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1 RT: Metapopulation dynamics of an annual plant  
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13 **Small-scale and regional spatial dynamics of an annual plant**  
14 **with contrasting sexual systems**  
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19 MARCEL E. DORKEN<sup>\*,1</sup>, ROBERT P. FRECKLETON<sup>2</sup>, JOHN R. PANNELL<sup>3</sup>  
20  
21

22 <sup>1</sup>Department of Biology, Trent University, 1600 West Bank Drive,  
23 Peterborough, ON, K9L 0G2, Canada

24 <sup>2</sup>Department of Animal and Plant Sciences, University of Sheffield,  
25 Sheffield, S10 2TN, UK

26 <sup>3</sup>Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne,  
27 Switzerland  
28  
29  
30  
31  
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33

34 <sup>\*</sup>Correspondence author: E-mail: marceldorken@trentu.ca

35 **Summary**

- 36 **1.** Plant demography is known to depend on both spatial dynamics and life history, but  
37 how these two factors interact is poorly understood. We conducted a longitudinal study of  
38 the wind-pollinated annual plant *Mercurialis annua* that varies geographically in its  
39 sexual system to investigate this interaction.
- 40 **2.** Metapopulation demographic models predict that regular population turnover should  
41 be a more common feature of monomorphic over dimorphic populations because males  
42 and females cannot found new populations by selfing but hermaphrodites can. We tested  
43 the prediction that rates of population turnover would be higher in monomorphic  
44 compared to dimorphic regions.
- 45 **3.** We surveyed 356 populations of *M. annua* along five regional transects in Morocco  
46 and the Iberian Peninsula over a three-year period to examine their demography and  
47 persistence. Each transect crossed a transition in the sexual system, from a monomorphic  
48 region where almost all populations were hermaphroditic to a dimorphic one in which  
49 most populations had separate sexes (males with females or hermaphrodites).
- 50 **4.** As predicted, rates of local apparent extinctions (i.e. the disappearance of adult  
51 plants) were 50% higher in monomorphic compared to dimorphic regions. Local  
52 extinctions appeared to be driven by changes in vegetation cover, with extinctions tending  
53 to occur in sites in which perennial cover also declined. This suggests that disturbance is a  
54 primary agent of local extinctions.
- 55 **5.** We further examined the influence of regional dynamics on local demographic  
56 properties by investigating patterns of spatial autocorrelation in population density across  
57 years. We found positive spatial autocorrelations in plant densities within regions for both  
58 sexual systems. However, these positive autocorrelations extended over shorter distances  
59 in monomorphic regions, perhaps as a result of greater population flux in these regions.
- 60 **6. *Synthesis:*** Our study shows that population dynamics may be influenced by processes  
61 acting at a range of spatial scales: within patches, across patches within sites, and across  
62 sites within regions, as well as by life-history variation. In *M. annua*, regional variation in  
63 apparent extinction rates is affected by life history and implicated in regulating the  
64 geographical distribution of populations with different sexual systems.

65 **Key-words:** androdioecy, demography, density-dependence, dioecy, *Mercurialis annua*,  
66 metapopulations, monoecy, plant population and community dynamics, sexual systems

67

## 68 **Introduction**

69 Understanding the distribution and abundance of plant species represents one of the most  
70 fundamental aims of plant ecology (Gurevitch *et al.* 2006). Contemporary patterns of  
71 **distribution and abundance** will ultimately reflect the accumulated outcome of processes  
72 that have acted on individuals and their populations over a range of temporal and spatial  
73 scales (Pannell & Dorken 2006). However, one of the key advances in plant ecology has  
74 been the recognition of the importance of on-going large-scale spatial dynamics rather  
75 than just those that occurred in the past (Husband & Barrett 1996; Thomas & Kunin 1999;  
76 Freckleton & Watkinson 2002; Hanski & Gaggiotti 2004; Alexander *et al.* 2012). This  
77 perspective includes metapopulation theory, which emphasizes the roles of colonisation  
78 and local extinction (Hanski & Gaggiotti 2004). Not all plant populations can be usefully  
79 characterized as metapopulations (Bullock *et al.* 2002; Freckleton & Watkinson 2002,  
80 2003). However, the regional persistence of many species depends as much on the  
81 availability of suitable habitat locally as on larger-scale processes (i.e. scales that  
82 encompass regional assemblages of populations) that include population turnover  
83 (Olivieri *et al.* 2016).

84

85 **Although the processes of colonization and extinction probably characterize all plant**  
86 **populations at some point in their history, the extent to which metapopulation dynamics**  
87 ***per se* influence the maintenance of species within particular regions is poorly known**  
88 **(Freckleton & Watkinson 2002).** Instead, regional patterns of species distributions may be  
89 more strongly influenced by processes acting locally, and that the patchy nature of plant  
90 species distributions may often better be described as ‘regional ensembles’ or ‘spatially  
91 extended populations’ in which local processes are sufficient to understand distributional  
92 patterns (Freckleton & Watkinson 2002). Many annual ruderals, for example, occur as  
93 ‘shifting clouds’ of individuals that are patchily distributed in an apparently uniform  
94 habitat matrix, such that the spatial location of patches moves around over time  
95 (Watkinson, Freckleton & Forrester 2000). Pannell & Obbard (2003) argued that the

96 dynamics of such ‘shifting clouds’ might also usefully be construed as metapopulations if  
97 the processes of patch movement involve dispersal and colonization, albeit over small  
98 spatial scales. Cavanaugh *et al.* (2014) referred to this issue as the ‘mega-patch problem’,  
99 and showed that shifting clouds can reflect the outcome of metapopulation processes  
100 involving colonization and extinction of local subpopulations.

101

102 Disturbance can have two different but complementary effects. On the one hand, it can  
103 bring about the local extinction of a given species (e.g. Ross *et al.* 2002), whereas, on the  
104 other hand, it potentially opens up new habitat for the colonization of ruderal species (e.g.  
105 Alexander *et al.* 2009), or it may arrest the process of succession that might otherwise  
106 bring about extinction of such species (Connell 1978). We still know very little about how  
107 succession and disturbance might vary over the geographical range of a species, and how  
108 this variation might affect patterns of plant species distribution and abundance. It seems  
109 clear that the population dynamics associated with succession and disturbance will be  
110 slowed by the presence of a soil seed bank, which can reduce times to extinction (Kalisz  
111 & McPeck 1993). However, although seed banks are clearly important in regulating  
112 metapopulation dynamics (Alexander *et al.* 2012) and have hindered the widespread use  
113 of a metapopulation concept for plants (Eriksson 1996), it is not well known how often  
114 populations recover from apparent local extinctions from a soil seed bank.

115

116 Although the possibility that regional processes (in whatever guise) influence the  
117 distribution of many plant species, very few empirical studies have been conducted to  
118 characterize their regional dynamics at an appropriate range of spatial scales. Even less is  
119 known about the processes that govern ongoing regional dynamics. However, some large-  
120 scale geographic studies have demonstrated the importance of regional processes in  
121 regulating plant distributions (reviewed in Freckleton and Watkinson 2002). In  
122 *Eichhornia paniculata*, for example, local extinction rates are high and the regional  
123 abundance of suitable habitat is associated with patterns of patch occupancy (Husband &  
124 Barrett 1998). Studies of *E. paniculata* have further revealed the importance of population  
125 turnover, evolutionary transitions to predominant self-fertilization, and long-distance  
126 colonization in regulating its distribution (Husband & Barrett 1991; 1993). The local

127 dynamics of *Silene latifolia* and *Helianthus annuus* also appear to involve the  
128 metapopulation processes of extinction and colonization, the operation of which can be  
129 predicted by data sampled over broad spatial scales (Moody-Weiss *et al.* 2008). However,  
130 at least for *H. annuus*, coarse-scale processes can be understood in terms of a simple  
131 scaling-up of local processes. These dynamics might therefore more readily be  
132 characterized by the term “spatially-extended populations” (*sensu* Freckleton &  
133 Watkinson 2002) than as true metapopulations with clear population turnover (Alexander  
134 *et al.* 2009; and see Alexander *et al.* 2012).

135

136 Theoretical work points to the importance of plant life histories, including trade-offs  
137 between competitive ability and dispersal (Levins & Culver 1971), seed size and number  
138 (Venable 1992), a capacity for uniparental reproduction, such as through asexuality or  
139 self-fertilization (Dorken & Pannell 2007), and sex allocation (Pannell *et al.* 2014) as  
140 important drivers of population dynamics. Indeed, sexual systems are likely to play a  
141 particularly important role in the local and regional dynamics of species with a colonising  
142 habit (reviewed in Pannell & Dorken 2006; Pannell *et al.* 2008; Pannell 2015). Self-  
143 compatible hermaphroditic species should enjoy higher colonization rates than those that  
144 are self-incompatible or dioecious, because selfing confers reproductive assurance when  
145 mates are limited (Baker 1955; Stebbins 1957; Pannell & Barrett 1998; Busch & Schoen  
146 2008). This idea, labelled ‘Baker’s law’ by Stebbins (1957), might explain why oceanic  
147 islands are often enriched for species with an ability for uniparental reproduction (Barrett  
148 1996), for the larger range sizes of selfing versus related outcrossing lineages  
149 (Grossenbacher *et al.* 2015), for the higher frequency of self-fertilization towards the edge  
150 of species’ ranges (Griffin & Willi 2014) or in smaller populations in areas with lower site  
151 occupancy rates (Eppley & Pannell 2007a; reviewed in Pannell *et al.* 2015).

152

153 Studies testing the predicted association between reproductive traits and population  
154 dynamics should ideally involve comparisons of populations that are similar in all but  
155 their reproductive traits. Although such species are rare, in a few species there is  
156 considerable variation in sexual system, e.g. in *Ecballium elaterium* (Costich 1995) and  
157 *Sagittaria latifolia* (Dorken, Friedman & Barrett 2002). In the current study, we present

158 results of a large-scale survey of the spatial dynamics of third such species, the annual  
159 plant *Mercurialis annua*. A remarkable feature of *M. annua* is the occurrence of repeated  
160 transitions between sexual systems over its geographic range (Pannell *et al.* 2008), spatial  
161 variation that is thought to have been influenced by large-scale heterogeneity in the  
162 relative importance of the spatial dynamics of the species (Pannell *et al.* 2014).

163

164 In previous work, Eppley and Pannell (2007a) described four transitions between regions  
165 characterized by sexually monomorphic (monoecious) and sexually dimorphic  
166 (androdioecious and dioecious) populations of *M. annua* in the Iberian Peninsula alone.  
167 Dimorphic populations tend to display greater site occupancy and population sizes than  
168 monomorphic populations that are facultative selfers (Eppley & Pannell 2007a).

169 Monomorphic populations show lower genetic diversity, greater genetic differentiation,  
170 and patterns of sex allocation that point to selection during frequent bouts of inbreeding  
171 (presumably when populations are sparse or recently colonised; Obbard, Harris & Pannell  
172 2006; Pujol *et al.* 2009). **Regional variation in the occurrence of dimorphic populations of**  
173 ***M. annua* might be explained by corresponding variation in rates of population turnover,**  
174 **because monomorphic populations can persist under higher rates of population turnover**  
175 **than dimorphic populations (Pannell 1997a). It also seems that a continent-wide**  
176 **expansion over a large latitudinal range has affected the genetic structure and sexual**  
177 **system of its populations (Pannell *et al.* 2014).** The distribution of sexual systems, patterns  
178 of occupancy abundance and genetic diversity among populations of *M. annua* thus all  
179 appear to be consistent with the importance of metapopulation dynamics. However, direct  
180 evidence demonstrating that these patterns are underpinned by metapopulation dynamics  
181 requires actual measures of population turnover and changes in population demography  
182 over time and these data have never been recorded.

183

184 In this study we report on a large-scale analysis of population dynamics of *M. annua* at a  
185 range of spatial scales, and relate the observed dynamics to predictions of how spatial  
186 dynamics should vary among populations with different sexual systems. We examined the  
187 population dynamics of *M. annua* over a three-year period across replicated quadrats in  
188 more than 300 populations spanning more than 10 degrees of latitude, including the four

189 sexual-system transitions studied in the Iberian Peninsula by Eppley and Pannell (2007a)  
190 as well as a fifth such transition from Morocco (Pannell *et al.* 2014; Figure 1). We  
191 addressed the following specific questions: (1) What are the principal causes of spatial  
192 and temporal variation in occupancy and abundance in *M. annua* (i.e. succession versus  
193 disturbance), and how do these vary over latitude? (2) To what extent are these site  
194 dynamics associated with variation in the sexual system? (3) Is the flux in population  
195 densities dampened by the occurrence of a soil seed bank and/or associated with changes  
196 in vegetation cover? (4) To what extent do range-level patterns of site occupancy reflect  
197 patterns of site suitability versus dispersal limitation of colonization? We show that sexual  
198 system indeed affects population dynamics at a range of scales, and that variation in life-  
199 history influences regional dynamics via impacts on local population flux.

200

## 201 **Methods**

### 202 STUDY SPECIES AND POPULATIONS

203 *Mercurialis annua* L. is a wind-pollinated annual plant that grows in ruderal and roadside  
204 habitats throughout central and Western Europe and around the Mediterranean Basin  
205 (Tutin *et al.* 1964). In the regions studied here, *M. annua* is a winter annual, with peak  
206 flowering occurring in February (Morocco) through April (Spain). Seeds are dispersed  
207 over short distances (up to ~1 m) by explosive release from 2- to 3-seeded capsules and  
208 may be secondarily dispersed by ants (Lisci & Pacini 1997). Seeds are also likely to be  
209 transported over substantial distances by humans (Taylor *et al.* 2012). *Mercurialis annua*  
210 does not naturally reproduce by vegetative propagation, so the number of plants is readily  
211 determined by counting the number of stems. Populations comprise one cohort of plants  
212 per year.

213

214 *Mercurialis annua* is a polyploid complex, with diploid, tetraploid and hexaploid  
215 populations distributed around the Mediterranean (Durand 1963, Durand & Durand 1992,  
216 Pannell, Obbard & Buggs 2004). Diploid populations, which occur in northern Spain and  
217 throughout western, central and eastern Europe, are dioecious (dimorphic), whereas  
218 tetraploid and hexaploid populations, distributed in the Iberian Peninsula and Morocco,  
219 are variously monoecious (monomorphic) or androdioecious (dimorphic where males co-

220 occur with functional hermaphrodites). For these hexaploid androdioecious populations,  
221 the mechanism of sex determination is relatively simple, with maleness determined by the  
222 possession of a Y chromosome. Thus, only males carry male-determining alleles, and they  
223 are the only phenotype that can sire male offspring in androdioecious populations (Pannell  
224 1997b).

225

226 For the present study, we sampled populations from five regions occupied by *M. annua* in  
227 the western Mediterranean Basin – four in the Iberian Peninsula and one in Morocco (Fig.  
228 1). These regions were chosen because they span transitions from one sexual system to  
229 another (Eppley and Pannell 2007). These regions covered the distribution of hexaploid  
230 *M. annua*, however the southernmost region (Morocco) included both hexaploid and  
231 tetraploid populations, while the northernmost regions (Catalonia and Galicia in Spain)  
232 included both hexaploids and diploids (Fig. S1). Despite differences in ploidy among  
233 some populations, *M. annua* throughout the entire range occupies similar habitat, and the  
234 ploidy levels cannot be distinguished morphologically, except in part via the sexual  
235 system.

236

#### 237 VARIATION IN OCCUPANCY AND ABUNDANCE

238 In 2004, we examined sites for the presence or absence of *M. annua* within each of the  
239 five regions chosen for the study. We used predetermined intervals or evenly spaced  
240 landmarks (usually highway-distance markings) to identify sampling localities without  
241 biasing the sample towards larger, more easily visible populations. The minimum distance  
242 between sites was 2 km. At each of these sites, we searched 100 m along each side of the  
243 road for the presence of *M. annua*. If *M. annua* was absent at a site, its absence was  
244 recorded. To reduce search time in areas where *M. annua* was uncommon, we continued  
245 driving until we were able to identify a population *M. annua* located at least the minimum  
246 distance from the previous site. This may have slightly biased our sampling in the first  
247 year somewhat to larger populations; however, as shown in the Results, population sizes  
248 fluctuated enormously, and many populations that were initially large became small or  
249 went extinct in later years. We continued searching for sites until we were no more than  
250 10 km from the nearest site already sampled. We then backtracked to the previously

251 sampled site and began searching in a new direction. This sampling protocol was repeated  
252 until at least 40 sites had been included per sexual system per transect. We were able to  
253 include our target number of sampling sites for all transects except for Transect 3. Our  
254 sampling protocol, together with the location of transitions between sexual  
255 monomorphism and dimorphism, determined locations of the boundaries for each region.

256

257 For all chosen sites with *M. annua* present, we delimited two small and two large plots  
258 using permanent landmarks and GPS readings. The first two plots (focal plot A &  
259 neighbouring plot B) were smaller to enable more accurate census taking. These plots  
260 were usually 2 m · 4 m rectangles, but for a small proportion of sites plots of different  
261 dimensions were used because of constraints in the distribution of habitat suitable for *M.*  
262 *annua* at the site or the position of walls, rocks, trees, etc. The two remaining plots (C &  
263 D), which represented a continuation of the habitat found in the focal plot, were typically  
264 2 m · 50 m rectangles. All plots were adjacent to one another except when landscape  
265 features prevented them from being so. All plots were photographed and mapped. We  
266 returned to all sites and plots during peak flowering in 2005 and 2006.

267

268 At each site, we counted all the plants in each focal plot. In the larger transect plots, plant  
269 numbers above 100 were estimated to the nearest 10. For each site, we estimated plot  
270 density by using a weighted density of the averaged densities in each of the four plots. We  
271 weighted the contribution of each plot by its area, i.e. so that the large transect plots  
272 contributed more to the mean than the smaller focal plots. We transformed our estimates  
273 of the density of plants per plot on a natural logarithmic scale. We evaluated annual  
274 fluctuations in the number of plants per plot by examining the difference in the log  
275 number of plants between years  $t$  and  $t + 1$ .

276

277 To estimate the fine-scale turnover in patch occupancy within sites ('patch extinction'),  
278 we calculated, for each site, the proportion of the focal patches that contained plants at  
279 time  $t$ , but which contained no plants at time  $t + 1$ . To generate a large-scale estimate of  
280 population turnover within regions, we inferred a population-scale extinction ('population  
281 extinction') if all four plots (A, B, C and D) became unoccupied. The possibility for

282 regeneration from a soil seed bank means that not all of these apparent extinctions  
283 represent true extirpations at a site (see below).

284

#### 285 SEED BANK AND VEGETATION COVER

286 In the final year of the study (2006), we collected soil samples from focal patches at  
287 which *M. annua* adults had been present in our initial survey in 2004 but from which  
288 plants were absent in 2006. Soil collection was possible from a total of 31 sites (11  
289 dimorphic and 20 monomorphic sites), though not at some sites that had been severely  
290 disturbed (e.g. covered in concrete). To collect the soil, we sampled soil from each of two  
291 30 cm · 30 cm plots in two randomly chosen areas within the plot by removing the upper  
292 3 cm layer of soil. Final soil volumes differed among samples because of variation in soil  
293 composition (e.g. rocks and stones were not collected). We examined the contribution of  
294 the soil seed bank to population persistence by dividing soil samples into two batches of  
295 equal weight (approx. 250 g), and placing these batches in germination trays under  
296 common glasshouse conditions in a fully randomized design. In each tray, soil batches  
297 were scattered in an even layer between two equal volumes of sterile compost to maintain  
298 moisture levels within trays. Trays were watered regularly and the number of *M. annua*  
299 seedlings was counted two weeks after sowing, a time-frame within which all viable seeds  
300 should have germinated (M. E. Dorken & J. R. Pannell, pers. obs.).

301

302 At each site, we recorded several variables relating to site quality as well as occupancy by  
303 other vegetation. In each of the focal and transect plots at each site, we estimated the  
304 percentage cover of other classes of vegetation using six categories: ~0% but present;  
305 <1%; <5%; <20%; <50%; >50%. The different cover classes considered were: bare soil;  
306 litter; grasses; annual forbs (and whether these were erect, prostrate, or rosette-forming);  
307 herbaceous perennials; and woody perennials. We also recorded the per cent cover of the  
308 perennial plants *Parietaria judaica*, *Oxalis pes-caprae*, and *Urtica dioica*, which  
309 commonly co-occurred with *M. annua* in the study regions.

310

#### 311 ASSESSMENT OF SITE SUITABILITY VERSUS DISPERSAL LIMITATION

312 To assess establishment success following simulated colonization, we experimentally  
313 sowed seeds at a further ten sites per region that were unoccupied in 2004. In particular,

314 we sowed seeds sampled from nearby locations at sites with bare soil and adjacent to  
315 permanent landmarks to test whether apparently unoccupied sites represented suitable  
316 habitat for *M. annua* plants (i.e. whether the distribution of *M. annua* is limited by  
317 dispersal or by the occurrence of suitable habitats). These sites were located several  
318 kilometres from our other sample sites and from any other populations of *M. annua*  
319 occurring along our roadside transects. Specifically, we sowed seeds at a site if *M. annua*  
320 had been absent from two consecutive locations visited (separated by intervals of 2 km,  
321 respectively) as well as along the intervening roadside. Because these sowings were  
322 conducted in the first year of the study and material from nearby localities was used (to  
323 limit the possibility that adaptation to regional climatic regimes would limit germination),  
324 we were restricted to using fresh plant material with varying numbers of ripening fruits.  
325 We sowed approximately 250 g of freshly harvested *M. annua* onto 20 x 20 cm square  
326 patches from which we had removed the upper layer of vegetation. This amounted to  
327 sowing at least one hundred seeds per site (M. E. Dorken & J. R. Pannell, unpublished  
328 data). These sites were mapped and revisited over the next two years to examine  
329 recruitment.

330

### 331 STATISTICAL ANALYSES

332 Spatial dynamics in plant densities per site, population growth rates, and the probability of  
333 patch extinctions were evaluated at a range of spatial scales. First, broader latitudinal  
334 trends, and differences, in population density and extinction were evaluated using mixed  
335 models. To meet linear model assumptions, we used the log of plant densities (Ives 2015)  
336 in patches A and B as the dependent variable. Latitude and sexual system (dimorphic  
337 versus monomorphic) were included as fixed effects. Year and transect, nested within  
338 year, were included as random effects to account for the hierarchical nature of the  
339 sampling design. Model fitting was performed using the lmer function from the lme4  
340 package (v. 1.1-12; Bates *et al.* 2015) in R (v. 3.3.0; R Core Team 2016). For this and all  
341 other mixed models described below, Type II tests of significance for fixed effects were  
342 calculated using the Anova function from the car package for R (v. 2.1-2; Fox &  
343 Weisberg 2011). Also for these analyses, our initial tests included ploidy as a fixed effect.  
344 However, parameter estimates for ploidy were not significant and were sometimes

345 correlated with estimates for sexual system. For these reasons, and because we used Type  
346 II tests of significance, we excluded ploidy as a factor in our analyses.

347

348 We similarly evaluated the association between latitude and population growth rates using  
349 a mixed model. Again, the log of population growth rates in focal patch A was the  
350 dependent variable and latitude and sexual system were the independent variables; we  
351 used the same nested random effects as described for the previous analysis. We evaluated  
352 latitudinal trends in the probability of extinction in focal patches and at the whole-site  
353 level using a generalized linear mixed model in which extinction occurrence was  
354 modelled as a binomial response variable and latitude and sexual system were included as  
355 fixed independent variables. The density of seed-producing plants in focal patch A in the  
356 previous census year was included as covariate in these analyses, and transect nested  
357 within year were included as random effects. Models were calculated using the glmer  
358 function in the lme4 package in R.

359

360 Second, we evaluated similarities in plant densities and population growth rates across  
361 sites within regions by measuring the magnitude of spatial autocorrelations among sites.  
362 Spatial autocorrelations were measured by calculating the value of Moran's  $I$  at 2.5 km  
363 intervals using the correlog function in the ncf package (v. 1.1-7; Bjornstad 2016) in R.  
364 Significance was assessed using permutation tests as implemented in the correlog  
365 function, with 999 permutations per calculated value of Moran's  $I$ .

366

367 Third, we evaluated patterns in plant densities per site, population growth rates, and the  
368 probability of patch extinction over smaller spatial scales by evaluating the  
369 correspondence in densities and extinctions between focal patch A and neighbouring  
370 patch B using pair-wise analyses. These two patches were chosen to evaluate concerted  
371 changes in demographic properties because they were of similar size and had similar soil  
372 and habitat characteristics. We used linear mixed models to evaluate the correspondence  
373 in plant densities in focal patch A versus neighbouring patch B. As above, we used the log  
374 of plant densities in each patch and included transect, nested within year, as random  
375 effects. We also evaluated the association between growth rates in focal patch A versus

376 neighbouring patch B using a mixed-effect model with the same nested random effects as  
377 for the previous analysis. As above, population growth rates in each patch were log-  
378 transformed. The correspondence of extinction rates in patches A and B was evaluated  
379 using a generalized linear mixed-effect model assuming binomial error and the same  
380 nested random effects as above. We also evaluated the association between population  
381 growth rates in patch B versus the occurrence of extinction events in focal patch A using  
382 linear mixed models in which extinction events in patch A were included as binary  
383 independent variables and nested random effects transect nested within year. All models  
384 described in this paragraph were calculated using the lmer function from the lme4  
385 package in R.

386

387 In dimorphic populations with males and hermaphrodites (i.e. androdioecious  
388 populations), small-scale changes in population densities can affect the maintenance of  
389 males via effects on their siring success (Dorken & Pannell 2008). Accordingly, we  
390 evaluated whether patch densities in one year were associated with the frequency of males  
391 in the following year with the expectation that higher plant densities should yield higher  
392 male frequencies (Eppley & Pannell 2007b). This analysis was conducted using a  
393 generalized linear model (glm function from the stats package in R) with the log of plant  
394 density and the year in which sex ratios were included as fixed effects. Model fitting  
395 required the use of a quasibinomial error distribution to account for overdispersion.

396

397 To evaluate whether there were associations between the occurrence of viable seeds in  
398 sites that had experienced an apparent extinction event and latitude and sexual system we  
399 used a generalized linear mixed-effects models; here we treated *M. annua* occurrence in  
400 the seed bank as a binary (presence/absence) and, in a separate analysis, as a numeric  
401 dependent variable (i.e. the number of seeds per sample). Transect was included as a  
402 random grouping variable. The total mass of soil per sample was used as an offset. Both  
403 models were calculated using the glmmadmb function in the glmmADMB package (v.  
404 0.8.3.3), adapted for use in R by Skaug *et al.* (2016) from the AD Model Builder by  
405 Fournier *et al.* (2012); the model involving a binary response variable assumed a binomial

406 error distribution, while the model involving count data assumed a Poisson error  
407 distribution and adjusting for zero inflation of the dependent variable.

408

409 We evaluated whether changes in vegetation characteristics were associated with changes  
410 in (log) population growth rates and the occurrence of patch extinction events using  
411 mixed-effects models with the lmer function in the lme4. For these analyses, the  
412 independent variables were year-to-year changes in the per cent cover of (i) bare ground,  
413 (ii) annuals, and (iii) perennials. Transect nested within year were included as random  
414 effects. For the test of the association between the probability of extinction in focal patch  
415 A and annual changes in vegetation characteristics, we used a generalized linear mixed  
416 model using a binomial error term (extinction events were coded as a binary, dependent  
417 variable).

418

419 We assessed whether the successful establishment of seeds following experimental  
420 sowing was associated with latitude and sexual system using the same approach as for the  
421 analysis of seed banks. The success of experimental sowings was included as a binary  
422 response variable assuming a binomial error distribution. As for the analysis of soil seed  
423 banks, transect was included as random grouping variable.

424

## 425 **Results**

### 426 SITE CHARACTERISTICS

427 Our sites tended to occur in areas heavily modified by human activities such as  
428 embankments, along walls or fence lines, or at the edges of farm fields (in total  
429 approximately 75% of all sites). In part, this reflected our road-side sampling strategy, but  
430 also *M. annua*'s ruderal habit. Of all sites in our census, the most common category  
431 involved plants growing along embankments (121 sites), many of which were also located  
432 immediately adjacent to the roadside (114 sites). A substantial proportion of sites were  
433 characterized by the growth of plants in habitats that provided some protection from  
434 trampling, with 116 sites directly next to a wall, fence, or around a post, and 58 sites  
435 around or between upright woody vegetation such as trees and thorny shrubs. Our sites

436 tended not to occur in areas dominated by herbaceous vegetation, but some did occur at  
437 field edges (48 sites) or in recently disturbed fields (26 sites).

438  
439 VARIATION IN OCCUPANCY AND ABUNDANCE

440 Plant densities within plots fluctuated greatly from one year to the next, often over orders  
441 of magnitude (Fig. 2b). Many focal plots occupied in 2004 or 2005 went locally extinct in  
442 the subsequent year. Indeed, of the 356 sites surveyed, 36% experienced an apparent local  
443 extinction in focal plot A in 2005 or 2006. Of the 89 focal plots apparently extirpated in  
444 2005, 35 remained so in 2006, with the remaining plots recovering from apparent  
445 extinction (Fig. 2b). At the whole site level, extinctions were less common, with 27  
446 apparent extinctions in 2005 and 2006. However, only one third of these sites (i.e. 9 sites)  
447 that were extinct in 2005 remained so in 2006; most apparent extinctions in 2006 were  
448 new events and, therefore, most sites experiencing apparent extinctions in 2005 recovered  
449 the next year. These fluctuations in plant densities within plots were also associated with  
450 more subtle demographic changes over time via effects on the frequency of males. In  
451 particular, in dimorphic regions in which populations had both males and hermaphrodites  
452 (i.e. androdioecious populations), the frequency of males in focal patch A was positively  
453 associated with the density of plants in the previous year ( $F_{1,146} = 8.90, P < 0.01$ ).

454  
455 Overall trends: Mean population densities per site declined systematically with latitude  
456 (Fig. 2a). Population densities were also associated with sexual system (Table 1a). On  
457 average, plant densities were 20% lower in monomorphic compared to dimorphic sites  
458 (back-transformed least-square means: density of monomorphic sites = 3.5 plants/m<sup>2</sup>,  
459 dimorphic sites: 4.4 plants/m<sup>2</sup>; Fig. 2b). The density of plants in the preceding year  
460 influenced the probability of extinction at the focal-patch and whole-site levels (Table 1c,  
461 d). Accordingly, the lower plant densities in monomorphic regions may have been  
462 responsible for higher probabilities of focal-patch and whole-site extinctions (Table 1c, d;  
463 Fig. 3), where the average probability of patch extinction was over 50% higher than in  
464 dimorphic regions (average probability of extinction in monomorphic regions = 0.24  
465 versus 0.17 in dimorphic regions). However, this large-scale regional variation in  
466 population densities did not appear to be driven by latitudinal variation in population  
467 growth rates or differences in growth rates between sexual systems (Table 1b).

468

469 Within regions: There were significant, positive spatial autocorrelations in plant densities  
470 over substantial areas that tended to decline at distances of more than 100 km, roughly  
471 coinciding with the distances between transects (Fig. 4). Over smaller spatial scales (up to  
472 50 km), spatial autocorrelations were similar for the two sexual systems. However, over  
473 larger scales (beyond 50 km), spatial autocorrelations were larger in magnitude in  
474 dimorphic than in monomorphic regions. In particular, for each year of the survey  
475 significant positive spatial autocorrelations in plant density extended over scales of up to  
476 ~100 km in dimorphic regions. By contrast, we detected fewer significant positive spatial  
477 autocorrelations in plant density in monomorphic regions, and significant autocorrelations  
478 tended not to extend over distances greater than 50 km.

479

480 Within sites: The density of plants in focal patch A was strongly associated with the  
481 density of plants in neighbouring patch B (Table 2a). This close correspondence in the  
482 number of plants between patches A and B over the three years of the study was reflected  
483 a strong positive association between growth rates over time (Table 2b, Fig. 5a). The  
484 concerted dynamics of paired patches A and B were also demonstrated by a positive  
485 association between the probability of extinction between patches (Table 2c) and a  
486 negative association between the growth rate of plants in patch B and the occurrence of an  
487 extinction in patch A (Table 2d, Fig. 5b).

488

#### 489 SEED BANK AND VEGETATION COVER

490 Viable seeds of *M. annua* were detected in nearly one third of soil samples (10 out of 31)  
491 from sites that had experienced an apparent local extinction (and for which it was possible  
492 to collect a soil sample). Among those samples in which we recovered *M. annua* plants,  
493 we counted an average of 3.5 *M. annua* seedlings (range = 1 to 15). There was no  
494 association between the number of *M. annua* seedlings per sample and sexual system or  
495 latitude (generalized linear mixed model: occurrence of *M. annua* seedlings =  $-8.08 +$   
496  $0.47 \times \text{sexual system} + 0.13 \times \text{latitude}$ ,  $\chi^2$  sexual system = 0.28,  $\chi^2$  latitude = 0.38,  $P$   
497 sexual system > 0.50,  $P$  latitude > 0.50). We obtained qualitatively similar results for the  
498 number of *M. annua* seedlings per sample (generalized linear mixed model: number of *M.*

499 *annua* seedlings =  $-3.96 - 0.69 \times \text{sexual system} + 0.10 \times \text{latitude}$ ,  $\chi^2$  sexual system = 1.06,  
500  $\chi^2$  latitude = 0.42,  $P$  sexual system > 0.30,  $P$  latitude > 0.50).

501

502 The rate of population growth in focal patch A was negatively associated with increases in  
503 the cover of soil and positively associated with increases in the cover of perennials (Table  
504 3a). Moreover, focal patch extinctions were associated with year-over-year changes in  
505 vegetation cover. In particular, the probability of an extinction event in site A increased  
506 when the per cent cover of perennial plants decreased from one year to the next (Table  
507 3b), pointing to disturbance as a primary driver of local patch extinction.

508

#### 509 ASSESSMENT OF SITE SUITABILITY VERSUS DISPERSAL LIMITATION

510 Sowings led to the establishment of populations in 53% of sites treated (48 sites of 90  
511 sites sown). The average number of plants recruited into these sites was  $18.4 \pm 32.6$  S.D.,  
512 with a range from 1 and 155. Of the 37 sites in which establishment occurred in the first  
513 year after sowing, 51% (19 sites) persisted until 2006. Among sites first established in  
514 2005, the average population growth rate (calculated by dividing the number of plants  
515 present in 2006 by the number in 2005) was less than one (geometric mean = 0.37; range:  
516 0 – 12), and was greater than one in only eight of the 37 sites. Moreover, there were no  
517 significant associations between the probability of successful establishment and sexual  
518 system or latitude (generalized linear mixed model: probability of establishment =  $2.70 -$   
519  $0.27 \times \text{sexual system} - 0.12 \times \text{latitude}$ ,  $\chi^2$  sexual system = 0.72,  $\chi^2$  latitude = 3.32,  $P$   
520 sexual system > 0.30,  $P$  latitude > 0.05).

521

#### 522 **Discussion**

523 Metapopulations are characterized by the extinction and colonization of local populations,  
524 i.e., changes in the occupancy of sites over time (Hanski & Gilpin 1991). Both these  
525 processes are difficult to assess in natural populations, and large geographic surveys  
526 conducted over multiple years are required to evaluate their importance (e.g. Husband &  
527 Barrett 1998). Such large-scale studies are rare, and the present study is among the largest  
528 of its kind in terms of the geographical extent and the number of local patches examined.  
529 From our study of 356 populations distributed across a wide geographic range over a

530 three-year period, we observed frequent apparent local extinctions and found that the  
531 dynamics of local populations were affected by regional dynamics. Specifically, variation  
532 in rates of disturbance and extinction coincided with regional differences in average  
533 population size, which in turn appeared to influence the presence versus the absence of  
534 males at the regional level. Our findings are consistent with the operation of  
535 metapopulation processes in the regulation of *M. annua* populations in the Iberian  
536 Peninsula and Morocco (and see Pannell *et al.* 2014). We argue that regional differences  
537 in these metapopulation dynamics influence the presence versus the absence of unisexual  
538 phenotypes within geographic regions. Below, we provide an overview of processes that  
539 appear to regulate the population dynamics of *M. annua*. We then argue that our results  
540 help to explain regional variation in sexual systems across this part of the species' range.  
541 Finally, we evaluate our results in light of the expected joint operation of local and  
542 regional processes in a metapopulation.

543

#### 544 SPATIAL AND TEMPORAL VARIATION IN OCCUPANCY AND ABUNDANCE

545 Metapopulation dynamics involve the joint action of local- and regional-level processes in  
546 the regulation of demography. Our data indicate that processes operating across this range  
547 of spatial scales influenced the population dynamics of *M. annua*. At the largest spatial  
548 scales considered, local population densities and the probability of local extinction were  
549 associated with latitude, indicating that climatic and/or ecological processes that co-varied  
550 with latitude in the Iberian Peninsula and Morocco affected population demography  
551 across the species' range (e.g., temperature, precipitation, disturbances associated with  
552 agriculture and grazing). Higher-density populations occurred further south, and these  
553 populations were also less likely to become extinct. Our data further indicate that these  
554 two spatial patterns are linked via local dynamics, because population turnover was much  
555 more likely in smaller than in larger populations. Although regional, metapopulation  
556 processes can be analysed via the scaling-up of data from smaller spatial scales (Moody-  
557 Weis *et al.* 2008), the latitudinal effects observed here were only apparent when  
558 comparing among transects and could not have been detected by scaling up from data  
559 collected within transects. This implies that large-scale spatial dynamics are likely to be  
560 underestimated by scaling up.

561

562 At regional levels (i.e. among transects), we identified a significant association between  
563 the presence of unisexual plants within regions and extinction rates. Moreover, we  
564 detected spatial autocorrelations in **the density of *M. annua* within populations** that  
565 extended over distances that roughly coincided with the length of our transects. These  
566 spatial autocorrelations in population size may reflect differences in extinction rates  
567 between transects characterized by monomorphic versus dimorphic populations. In  
568 particular, the spatial autocorrelations suggest that in regions with lower rates of turnover,  
569 plant densities were lower and more variable among populations within transects (i.e. in  
570 monomorphic regions). This lack of demographic cohesion in the monomorphic regions  
571 of *M. annua* is also apparent from patterns of genetic diversity, with lower genetic  
572 diversity and greater genetic differentiation in monomorphic regions than in neighbouring  
573 dimorphic regions (Obbard, Harris & Pannell 2006). Together, both genetic and  
574 ecological data are consistent with the hypothesis that regional processes influence the  
575 local population dynamics of *M. annua*.

576

#### 577 SEXUAL SYSTEMS AND POPULATION DYNAMICS

578 Unisexual phenotypes are expected to be at a strong disadvantage in regions characterized  
579 by high rates of population turnover because of their inability to establish new populations  
580 by self-fertilization (Pannell & Barrett 1998; Pannell 2015). **Consistent with this**  
581 **expectation, we found lower rates of population and patch extinctions in dimorphic**  
582 **compared to monomorphic regions. These results align not only with predictions arising**  
583 **from Baker's law** (Pannell 2015; Pannell *et al.* 2015), but also with specific predictions  
584 for the effect of population turnover on the maintenance of unisexual phenotypes at the  
585 landscape level (Pannell 1997a). Plants from monomorphic populations of *M. annua* are  
586 not mate-limited (Hesse & Pannell 2011) and therefore should be less affected by Allee  
587 effects during colonization. Males, on the other hand, are expected to be maintained only  
588 in large populations that are sufficiently dense (Pannell 1997a, Pannell *et al.* 2014). There  
589 is some evidence for higher rates of population turnover in monomorphic (monoecious)  
590 compared to dimorphic (dioecious) populations of *Sagittaria latifolia* (Dorken & Barrett  
591 2003). For *S. latifolia* these effects have also been invoked to explain why monomorphic

592 populations are more common at the northern range limit, where the colonization  
593 advantage to cosexual plants appear to be important in regulating patterns of patch  
594 occupancy (Yakimowski & Barrett 2014). By contrast, in *M. annua* data from studies of  
595 population genetics (Obbard, Harris & Pannell 2006), regional patterns of patch  
596 occupancy (Eppley & Pannell 2007a), patterns of sex allocation (Pannell *et al.* 2014) and  
597 patterns of population turnover (this study) are all point to the importance of  
598 metapopulation dynamics in shaping the geographical distribution of gender variation and  
599 sexual systems.

600

601 The maintenance of unisexual *M. annua* at the landscape level requires lower extinction  
602 rates than are required for the maintenance of hermaphroditic populations, but also higher  
603 population densities (Eppley & Pannell 2007b, Pannell *et al.* 2014). Consistent with this  
604 expectation, we found higher plant densities in dimorphic compared to monomorphic  
605 regions. Moreover, we detected spatial autocorrelations in plant densities that ranged over  
606 larger distances in dimorphic than monomorphic regions. Together, these two results are  
607 consistent with expectations from a model examining the effect of metapopulation  
608 dynamics on the maintenance of gender dimorphic populations (Pannell 1997a).  
609 Specifically, the geographical clustering of local populations with high densities is  
610 expected to promote the regional maintenance of dimorphic sexual systems by increasing  
611 the likelihood of successful immigration by unisexual plants (Pannell 1997a; Eppley &  
612 Pannell 2007b; Pannell *et al.* 2014). This is because only males can sire male offspring  
613 (only males carry male-determining alleles, and half of the progeny they sire are sons;  
614 Pannell 1997b; Russell and Pannell 2014), and high population densities increase siring  
615 opportunities (Eppley & Pannell 2007b) and, consequently, the frequency of males in  
616 subsequent generations (Dorken & Pannell 2008).

617

618 In dimorphic regions where males coexist with hermaphrodites (androdioecious regions),  
619 male frequencies ranged between 0% and nearly 50%. Our observation of substantial  
620 annual variation in population densities can help to explain this variation. Population  
621 densities influence whether the pollen dispersed from male plants is likely to come into  
622 contact with hermaphrodite stigmas (Eppley & Pannell 2007b). Accordingly, we found

623 that plant densities in one year affected the frequency of unisexual plants in the  
624 subsequent year. This finding is consistent with a previous study of evolutionary  
625 trajectories in the frequency of males of *M. annua* under experimentally manipulated  
626 densities (Dorken & Pannell 2008). More generally, these findings together suggest that  
627 encounter rates of hermaphrodites regulate male frequencies over time, as also shown, for  
628 example, for *Caenorhabditis elegans* (Lopes *et al.* 2008). In both animals and plants,  
629 therefore, these encounter rates depend on population density, which affects how often  
630 males (or their pollen) ‘encounter’ hermaphrodites.

631

632 LOCAL EXTINCTIONS, VEGETATION DYNAMICS, AND THE SOIL SEED BANK

633 As expected for a ruderal species, we found that disturbance influenced patch  
634 demography and the probability of patch and population turnover of *M. annua*  
635 *populations*. Although we did not measure disturbance directly, we found that population  
636 growth rates were reduced for patches that showed an increase in soil cover between  
637 years, a potential index of disturbance. Moreover, reductions in perennial cover, which are  
638 expected to accompany individual and population-level disturbance (Pickett *et al.* 1989),  
639 **were similarly associated with lower population growth rates and a higher extinction risk.**  
640 For annual and short-lived perennial plants generally, disturbance can be expected to have  
641 opposing effects on the persistence of populations. On one hand, disturbance may reduce  
642 the probability of population persistence if it reduces the survival and seed production of  
643 vegetative and sexually mature plants (Elder & Doak 2006; **Crawley 2004**). On the other  
644 hand, disturbance is expected to have positive demographic effects through enhanced  
645 opportunities for seed recruitment (Turnbull *et al.* 2000) **and reduced competition**  
646 **(Crawley 2004)**. These dual effects can yield net-neutral effects of disturbance for the  
647 persistence of populations of some species of short-lived plants within geographic regions  
648 (e.g. the annual *Helianthus annuus* and the short-lived perennial *Silene latifolia*; Moody-  
649 Weis *et al.* 2008). However, insofar as changes in perennial cover accurately reflect  
650 patterns of disturbance across the sites that we surveyed, our results are not consistent  
651 with the inference of net-neutral effects.

652

653 Whatever its specific driver, extinction is the ultimate fate of any local population. Across  
654 the approximately 350 populations surveyed in this study, we detected 54 apparent  
655 extinctions, with populations at more than 15% of whole sites disappearing. These  
656 extinction rates fall in the range of those found in other studies of annual and perennial  
657 plant metapopulations (e.g. 36% for annual *Eichhornia paniculata*; Husband & Barrett  
658 1998; 9-30% for perennial *Silene latifolia*; Antonovics *et al.* 1994; 2-12% for perennial  
659 *Pedicularis furbishiae*; Menges 1990; ~5% per year for perennial *Silene tatarica*;  
660 Jäkäläniemi *et al.* 2005). Although populations with fewer plants were more likely to  
661 become extinct, several populations with more than 500 plants in the previous year also  
662 crashed to zero. Because *M. annua* has a soil seed bank, as our study confirms, the  
663 disappearance of adult plants from sites does not imply local extinction. Indeed, the  
664 frequent post-extinction recovery of populations in 2006 to sizes as large as, or larger  
665 than, our initial observations indicate that soil seed banks play an important role in  
666 population regeneration. For these populations, apparent extinctions were clearly  
667 transient. However, one third of sites experiencing local extinction in 2005 did not  
668 reappear in 2006. In spite of a seed bank, extinction may have been permanent for some  
669 of these sites; disappearance of *M. annua* from whole sites, which in most cases would  
670 have involved  $> 100 \text{ m}^2$  of surveyed habitat, tended to occur via large-scale disturbances  
671 associated with human activities, often through the reconfiguration or development of the  
672 land (e.g. road or house building).

673

#### 674 PATTERNS OF SITE SUITABILITY VERSUS DISPERSAL LIMITATION

675 Classical metapopulation theory assumes that local populations are embedded in a matrix  
676 of unsuitable habitat (Hanski 1998). The difficulty of assessing habitat suitability for  
677 plants (Münzbergová & Herben 2004) has impeded progress towards understanding the  
678 importance metapopulation processes (Freckleton & Watkinson 2002; but see, for  
679 example, Husband & Barrett 1998; Snäll, Ehrlén & Rydin 2005). However, in the present  
680 study, we were able to evaluate habitat suitability in two ways. First, for a subset of *M.*  
681 *annua* phenotypes, habitat suitability could be determined unambiguously: for male  
682 plants, suitable habitat patches are those in which hermaphrodites occur above a threshold  
683 density (Pannell *et al.* 2014; and see below). The second, more direct, method used to

684 assess habitat suitability was to sow seeds into systematically chosen unoccupied habitat  
685 patches that occurred in similar habitat types and in close proximity to occupied patches.  
686 This approach revealed that, on average, population growth rates in these unoccupied  
687 patches were positive in approximately 22% of sites in which seeds were recruited the  
688 year after sowing. By comparison, average population growth rates for populations extant  
689 in 2004 were positive in approximately 56% of sites. It would thus appear that the matrix  
690 of habitats surrounding local populations of *M. annua* tends to be less suitable than  
691 occupied habitats, but that the distribution of *M. annua* in the Iberian Peninsula and  
692 Morocco is at least partially limited by seed dispersal. Our data for *M. annua* thus suggest  
693 that available habitat likely occurs as (albeit cryptic) islands in a matrix of less suitable  
694 habitat.

695  
696 Our finding of some degree of dispersal limitation in *M. annua* is consistent with other  
697 seed-release experiments conducted in different types of habitats. Seed sowing  
698 experiments involving five species of forest herbs (Ehrlén *et al.* 2006) and six species  
699 occurring in a wet-meadow community (Vítová & Lepš, 2011) allowed the respective  
700 authors to infer some degree of dispersal limitation for most of the species studied. These  
701 inferences were made even though, as in the current study, population sizes for  
702 experimentally sown sites tended to decline over the eleven- (Ehrlén *et al.* 2006) and five-  
703 year (Vítová & Lepš 2011) time frames of these two studies, respectively. It is important  
704 to note, however, that population declines in the wet-meadow study occurred despite the  
705 fact that half of the species used were already resident in the community into which seeds  
706 were sown, indicating that these plants can form self-sustaining populations even if the  
707 numbers of plants in experimental plots declined (Vítová & Lepš 2011). Clearly,  
708 therefore, population declines are not themselves fully indicative of habitat suitability, and  
709 measures of population growth rates might underestimate the proportion of suitable  
710 unoccupied habitat. In this context it is important to note that many natural populations of  
711 *M. annua* with large sizes in our survey (presumably occupying suitable habitat) declined  
712 in size from one year to the next. It nevertheless seems reasonable to conclude that even if  
713 22% of unoccupied sites are suitable for viable populations of *M. annua*, as our  
714 experiment suggests, the clear difference in population growth rates between occupied

715 and unoccupied habitats indicates that potentially colonisable sites in the matrix of  
716 unoccupied habitat tend to be less suitable than those that are already occupied.

717

718 The requirement by males for the availability of mating partners points to an alternate  
719 perspective for defining suitable habitat for *M. annua*: suitable habitats for the  
720 maintenance of males (or male-determining alleles) are local populations in which  
721 hermaphrodites occur at a density higher than a threshold that allows them sufficient  
722 siring success. In dimorphic regions in the Iberian Peninsula and Morocco, where males  
723 and hermaphrodites coexist (androdioecious regions), this threshold occurs at about 7  
724 plants per m<sup>2</sup>: i.e., males can invade sites with hermaphrodites at densities greater than  
725 this threshold (Pannell *et al.* 2014). Considering only those sites in which males were  
726 present in the initial survey of sites in 2004, 40% had plant densities at or above 7 plants  
727 per m<sup>2</sup> (in plots A or B; 92 sites), compared to only 22% of 184 sites in fully  
728 monomorphic zones (Chi-squared = 9.51, d.f. = 1,  $P < 0.01$ ). Males thus do indeed occur  
729 preferentially in areas in which plant densities are higher. Together with regional  
730 differences in patch extinction rates discussed above, differences in the availability of  
731 suitable habitat patches for *M. annua* males (i.e. patches that exceed the minimum density  
732 for the maintenance of males) might explain why males are common in some regions, but  
733 not others. Taken together, our findings of dispersal limitation, unsuitable habitat in the  
734 matrix between occupied sites, and at least some permanent local extinctions, suggest that  
735 *M. annua* in the Iberian Peninsula and Morocco has important hallmarks of a classical  
736 metapopulation.

737

### 738 CONCLUSIONS

739 The importance of metapopulation dynamics in shaping the distribution and abundance of  
740 plant species has attracted considerable attention but has remained somewhat  
741 controversial (Eriksson 1996; Husband & Barrett 1996; Freckleton & Watkinson 2002;  
742 Alexander *et al.* 2012), not only because seed-bank dynamics complicate how apparent  
743 extinctions should be interpreted, but also because it is often difficult to distinguish  
744 suitable from less suitable habitat (Freckleton & Watkinson 2002; Münzbergová &  
745 Herben 2004). By studying the spatial dynamics of a plant in which a key life-history

746 trait, the sexual system, varies over space at a number of scales, we have found  
747 considerable evidence for a metapopulation structure and dynamic in an annual plant.  
748 This is particularly notable because the spatial dynamics of *M. annua* might appear to be  
749 those of a spatially extended population or a shifting cloud rather than a metapopulation.  
750 However, the fluctuations in occupancy and local abundance and particularly the spatial  
751 and temporal variation in the frequency of males are difficult to explain without invoking  
752 processes acting at larger geographic scales.

753

754 Although the atypical sexual system variation found in *M. annua* has allowed us to infer  
755 the importance of large-scale dynamics, in other respects *M. annua* is a typical ruderal  
756 weed. It is interesting to observe that several other species that have been studied from a  
757 metapopulation perspective (e.g. *Eichhornia paniculata*, Husband & Barrett 1998;  
758 *Sagittaria latifolia*, Dorken & Barrett 2003; *Silene vulgaris*, Taylor, Trimble & McCauley  
759 1999) also vary in their sexual systems, and that the spatial analysis of this variation  
760 pointed to the likely importance of spatial dynamics in their ecology. It seems likely that  
761 the ecology of many typical ruderal weeds will similarly be influenced by large-scale  
762 processes, even if the imprint of these processes is less obvious. Such species are  
763 ultimately characterised by a need to colonise new patches, and key aspects of their  
764 ecology and demography are likely to have been shaped by this need.

765

## 766 **Author's Contributions**

767 All authors conceived the ideas and designed methodology; MED collected the data;  
768 MED analysed the data; MED and JRP led the writing of the manuscript. All authors  
769 contributed critically to the drafts and gave final approval for publication.

770

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780

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Table 1. Mixed models of the effects of latitude and sexual system on the demographic properties of 350 populations of *Mercurialis annua* censused annually in the Iberian Peninsula and Morocco over a three-year period. Response variables are indicated in the first column. These were: (a) the  $\log_e$  of plant densities in the focal plot A and reference plot B; (b) the  $\log_e$  of the population growth rate parameter ( $\lambda$ ) for focal plot A; (c) the probability of apparent local extinction for focal plot A; and (d) the probability of apparent extinction of entire sites. For fixed effects, values are the parameter estimates and their standard errors in parentheses. Tests of significance for fixed effects are reported as Chi-squared values. For random effects, standard deviations of the intercept parameter are reported.

Response	Fixed effects				Random effects	
	Intercept	Sexual system	Latitude	Plant density	Year	Transect[Year]
a) $\text{Log}(\text{Density}_{AB}+1)$	0.11 (0.08)	-0.22 (0.07) $\chi^2 = 10.81^{**}$	-0.12 (0.02) $\chi^2 = 35.91^{***}$	NA	0.05	0.21
b) $\text{Log}(\lambda_A+1)$	-0.01 (0.06)	-0.00 (0.06) $\chi^2 = 0.00$	-0.02 (0.01) $\chi^2 = 2.32$	NA	0.00	0.09
c) $\text{Extinct}_A$	-1.05 (0.21)	0.45 (0.19) $\chi^2 = 5.53^*$	0.12 (0.04) $\chi^2 = 6.89^{**}$	-0.40 (0.10) $\chi^2 = 14.81^{***}$	0.00	0.30
d) $\text{Extinct}_{\text{Site}}$	-3.24 (0.31)	0.77 (0.31) $\chi^2 = 6.26^*$	0.18 (0.07) $\chi^2 = 7.25^{**}$	-0.35 (0.17) $\chi^2 = 4.29^*$	0.00	0.30

\*P < 0.05; \*\* P > 0.01; \*\*\* P > 0.001

Table 2. Pairwise analyses of patch demographics in focal plot A and neighbouring plot B. For (a) - (c) the response and predictor variables are the corresponding measurements from the two plots. For (d), the response and predictor variables differ, as indicated by the subscript. All analyses involved some combination of three different measurements of patch demography: the  $\log_e$  of plant densities, the  $\log_e$  of the population growth rate parameter ( $\lambda$ ), and the probability of apparent local extinction. For fixed effects, values are the parameter estimates and their standard errors in parentheses. Tests of significance for fixed effects are reported as Chi-squared values. For random effects, standard deviations of the intercept parameter are reported.

Plot A	Fixed effects		Random effects	
	Intercept	Plot B	Year	Transect[Year]
a) Log(Density+1)	-0.02 (0.07)	0.62 (0.02) $\chi^2 = 719.9^{***}$	0.00	0.26
b) Log( $\lambda$ +1)	-0.00 (0.04)	0.50 (0.04) $\chi^2 = 139.2^{***}$	0.00	0.05
c) Extinction	-1.76 (0.19)	1.99 (0.22) $\chi^2 = 80.83^{***}$	0.00	0.45
d) Extinct <sub>A</sub> versus Log( $\lambda_B$ +1)	-5.86 (4.53)	-1.58 (0.34) $\chi^2 = 21.97^{***}$	4.41	0.35

\*\*\* P > 0.001

Table 3. Mixed models of the effects of yearly changes in vegetation characteristics on the demographic properties of 350 populations of *Mercurialis annua* censused annually in the Iberian Peninsula and Morocco over a three-year period. Response variables are indicated in the first column. These were: (a) the  $\log_e$  of the population growth rate parameter ( $\lambda$ ) for focal plot A, and (b) the probability of apparent local extinction for focal plot A. Explanatory variables were the annual difference in the per cent cover of soil, other annual (non *M. annua*) plants, and perennials, in year  $t$  minus the value in year  $t - 1$ . For fixed effects, values are the parameter estimates, and their standard errors in parentheses. Tests of significance for fixed effects are reported as Chi-squared values. For random effects, standard deviations of the intercept parameter are reported.

Response	Fixed effects				Random effects	
	Intercept	$\Delta_{\text{Soil}}$	$\Delta_{\text{Annuals}}$	$\Delta_{\text{Perennials}}$	Year	Transect[Year]
a) $\text{Log}(\lambda_A+1)$	0.00 (0.04)	-0.36 (0.13)	-0.02 (0.20)	0.36 (0.17)	0.00	0.09
		$\chi^2 = 7.34^{**}$	$\chi^2 = 0.02$	$\chi^2 = 4.57^*$		
a) $\text{Extinct}_A$	-1.32 (0.21)	0.61 (0.38)	-0.90 (0.61)	-1.22 (0.48)	0.00	0.58
		$\chi^2 = 2.62$	$\chi^2 = 2.16$	$\chi^2 = 6.52^*$		

\* $P < 0.05$ ; \*\*  $P > 0.01$ ; \*\*\*  $P > 0.001$

## Figure Legends

Figure 1. Map of the study region indicating the location of the five transects and the 356 study sites. Grey squares indicate sites in gender-dimorphic regions; red circles indicate sites in monomorphic regions.

Figure 2. Variation in the density of plants in focal plots across space (A) and time (B). Red circles and lines refer to plots sampled in regions monomorphic for gender. Black circles and lines refer to plots sampled in regions dimorphic for gender. The lines in (A) indicate the results of a linear model with latitude and sexual system as additive fixed effects.

Figure 3. Differences in the binomial probability of extinction in focal plots between monomorphic (dashed lines, red polygon) and dimorphic regions (solid lines, grey polygons) as a function of the density of plants in the previous year. Lines at the outer edge of each polygon indicate the 95% CI from a generalized linear model that included latitude, sexual system and the density of plants in the previous census year as fixed additive effects.

Figure 4. Differences in the magnitude of spatial autocorrelations (measured as Moran's  $I$ ) in the density of plants in focal plots in each of the three survey years. For graphing purposes, only those points occurring at intervals of  $\sim 2.5$  km over the first 5 km and  $\sim 10$  km intervals thereafter are plotted. Red circles refer to data from regions that were monomorphic for gender. Black circles refer to data from dimorphic regions.

Figure 5. Concerted dynamics within sites measured as the correspondence in growth rates (A) between plots and the association between extinction events in focal plot A and (B) growth rates in reference plot B. The correspondence in the growth rates of plants for focal plot A and reference plot B is shown for the interval 2004 – 2005 in (A). Similar results were obtained for growth rates for the interval 2005 – 2006. In (B), the data are plotted for both survey intervals (i.e. 2004 – 2005 & 2005 – 2006).