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► **To cite this version:**

Jeanne Tonnabel, Etienne Klein, Ophélie Ronce, Sylvie Oddou-muratorio, François Rousset, et al.. Sex-specific spatial variation in fitness in the highly dimorphic *Leucadendron rubrum*. *Molecular Ecology*, Wiley, 2021, 30 (7), pp.1721-1735. 10.1111/mec.15833 . hal-03279442

HAL Id: hal-03279442

<https://hal.inrae.fr/hal-03279442>

Submitted on 25 Nov 2021

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

2

3 Running title: Sex-specific spatial variation in fitness

4 Jeanne Tonnabel^{1,2,*§}, Etienne K. Klein³, Ophélie Ronce^{1,4}, Sylvie Oddou-Muratorio⁵, François
5 Rousset¹, Isabelle Olivieri¹, Alexandre Courtiol^{6†}, Agnès Mignot^{1†}

6 ¹ ISEM, Université de Montpellier, CNRS, IRD, EPHE Montpellier, France.

7 ² Department of Ecology and Evolution, Le Biophore, UNIL-SORGE, University of Lausanne, CH-
8 1015 Lausanne, Switzerland.

9 ³ INRAE, BioSP, F-84000, Avignon, France.

10 ⁴ CNRS, Biodiversity Research Center, University of British Columbia, Vancouver, Canada

11 ⁵ INRAE, URFM, F-84000, Avignon, France.

12 ⁶ Department of Evolutionary Genetics, Leibniz Institute for Zoo and Wildlife Research, 10315
13 Berlin, Germany.

14 [†]Co-senior authors

15 * Corresponding author: jeanne.tonnabel@cefe.cnrs.fr

16 [§] Current address: Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, CNRS, UM,
17 Université Paul Valéry Montpellier, EPHE, 1919 route de Mende, 34293 Montpellier Cedex 5,
18 France.

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

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

59 The sex-specific cost of reproduction hypothesis posits that sexes should diverge in
60 morphology to satisfy their respective reproductive needs (Freeman *et al.*, 1976; Delph & Bell,
61 2008). Such divergence can emerge when reproduction involves a stronger cost in one sex than in
62 the other, or when the reproductive costs of each sex imply different resource 'currencies' (Freeman
63 *et al.*, 1976; Obeso, 2002). Several studies have shown that pollen production in males strongly
64 relies on nitrogen, while female reproduction is mostly limited by carbon and water (e.g. Antos &
65 Allen, 1990; McDowell *et al.*, 2000; Harris & Pannell, 2008; van Drunen & Dorken, 2012). Males
66 and females of dioecious plants have evolved divergent strategies of plastic allocation to resource-
67 harvesting organs (see Tonnabel *et al.*, 2017 for a review), probably to harvest the resources most

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

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

94 2012; Harder & Prusinkiewicz, 2013; Tonnabel *et al.*, 2019b). Wind-pollinated plants tend to evolve
95 larger degrees of sexual dimorphism than insect-pollinated lineages, because pollinators require
96 similarity of floral morphology to successfully transfer pollen (Tonnabel *et al.*, 2014; Welsford *et*
97 *al.*, 2016). Wind-pollinated plants, which typically show large inter-individual variation in fertility
98 (Schoen & Stewart, 1987; Ahee *et al.*, 2015), may thus be particularly subject to sexually
99 antagonistic selection.

100 In the presence of genetic variation for sexual dimorphism, each sex should, in principle,
101 ultimately reach its optimal trait value, and thereby resolve sexually antagonistic selection (Lande,
102 1980). Yet, a shared genetic basis of traits between sexes may temporally constrain the evolution of
103 their morphological divergence (Lande, 1980). In constant and homogeneous environments, theory
104 predicts that, with strong positive genetic correlations between sexes, opposite directional selection
105 gradients between sexes should emerge early during adaptation and persist for a long time before the
106 sexual conflict is resolved (Lande, 1980; Connallon & Hall, 2016). Consequently, one would expect
107 evidence for antagonistic selection between sexes to be relatively common. The compilation of
108 numerous sex-specific selection gradients in animals showed, however, a large diversity of patterns,
109 including cases of aligned selection across sexes (Cox & Calsbeek, 2009). In plants, documented
110 patterns of sex-specific selection provided mixed support for sexually antagonistic selection: sex-
111 specific selection gradients have been found to have opposite signs in both insect- and wind-
112 pollinated species (Delph *et al.*, 2011; Castilla *et al.*, 2014; Tonnabel *et al.*, 2019b) but to have the
113 same sign in other studies (Oddou-Muratorio *et al.*, 2018; Barrio & Teixido, 2014). More recent
114 theory suggests that temporal and spatial variation in selection pressures may explain the lack of
115 signal for sexually antagonistic selection, despite differences in the optimal phenotypes of males and
116 females (Connallon, 2015; Connallon & Hall, 2016; Zafitscher & Connallon, 2017).

117 Estimating sex-specific selection gradients requires, first, estimating male and female
118 individual fitness, and, second, relating trait values and fitness estimates. Using genotypes of
119 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

185 *Leucadendron rubrum* is a dioecious wind-pollinated shrub species endemic to the Western Cape of
186 South Africa (Rebelo, 2001) where natural fires occur every 10-15 years (van Wilgen *et al.*, 2010;
187 Kraaij *et al.*, 2011). *L. rubrum* belongs to the Proteaceae family and flowers from August to
188 September. Seed recruitment is constrained to a short period following fires, and seeds released
189 between fires typically fail to establish due to competition (Bond, 1984). *L. rubrum* typically starts
190 flowering at 2-3 years, and seeds are retained in woody cones for several years (Harris & Pannell,
191 2010). Seeds therefore form a 'serotinous' seed bank, which persists until fire kills the plants,
192 allowing cone opening and wind dispersal of fruits via their plumed perianth (Williams, 1972;
193 Rebelo, 2001). In serotinous species, disruption of water intake to the cone (caused by broken
194 branch or plant death) was shown to lead to seed release suggesting a water cost to keep the cones
195 closed (Treurnicht *et al.*, 2016; Martín-Sanz *et al.*, 2017). Thus, mother death or any event leading
196 to cone opening before the advent of fire results in seed release in poor conditions for recruitment
197 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 10 μ M composed of 5 μ L of Multiplex Master mix (2X), 1 μ L of
245 primer sequences (1 μ M), 1 μ L of DNA extracts and 3 μ L 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 NM π (Version 1.0, Chybicki, 2017) to estimate the per-marker genotyping errors.

260 **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 $NM\pi$ (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 (v), 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, (v) 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 $NM\pi$ (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 , ν , 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

337 for different spatial distributions of random effects between sexes (publicly available in spaMM
338 since version 2.6.0). The classical Matérn correlation function was used to model the spatial
339 autocorrelation of random effects, separately for each sex, as a function of the distance between
340 individuals. The Matérn correlation model involves two parameters: the smoothness parameter (ν),
341 and the scaling parameter for distances (ρ). We compared models fits considering (1) no spatial
342 autocorrelation, (2) the same spatial autocorrelation for both sexes and (3) two sex-specific spatial
343 autocorrelation structures. We used likelihood ratio tests (LRTs) to (i) first test for a sex-specific
344 spatial structure in morphology, by comparing models with a different structure of random effects
345 but the same fixed effects, and (ii) to test for sexual dimorphism, by comparing the selected model
346 in step (i) to a model fitted with a similar structure of random effects, but without sex as a fixed
347 effect. Models were fitted either by maximum likelihood, for performing LRTs between models
348 differing in their fixed-effects structure, or by restricted maximum likelihood, for LRTs between
349 models differing in their random-effect structures and for computing the predictions from the model
350 fits. We also examined whether male and female plants were spatially segregated (*i.e.* whether the
351 sex ratio was spatially autocorrelated) using a binomial generalized linear mixed model (GLMM)
352 with sex as the response variable and compared model fits with or without a spatially autocorrelated
353 random effect as described above. Finally, we tested whether the number of cones produced by
354 females displayed a non-uniform spatial distribution by comparing models including cone number
355 as the response variable, plant density (see below for its calculation) as a fixed factor, and either a
356 spatial random effect or not.

357

358 **Multivariate sex-specific selection analysis**

359 Inspired by the multivariate framework of Lande and Arnold (1983), we examined in a single full
360 model the relationship between the relative effective fecundity as the response variable and, the
361 following explanatory variables: canopy diameter, leaf area, plant density, sex, and the interaction
362 between each of the three former explanatory variables and sex. We fitted generalized linear mixed-

363 effects models (Gamma GLMM with logarithm link function) to describe the variation in effective
364 fecundity, while including spatially autocorrelated random effects. We checked that a model
365 predicting effective fecundity using a Gamma distribution with a log link performed better than
366 models assuming a different candidate distribution (compare gamma log link: $cAIC=18.7$ with
367 gaussian with a link identity: $cAIC=139$; or gaussian with a log link: $cAIC=126$ – $cAIC$ is a metric
368 similar to the traditional AIC , except that it measures prediction performance conditionally on the
369 realization of the random effects, Vaida & Blanchard, 2005). We followed the same procedure as
370 described for the analysis of sexual dimorphism (see previous section) to fit the models using the R
371 package `spaMM` and to identify the best fitting random spatial structure (*i.e.* comparing a sex-
372 specific spatial structure, a common spatial structure and a lack of it). We were thus able to compare
373 the patterns of spatial variation of residual effective fecundity between males and females, once the
374 effects of local density and variation in morphology were included as fixed effects in our global
375 model. Spatial autocorrelation in effective fecundity may then reflect spatial variation in
376 unmeasured environmental variables (such as water availability) or unmeasured plant traits.
377 Different spatial structures between sexes therefore inform on the differential sensitivities of their
378 effective fecundities to variation in such unmeasured variables. We took into account the variation
379 in uncertainty of the individual effective fecundity estimates by parameterizing the residual variance
380 as a function of the variance in MCMC estimates of individual fecundity during the fitting (see
381 Supplementary Method S4). We again fitted models with distinct residual variances for each sex.
382 Because our MEMMseedlings model estimated large effective fecundity for several plants located
383 in one part of the study population, we performed a sensitivity analysis testing the robustness of our
384 results to the removal of all individuals with standardized effective fecundity greater than four
385 standard errors (for all statistical models treating effective fecundity as response variable). Five
386 females and one male were removed in this sensitivity analysis, including four individuals that were
387 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

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

432 Females had significantly smaller canopy diameters (i.e., first and second diameter measures; Figs.
433 1a, S4c, Table S4), but they were not clearly shorter (Fig. S4a, Table S4). Females had also leaves
434 with a larger area than males (Fig. 1b, Table S4). Correlated measures of leaf morphology (Table
435 S3) showed similar sexual dimorphism, as females displayed longer and wider leaves than males
436 (Fig. S4e,f, Table S4).

437
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).

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

446
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 $\nu=0.81$ 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 $NM\pi$ 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 $NM\pi$ 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 ($\chi^2=2238$, $df=3$, $p<0.0001$;
 480 Fig. S9). Cone number was significantly correlated with relative effective fecundity but the effect
 481 size was small (using standardized cone number, $\beta=0.286$, $\chi^2=6.02$, $df=1$, $p=0.0141$) and the two
 482 spatial distributions were not fully aligned (Fig. 3a vs. S9).

484 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 ($\beta=0.171$; LRT: $\chi^2=42.7$,
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 ($\beta=0.904$; LRT: $\chi^2=78.8$, $df=1$, $p<0.001$). 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: $\chi^2=0.709$, $df=3$, $p=0.871$), or each of them separately ((leaf
497 area)²: $\chi^2=0.129$, $df=1$, $p=0.719$; (canopy diameter)²: $\chi^2=0.118$, $df=1$, $p=0.731$; leaf area x canopy
498 diameter: $\chi^2=0.378$, $df=1$, $p=0.539$).

500 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

507

508

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

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

525 **No contemporary sexually antagonistic selection despite strong sexual dimorphism**

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

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

549 Only 17% of studies estimating selection gradients in animals identified sexually
550 antagonistic selection (Cox & Calsbeek, 2009). The paucity of evidence for sexually antagonistic
551 selection, with which our study concurs, is inconsistent with the idea that genetic correlations
552 between sexes should maintain sexually antagonistic selection over long periods of time (Lande,
553 1980). To explain this inconsistency, both theory and experiments have suggested that temporal or
554 spatial ecological changes may result in variable pattern of selection acting on males and females,
555 with both sexes displaying trait values remaining far away from their ever changing ecological
556 optimum (Kokko & Rankin, 2006; Delph *et al.*, 2011; Sheridan & Bickford, 2011; Long *et al.*,
557 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

610 scarce, but they typically also indicate fat-tailed kernels in both insect- (Austerlitz *et al.*, 2004;
611 Oddou-Muratorio *et al.*, 2005; but see Matter *et al.*, 2013) and wind-pollinated species (Austerlitz *et*
612 *al.*, 2004; Goto *et al.*, 2006; Gaüzere *et al.*, 2013; Geber *et al.*, 2014 but see Ahee *et al.*, 2015). Our
613 estimated pollen dispersal kernel showed a markedly fat-tailed distribution, whereby a large
614 proportion of pollen was able to disperse over large distances; similar large distance pollen dispersal
615 was reported in both wind-pollinated and animal-pollinated species (e.g. Devaux *et al.*, 2005;
616 O'Connell *et al.*, 2007). Given the large estimates of pollen dispersal distances and the short
617 distance to the nearest population, the low estimates of pollen immigration are unexpected,
618 especially given the same order of magnitude as seed immigration rate. This discrepancy is
619 nevertheless consistent with other studies showing that the amount of long distance dispersal
620 inferred by spatially explicit parentage modeling is not always congruent with the amount predicted
621 by dispersal kernels inferred from local dispersal events (Chybicki & Oleksa, 2018; Hardy *et al.*,
622 2019). Such inconsistencies may emerge when extrapolation of dispersal kernels does not properly
623 account for an increased probability of encountering obstacles between populations.

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

Acknowledgments

636 We dedicate this manuscript to IO who passed away before the completion of this study, which she
637 initiated. She inspired and is still inspiring our research in many ways. We are grateful to Nicolas
638 Bierne and Pierre-Alexandre Gagnaire for their helpful advice on population genetic structure
639 analysis, to John Pannell for helpful discussions and English editing, to Jeremy Midgley for help in
640 the field and attracting our interest in this system. Elodie Flaven-Noguier, Fabienne Justy and
641 Clémence Hatt helped with the DNA extractions, genotyping and molecular biology protocols. This
642 work was supported by a grant from the FRB to IO and AM, from the ANR “Evorange”, ANR-09-
643 PEXT-011 to OR and from the ANR “MeCC”, ANR-13-ADAP-006 to OR, EKK and SOM. JT was
644 supported by a grant to John Pannell from the FNS, 31003A_163384. OR acknowledges support
645 from the Peter Wall Institute of Advanced Studies, UBC, and from CNRS.

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Data accessibility

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

Author contributions

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

Figure captions

Figure 1: Sexual dimorphism in canopy diameter in cm (A.) and leaf area in cm² (B.) of the study population *L. rubrum*. Points are prediction from models accounting for the spatial distribution of traits within each sex and error bars are 95% confidence intervals around mean predictions.

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

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

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

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

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

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

Figure S4: Sexual dimorphism in plant height in cm (A.), in canopy first and second diameters in cm (B. & C.), in leaf area in cm² (D.), in leaf length in cm (E.) and in leaf width in cm (F.). Raw data have been jittered around their x-axis value for visualization purposes and overlaid with both a violin plot and a boxplot using default settings in the R package ggplot2 version 3.1.0 (Wickham, 2016).

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

959

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

962

963 **Figure S7:** Comparisons of conditional likelihood between the model presented in the main text
964 accounting for spatial structure of pollen dispersal (in green) and a model neglecting such a spatial
965 structure of pollen dispersal (in brown) as a function of Bayesian iterations which were run for
966 50,000 steps. These simulations were run using uniform prior distributions with the following
967 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
968 parameters m_s , m_p , v , δ_s , b_s , δ_p and b_p , except for the second model in which δ_p and b_p were not
969 modeled.

970

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

974

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

978

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







