Sex-specific spatial variation in fitness in the highly dimorphic *Leucadendron rubrum*

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3 Running title: Sex-specific spatial variation in fitness

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Abstract

Sexual dimorphism in plants may emerge as a result of sex-specific selection on traits enhancing access to nutritive resources and/or to sexual partners. We here investigated sex-specific differences in selection of sexually dimorphic traits and in the spatial distribution of effective fecundity (our fitness proxy) in a highly dimorphic dioecious wind-pollinated shrub, *Leucadendron rubrum*. In particular, we tested for the effect of density on male and female effective fecundity. We used spatial and genotypic data of parent and offspring cohorts to jointly estimate individual male and female effective fecundity on the one hand and pollen and seed dispersal kernels on the other hand. This methodology was here adapted to the case of dioecious species. Explicitly modeling dispersal avoids the confounding effects of heterogeneous spatial distribution of mates and sampled seedlings on the estimation of effective fecundity. We also estimated selection gradients on plant traits while modeling sex-specific spatial autocorrelation in fecundity. Males exhibited spatial autocorrelation in effective fecundity at a smaller scale than females. A higher local density of plants was associated with lower effective fecundity in males but was not related to female effective fecundity. These results suggest sex-specific sensitivities to environmental heterogeneity in *L. rubrum*. Despite these sexual differences, we found directional selection for wider canopies and smaller leaves in both sexes, and no sexually antagonistic selection on strongly dimorphic traits in *L. rubrum*. Many empirical studies in animals similarly failed to detect sexually antagonistic selection in species expressing strong sexual dimorphism, and we discuss reasons explaining this common pattern.

Keywords: sexual dimorphism, sexual selection, selection gradients, dispersal kernels, cost of reproduction, spatial structure

Introduction

Plant species with separate sexes are relatively uncommon (*i.e.* 5-6%, Renner, 2014). Separate sexes have nonetheless evolved repeatedly among flowering plants (Renner, 2014), and such transitions often given rise to the evolution of morphological differences between sexes (Geber *et al.,* 1999; Puixeu *et al.,* 2019). The degree of sexual dimorphism has also switched multiple times from low to high along the evolutionary history of certain dioecious plant lineages (Tonnabel *et al.,* 2014). Both *sex-specific costs of reproduction* and *male-male competition to access ovules* have been suggested as potential forces causing the evolution of such dimorphism. These two factors could trigger sexually antagonistic selection (Delph & Ashman, 2006; Moore & Pannell, 2011), whereby selection exerts forces in opposite directions in each sex towards sex-specific optima (Cox & Calsbeek, 2009). The goal of this study is to estimate sex-specific fitness as well as the strength and form of selection acting on morphological traits in each sex, in a highly dimorphic dioecious wind-pollinated plant species. To do so, we combine, and adapt to the case of dioecious species, recently developed statistical methods estimating *effective fecundity*, a proxy for fitness, and its dependence on morphological traits, while explicitly modeling various spatial effects that could bias such estimations.

The sex-specific cost of reproduction hypothesis posits that sexes should diverge in morphology to satisfy their respective reproductive needs (Freeman *et al.,* 1976; Delph & Bell, 2008). Such divergence can emerge when reproduction involves a stronger cost in one sex than in the other, or when the reproductive costs of each sex imply different resource 'currencies' (Freeman *et al.,* 1976; Obeso, 2002). Several studies have shown that pollen production in males strongly relies on nitrogen, while female reproduction is mostly limited by carbon and water (e.g. Antos & Allen, 1990; McDowell *et al.,* 2000; Harris & Pannell, 2008; van Drunen & Dorken, 2012). Males and females of dioecious plants have evolved divergent strategies of plastic allocation to resource-harvesting organs (see Tonnabel *et al.,* 2017 for a review), probably to harvest the resources most

needed for their respective reproduction. The cost of reproduction is generally higher in females than in males, at least considering the cost per reproductive structure. However, at the scale of the whole plant, this trend is often reversed in wind-pollinated plants, which produce large amounts of pollen (Obeso, 2002; Harris & Pannell, 2008; Tonnabel *et al.*, 2017). In some dioecious species inhabiting fire-prone environments, the cost of reproduction markedly differs between sexes because females need to maintain a canopy-stored ('serotinous') seed bank (released by fire). As water intake is necessary to maintain cones closed and prevent seed release during unfavorable period between two fires (Martín-Sanz *et al.*, 2017), we may expect selection for enhanced water conduction to have favored a divergent plant architecture between sexes. Consistent with this prediction, the evolution of longer maintenance of cones in the canopy is indeed associated with the evolution of higher sexual dimorphism in the genus *Leucadrendron* (Harris & Pannell, 2010).

The evolution of sex-specific differences in vegetative traits may also originate from selection for male morphologies that are better at dispersing pollen and therefore at accessing mates (Tonnabel *et al.*, 2019a,b). The male-male competition hypothesis postulates that male reproduction, by being mostly limited by mating opportunities, selects for males that exhibit traits enhancing their competitive abilities (Bateman, 1948; Arnold, 1994). Several studies have pinpointed the importance of male-male competition in shaping male reproductive and floral traits. These studies showed more extravagant floral displays in males than in females to attract pollinators (e.g. Bond & Maze, 1999; Elle & Meagher, 2000; Wright & Meagher, 2004; Delph & Ashman, 2006; Waelti *et al.*, 2009; Schiestl & Johnson, 2013; Dorken & Perry, 2017), variation in male flowering phenology to track the female phenology (Delph & Herlihy, 2011; Forrest, 2014), increased pollen grain competitive performance in response to polyandry (Lankinen *et al.*, 2017) and morphological evolution of structures that disperse pollen, which prevents the attachment of competing pollen to the pollinator (Coccuci *et al.*, 2014). In wind-pollinated plants, sexual selection may also target vegetative traits such as plant size, branch length or the length of male flower peduncles, which can facilitate pollen dispersal (Klinkhamer *et al.*, 1997; Eppley & Pannell, 2007; Pickup & Barrett,

2012; Harder & Prusinkiewicz, 2013; Tonnabel *et al.,* 2019b). Wind-pollinated plants tend to evolve larger degrees of sexual dimorphism than insect-pollinated lineages, because pollinators require similarity of floral morphology to successfully transfer pollen (Tonnabel *et al.,* 2014; Welsford *et al.,* 2016). Wind-pollinated plants, which typically show large inter-individual variation in fertility (Schoen & Stewart, 1987; Ahee *et al.,* 2015), may thus be particularly subject to sexually antagonistic selection.

In the presence of genetic variation for sexual dimorphism, each sex should, in principle, ultimately reach its optimal trait value, and thereby resolve sexually antagonistic selection (Lande, 1980). Yet, a shared genetic basis of traits between sexes may temporally constrain the evolution of their morphological divergence (Lande, 1980). In constant and homogeneous environments, theory predicts that, with strong positive genetic correlations between sexes, opposite directional selection gradients between sexes should emerge early during adaptation and persist for a long time before the sexual conflict is resolved (Lande, 1980; Connallon & Hall, 2016). Consequently, one would expect evidence for antagonistic selection between sexes to be relatively common. The compilation of numerous sex-specific selection gradients in animals showed, however, a large diversity of patterns, including cases of aligned selection across sexes (Cox & Calsbeek, 2009). In plants, documented patterns of sex-specific selection provided mixed support for sexually antagonistic selection: sex-specific selection gradients have been found to have opposite signs in both insect- and wind-pollinated species (Delph *et al.,* 2011; Castilla *et al.,* 2014; Tonnabel *et al.,* 2019b) but to have the same sign in other studies (Oddou-Muratorio *et al.,* 2018; Barrio & Teixido, 2014). More recent theory suggests that temporal and spatial variation in selection pressures may explain the lack of signal for sexually antagonistic selection, despite differences in the optimal phenotypes of males and females (Connallon, 2015; Connallon & Hall, 2016; Zafitscher & Connallon, 2017).

Estimating sex-specific selection gradients requires, first, estimating male and female individual fitness, and, second, relating trait values and fitness estimates. Using genotypes of established seedlings and their potential parents, traditional methods first achieve categorical

120   parentage assignments to then estimate individual realized reproductive successes used as fitness

121   estimates. In the next generation methods, genotypes are combined with spatial localization of

122   sampled individuals, through spatially explicit mating models (SEMMs), to disentangle the effect of

123   fecundity from that of the distance between mating pairs (and the distance between mothers and

124   seedlings) on reproductive success (e.g. Oddou-Muratorio *et al.*, 2005). To do so, dispersal is

125   explicitly modeled and dispersal kernels are estimated for both seeds and pollen. A Bayesian

126   method was introduced in this framework to estimate individual male and female *effective*

127   *fecundities* (MEMM, Klein *et al.*, 2008 for seed sampling on mother trees; MEMMseedlings,

128   Oddou-Muratorio *et al.*, 2018 for seedling sampling designs). This method considers the likelihood

129   of genotypes conditional on the position of seedlings, so it is unaffected by any process acting on

130   the distribution of seedlings, be it the potential parents' positions, or habitat suitability and

131   disturbances. It analyses seedling genotypes in terms of (1) overall reproductive contribution of each

132   potential parent as determined jointly by gamete production, gamete fertilization rates, seed

133   maturation and germination, and seedling survival until census; (2) dispersal events in terms of

134   estimated dispersal kernels and (3) pollen or seedling competition by a mass action law. Effective

135   fecundity refers only to relative values of the first component for each parent. It varies with, e.g.,

136   male-male competitive ability through differences in overall pollen production and their subsequent

137   ovule fertilization abilities, but not with competitive effects dependent on the composition of

138   competitors within the pollen cloud generated by uneven spatial distribution of mates. We here

139   extend this methodology to dioecious species. This spatially explicit approach avoids spatial bias in

140   effective fecundity estimation, typically generated by sampling seedlings non-uniformly with

141   respect to the positions of their parents or by the confounding effects of heterogeneous spatial

142   distribution of mates (Oddou-Muratorio *et al.*, 2018). Used as a proxy for fitness, effective fecundity

143   thus provides the expected relative reproductive success if putative mates (for male fecundity) and

144   regeneration sites (for female fecundity) were uniformly distributed in space, and all offspring could

145 establish and be sampled (Klein *et al.,* 2013). It therefore attenuates the impact of stochastic effects

146 associated with sampling methods on fitness estimates.

147   Relating fitness estimates to plant traits using the selection gradients methodology proposed

148 by Lande & Arnold (1983) can further suffer from specific statistical bias in sessile organisms living

149 in heterogeneous environments. Indeed, small-scale spatial variation in resources fundamental to

150 plant physiology, including sex-specific reproduction, is common across a range of habitat types

151 (Silvertown *et al.,* 1999; Araya *et al.,* 2011). To disentangle the fitness effect of plant characteristics

152 (such as their ability to harvest resources, which may be sex-specific) from that of the environment

153 (such as the spatial distribution of resources), the spatial distribution of individuals must be

154 accounted for (Rausher, 1992). Indeed, not modeling explicitly the spatial autocorrelation of

155 unmeasured ecological variables affecting fitness can lead to detect false-positive effects of traits on

156 fitness, as on any other response (Guillot & Rousset, 2013). To address this problem, we fitted

157 mixed-effect models with spatially autocorrelated random-effects, using the spaMM package

158 (Rousset & Ferdy, 2014). To our knowledge, it is the first time that spatial effects are taken into

159 account in the estimation of selection gradients. Moreover, spatial variation in plant density and the

160 local sex ratio may generate spatial variation in competition for resources, which can be studied by

161 analyzing their fixed effects on plant fitness. In conclusion, our MEMMseedlings model controls for

162 spatial confounding effects on estimations of effective fecundity relative to spatial sampling biases

163 and to the spatial heterogeneity of plant distribution (potentially impacting competition among

164 males), while our spaMM procedure controls for spatial environmental heterogeneity.

165   We applied our methodology to *Leucadendron rubrum*, a dioecious wind-pollinated

166 serotinous shrub, endemic to the fire-prone South-African fynbos. *L. rubrum* displays extreme

167 sexual dimorphism (Fig. S1), with males being typically more highly branched, having smaller

168 leaves and taller stature than females (Harris & Pannell, 2010; Welsford *et al.,* 2014; Welsford *et*

169 *al.,* 2016). A single recruitment pulse typically occurs after fire, killing all adult trees and releasing

170 seeds stored in their canopy seed bank (Cowling & Lamont, 1987). This particular life-cycle allows

171 the estimation of life-time effective fecundity by sampling seedlings only once (*i.e.* after the fire

172 event). Furthermore, because recruitment is synchronized by fire, all sampled adult individuals in

173 the population have the same age (Bond, 1984). The strong sexual dimorphism of *L. rubrum* has

174 been previously hypothesized to be the consequence of sex-specific resource requirements (Harris &

175 Pannell, 2010). Indeed, the cost of reproduction in *L. rubrum* is likely to differ strongly between

176 sexes due to the cost of maintaining the canopy-stored ('serotinous') seed bank in females (Martín-

177 Sanz *et al.,* 2017). We hypothesized that, because of such maternal care, female fitness may be more

178 sensitive to water availability than male fitness. Owing to these differences in resource requirement

179 for reproduction, we therefore tested whether male and female effective fecundities (as defined

180 above) display different spatial structure and whether the observed strong sexual dimorphism is

181 associated with sex-specific selection gradients (Lande, 1980).

Materials and methods

Study species and site

Leucadendron rubrum is a dioecious wind-pollinated shrub species endemic to the Western Cape of

South Africa (Rebelo, 2001) where natural fires occur every 10-15 years (van Wilgen *et al.,* 2010;

Kraaij *et al.,* 2011). *L. rubrum* belongs to the Proteaceae family and flowers from August to

September. Seed recruitment is constrained to a short period following fires, and seeds released

between fires typically fail to establish due to competition (Bond, 1984). *L. rubrum* typically starts

flowering at 2-3 years, and seeds are retained in woody cones for several years (Harris & Pannell,

2010). Seeds therefore form a 'serotinous' seed bank, which persists until fire kills the plants,

allowing cone opening and wind dispersal of fruits via their plumed perianth (Williams, 1972;

Rebelo, 2001). In serotinous species, disruption of water intake to the cone (caused by broken

branch or plant death) was shown to lead to seed release suggesting a water cost to keep the cones

closed (Treurnitcht *et al.,* 2016; Martín-Sanz *et al.,* 2017). Thus, mother death or any event leading

to cone opening before the advent of fire results in seed release in poor conditions for recruitment

and ultimately in the loss of progeny.

The study population was located at Bainskloof pass (33°32'21.25"S 19°10'12.10"E) and was

contained in a rectangle of 135x110 meters (Fig. S2). We studied all adult individuals of our focal

population. Another population of *L. rubrum* was located at a distance of 310 meters (smallest

distance found between two plants from the two populations). All adults of *L. rubrum* of the focal

population (*i.e.* 86 females and 88 males) were mapped (see Supplementary Methods S1), sampled

for DNA analyses and measured for several traits in 2004. In summer 2006, a fire burnt the

population, killing all adults. A total of 1,265 seedlings were mapped, and their leaves were sampled

in the following Fall (February 2007), four to five months after the fire. The spatial distribution of

adults and seedlings is shown in Fig. S2. In one part of the study site, a ditch had been dug for

construction after seeds had dispersed, so we were unable to determine the undisturbed positions of

208   172 seedlings located in that area which we therefore eliminated from the dataset. However, the

209   effective fecundity of adults in this area can still be estimated without bias induced by the

210   disturbance, thanks to the use of MEMMseedlings (see below).

211   When sampling seedlings, the presence of seedlings from another closely related sympatric

212   species (*Leucadendron salignum* P.J. Bergins) rendered the identification of *L. rubrum* juveniles

213   difficult. To ensure that only juveniles of *L. rubrum* were included in later analyses, we genotyped

214   juveniles (see below for details on the genotyping protocol), as well as adults from both species.

215   This analysis aimed at assigning seedlings to either species and its results are described in

216   Supplementary Method S2 and Fig. S3. We did not find evidence for the existence of hybrids

217   between *L. rubrum* and *L. salignum*. In addition, 254 juveniles were excluded after genotyping as

218   they belonged to *L. salignum*.

219

220   **Measurements of adult traits in the field**

221   For adult shrubs, we measured in 2004 three traits describing plant architecture and three traits

222   describing leaf morphology (available at doi:10.5061/dryad.ngf1vhhst). All six traits are known to

223   be sexually dimorphic in this species (Harris & Pannell, 2010; Welsford *et al.*, 2014, 2016; Fig. S4).

224   The three traits describing plant architecture were (1) plant height, (2) the first diameter defined as

225   the greatest horizontal diameter of the plant (hereafter, canopy diameter), and (3) the second

226   horizontal diameter defined as the diameter perpendicular to the first diameter (hereafter, second

227   diameter). Several leaves were collected randomly along branches of each adult, dried and

228   photographed. Pictures were analyzed to measure the three traits describing leaf morphology: (1)

229   leaf area, (2) length and (3) width using ImageJ (Schneider *et al.*, 2012). The number of leaves

230   analyzed per adult ranged from 10 to 23 with an average of 20.3. In females, we counted the number

231   of cones in the last two cohorts (cones produced in the last two seasons of cone production and

232   maintained closed since). Because older cohorts were not counted, this measure reflects cone

233 production rather than the maintenance of the serotinous seed bank. We did not count male cones

234 because they were too numerous.

235

236 **Microsatellite genotyping**

237 We genotyped both adults and their progeny in our focal population (available at

238 doi:10.5061/dryad.ngf1vhhst). For both adults and seedlings, sampled leaves were preserved in

239 silica gel prior to DNA extraction using a modified version of the CTAB protocol (Justy *et al.*,

240 2009). We designed two polymerase chain reaction (PCR) multiplexes for amplifying DNA at 4

241 microsatellite loci, each involving primers with different fluorescent labels (Multiplex 1: 4F8, 3C9,

242 1C7, 1C3; Multiplex 2: 3B11, 2B2, 1D7, 1B8; markers developed by Justy *et al.*, 2009). PCRs were

243 performed using the Qiagen Multiplex PCR Kit (Qiagen, Hilden, Germany); each PCR reaction was

244 performed in a final volume of 10μM composed of 5μL of Multiplex Master mix (2X), 1μL of

245 primer sequences (1μM), 1μL of DNA extracts and 3μL of sterile water. PCR reactions were

246 performed on a Mastercycler pro thermocycler (Eppendorf, vapo.protect) with an initial

247 denaturation step of 15min at 95 °C, 35 cycles of 30s at 94 °C, 1min30s at the T_m temperature (M1:

248 54°C, M2: 53°C) and 1min at 72 °C, and a final step of 30min at 60°C. Genotyping was performed

249 on an ABI3500XL sequencer. The genotypes of all adults and offspring were scored using

250 GeneMapper at the eight microsatellite loci, which exhibited between five and 23 alleles (Table S1

251 for information per marker). After excluding individuals that did not amplify, our dataset contained

252 82 females, 85 males and 869 juveniles, corresponding to an amplification failure of roughly 8% for

253 both adults and juveniles. For each microsatellite marker, we used CERVUS (version 3.0.7;

254 Kalinowski *et al.*, 2007) to estimate the non-exclusion probabilities of the first parent, the second

255 parent and parent pairs, to test for Hardy-Weinberg equilibrium, and to compute null allele

256 frequencies (Table S1). Non-exclusion probabilities correspond to the probabilities that the set of

257 loci will not exclude an unrelated candidate parent (or parent pair) of an arbitrary offspring. Finally,

258 we used NMπ (Version 1.0, Chybicki, 2017) to estimate the per-marker genotyping errors.

259

Joint estimation of effective fecundities and both pollen and seed dispersal kernels

261 We used a method that uses information about the genotype and the spatial location of adults and

262 seedlings to jointly estimate pollen and seed dispersal kernels and the individual male and female

263 *effective fecundities* – a proxy for fitness (see the Introduction). Our method builds on the Mixed

264 Effects Mating Model, MEMMseedlings (Oddou-Muratorio *et al.*, 2018), which models mating and

265 dispersal events in a hermaphroditic plant population to estimate the selfing rate, immigration rates

266 and dispersal kernels for both pollen and seeds as well as the variance in male and female effective

267 fecundity (*i.e.* using random individual effects). We modified the MEMMseedlings algorithm to

268 produce a new version that handles separate sexes, with distinct spatial distributions of male and

269 female plants (see Supplementary Method S3, available at

270 https://gitlab.paca.inrae.fr/pub/tonnabel_mol_ecol.).

271 MEMMseedlings takes into account both the variation in fecundity among individuals and

272 the relative positions of putative parents and seedlings when computing the likelihood of observed

273 genotypes conditional to dispersal parameter and individual fecundity estimations. In

274 MEMMseedlings, putative parents that are more distant from a seedling have a lower parentage

275 probability. This model also describes mate competition through a mass action law, *i.e.* the

276 contribution of a given male to the pollen cloud of a given female is diluted among the contributions

277 of all other males. For these reasons, the model can estimate variation in effective fecundities,

278 separately from different sources of spatial variation in reproductive success, linked to (i) spatial

279 biases in seedling sampling, (ii) the spatial distribution of mates, or (iii) edge effects. Accordingly,

280 we checked that the estimated effective fecundity of adult plants located on the border of our study

281 population was not different than elsewhere in the study population by generalized linear mixed

282 models (results not shown). Our model assumes the same pollen (or seed) dispersal kernels for each

283 male (or respectively female) individual, and isotropic wind dispersal patterns. Given that

284 anisotropy can sometimes be found in wind-pollinated plants (Austerlitz *et al.* 2007), we confirmed

285 an absence of signal for anisotropy using NMπ (see Supplementary Method S3). MEMMseedlings

286 estimates a relative measure of effective fecundity, scaled by the average effective fecundity, (see

287 equation (1) in Supplementary methods S3), which is therefore unitless.

288   Given the life cycle of *L. rubrum* and the sampling of seedlings after the fire, our estimated

289 effective fecundity integrates the effect of variation between individuals, either male or female, not

290 only for pollen and ovule production, but also for pollen export, fertilization rate, seed maturation

291 and dispersal, maintenance of seeds within the cones (degree of serotiny), adult survival until the

292 fire, seed germination and juvenile survival until the seedling census. Seeds released after the fire

293 and previously stored in the canopy were potentially fertilized in different years. Because adults of

294 *L. rubrum* do not survive fire, the establishment of progeny after a fire thus represents their entire

295 lifetime reproduction.

296   Briefly, our MEMMseedlings model combines genotypes data and spatial distribution data

297 for both adults and offspring to estimate, in a Bayesian framework, individual male and female

298 effective fecundities (F_k and R_j, respectively), the seed immigration rate (m_s), the pollen immigration

299 rate (m_p), the rate of pollen export to the pollen cloud of non-local mothers (υ), the mean seed

300 dispersal distance (δ_s), the mean pollen dispersal distance (δ_p), a parameter affecting the shape of the

301 seed dispersal kernel (b_s) and that of the pollen dispersal kernel (b_p). The estimation of pollen and

302 seed immigration rates (m_s and m_p) and, the rate of pollen export to the pollen cloud of non-local

303 mothers, (υ) depends on the actual process of immigration, but is also affected by the fact that

304 around 8% of the parents were excluded from the analysis due to a lack of amplification.

305 Immigration rates therefore include the probabilities of maternity and paternity attributable to

306 unsampled parents. Both pollen and seed immigration rates are therefore likely overestimated.

307 Finally, when computing Mendelian transition probabilities between seedlings and putative parents,

308 MEMMseedlings considers genotyping errors by allowing a parent-offspring genetic discrepancy at

309 a maximum of one locus, and at each locus, the probability to mistype any allele was fixed using the

310 per-marker genotyping error rates estimated by NMπ (see Supplementary Method S3). To describe

311 the quality of parentage assignments associated with the dataset, MEMMseedlings computes the

312 posterior probabilities for all seedlings for which (i) both parents are known among the genotyped

313 parents, (ii) only the mother, or (iii) the father is known, and (iv) none of the parents is known.

314   Estimates of dispersal kernels are based on dispersal events within the population, even if the

315 parametric model implies dispersal in unbounded space (beyond the maximal male-female and

316 female-seed distances found in our study population, respectively 106.4 and 139 meters for pollen

317 and seeds dispersal). To describe dispersal within the study population, we computed, from the

318 estimated kernels, the predicted proportion of seeds and pollen that dispersed within the population

319 range and the predicted proportion that dispersed within an arbitrary short distance of 20m.

320   We estimated the model parameters using two MCMC chains of 50,000 steps and a burn-in

321 of 10,000 steps each. We used uniform prior distributions for the parameters m_s, m_p, υ, δ_s, b_s, δ_p and

322 b_p within the intervals [0.01,1.00], [0.01,1.00], [0.00,1.00], [1.00,100], [0.01,1.00], [1.00,30000] and

323 [0.01,10.0], respectively. For individual effective fecundity estimates (F_k *or* R_j), values were

324 sampled every 20 iterations to decrease autocorrelation and averaged after concatenating the two

325 chains. For each of these stored iterations, we also computed the variance in effective fecundity

326 estimates among individuals. Credibility intervals at 95% were calculated for all estimated

327 parameters, as well as the mean value across all iterations and chains (Table 1).

328

329 **Sex differences in morphology, spatial distribution and analysis of number of cones**

330 We tested for sex differences in morphology using Linear Mixed-effects Models (LMM) with

331 spatially autocorrelated random effects. We analyzed all measured adult traits describing either plant

332 architecture or leaf morphology. Random individual effects can be spatially autocorrelated, for

333 instance, due to spatial variation in some ecological variables not included in the model. We fitted

334 models with morphology as the response variable and sex as a fixed effect using the R package

335 spaMM version 3.3.0 (Rousset & Ferdy, 2014) in R 4.0.2 (R Core Team, 2020). We fitted models

336 with distinct residual variances for each sex. We updated the code of the spaMM package to allow

for different spatial distributions of random effects between sexes (publicly available in spaMM

since version 2.6.0). The classical Matérn correlation function was used to model the spatial

autocorrelation of random effects, separately for each sex, as a function of the distance between

individuals. The Matérn correlation model involves two parameters: the smoothness parameter (v),

and the scaling parameter for distances (ρ). We compared models fits considering (1) no spatial

autocorrelation, (2) the same spatial autocorrelation for both sexes and (3) two sex-specific spatial

autocorrelation structures. We used likelihood ratio tests (LRTs) to (i) first test for a sex-specific

spatial structure in morphology, by comparing models with a different structure of random effects

but the same fixed effects, and (ii) to test for sexual dimorphism, by comparing the selected model

in step (i) to a model fitted with a similar structure of random effects, but without sex as a fixed

effect. Models were fitted either by maximum likelihood, for performing LRTs between models

differing in their fixed-effects structure, or by restricted maximum likelihood, for LRTs between

models differing in their random-effect structures and for computing the predictions from the model

fits. We also examined whether male and female plants were spatially segregated (*i.e.* whether the

sex ratio was spatially autocorrelated) using a binomial generalized linear mixed model (GLMM)

with sex as the response variable and compared model fits with or without a spatially autocorrelated

random effect as described above. Finally, we tested whether the number of cones produced by

females displayed a non-uniform spatial distribution by comparing models including cone number

as the response variable, plant density (see below for its calculation) as a fixed factor, and either a

spatial random effect or not.

Multivariate sex-specific selection analysis

Inspired by the multivariate framework of Lande and Arnold (1983), we examined in a single full

model the relationship between the relative effective fecundity as the response variable and, the

following explanatory variables: canopy diameter, leaf area, plant density, sex, and the interaction

between each of the three former explanatory variables and sex. We fitted generalized linear mixed-

effects models (Gamma GLMM with logarithm link function) to describe the variation in effective fecundity, while including spatially autocorrelated random effects. We checked that a model predicting effective fecundity using a Gamma distribution with a log link performed better than models assuming a different candidate distribution (compare gamma log link: cAIC=18.7 with gaussian with a link identity: cAIC=139; or gaussian with a log link: cAIC=126 – cAIC is a metric similar to the traditional *AIC*, except that it measures prediction performance conditionally on the realization of the random effects, Vaida & Blanchard, 2005). We followed the same procedure as described for the analysis of sexual dimorphism (see previous section) to fit the models using the R package spaMM and to identify the best fitting random spatial structure (*i.e.* comparing a sex-specific spatial structure, a common spatial structure and a lack of it). We were thus able to compare the patterns of spatial variation of residual effective fecundity between males and females, once the effects of local density and variation in morphology were included as fixed effects in our global model. Spatial autocorrelation in effective fecundity may then reflect spatial variation in unmeasured environmental variables (such as water availability) or unmeasured plant traits. Different spatial structures between sexes therefore inform on the differential sensitivities of their effective fecundities to variation in such unmeasured variables. We took into account the variation in uncertainty of the individual effective fecundity estimates by parameterizing the residual variance as a function of the variance in MCMC estimates of individual fecundity during the fitting (see Supplementary Method S4). We again fitted models with distinct residual variances for each sex. Because our MEMMseedlings model estimated large effective fecundity for several plants located in one part of the study population, we performed a sensitivity analysis testing the robustness of our results to the removal of all individuals with standardized effective fecundity greater than four standard errors (for all statistical models treating effective fecundity as response variable). Five females and one male were removed in this sensitivity analysis, including four individuals that were particularly close from each other.

388　　　We chose to investigate the selection gradients for two morphological predictors only

389　(canopy diameter and leaf area), because several of the six morphological traits were highly

390　correlated (Table S3). Notably, all three traits describing plant architecture were strongly correlated

391　with each other (*i.e.* plant height, canopy diameter and second diameter, Table S3). Similarly, our

392　three measures of leaf morphology were strongly correlated with each other (*i.e.* leaf area, length

393　and width, Table S3). Estimation of multivariate selection gradients and their interpretation could be

394　confused by such strong correlations between traits (see Chong *et al.,* 2018 for a review). We

395　therefore retained only two morphological traits in our selection analysis (but similar results were

396　obtained for other combinations of traits). We standardized the two focal traits using z-scores based

397　on the mean and variance values of the traits calculated separately for each sex. We confirmed that

398　leaf area significantly differed between individuals by comparing, within each sex, models

399　predicting leaf area with *vs*. without an individual-level random effect using an exact restricted

400　likelihood ratio test (Crainiceanu and Ruppert, 2004) implemented in package RLRsim 3.1-6

401　(Scheipl *et al.,* 2008): for females, likelihood ratio (LR)=1573.9, p<0.001; for males, LR=625.1,

402　p<0.001.

403　　　We compared the performance of local plant density measured at different scales in

404　explaining variation in male and female effective fecundity (see Supplementary Method S5). We did

405　not transform plant density into z-scores since this predictor is not an individual trait and thus its

406　associated slope should not be considered as a selection gradient. To compare models explaining

407　variation in effective fecundity with different scales used to compute plant density, we used *cAIC*.

408　The best model included the density of plants in a quadrat of 12x12m around the focal individual.

409　We therefore retained this metric to compute the values of plant density used in our all subsequent

410　analyses.

411　　　To test for the significance of selection gradients, we first compared the fit of the full model

412　to the fit of nested models in which one of the three predictors of interest (*i.e.* canopy diameter, leaf

413　area and plant density) had been removed, both as a main effect and in interactions. This revealed

414   whether there was any effect of the focal predictor. Second, we compared the full model to models

415   in which only the interaction between sex and one of the three variables of interest had been

416   removed. This allowed us to test whether the effect of the predictor was different between sexes. We

417   also built separate GLMMs for each sex, predicting effective fecundity from the three predictors of

418   interest. We used these sex-specific models to test the effect of each predictor in each sex, if and

419   only if, the interaction between sex and a given predictor was significant. We compared the fit of

420   our full model, which considers linear selection gradients only, to the fit of a similar model

421   including quadratic and correlational selection terms for canopy diameter and leaf area, and to

422   model fits including one quadratic or correlational term at a time.

423   We also estimated selection gradients for the same morphological traits (canopy diameter

424   and leaf area), using as a proxy for fitness, not the estimated effective fecundity but the actual

425   number of cones empirically counted on female plants. We predicted the number of female cones

426   from traits using a Poisson GLMM with spatially autocorrelated random effects and plant density as

427   a covariate in addition to the two focal traits. Finally, we predicted the female effective fecundity

428   from the number of empirically counted cones, also with spatially autocorrelated random effects and

429   plant density as a covariate.

Results

431

432   ***L. rubrum* showed strong sexual dimorphism in morphology**

433 Females had significantly smaller canopy diameters (i.e., first and second diameter measures; Figs.

434 1a, S4c, Table S4), but they were not clearly shorter (Fig. S4a, Table S4). Females had also leaves

435 with a larger area than males (Fig. 1b, Table S4). Correlated measures of leaf morphology (Table

436 S3) showed similar sexual dimorphism, as females displayed longer and wider leaves than males

437 (Fig. S4e,f, Table S4).

438   Spatial structure in the canopy diameter did not clearly differ between sexes, as the fit of a

439 linear mixed model including sex-specific spatially autocorrelated random effects did not produce a

440 likelihood significantly higher than the fit of the model with the same distribution of spatial random

441 effects in both sexes (Table S4). However, a spatially structured random effect considerably

442 improved the fit over the models without it (Table S4; Fig. S5). In contrast, leaf area showed neither

443 a sex-specific spatial structure nor a general spatial structure, (Table S4). Similarly, we found no

444 significant spatial structure for sex ratio (Table S4; Fig. S6).

445

446   **Dispersal occurred on a smaller spatial scale for seed than for pollen**

447 For both pollen and seed dispersal kernels, our analysis revealed fat-tailed dispersal kernels (*i.e. b_s*

448 and b_p lower than one; Fig. 2 and Table 1). Seed and pollen immigration rates were of the same

449 order of magnitude (11% and 15% for seed and pollen respectively). Seed dispersal occurred on a

450 smaller spatial scale than pollen dispersal: the mean estimated dispersal distance of seeds and pollen

451 were respectively of 10.6 and 11,041 meters. These estimated dispersal kernels predict that ca.

452 100% of seeds fell closer than the maximal female-seedling distance found in our population (*i.e.*

453 139 meters), while only 7.56% of pollen traveled a distance shorter than the maximal male-female

454 distance found in our population (*i.e.* 106.4 meters). Similarly, we estimated that 86% of seeds and

455 1.56% of pollen was dispersed within 20 meters. A fat-tailed pollen dispersal kernel accounting for

456   distance-dependent pollen dispersal nevertheless explained our data better than modeling a uniform

457   distribution of pollen dispersal distances (Fig. S7, see Supplementary Methods S3 for a description

458   of their comparison). Although we estimated a high probability for the pollen to travel long distance,

459   we estimated that about three quarters of the seedlings had a genotyped father in the population (1-

460   m_p=0.85 for seedlings with a known mother or υ=0.81 for seedlings with an unknown mother),

461   which is similar to the proportion found for mothers (1-m_s=0.89; Table 1). Estimations of dispersal

462   kernels with the NMπ algorithm yielded similar parameter estimation, yet with a notable shorter

463   estimate of mean pollen dispersal distance (Table 1 *vs.* S2). The estimates of dispersal kernels with

464   NMπ were robust to the inclusion of anisotropy in dispersal events (results not shown).

465

466   **Autocorrelation in effective fecundity occurred on a smaller spatial scale for males**

467   **than females**

468   Effective fecundity estimations were carried out using a set of 8 microsatellite markers containing

469   between 6 and 24 alleles, showing non-exclusion probabilities of parent pairs ranging between 0.12

470   to 0.58 and genotyping error rates ranging from 0.9% to 5.5% (Table S1). The combination of the

471   genotype data and plant spatial distribution data provided information to assign two parents to ~88%

472   of seedlings (Figure SM3 in Supplementary Methods S3).

473   We detected a clear sex-specific spatial structure for effective fecundity (Table S5). We

474   found different spatial variation in effective fecundity for each sex, with coarse-grained and fine-

475   grained spatial effects for females and males, respectively (Fig. 3a *vs.* 3b). These results were robust

476   to the removal of plants with standardized effective fecundity greater than four standard errors,

477   which only slightly affected the previous conclusion (Table S5; Fig. S8). Several plants with large

478   effective fecundity were found in the disturbed area (Fig. 3). The number of empirically counted

479   cones on female plants also displayed a significant spatial autocorrelation (χ^2=2238, *df*=3, *p*<0.0001;

480   Fig. S9). Cone number was significantly correlated with relative effective fecundity but the effect

481   size was small (using standardized cone number, β=0.286, χ^2=6.02, *df*=1, *p*=0.0141) and the two

482   spatial distributions were not fully aligned (Fig. 3a *vs.* S9).

483

Selection for higher leaf area and wider canopies similar in both sexes

485 Our spatially corrected selection gradient approach revealed that the leaf area was negatively

486 associated with effective fecundity (Table 2 and S5; Fig. 4), with similar slopes in both sexes as

487 shown by a non-significant interaction between leaf area and sex (Table S5). Yet, the leaf area was

488 positively correlated to the number of counted cones on female plants (β=0.171; LRT: χ^2=42.7,

489 df=1, p<0.001). Larger canopy diameter was significantly associated with higher effective fecundity

490 (Table 2 and S5; Fig. 4). Accordingly, female plants with wider canopies displayed higher numbers

491 of empirically counted cones (β=0.904; LRT: χ^2=78.8, df=1, p<0.001). The increase in effective

492 fecundity with increasing canopy diameter was similar in both sexes, as shown by a non-significant

493 interaction between sex and canopy diameter (Table S5). Our estimates of selection gradients were

494 robust to the removal of plants with effective fecundity greater than four standard errors (Table S5;

495 Fig. S10). We found no signal for non-linear selection, either by including all three quadratic and

496 correlational terms at once (LRTs: χ^2=0.709, df=3, p=0.871), or each of them separately ((leaf

497 area)^2: χ^2=0.129, df=1, p=0.719; (canopy diameter)^2: χ^2=0.118, df=1, p=0.731; leaf area x canopy

498 diameter: χ^2=0.378, df=1, p=0.539).

499

The effect of plant density on effective fecundity is sex-specific

501 The effect of plant density on effective fecundity (Fig. S6) differed between sexes, as revealed by a

502 significant interaction between sex and plant density (Table S5; Fig. 4c). Plant density was

503 negatively associated with male effective fecundity, but female effective fecundity showed no

504 association with plant density (Table S5). The effect of the interaction between sex and plant density

505 was however only marginally significant when the plants with the highest effective fecundity were

506 removed in the robustness analysis (Table S5; Fig. S10).

Discussion

Novel methods for dealing with spatial bias affecting selection estimates in plants

Technical and methodological improvements in parentage assignments now allow for estimation of plant fitness in natural populations from genetic data, and provide the link between fitness and plant traits through selection gradients analyses (e.g. Meagher & Thompson, 1986; Burczyk & Prat, 1997; Burczyk *et al.*, 2006; van Kleunen & Burczyk, 2008). We have developed a methodology that estimates effective fecundity in dioecious plants while accounting for biases associated with their spatial distribution. Beyond the interest of documenting spatial patterns of seed and pollen dispersal, the addition of this spatially explicit component to classical parentage methods (Jones, 2010) improves the estimation of effective fecundity in the presence of confounding effects, such as spatial bias in sampling descendants, spatial variation in the intensity of mate competition triggered by a non-uniform distribution of mates, or border effects (Oddou-Muratorio *et al.*, 2018). We investigated effects of traits on effective fecundity by classical selection gradient methods (Lande & Arnold, 1983), in which we explicitly modeled the effect of spatially correlated unmeasured environmental factors on effective fecundity. This newly developed framework will be particularly suited to estimating selection in natural populations, given that spatial biases are typically difficult to avoid regarding both sampling and uncontrolled factors.

No contemporary sexually antagonistic selection despite strong sexual dimorphism

The signal we found for selection of larger canopy diameters in both sexes may indicate a 'budget effect' of plant size, where larger plants acquire more resources that can be reallocated to gamete production (Delph & Ashman, 2006). In females, the number of counted cones was positively related to canopy diameter. However, cone number only poorly explained effective fecundity. The spatial distribution of cone number and female effective fecundity were moreover not fully matching, suggesting that processes occurring after cone production, such as cone maintenance or mother plant survival affect the female effective fecundity. In males, selection for wider canopies

could be linked to flower production if both sexes are subject to similar ontogenetic constraints. We found evidence for similar selection for smaller leaf area in both sexes. Smaller leaves were previously shown to be correlated in *L. rubrum* with thinner, and more numerous, branches and less efficient water transport from roots to branch apex (Harris, 2007). Selection for smaller leaves in males may reflect selection for greater number of inflorescences held on more flexible branches, a trait long hypothesized to enhance pollen dispersal (Klinkhamer *et al.*, 1997). Smaller leaves may also represent a decreased mechanical hindrance to pollen dispersal. Selection for smaller leaves in females, however, contradicts our expectation of selection for enhanced water transport to the cones. The number of cones counted on females was furthermore positively related to leaf area. The fact that leaf area relates to the number of cones, and to effective fecundity in opposite ways, suggests that any positive effects of leaf area on fecundity through female cone production may have been masked by trade-offs with other key life history components for serotinous plants (e.g. adult survival until the fire). In the absence of positive genetic correlation between sexes, sexual conflicts may be resolved once each sex reaches its respective optimum. We however did not find evidence for stabilizing selection in the study population, which one could expect if each sex was at its optimum with sufficient genetic variation in the studied traits.

Only 17% of studies estimating selection gradients in animals identified sexually antagonistic selection (Cox & Calsbeek, 2009). The paucity of evidence for sexually antagonistic selection, with which our study concurs, is inconsistent with the idea that genetic correlations between sexes should maintain sexually antagonistic selection over long periods of time (Lande, 1980). To explain this inconsistency, both theory and experiments have suggested that temporal or spatial ecological changes may result in variable pattern of selection acting on males and females, with both sexes displaying trait values remaining far away from their ever changing ecological optimum (Kokko & Rankin, 2006; Delph *et al.*, 2011; Sheridan & Bickford, 2011; Long *et al.*, 2012; Berger *et al.*, 2014; Connallon, 2015; Connallon & Hall, 2016). Recent theoretical

558 developments showed that positive inter-sexual covariance for resource acquisition traits could also

559 impede the identification of sexually antagonistic selection (Zafitschek & Connallon, 2017).

560 An alternative explanation to the lack of detected antagonistic selection is that antagonistic

561 selection is present but masked by a positive correlation between a locally varying unmeasured

562 ecological factor and both effective fecundity and a focal morphological trait (Price *et al.*, 1988). A

563 large body of theoretical work also suggests that the combination of a strong sexual dimorphism

564 with a lack of sexually antagonistic selection found in *L. rubrum* may result from adaptation to

565 changing ecological conditions, which cause patterns of selection between sexes to align. A longer

566 fire return interval, or low resource availability, are predicted to select for increased resource

567 allocation to plant survival and a lower allocation to cone maintenance (Tonnabel *et al.*, 2012). That

568 is because serotinous plants need to survive until fire to reproduce and can therefore afford to

569 maintain cones over long periods of time only if it does not come at the expense of their own

570 survival up until the fire. These particular ecological conditions may have weakened selection in

571 females for traits improving current water conductance and cone maintenance, and favored instead

572 traits improving cone production and adult survival. Understanding the emergence of sexual

573 dimorphism through sex-specific selection estimations will therefore require either experimental

574 protocols controlling environmental conditions or extensive estimations of spatio-temporal variation

575 in sex-specific selection in natural populations. Long-term studies in animals have indeed

576 commonly found large temporal variation in selection pressures acting on various traits (e.g. Grant

577 & Grant, 2002; Reimchen & Nosil, 2002; Reed *et al.*, 2013; Acker *et al.*, 2015), including both

578 temporal and spatial variation in the direction of sexually antagonist selection pressure on sexually

579 dimorphic traits (Fargevieille, 2016).

580 **Sex-specific spatial distribution of effective fecundities**

581 The observation that reproductive costs differ between males and females (e.g. Antos & Allen,

582 1990; McDowell *et al.*, 2000; Harris & Pannell, 2008; van Drunen & Dorken, 2012) has been

583 pivotal to discussions on the evolution of sexual dimorphism in plants (Freeman *et al.*, 1976; Delph

584 & Bell, 2008). Resources key to male and female reproduction commonly display small-scale

585 variation in the wild (Silvertown *et al.,* 1999; Araya *et al.,* 2011). Therefore, it is a simple corollary

586 of the sex-specific cost of reproduction hypothesis that male and female fitness should often exhibit

587 different spatial patterns in natural populations, as found in our study population. These sex-specific

588 spatial patterns of fitness variation call for future studies relating small-scale variation in key

589 resource types (Silvertown *et al.,* 1999; Araya *et al.,* 2011) and plant fitness in both males and

590 females.

591 **Only male effective fecundity was affected by density**

592 Male effective fecundity was negatively associated with plant density while no association was

593 found for females. The negative effect of plant density on male effective fecundity might be

594 triggered by increased competition over nutritive resources affecting pollen production, by negative

595 effects of a closed canopy on pollen dispersal, or by competition effects at the seedling stage

596 affecting their offspring. The lack of an effect of plant density on female reproduction suggests that,

597 either they are less affected than males by competition with other plants, or that the negative effects

598 of competition are counter-balanced by positive effects of reproducing in a high density patch. In

599 both cases, it suggests different reproductive needs and ecology in males and females. Plant density

600 was shown to negatively affect both male and female effective fecundity in a wind-pollinated tree

601 (Oddou-Muratorio *et al.,* 2018), and was also shown to impede pollen dispersal in a wind-pollinated

602 herb (Tonnabel *et al.,* 2019b). We note however that this sex-specific effect of density on effective

603 density was only marginally significant when removing individuals with large fecundity.

604 **Pollen and seed dispersal kernels typical of plant dispersal behaviour**

605 Our spatially explicit method allowed the estimation of dispersal kernels, which revealed a fat-tailed

606 seed dispersal kernel in the anemochorous *L. rubrum.* Most seeds dispersed close to the mother

607 plant, but some fraction dispersed much further. Similarly, a meta-analysis including species from

608 various plant families, continents, vegetation types and growth forms found a predominance of fat-

609 tailed seed dispersal kernels (Bullock *et al.,* 2017). Investigations of pollen dispersal kernels are

scarce, but they typically also indicate fat-tailed kernels in both insect- (Austerlitz *et al.,* 2004; Oddou-Muratorio *et al.,* 2005; but see Matter *et al.,* 2013) and wind-pollinated species (Austerlitz *et al.,* 2004; Goto *et al.,* 2006; Gaüzere *et al.,* 2013; Geber *et al.,* 2014 but see Ahee *et al.,* 2015). Our estimated pollen dispersal kernel showed a markedly fat-tailed distribution, whereby a large proportion of pollen was able to disperse over large distances; similar large distance pollen dispersal was reported in both wind-pollinated and animal-pollinated species (e.g. Devaux *et al.,* 2005; O'Connell *et al.,* 2007). Given the large estimates of pollen dispersal distances and the short distance to the nearest population, the low estimates of pollen immigration are unexpected, especially given the same order of magnitude as seed immigration rate. This discrepancy is nevertheless consistent with other studies showing that the amount of long distance dispersal inferred by spatially explicit parentage modeling is not always congruent with the amount predicted by dispersal kernels inferred from local dispersal events (Chybicki & Oleksa, 2018; Hardy *et al.,* 2019). Such inconsistencies may emerge when extrapolation of dispersal kernels does not properly account for an increased probability of encountering obstacles between populations.

In conclusion, we found sex-specific variation in fitness in a natural population of a highly dimorphic plant species, despite similar directional selection in both sexes. Plant density impacted males and females differently, suggesting that sexes may display different sensitivities to competition over resources, regardless of competition for mates. The fixed life-form of plants might often generate spatial structure in fitness, as displayed in our study population. We therefore advocate for the generalization of spatial methods for estimating selection gradients, combined with spatially explicit fitness estimation methods for estimating selection acting on plants in the wild. In the long run, such methods should also account for the sex-specific temporal variation in plant phenology and the relatedness between potential mates as both can also influence fitness (Ismail & Kokko, 2019) and are likely to show spatial patterns.

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646 **References**

647

648 Acker P, Grégoire A, Rat M, Spottiswoode CN, van Dijk RE, Paquet M, Kaden JC, Pradel R,

649   Hatchwell BJ, Covas R, Doutrelant C. 2015. Disruptive viability selection on a black

650   plumage trait associated with dominance. *Journal of Evolutionary Biology* **28**: 2027-2041.

651 Ahee JE, Van Drunen WE, Dorken ME. 2015. Analysis of pollination neighbourhood size using

652   spatial analysis of pollen and seed production in broadleaf cattail (*Typha latifolia*). *Botany*

653   **93**: 91-100.

654 Antos JA, Allen GA. 1990. A comparison of reproductive effort in the dioecious shrub *Oemleria*

655   *cerasiformis* using nitrogen, energy and biomass as currencies. *The American Midland*

656   *Naturalist* **124**: 254-262.

657 Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G. 2011. A fundamental,

658   eco-hydrological basis for niche segregation in plant communities. *New Phytologist* **189**:

659   253-258.

660 Arnold SJ. 1994. Bateman's principles and the measurement of sexual selection in plants and

661   animals. *The American Naturalist* **144**: S126-S149.

662 Austerlitz F, Dick CW, Dutech C, Klein EK, Oddou-Muratorio S, Smouse PE, Sork VL. 2004.

663   Using genetic markers to estimate the pollen dispersal curve. *Molecular Ecology* **13**: 937-

664   954.

665 Austerlitz F, Dutech C, Smouse PE, Davis F, Sork VL. 2007. Estimating anisotropic pollen

666   dispersal: a case study in *Quercus lobata*. *Heredity* **99**: 193-204.

667 Barrio M, Teixido AL. (2015) Sex-dependent selection on flower size in a large-flowered

668   Mediterranen specie: experimental approach with *Cistus ladanifer*. *Plant Systematics and*

669   *Evolution* **301**:113-124.

670 Bateman AJ. 1948. Intra-sexual selection in Drosophila. *Heredity* **2**: 349-368.

Berger D, Grieshop K, Lind MI, Goenaga J, Maklakov AA, Arnqvist G. 2014. Intralocus sexual conflict and environmental stress. *Evolution* **68**: 2184-2196.

Bond WJ, Maze KE. 1999. Survival costs and reproductive benefits of floral display in a sexually dimorphic dioecious shrub, *Leucadendron xanthoconus. Evolutionary Ecology* **13**: 1-18.

Bond WJ. 1984. Fire survival of Cape Proteaceae influence of fire season and seed predators. *Vegetatio,* **56**:65-74.

Bullock JM, Gonzàlez LM, Tamme R, Götzenberger L, White SM, Pärtel M, Hooftman DAP. 2017. A synthesis of empirical plant dispersal kernels. *Journal of Ecology* **105**: 6-19.

Burczyk J, Adams WT, Birkes DS, Chybicki IJ. 2006. Using genetic markers to directly estimate gene flow and reproductive success parameters in plants on the basis of naturally regenerated seedlings. *Genetics* **173**: 363-372.

Burczyk JL, Prat D. 1997. Male reproductive success in *Pseudotsuga menziesii* (Mirb.) France: the effects of spatial structure and flowering characteristics. *Heredity* **79**: 638-647.

Castilla AR, Alonso C, Herrera CM. 2014. Sex-specific selection and geographical variation in gender divergence in a gynodioecious shrub. *Plant biology* **17**:186-193.

Chong VK, Fung HF, Stinchcombe JR. 2018. A note on measuring natural selection on principal component scores. *Evolution letters* **2**:272-280.

Chybicki IJ. 2018. NMπ—improved reimplementation of NM+, a software for estimating gene dispersal and mating patterns. *Molecular ecology resources* **18***:*159-168.

Chybicki IJ. Oleska A. 2018. Seed and pollen gene dispersal in *Taxus baccata,* a dioecious conifer in the face of strong population fragmentation. *Annals of Botany* **122**:409-421.

Cocucci AA, Marino S, Baranzelli M, Wiemer AP, Sérsic A. 2014. The buck in the milkweed: evidence of male-male interference among pollinaria on pollinators. *New Phytologist* **203**: 280-286.

695   Connallon T. 2015. The geography of sex-specific selection, local adaptation, and sexual

696   dimorphism. *Evolution* **69**: 2333-2344.

697   Connallon T, Hall MD. 2016. Genetic correlations and sex-specific adaptation in changing

698   environments. *Evolution* **70**: 2186-2198.

699   Cowling RM, Lamont BB. 1987. Post-fire recruitment of four co-occurring *Banksia* species.

700   *Journal of Applied Ecology* **24**: 645-658.

701   Cox RM, Calsbeek R. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution

702   of intralocus sexual conflict. *The American Naturalist* **173**: 176-187.

703   Crainiceanu CM, Ruppert, D. 2004. Likelihood ratio tests in linear mixed models with one variance

704   component. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **66**:

705   165-185.

706   Delph LF, Herlihy CR. 2012. Sexual, fecundity, and viability selection on flower size and number in

707   a sexually dimorphic plant. *Evolution* **66**: 1154-1166.

708   Delph LF, Andicoechea J, Steven JC, Herlihy CR, Scarpino SV, Bell DL. 2011. Environment-

709   dependent intralocus sexual conflict in a dioecious plant. *New Phytologist* **192**: 542-552.

710   Delph LF, Ashman TL. 2006. Trait selection in flowering plants: how does sexual selection

711   contribute? *Integrative and Comparative Biology* **46**: 465-472.

712   Delph LF, Bell DL. 2008. A test of the differential-plasticity hypothesis for variation in the

713   degree of sexual dimorphism in *Silene latifolia. Evolutionary Ecology Research* **10**: 61-75.

714   Devaux C, Lavigne C, Falentin-Guyomarc'h H, Vautrin S, Lecomte J, Klein EK. 2005. High

715   diversity of oilseed rape pollen clouds over an agro ecosystem indicates long distance

716   dispersal. *Molecular Ecology* **14**: 2269-2280.

717

718 Dorken ME, Perry LE. 2017. Correlated paternity measures mate monopolization and scales with

719   the magnitude of sexual selection. *Journal of Evolutionary Biology* **30**: 377-387.

720 Elle, E. & Meagher, TR. 2000. Sex allocation and reproductive success in the andromonoecious

721   perennial *Solanum carolinense* (Solanaceae). II Paternity and functional gender. *The*

722   *American Naturalist* **156**: 622-636.

723 Eppley SM, Pannell JR. 2007. Density-dependent self-fertilization and male *versus* hermaphrodite

724   siring success in an androdioecious plant. *Evolution* **61**: 2349-2359.

725 Fargevieille A. 2016. Sexual selection and the evolution of female ornaments: an examination of

726   female plumage colouration using comparative analyses and long-term data sets collected

727   in blue tit (*Cyanistes caeruleus*) populations. Animal biology. Université Montpellier,

728   English.   NNT:2016MONTT127. Tel-01647685

729 Forrest JRK. 2014. Plant size, sexual selection, and the evolution of protandry in dioecious plants.

730   *The American Naturalist* **184**: 338-351.

731 Freeman DC, Klikoff LG, Harper KT. 1976. Differential resource utilization by the sexes of

732   dioecious plants. *Science* **193**: 597-599.

733 Gauzère J, Klein EK, Oddou-Muratorio S. 2013. Ecological determinants of mating system

734   within and between three *Fagus sylvatica* populations along an elevational gradient.

735   *Molecular Ecology* **19**: 5001-5015.

736 Geber MA, Dawson TE, Delph LF. 1999. *Sexual and gender dimorphism in flowering plants*.

737   Springer-Verlag: Heidelberg.

738 Geber S, Chadoeuf J, Gugerli F, Lascoux M, Buiteveld J, Cottrel J, Dounavi A, Fineschi S, Forrest

739   LL, Fogelqvist J. et al. 2014. High rates of gene flow by pollen and seed in oak populations

740   across Europe. *Plos One* **9**: e85130.

63

Goto S, Shimatani K, Yoshimaru H, Takahashi Y. 2006. Fat-tailed gene flow in the dioecious canopy tree species *fraxinus mandshurica var. japonica* revealed by microsatellites. *Molecular Ecology* **15**: 2985-2996.

Grant PR, Grant BR. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707-711.

Guillot G, Rousset F. 2018. Dismantling the Mantel tests. *Methods in Ecology and Evolution* **4**: 336-344.

Harder LD, Prusinkiewicz P. 2013. The interplay between inflorescence development and function as the crucible of architectural diversity. *Annals of Botany* **112**: 1477-1493.

Hardy OJ, Delaide B, Hainaut H, Gillet J-F, Gillet P, Kaymak E, Vankercklove N, Dumini J, Doucet J-L. (2019) Seed and pollen dispersal distances in two African legume timber trees and their reproductive potential under selective logging. *Molecular Ecology* **28**:3119-3134.

Harris MS, Pannell JR. 2008. Roots, shoots and reproduction: sexual dimorphism in size and costs of reproductive allocation in an annual herb. *Proceedings of the Royal Society B – Biological Sciences* **275**: 2595-2602.

Harris MS, Pannell JR. 2010. Canopy seed storage is associated with sexual dimorphism in the woody dioecious genus *Leucadendron*. *Journal of Ecology* **98**: 509-515.

Harris MS. 2007. *The evolution of sexual dimorphism in flowering plants*. PhD thesis, University of Oxford, England.

Ismail SA, Kokko H. 2019. An analysis of mating biases in trees. *Molecular Ecology* in press, doi:10.1111/mec.15312.

Jones AG, Small CM, Paczolt KA, Ratterman NL. 2010. A practical guide to methods of parentage analysis. *Molecular Ecology Resources* **10**: 6-30.

Justy F, Midgley J, Olivieri I. 2009. Isolation and characterization of ten microsatellites markers in *Leucadendron rubrum* (Proteaceae). *Molecular Ecology Resources database* **9**: 1375-1429.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**: 1099-1106.

Klein EK, Desassis N, Oddou-Muratorio S. 2008. Pollen flow in the wildservice tree, S*orbus torminalis* (L.) Crantz. IV. Whole interindividual variance of male fecundity estimated jointly with the dispersal kernel. *Molecular Ecology* **17**: 3323-3336.

Klein EK, Bontemps A, Oddou-Muratorio S. 2013. Seed dispersal kernels estimated from genotypes of established seedlings: does density   dependent mortality matter? *Methods in ecology and Evolution* **4**:1059-1069.

Klinkhamer PGL, de Jong TJ, Metz H. 1997. Sex and size in cosexual plants. *Trends in Ecology and Evolution* **12**: 260-265.

Kokko H, Rankin DJ. 2006. Lonely hearts or sex in the city? Density- dependent effects in mating systems. *Philosophical Transaction of the Royal Society B* **361**: 319-334.

Kraaij T, Cowling RM, van Wilgen BW. 2011. Past approaches and future challenges to the management of fire and invasive alien plants in the new Garden Route National Park. *South African Journal of Science* **107**: doi:10.4102/sajs.v107i9/10.633.

Lande R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* **34**: 292-305.

Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* **37**: 1210-1226.

67

786   Lankinen A, Hybdom S, Strandh M. 2017. Sexually antagonistic evolution caused by male-male

787   competition in the pistil. *Evolution* **71**: 2359:2369.

788   Long TAF, Agrawal AF, Rowe L. 2012. The effect of sexual selection on offspring fitness depends

789   on the nature of genetic variation. *Current Biology* **22**: 204-208.

790   Martín-Sanz RC, Callejas-Días M, Tonnabel J, Climent JM. 2017. Maintenance costs of serotiny in

791   a variably serotinous pine: the role of water supply. *PlosOne* **12**: e0181648.

792   Matter P, Kettle CJ, Ghazoul J, Hahn T, Pluess AR. 2013. Evaluating contemporary pollen

793   dispersal in two common grassland species *Ranunculus bulbosus L. (Ranunculaceae)* and

794   *Trifolium montanum L. Fabaceae* using an experimental approach. *Plant Biology* **15**: 583-

795   592.

796   McDowell SCL, McDowell NG, Marshall JD, Hultine K. 2000. Carbon and nitrogen allocation to

797   male and female reproduction in Rocky Mountain Douglas-fir (P*seudotsuga menziesii var.*

798   *galuca*, Pinaceae). *American Journal of Botany* **87**: 539-546.

799   Meagher TR, Thompson EA. 1986. The relationship between single parent and parent pair

800   likelihoods in genealogy reconstruction. *Theoretical Population Biology* **29**: 87-106.

801   Moore JC, Pannell JR. 2011. Sexual selection in plants. *Current Biology* **21**: R176-R182.

802   Obeso JR. 2002. The cost of reproduction in plants. *New Phytologist* **155**: 321-348.

803   O'Connell LM, Mosseler A, Rajora OP. 2007. Extensive long-distance pollen dispersal in a

804   fragmented landscape maintains genetic diversity in white spruce. *Journal of Heredity* **98***:*

805   640-645.

806   Oddou-Muratorio S, Klein EK, Austerlitz F. 2005. Pollen flow in the wildservice tree, *Sorbus*

807   *torminalis* (L.) crantz. II. Pollen dispersal and heterogeneity in mating success inferred from

808   parent-offspring analysis. *Molecular Ecology* **14**: 4441-4452.

809 Oddou-Muratorio S, Gauzère J, Bontemps A, Rey J-F, Klein EK. 2018. Tree, sex and size:
810   ecological determinants of male vs. female fecundity in three *Fagus sylvatica* stands.
811   *Molecular Ecology* **27**:3131-3145.

812 Pickup M, Barrett SCH. 2012. Reversal of height dimorphism promotes pollen and seed dispersal in
813   a wind-pollinated dioecious plant. *Biology Letters* **8**: 397-404.

814 Price T, Kirkpatrick M, Arnold SJ. 1988. Directional selection and the evolution of breeding date in
815   birds. *Science* **240**: 798-799.

816 Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus
817   genotype data. *Genetics* **155**: 945-959.

818 Puixeu G, Pickup M, Field DL, Barrett SCH. 2019. Variation in sexual dimorphism in a wind-
819   pollinated plant: the influence of geographical context and life-cycle dynamics. *New*
820   *Phytologist*, **224**:1108-1120.

821 R Core Team (2020) R: A Language and Environment for Statistical Computing, R Foundation for
822   Statistical Computing, Vienna, Austria, https://www.R-project.org.

823 Rausher, M.D. 1992. The measurement of selection on quantitative traits: biases due to
824   environmental covariances between traits and fitness. *Evolution*, **46**:616-626.

825 Rebelo AG. 2001. *A field guide to the Proteas of Southern Africa*. Vlaeberg, Cape Town: Fernwood
826   Press.

827 Reed TE, Jenouvrier S, Visser ME. Phenological mismatch strongly affects individual fitness but
828   not population demography in a woodland passerine. *Journal of Animal Ecology*, **82**: 131-
829   144.

830 Reimchen TE, Nosil P. 2002. Temporal variation in divergent selection on spine number in
831   three spine stickleback. *Evolution*, **56**: 2472-2483.

71

832 Renner SS. 2014. The relative and absolute frequencies of angiosperm sexual systems: Dioecy,

833   monoecy, gynodioecy, and an updated online database. *American Journal of Botany*

834   **101**: 1588-1596.

835 Rousset F, Ferdy J-B. 2014. Testing environmental and genetic effects in the presence of spatial

836   autocorrelation. *Ecography* **37**: 781-790.

837 Scheipl F, Greven S, Kuechenhoff H. 2008. Size and power of tests for a zero random effect

838   variance or polynomial regression in additive and linear mixed models. *Computational*

839   *Statistics & Data Analysis* **52**:3283-3299.

840 Schiestl FP, Johnson SD. 2013. Pollinator mediated evolution of floral signals. *Trends in Ecology*

841   *and Evolution* **28**: 307-315.

842 Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis.

843   *Nature methods* **9**: 671-675.

844 Schoen DJ, Stewart SC. 1987. Variation in male fertilities and pairwise mating probabilities in

845   *Picea glauca*. *Genetics* **116**: 141-152.

846 Sheridan JA, Bickford D. 2011. Shrinking body size as an ecological response to climate change.

847   *Nature Climate Change* **1**: 401-406.

848 Silvertown J, Dood ME, Gowing DJG, Mountford JO. 1999. Hydrologically defined niches reveal a

849   basis for species richness in plant communities. *Nature* **400**: 61-63.

850 Tonnabel J, Van Dooren T, Midgley J, Haccou P, Mignot A, Ronce O, Olivieri I. 2012. Optimal

851   resource allocation in a serotinous non-sprouting plant species under different fire regimes.

852   *Journal of Ecology* **100**: 1464-1474.

Tonnabel J, Mignot A, Douzery EJP, Rebelo T, Schurr F, Midgley J, Illing N, Justy F, Orcel D, Olivieri I. 2014. Convergent and correlated evolution of major life-history traits in the angiosperm genus *Leucadendron* (Proteaceae). *Evolution* **68**: 2775-2792.

Tonnabel J, David P, Pannell JR. 2017. Sex-specific strategies of resource allocation in response to competition for light in a dioecious plant. *Oecologia* **185**:675-686.

Tonnabel J, David P, Pannell JR. 2019a. Do metrics of sexual selection conform to Bateman's principles in a wind-pollinated plant? *Proceedings of the Royal Society, B* 20190532.

Tonnabel J, David P, Klein EK, Pannell JR. 2019b. Sex-specific selection on plant architecture through 'budget' and 'direct' effects in experimental populations of a wind pollinated herb. *Evolution* **73**:897-912.

Treurnicht M, Pagel J, Esler KJ, Schutte-Vlok A-L, Nottebrock H, Rebelo AG, Schurr FM. 2016. Environmental drivers of demographic variation across the global geographical range of 26 plant species. *Journal of Ecology* **104**: 331-342.

Vaida F, Blanchard S. 2005. Conditional akaike information for mixed-effects models. *Biometrika* **92**:351-370.

van Drunen WE, Dorken ME. 2012. Trade-offs between clonal and sexual reproduction in *Sagittaria latifolia* (Alismataceae) scale up to affect the fitness of entire clones. *New Phytologist* **196**: 606-616.

van Kleunen M, Burczyk J. 2008. Selection on floral traits through male fertility in a natural plant population. *Evolutionary Ecology* **22**: 39-54.

van Wilgen BW, Forsyth GG, de Klerk H, Das S, Khuluse S, Schmitz P. 2010. Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology,* **47**: 631-638.

Waelti MO, Page PA, Widmer A, Schiesti FP. 2009. How to be an attractive male: floral dimorphism and attractiveness to pollinators in a dioecious plant. *BMC Evolutionary Biology* **9**: 190.

Welsford MR, Hobbhahn N, Midgley JJ, Johnson SD. 2016. Floral trait evolution associated with shifts between insect and wind pollination in the dioecious genus *Leucadendron* (Proteaceae). *Evolution* **70**: 126-139.

Welsford, M. R., Midgley, J. J., & Johnson, S. D. 2014. Experimental evaluation of insect pollination versus wind pollination in *Leucadendron* (Proteaceae). *International journal of plant sciences* **175**: 296-306.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

Williams IJM. 1972. A revision of the genus *Leucadendron* (*Proteaceae*). *Contrib. Bol. Herb* **3**: 1-425.

Wright JW, Meagher TR. 2004. Selection on floral characters in natural Spanish populations of *Silene latifolia*. *Journal of Evolutionary Biology* **17**: 382-395.

Zajitschek F, Connallon T. 2017. Partitioning of resources: the evolutionary genetics of sexual conflict over resource acquisition and allocation. *Journal of Evolutionary Biology* **30**: 826-838.

Data accessibility

All genotype and morphological trait data are available in Dryad at doi:10.5061/dryad.ngf1vhhst. The new MEMMseedlings source code for dioecious species is available at https://gitlab.paca.inrae.fr/pub/tonnabel_mol_ecol. The new version of spaMM is publicly available in spaMM since version 2.6.0 at https://CRAN.R-project.org/package=spaMM.

Author contributions

IO, AM and AC designed the study, collected data, and mapped the plants; EKK produced the mating model; FR implemented methods allowing fitting of sex-specific spatial random effects in spaMM; FR and AC designed the statistical procedures for measuring selection gradients in the presence of spatial autocorrelation; JT and AC performed the analyses; JT produced the genotyping dataset and drafted the manuscript; all authors discussed the results and edited the manuscript.

905 **Figure captions**

906

907 **Figure 1:** Sexual dimorphism in canopy diameter in cm (A.) and leaf area in cm^2 (B.) of the study
908 population *L. rubrum*. Points are prediction from models accounting for the spatial distribution of
909 traits within each sex and error bars are 95% confidence intervals around mean predictions.

910

911 **Figure 2:** Dispersal kernels estimated under the Bayesian model for seed dispersal (A.) and for
912 pollen dispersal (B.). Filled lines correspond to the posterior mean dispersal kernels obtained by
913 averaging parameters of the concatenation of two Markov chains of 50,000 steps (burn-in phase of
914 10,000 steps). Grey lines illustrate the uncertainty around the averaged dispersal kernel and
915 correspond to the kernels estimated on each iteration of the MCMC. Both dispersal kernels are
916 represented within the minimal and maximal distances existing in our population between females
917 and seedlings for seeds (A.) and between males and females for pollen (B.), *i.e.*, respectively, the
918 maximal female-seedling and male-female distances in our population. The extrapolation of
919 dispersal kernels beyond these limits are not represented in the plots.

920

921 **Figure 3:** Spatial prediction of the relative effective fecundity in males (A.) and females (B.) as
922 predicted by a generalized linear mixed-effect model, our full model, including all fixed effects (sex,
923 canopy diameter, leaf area, plant density, and the interaction between each of the three latter
924 variables and sex) as well as one spatially autocorrelated random effect for each sex. Relative
925 fecundity represents our measure of relative effective fecundity estimated by our MEMMseedlings
926 model, and circles represent the localization of individual plants.

927

928 **Figure 4:** Partial-dependence effect plots of leaf area (A.), canopy diameter (B.) and plant density
929 (C.) on the relative effective fecundity as predicted by our full model. Points indicate observed trait
930 values as well as the relative effective fecundity ± SD stemming from MCMC estimations. Curves
931 indicate model predictions computed as partial-dependence effects ± 95% confidence intervals.
932 Relative fecundity designates our measure of relative effective fecundity.

933

934 **Figure S1:** Pictures of females and males *Leucadendron rubrum* plants (A.), and of male (B.) and
935 female (C.) inflorescences magnification. Credit picture: Isabelle Olivieri.

936

937 **Figure S2:** Map of the study site showing distribution of females (red circles), males (blue
938 triangles), juveniles (green crosses), non-genotyped females (red full circles) and non-genotyped
939 males (blue full circles). One non-genotyped male that was located nearby the population is not
940 represented in the map.

941

942 **Figure S3:** Results of a genetic analysis of the sampled individuals using the software
943 STRUCTURE (Pritchard *et al.*, 2000). Four types of samples were tested: juvenile plants of the
944 third undetermined morphological group and, adult plants of *L. salignum* and of *L. rubrum* and
945 juvenile plants of *L. rubrum*. Four genetic groups were selected by this analysis and are represented
946 here by four different colors (*i.e.* blue, orange, pink and yellow). Individuals are displayed on two
947 different panels (A. and B.) only for the sake of readability but all individuals belong to the same
948 dataset described in Supplementary Methods S2.

949

950 **Figure S4:** Sexual dimorphism in plant height in cm (A.), in canopy first and second diameters in
951 cm (B. & C.), in leaf area in cm^2 (D.), in leaf length in cm (E.) and in leaf width in cm (F.). Raw
952 data have been jittered around their x-axis value for visualization purposes and overlaid with both a
953 violin plot and a boxplot using default settings in the R package ggplot2 version 3.1.0 (Wickham,
954 2016).

955

Figure S5: Prediction of canopy diameter in males (A.) and females (B.) as predicted by a linear mixed-effect models including sex as a fixed effect as well as one spatially autocorrelated random effect for each sex.

Figure S6: Density for all individuals (A.), for males (B.) and for females (C.) as numbers of individuals in quadrats of 12x12 meters.

Figure S7: Comparisons of conditional likelihood between the model presented in the main text accounting for spatial structure of pollen dispersal (in green) and a model neglecting such a spatial structure of pollen dispersal (in brown) as a function of Bayesian iterations which were run for 50,000 steps. These simulations were run using uniform prior distributions with the following intervals [0.01,1.00], [0.01,1.00], [0.00,1.00], [1.00,100], [0.01,10], [1.00,30000], [0.01,1.10] for the parameters m_s, m_p, υ, δ_s, b_s, δ_p and b_p, except for the second model in which δ_p and b_p were not modeled.

Figure S8: Replicate of Fig. 3 after the removal of individuals with effective fecundity greater than four standard errors (*i.e.* five females and one male). See Fig. 3 for legend details. Red crosses correspond to the locations of plants removed in the sensitivity analysis.

Figure S9: Spatial prediction of the number of empirically counted cones as predicted by a generalized linear mixed-effect model including all fixed effects (canopy diameter, leaf area, plant density) as well as one spatially autocorrelated random effect.

Figure S10: Replicate of Fig. 4 after the removal of individuals with effective fecundity greater than four standard errors (*i.e.* five females and one male). See Fig. 4 for legend details.

981

A.

B.

A.

B.

A. Males

B. Females