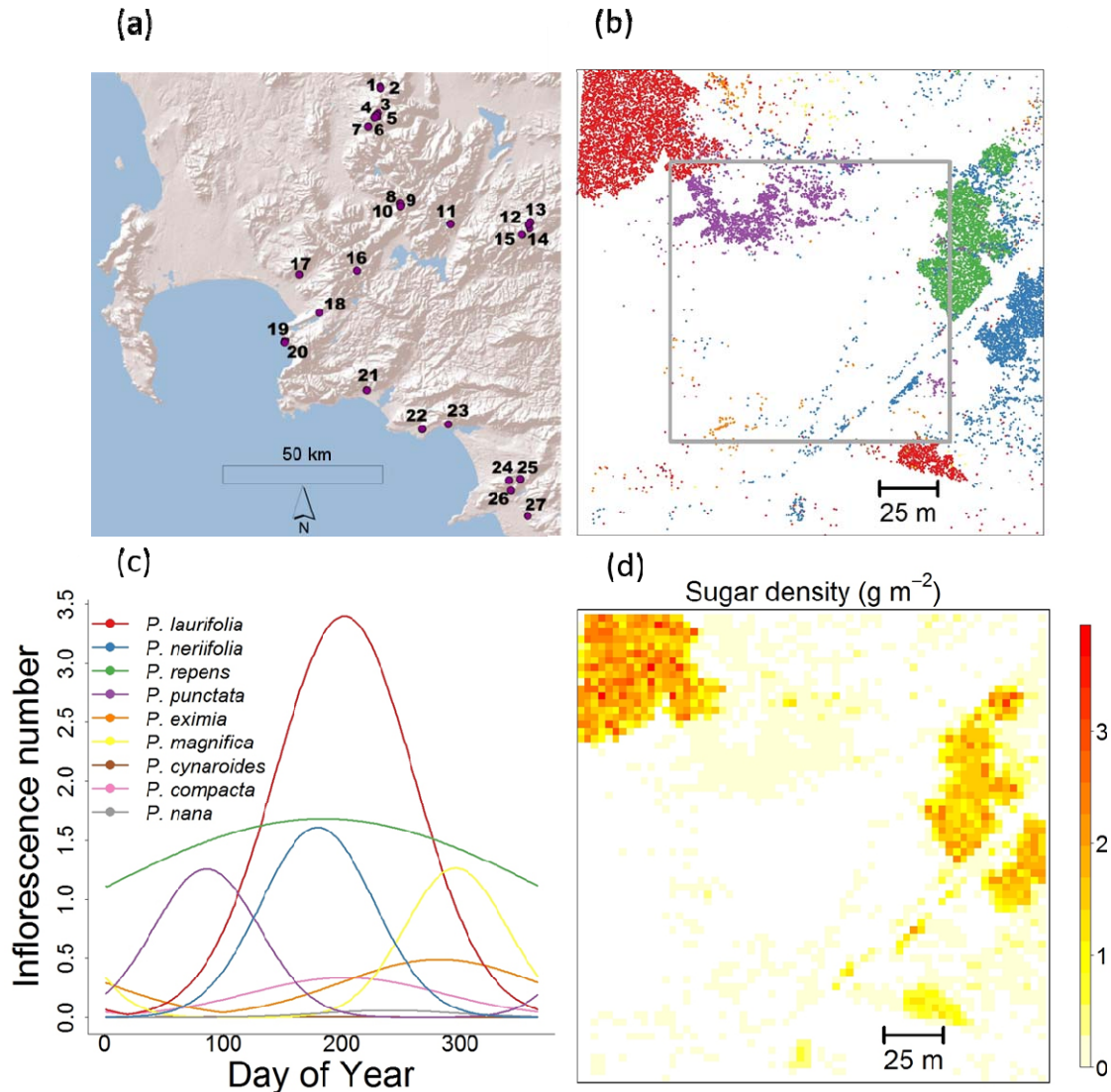
642 surrounded by inflorescences of equal quality (left) or lower quality (right). (c) Effects of

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

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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

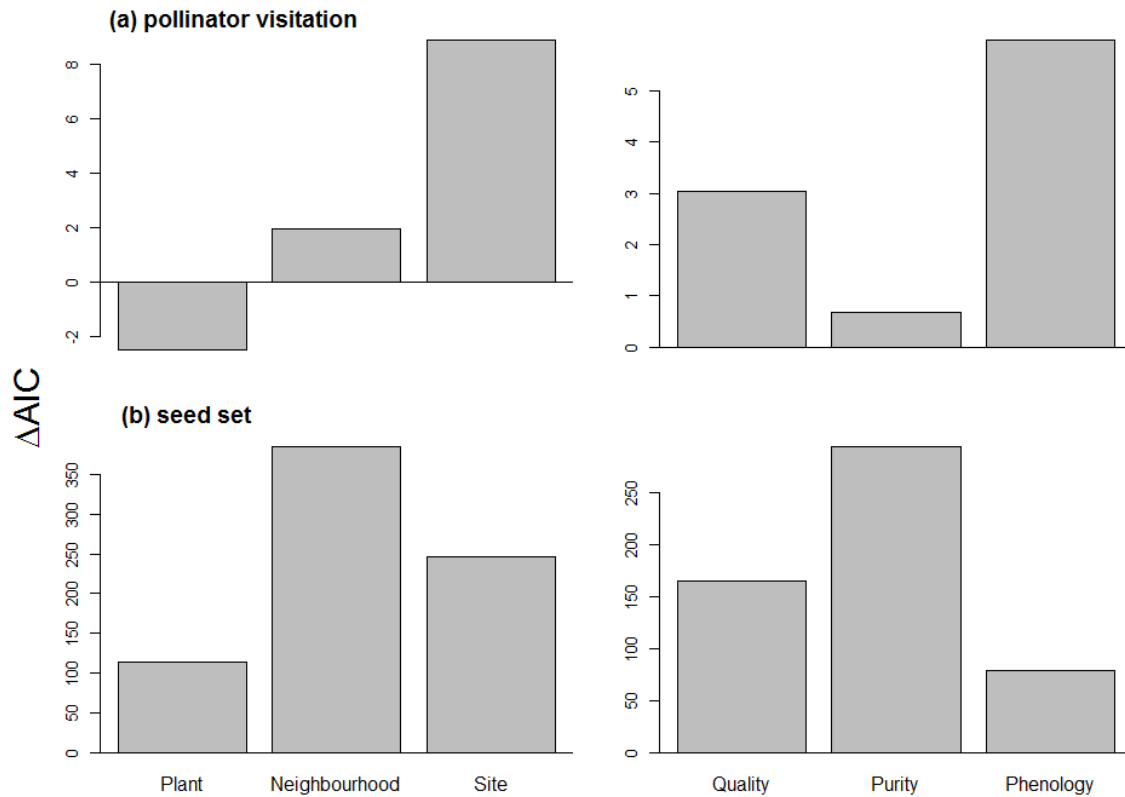
651 individuals on study site 4 with colours indicating different *Protea* species (see legend in (c)).

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).

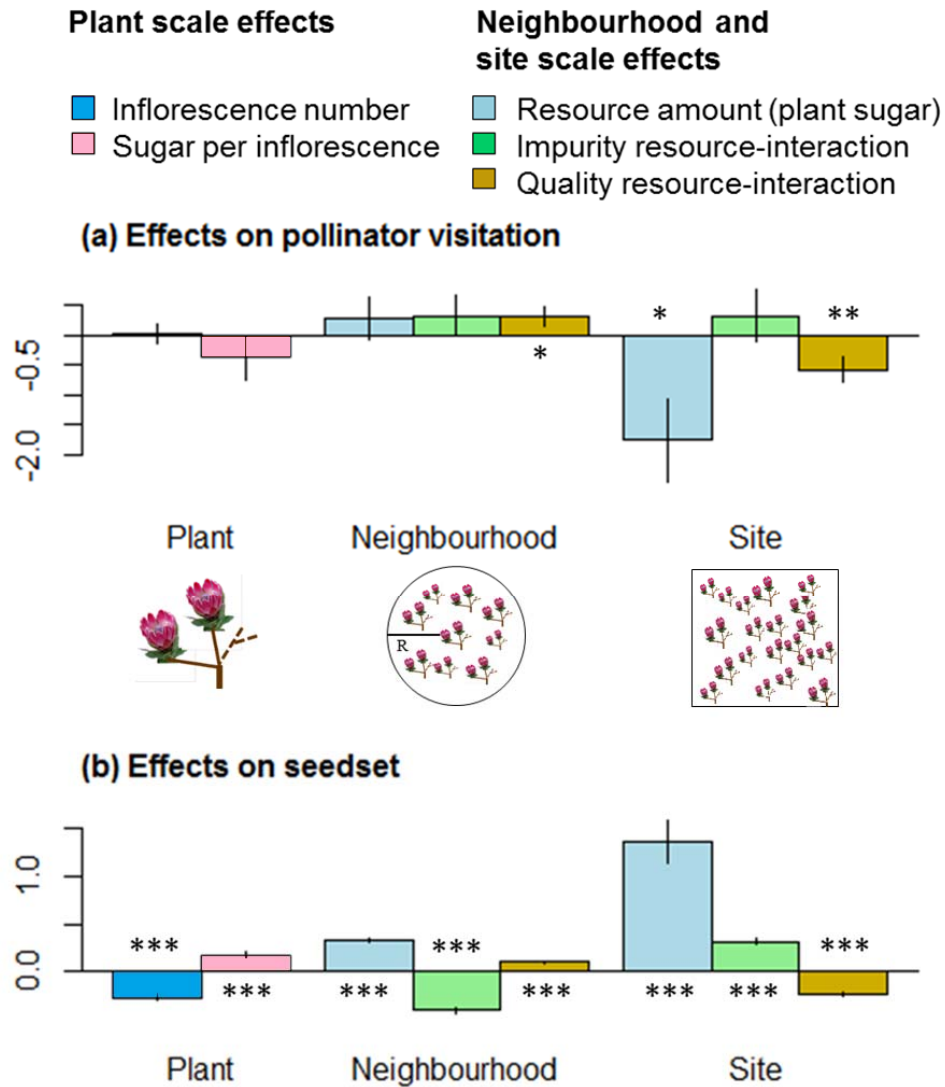
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657 Figure 3: Relevance of different aspects of floral resource-landscapes for (a) pollinator
658 visitation per inflorescence and (b) seed set per inflorescence. The left panels show the
659 relevance of floral resources at three spatial scales, the 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