Article:

Dorken, M.E., Freckleton, R.P. orcid.org/0000-0002-8338-864X and Pannell, J.R. (2017) Small-scale and regional spatial dynamics of an annual plant with contrasting sexual systems. Journal of Ecology, 105 (4). pp. 1044-1057. ISSN 0022-0477

https://doi.org/10.1111/1365-2745.12719

RT: Metapopulation dynamics of an annual plant

Small-scale and regional spatial dynamics of an annual plant with contrasting sexual systems

MARCEL E. DORKEN*[,1], ROBERT P. FRECKLETON[2], JOHN R. PANNELL[3]

[1]Department of Biology, Trent University, 1600 West Bank Drive,
Peterborough, ON, K9L 0G2, Canada
[2]Department of Animal and Plant Sciences, University of Sheffield,
Sheffield, S10 2TN, UK
[3]Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne,
Switzerland

*Correspondence author: E-mail: marceldorken@trentu.ca

Summary

1. Plant demography is known to depend on both spatial dynamics and life history, but how these two factors interact is poorly understood. We conducted a longitudinal study of the wind-pollinated annual plant *Mercurialis annua* that varies geographically in its sexual system to investigate this interaction.

2. Metapopulation demographic models predict that regular population turnover should be a more common feature of monomorphic over dimorphic populations because males and females cannot found new populations by selfing but hermaphrodites can. We tested the prediction that rates of population turnover would be higher in monomorphic compared to dimorphic regions.

3. We surveyed 356 populations of *M. annua* along five regional transects in Morocco and the Iberian Peninsula over a three-year period to examine their demography and persistence. Each transect crossed a transition in the sexual system, from a monomorphic region where almost all populations were hermaphroditic to a dimorphic one in which most populations had separate sexes (males with females or hermaphrodites).

4. As predicted, rates of local apparent extinctions (i.e. the disappearance of adult plants) were 50% higher in monomorphic compared to dimorphic regions. Local extinctions appeared to be driven by changes in vegetation cover, with extinctions tending to occur in sites in which perennial cover also declined. This suggests that disturbance is a primary agent of local extinctions.

5. We further examined the influence of regional dynamics on local demographic properties by investigating patterns of spatial autocorrelation in population density across years. We found positive spatial autocorrelations in plant densities within regions for both sexual systems. However, these positive autocorrelations extended over shorter distances in monomorphic regions, perhaps as a result of greater population flux in these regions.

6. *Synthesis:* Our study shows that population dynamics may be influenced by processes acting at a range of spatial scales: within patches, across patches within sites, and across sites within regions, as well as by life-history variation. In *M. annua*, regional variation in apparent extinction rates is affected by life history and implicated in regulating the geographical distribution of populations with different sexual systems.

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

Introduction

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

Although the processes of colonization and extinction probably characterize all plant populations at some point in their history, the extent to which metapopulation dynamics *per se* influence the maintenance of species within particular regions is poorly known (Freckleton & Watkinson 2002). Instead, regional patterns of species distributions may be more strongly influenced by processes acting locally, and that the patchy nature of plant species distributions may often better be described as ‘regional ensembles’ or ‘spatially extended populations’ in which local processes are sufficient to understand distributional patterns (Freckleton & Watkinson 2002). Many annual ruderals, for example, occur as ‘shifting clouds’ of individuals that are patchily distributed in an apparently uniform habitat matrix, such that the spatial location of patches moves around over time (Watkinson, Freckleton & Forrester 2000). Pannell & Obbard (2003) argued that the dynamics of such ‘shifting clouds’ might also usefully be construed as metapopulations if the processes of patch movement involve dispersal and colonization, albeit over small spatial scales. Cavanaugh *et al.* (2014) referred to this issue as the ‘mega-patch problem’, and showed that shifting clouds can reflect the outcome of metapopulation processes involving colonization and extinction of local subpopulations.

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

Although the possibility that regional processes (in whatever guise) influence the distribution of many plant species, very few empirical studies have been conducted to characterize their regional dynamics at an appropriate range of spatial scales. Even less is known about the processes that govern ongoing regional dynamics. However, some large-scale geographic studies have demonstrated the importance of regional processes in regulating plant distributions (reviewed in Freckleton and Watkinson 2002). In *Eichhornia paniculata*, for example, local extinction rates are high and the regional abundance of suitable habitat is associated with patterns of patch occupancy (Husband & Barrett 1998). Studies of *E. paniculata* have further revealed the importance of population turnover, evolutionary transitions to predominant self-fertilization, and long-distance colonization in regulating its distribution (Husband & Barrett 1991; 1993). The local dynamics of *Silene latifolia* and *Helianthus annuus* also appear to involve the metapopulation processes of extinction and colonization, the operation of which can be predicted by data sampled over broad spatial scales (Moody-Weiss *et al.* 2008). However, at least for *H. annuus*, course-scale processes can be understood in terms of a simple scaling-up of local processes. These dynamics might therefore more readily be characterized by the term “spatially-extended populations” (*sensu* Freckleton & Watkinson 2002) than as true metapopulations with clear population turnover (Alexander *et al.* 2009; and see Alexander *et al.* 2012).

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

Studies testing the predicted association between reproductive traits and population dynamics should ideally involve comparisons of populations that are similar in all but their reproductive traits. Although such species are rare, in a few species there is considerable variation in sexual system, e.g. in *Ecballium elaterium* (Costich 1995) and *Sagittaria latifolia* (Dorken, Friedman & Barrett 2002). In the current study, we present results of a large-scale survey of the spatial dynamics of third such species, the annual plant *Mercurialis annua*. A remarkable feature of *M. annua* is the occurrence of repeated transitions between sexual systems over its geographic range (Pannell *et al.* 2008), spatial variation that is thought to have been influenced by large-scale heterogeneity in the relative importance of the spatial dynamics of the species (Pannell *et al.* 2014).

In previous work, Eppley and Pannell (2007a) described four transitions between regions characterized by sexually monomorphic (monoecious) and sexually dimorphic (androdioecious and dioecious) populations of *M. annua* in the Iberian Peninsula alone. Dimorphic populations tend to display greater site occupancy and population sizes than monomorphic populations that are facultative selfers (Eppley & Pannell 2007a). Monomorphic populations show lower genetic diversity, greater genetic differentiation, and patterns of sex allocation that point to selection during frequent bouts of inbreeding (presumably when populations are sparse or recently colonised; Obbard, Harris & Pannell 2006; Pujol *et al.* 2009). Regional variation in the occurrence of dimorphic populations of *M. annua* might be explained by corresponding variation in rates of population turnover, because monomorphic populations can persist under higher rates of population turnover than dimorphic populations (Pannell 1997a). It also seems that a continent-wide expansion over a large latitudinal range has affected the genetic structure and sexual system of its populations (Pannell et al. 2014). The distribution of sexual systems, patterns of occupancy abundance and genetic diversity among populations of *M. annua* thus all appear to be consistent with the importance of metapopulation dynamics. However, direct evidence demonstrating that these patterns are underpinned by metapopulation dynamics requires actual measures of population turnover and changes in population demography over time and these data have never been recorded.

In this study we report on a large-scale analysis of population dynamics of *M. annua* at a range of spatial scales, and relate the observed dynamics to predictions of how spatial dynamics should vary among populations with different sexual systems. We examined the population dynamics of *M. annua* over a three-year period across replicated quadrats in more than 300 populations spanning more than 10 degrees of latitude, including the four sexual-system transitions studied in the Iberian Peninsula by Eppley and Pannell (2007a) as well as a fifth such transition from Morocco (Pannell *et al.* 2014; Figure 1). We addressed the following specific questions: (1) What are the principal causes of spatial and temporal variation in occupancy and abundance in *M. annua* (i.e. succession versus disturbance), and how do these vary over latitude? (2) To what extent are these site dynamics associated with variation in the sexual system? (3) Is the flux in population densities dampened by the occurrence of a soil seed bank and/or associated with changes in vegetation cover? (4) To what extent do range-level patterns of site occupancy reflect patterns of site suitability versus dispersal limitation of colonization? We show that sexual system indeed affects population dynamics at a range of scales, and that variation in life-history influences regional dynamics via impacts on local population flux.

Methods

STUDY SPECIES AND POPULATIONS

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

Mercurialis annua is a polyploid complex, with diploid, tetraploid and hexaploid populations distributed around the Mediterranean (Durand 1963, Durand & Durand 1992, Pannell, Obbard & Buggs 2004). Diploid populations, which occur in northern Spain and throughout western, central and eastern Europe, are dioecious (dimorphic), whereas tetraploid and hexaploid populations, distributed in the Iberian Peninsula and Morocco, are variously monoecious (monomorphic) or androdioecious (dimorphic where males cooccur with functional hermaphrodites). For these hexaploid androdioecious populations, the mechanism of sex determination is relatively simple, with maleness determined by the possession of a Y chromosome. Thus, only males carry male-determining alleles, and they are the only phenotype that can sire male offspring in androdioecious populations (Pannell 1997b).

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

VARIATION IN OCCUPANCY AND ABUNDANCE

In 2004, we examined sites for the presence or absence of *M. annua* within each of the five regions chosen for the study. We used predetermined intervals or evenly spaced landmarks (usually highway-distance markings) to identify sampling localities without biasing the sample towards larger, more easily visible populations. The minimum distance between sites was 2 km. At each of these sites, we searched 100 m along each side of the road for the presence of *M. annua*. If *M. annua* was absent at a site, its absence was recorded. To reduce search time in areas where *M. annua* was uncommon, we continued driving until we were able to identify a population *M. annua* located at least the minimum distance from the previous site. This may have slightly biased our sampling in the first year somewhat to larger populations; however, as shown in the Results, population sizes fluctuated enormously, and many populations that were initially large became small or went extinct in later years. We continued searching for sites until we were no more than 10 km from the nearest site already sampled. We then backtracked to the previously sampled site and began searching in a new direction. This sampling protocol was repeated until at least 40 sites had been included per sexual system per transect. We were able to include our target number of sampling sites for all transects except for Transect 3. Our sampling protocol, together with the location of transitions between sexual monomorphism and dimorphism, determined locations of the boundaries for each region.

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

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

To estimate the fine-scale turnover in patch occupancy within sites (‘patch extinction’), we calculated, for each site, the proportion of the focal patches that contained plants at time t, but which contained no plants at time $t + 1$. To generate a large-scale estimate of population turnover within regions, we inferred a population-scale extinction (‘population extinction’) if all four plots (A, B, C and D) became unoccupied. The possibility for regeneration from a soil seed bank means that not all of these apparent extinctions represent true extirpations at a site (see below).

SEED BANK AND VEGETATION COVER

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

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

ASSESSMENT OF SITE SUITABILITY VERSUS DISPERSAL LIMITATION

To assess establishment success following simulated colonization, we experimentally sowed seeds at a further ten sites per region that were unoccupied in 2004. In particular, we sowed seeds sampled from nearby locations at sites with bare soil and adjacent to permanent landmarks to test whether apparently unoccupied sites represented suitable habitat for *M. annua* plants (i.e. whether the distribution of *M. annua* is limited by dispersal or by the occurrence of suitable habitats). These sites were located several kilometres from our other sample sites and from any other populations of *M. annua* occurring along our roadside transects. Specifically, we sowed seeds at a site if *M. annua* had been absent from two consecutive locations visited (separated by intervals of 2 km, respectively) as well as along the intervening roadside. Because these sowings were conducted in the first year of the study and material from nearby localities was used (to limit the possibility that adaptation to regional climatic regimes would limit germination), we were restricted to using fresh plant material with varying numbers of ripening fruits. We sowed approximately 250 g of freshly harvested *M. annua* onto 20 x 20 cm square patches from which we had removed the upper layer of vegetation. This amounted to sowing at least one hundred seeds per site (M. E. Dorken & J. R. Pannell, unpublished data). These sites were mapped and revisited over the next two years to examine recruitment.

STATISTICAL ANALYSES

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

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

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

Third, we evaluated patterns in plant densities per site, population growth rates, and the probability of patch extinction over smaller spatial scales by evaluating the correspondence in densities and extinctions between focal patch A and neighbouring patch B using pair-wise analyses. These two patches were chosen to evaluate concerted changes in demographic properties because they were of similar size and had similar soil and habitat characteristics. We used linear mixed models to evaluate the correspondence in plant densities in focal patch A versus neighbouring patch B. As above, we used the log of plant densities in each patch and included transect, nested within year, as random effects. We also evaluated the association between growth rates in focal patch A versus neighbouring patch B using a mixed-effect model with the same nested random effects as for the previous analysis. As above, population growth rates in each patch were log-transformed. The correspondence of extinction rates in patches A and B was evaluated using a generalized linear mixed-effect model assuming binomial error and the same nested random effects as above. We also evaluated the association between population growth rates in patch B versus the occurrence of extinction events in focal patch A using linear mixed models in which extinction events in patch A were included as binary independent variables and nested random effects transect nested within year. All models described in this paragraph were calculated using the lmer function from the lme4 package in R.

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

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

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

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

Results

SITE CHARACTERISTICS

Our sites tended to occur in areas heavily modified by human activities such as embankments, along walls or fence lines, or at the edges of farm fields (in total approximately 75% of all sites). In part, this reflected our road-side sampling strategy, but also *M. annua*'s ruderal habit. Of all sites in our census, the most common category involved plants growing along embankments (121 sites), many of which were also located immediately adjacent to the roadside (114 sites). A substantial proportion of sites were characterized by the growth of plants in habitats that provided some protection from trampling, with 116 sites directly next to a wall, fence, or around a post, and 58 sites around or between upright woody vegetation such as trees and thorny shrubs. Our sites tended not to occur in areas dominated by herbaceous vegetation, but some did occur at field edges (48 sites) or in recently disturbed fields (26 sites).

VARIATION IN OCCUPANCY AND ABUNDANCE

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

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

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

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

SEED BANK AND VEGETATION COVER

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

annua seedlings = -3.96 – 0.69 × sexual system + 0.10 × latitude, χ^2 sexual system = 1.06, χ^2 latitude = 0.42, *P* sexual system > 0.30, *P* latitude > 0.50).

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

ASSESSMENT OF SITE SUITABILITY VERSUS DISPERSAL LIMITATION

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

Discussion

Metapopulations are characterized by the extinction and colonization of local populations, i.e., changes in the occupancy of sites over time (Hanski & Gilpin 1991). Both these processes are difficult to assess in natural populations, and large geographic surveys conducted over multiple years are required to evaluate their importance (e.g. Husband & Barrett 1998). Such large-scale studies are rare, and the present study is among the largest of its kind in terms of the geographical extent and the number of local patches examined. From our study of 356 populations distributed across a wide geographic range over a three-year period, we observed frequent apparent local extinctions and found that the dynamics of local populations were affected by regional dynamics. Specifically, variation in rates of disturbance and extinction coincided with regional differences in average population size, which in turn appeared to influence the presence versus the absence of males at the regional level. Our findings are consistent with the operation of metapopulation processes in the regulation of *M. annua* populations in the Iberian Peninsula and Morocco (and see Pannell *et al.* 2014). We argue that regional differences in these metapopulation dynamics influence the presence versus the absence of unisexual phenotypes within geographic regions. Below, we provide an overview of processes that appear to regulate the population dynamics of *M. annua*. We then argue that our results help to explain regional variation in sexual systems across this part of the species' range. Finally, we evaluate our results in light of the expected joint operation of local and regional processes in a metapopulation.

SPATIAL AND TEMPORAL VARIATION IN OCCUPANCY AND ABUNDANCE

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

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

SEXUAL SYSTEMS AND POPULATION DYNAMICS

Unisexual phenotypes are expected to be at a strong disadvantage in regions characterized by high rates of population turnover because of their inability to establish new populations by self-fertilization (Pannell & Barrett 1998; Pannell 2015). Consistent with this expectation, we found lower rates of population and patch extinctions in dimorphic compared to monomorphic regions. These results align not only with predictions arising from Baker's law (Pannell 2015; Pannell *et al.* 2015), but also with specific predictions for the effect of population turnover on the maintenance of unisexual phenotypes at the landscape level (Pannell 1997a). Plants from monomorphic populations of *M. annua* are not mate-limited (Hesse & Pannell 2011) and therefore should be less affected by Allee effects during colonization. Males, on the other hand, are expected to be maintained only in large populations that are sufficiently dense (Pannell 1997a, Pannell *et al.* 2014). There is some evidence for higher rates of population turnover in monomorphic (monoecious) compared to dimorphic (dioecious) populations of *Sagittaria latifolia* (Dorken & Barrett 2003). For *S. latifolia* these effects have also been invoked to explain why monomorphic populations are more common at the northern range limit, where the colonization advantage to cosexual plants appear to be important in regulating patterns of patch occupancy (Yakimowski & Barrett 2014). By contrast, in *M. annua* data from studies of population genetics (Obbard, Harris & Pannell 2006), regional patterns of patch occupancy (Eppley & Pannell 2007a), patterns of sex allocation (Pannell *et al.* 2014) and patterns of population turnover (this study) are all point to the importance of metapopulation dynamics in shaping the geographical distribution of gender variation and sexual systems.

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

In dimorphic regions where males coexist with hermaphrodites (androdioecious regions), male frequencies ranged between 0% and nearly 50%. Our observation of substantial annual variation in population densities can help to explain this variation. Population densities influence whether the pollen dispersed from male plants is likely to come into contact with hermaphrodite stigmas (Eppley & Pannell 2007b). Accordingly, we found that plant densities in one year affected the frequency of unisexual plants in the subsequent year. This finding is consistent with a previous study of evolutionary trajectories in the frequency of males of *M. annua* under experimentally manipulated densities (Dorken & Pannell 2008). More generally, these findings together suggest that encounter rates of hermaphrodites regulate male frequencies over time, as also shown, for example, for *Caenorhabditis elegans* (Lopes *et al.* 2008). In both animals and plants, therefore, these encounter rates depend on population density, which affects how often males (or their pollen) 'encounter' hermaphrodites.

LOCAL EXTINCTIONS, VEGETATION DYNAMICS, AND THE SOIL SEED BANK

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

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

PATTERNS OF SITE SUITABILITY VERSUS DISPERSAL LIMITATION

Classical metapopulation theory assumes that local populations are embedded in a matrix of unsuitable habitat (Hanski 1998). The difficulty of assessing habitat suitability for plants (Münzbergová & Herben 2004) has impeded progress towards understanding the importance metapopulation processes (Freckleton & Watkinson 2002; but see, for example, Husband & Barrett 1998; Snäll, Ehrlén & Rydin 2005). However, in the present study, we were able to evaluate habitat suitability in two ways. First, for a subset of *M. annua* phenotypes, habitat suitability could be determined unambiguously: for male plants, suitable habitat patches are those in which hermaphrodites occur above a threshold density (Pannell *et al.* 2014; and see below). The second, more direct, method used to assess habitat suitability was to sow seeds into systematically chosen unoccupied habitat patches that occurred in similar habitat types and in close proximity to occupied patches. This approach revealed that, on average, population growth rates in these unoccupied patches were positive in approximately 22% of sites in which seeds were recruited the year after sowing. By comparison, average population growth rates for populations extant in 2004 were positive in approximately 56% of sites. It would thus appear that the matrix of habitats surrounding local populations of *M. annua* tends to be less suitable than occupied habitats, but that the distribution of *M. annua* in the Iberian Peninsula and Morocco is at least partially limited by seed dispersal. Our data for *M. annua* thus suggest that available habitat likely occurs as (albeit cryptic) islands in a matrix of less suitable habitat.

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

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

CONCLUSIONS

The importance of metapopulation dynamics in shaping the distribution and abundance of plant species has attracted considerable attention but has remained somewhat controversial (Eriksson 1996; Husband & Barrett 1996; Freckleton & Watkinson 2002; Alexander *et al.* 2012), not only because seed-bank dynamics complicate how apparent extinctions should be interpreted, but also because it is often difficult to distinguish suitable from less suitable habitat (Freckleton & Watkinson 2002; Münzbergová & Herben 2004). By studying the spatial dynamics of a plant in which a key life-history trait, the sexual system, varies over space at a number of scales, we have found considerable evidence for a metapopulation structure and dynamic in an annual plant. This is particularly notable because the spatial dynamics of *M. annua* might appear to be those of a spatially extended population or a shifting cloud rather than a metapopulation. However, the fluctuations in occupancy and local abundance and particularly the spatial and temporal variation in the frequency of males are difficult to explain without invoking processes acting at larger geographic scales.

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

Author's Contributions

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

Acknowledgements

We thank Elze Hesse, Benoit Pujol, and Rebecca Anderson for assistance in the field, Stephen Bonser and two anonymous reviewers for comments on a previous version of the manuscript, the Natural Environment Research Council (NERC UK; NER/B/S/2003/00248) and the Swiss National Research Council for research grants to JRP, the University of Oxford and St. Hugh’s College for a Career Development Fellowship to MED, and the Natural Sciences and Engineering Research Council (NSERC Canada) for a post-doctoral fellowship and Discovery Grant to MED. The authors declare no conflicts of interest.

References

Alexander, H.M., Foster, B.L., Ballantyne, F., Collins, C.D., Antonovics, J. & Holt, R.D. (2012) Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. *Journal of Ecology*, **100**, 88–103.

Alexander, H.M., Pilson, D., Moody-Weis, J. & Slade, N.A. (2009) Geographic variation in dynamics of an annual plant with a seed bank. *Journal of Ecology*, **97**, 1390–1400.

Antonovics, J., Thrall, P., Jarosz, A. & Stratton, D. (1994) Ecological genetics of metapopulations: the *Silene-Ustilago* plant-pathogen system. *Ecological genetics* (ed. L. Real), pp. 146–170. Princeton University Press, Princeton, NJ, USA.

Baker, H.G. (1955) Self-compatibility and establishment after "long-distance" dispersal. *Evolution*, **9**, 347–348.

Barrett, S.C.H. (1996) The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **351**, 725–733.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Bjornstad, O.N. (2016) ncf: Spatial Nonparametric Covariance Functions. R package version 1.1-7. https://CRAN.R-project.org/package=ncf

Bullock, J.M., Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002) Plant dispersal and colonization processes at local and landscape scales. *Dispersal Ecology* (eds. J. M. Bullock, R.E. Kenward & R.S. Hails), pp. 279–302. Blackwell Science, Oxford, UK.

Busch, J.W. & Schoen, D. J. (2008) The evolution of self-incompatibility when mates are limiting. *Trends in Plant Science*, **13**, 128–136.

Cavanaugh, K.C., Siegel, D.A., Raimondi, P.T. & Alberto, F. (2014) Patch definition in metapopulation analysis: a graph theory approach to solve the mega-patch problem. *Ecology*, **95**, 316–328.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Costich, D.E. (1995) Gender specialization across a climatic gradient: experimental comparison of monoecious and dioecious *Ecballium*. *Ecology*, **76**, 1036–1050.

Crawley, M.J. (2004) Timing of disturbance and coexistence in a species-rich ruderal plant community. *Ecology*, **85**, 3277–3288.

Dorken, M.E. & Pannell, J.R. (2007) The maintenance of hybrid zones across a disturbance gradient. *Heredity*, **99**, 89–101.

Dorken, M.E. & Barrett, S.C.H. (2003) Life-history differentiation and the maintenance of monoecy and dioecy in *Sagittaria latifolia* (Alismataceae). *Evolution*, **57**, 1973–1988.

Dorken, M.E., Friedman, J. & Barrett, S.C.H. (2002) The evolution and maintenance of monoecy and dioecy in *Sagittaria latifolia* (Alismataceae). *Evolution*, **56**, 31–41.

Dorken, M.E. & Pannell, J.R. (2008) Density-dependent regulation of the sex ratio in an annual plant. *American Naturalist*, **171**, 824–830.

Durand, B. (1963) Le complexe *Mercurialis annua* L. s.l.: une étude biosystématique. *Annales des Sciences Naturelles, Botanique, Paris* **12**, 579–736.

Durand, R. & Durand, B. (1992) Dioecy, monoecy, polyploidy and speciation in annual mercuries. *Bulletin de la Société botanique de France. Lettres botaniques*, **139**, 377–399.

Ehrlén, J., Münzbergová, Z., Diekmannm M. & Eriksson, O. (2006) Long-term assessment of seed limitation in plants: results from an 11-year experiment. *Journal of Ecology*, **94**, 1224–1232.

Elderd, B.D. & Doak, D.F. (2006) Comparing the direct and community-mediated effects of disturbance on plant population dynamics: flooding, herbivory and *Mimulus guttatus*. *Journal of Ecology*, **94**, 656–669.

Eppley, S.M. & Pannell, J.R. (2007a) Sexual systems and measures of occupancy and abundance in an annual plant: testing the metapopulation model. *American Naturalist*, **169**, 20–28.

Eppley, S.M. & Pannell, J.R. (2007b) Density-dependent self-fertilization and male versus hermaphrodite siring success in an androdioecious plant. *Evolution*, **61**, 2349–2359.

Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. & Sibert, J. (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, **27**, 233–249.

Fox, J. & Weisberg, S. (2011) An R Companion to Applied Regression, Second Edition. Sage, Thousand Oaks, CA, USA.

Freckleton, R.P. & Watkinson, A.R. (2003) Are all plant populations metapopulations? *Journal of Ecology*, **91**, 321–324.

Freckleton, R.P. & Watkinson, A.R. (2002) Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. *Journal of Ecology*, **90**, 419–434.

Griffin, P.C. & Willi Y. (2014) Evolutionary shifts to self-fertilisation restricted to geographic range margins in North American *Arabidopsis lyrata*. *Ecology Letters*, 17:484–490.

Grossenbacher, D., Briscoe Runquist, R., Goldberg, E.E. & Brandvain, Y. (2015) Geographic range size is predicted by plant mating system. *Ecology Letters*, **18**, 706–713.

Gurectich, J., Scheiner, S. M., & Fox, G. A. (2006) *The Ecology of Plants*. Sinauer Associates, Sunderland.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.

Hanski, I. & Gaggiotti, O. E. 2004. Ecology, genetics, and evolution of metapopulations. Academic Press. Burlington, MA, USA.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, **42**, 3–16.

Hesse, E. & Pannell, J.R. (2011) Density-dependent pollen limitation and reproductive assurance in a wind-pollinated herb with contrasting sexual systems. *Journal of Ecology*, **99**, 1531–1539.

Husband, B.C. & Barrett, S.C.H. (1998) Spatial and temporal variation in population size of *Eichhornia paniculata* in ephemeral habitats: implications for metapopulation dynamics. *Journal of Ecology*, **86**, 1021–1031.

Husband, B.C. & Barrett, S.C.H. (1996) A metapopulation perspective in plant population biology. *Journal of Ecology*, **84**, 461–469.

Husband, B.C. & Barrett, S.C.H. (1991) Colonization history and population genetic structure of *Eichhornia paniculata* in Jamaica. *Heredity*, **66**, 287–296.

Husband, B.C. & Barrett, S.C.H. (1993) Multiple origins of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae): inferences from style morph and isozyme variation. *Journal of Evolutionary Biology*, **6**, 591–608.

Ives, A.R. (2015) For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution* **6**, 828–835.

Jäkäläniemi, A., Tuomi. J., Siikamäki, P. & Kilpiä, A. (2005) Colonization-extinction and patch dynamics of the perennial riparian plant, *Silene tatarica*. *Journal of Ecology*, **93**, 670–680.

Kalisz, S. & McPeek, M.A. (1993) Extinction dynamics, population growth and seed banks. *Oecologia*, **95**, 314–320.

Levins, R. & Culver, D. (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences*, **68**, 1246–1248.

Lisci, M. & Pacini, E. (1997) Fruit and seed structural characteristics and seed dispersal in *Mercurialis annua* L. (Euphorbiaceae). *Acta Societatis Botanicorum Poloniae*, **66**, 379–386.

Lopes, P.C., Sucena, É., Santos, M.E. & Magalhães, S. (2008) Rapid experimental evolution of pesticide resistance in *C. elegans* entails no costs and affects the mating system. *PLoS ONE*, **3**, e3741–e3741.

Münzbergová, Z. & Herben, T. (2004) Identification of suitable unoccupied habitats in metapopulation studies using co-occurrence of species. *Oikos*, **105**: 408–414.

Menges, E.S. (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.

Moody-Weis J., Antonovics, J., Alexander, H.M. & Pilson, D. (2008) Predicting local colonization and extinction dynamics from coarser-scale surveys. *Ecography*, **31**, 61–72.

Nee, S. & May, R.M. (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology*, **61**, 37–40.

Obbard, D.J., Harris, S.A. & Pannell, J.R. (2006) Sexual systems and population genetic structure in an annual plant: testing the metapopulation model. *American Naturalist*, **167**, 354–366.

Olivieri, I., Tonnabel, J., Ronce, O. & Mignot, A. (2016) Why evolution matters for species conservation: perspectives from three case studies of plant metapopulations. *Evolutionary Applications*, **9**, 196–211.

Pannell, J. (1997a) The maintenance of gynodioecy and androdioecy in a metapopulation. *Evolution*, **51**, 10–20.

Pannell, J. (1997b) Mixed genetic and environmental sex determination in an androdioecious population of *Mercurialis annua*. *Heredity*, **78**, 50–56.

Pannell, J.R. (2015) Evolution of the mating system in colonizing plants. *Molecular Ecology*, **24**, 2018–2037.

Pannell, J. R. & Dorken, M. E. (2006) Colonisation as a common denominator in plant metapopulations and range expansions: effects on genetic diversity and sexual systems *Landscape Ecology*, **21**, 837–848.

Pannell, J.R. & Barrett, S.C.H. (1998) Baker's law revisited: reproductive assurance in a metapopulation. *Evolution*, **52**, 657–668.

Pannell, J.R., Auld, J.R., Brandvain, Y., Burd, M., Busch, J.W., Cheptou, P.-O., Conner, J.K., Goldberg, E.E., Grant, A.-G., Grossenbacher, D.L., Hovick, S.M., Igic, B., Kalisz, S., Petanidou, T., Randle, A., Rubio de Casas, R., Pauw, A., Vamosi, J. & Winn A.A. (2015) The scope of Baker's law. *New Phytologist*, **208**, 656–667.

Pannell, J.R., Dorken, M.E., Pujol, B. & Berjano, R. (2008) Gender variation and transitions between sexual systems in *Mercurialis annua* (Euphorbiaceae). *International Journal of Plant Sciences*, **169**, 129–139.

Pannell, J.R., Eppley, S.M., Dorken, M.E. & Berjano, R. (2014) Regional variation in sex ratios and sex allocation in androdioecious *Mercurialis annua*. *Journal of Evolutionary Biology*, **27**, 1467–1477.

Pannell, J.R. & Obbard, D.J. (2003) Probing the primacy of the patch: what makes a metapopulation? *Journal of Ecology*, **91**, 485–488.

Pannell, J.R., Obbard, D.J. & Buggs, R.J.A. (2004) Polyploidy and the sexual system: what can we learn from *Mercurialis annua*? *Biological Journal of the Linnean Society*, **82**, 547–560.

Pickett, S., Kolasa, J., Armesto, J. & Collins, S. (1989). The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*, **54**, 129–136.

Pujol, B., Zhou, S.R., Vilas, J.S. & Pannell, J.R. (2009) Reduced inbreeding depression after species range expansion. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 15379–15383.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ross, K.A, Fox, B.J., and Fox, M.D. (2002) Changes to plant species richness in forest fragments: fragment age, disturbance and fire history may be as important as area. *Journal of Biogeography*, **29**, 749–765.

Russell, J.R.W., and Pannell, J.R. (2014) Sex determination in dioecious *Mercurialis annua* and its close diploid and polyploid relatives. *Heredity* **114**, 262–271.

Skaug, H., Fournier, D., Bolker, B., Magnusson, A. & Nielsen, A. (2015) Generalized linear mixed models using AD model builder. *R package version 0.8.3.3*

Snäll, T., Ehrlén, J. & Rydin, H. (2005) Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology*, **86**, 106–115.

Stebbins, G.L. (1957) Self-fertilization and population variability in the higher plants. *American Naturalist*, **91**, 337–354.

Taylor, D.R., Trimble, S. & McCauley, D.E. (1999) Ecological genetics of gynodioecy in *Silene vulgaris*: relative fitness of females and hermaphrodites during the colonization process. *Evolution*, **53**, 745–751.

Taylor, K., Brummer, T., Taper, M.L., Wing, A. and Rew, L.J. (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. *Diversity and Distributions*, **18**, 942–951.

Thomas, C.D. & Kunin, W.E. (1999) The spatial structure of populations. *Journal of Animal Ecology*, **68**, 647–657.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? a review of seed sowing experiments. *Oikos*, **88**, 225–238.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M.& Webb, D.A. (1964) Flora Europaea. Cambridge University Press, Cambridge, UK.

Venable, D.L. (1992) Size-number trade-offs and the variation of seed size with plant resource status. *American Naturalist*, **140**, 287–304.

Vítová, A. & Lepš, J. (2011) Experimental assessment of dispersal and habitat limitation in an oligotrophic wet meadow. *Plant Ecology*, **212**, 1231–1242.

Watkinson, A.R., Freckleton, R.P. & Forrester, L. (2000) Population dynamics of *Vulpia ciliata*: regional, patch and local dynamics. *Journal of Ecology*, **88**, 1012–1029.

Yakimowski, S.B. & Barrett, S.C.H. (2014) Variation and evolution of sex ratios at the northern range limit of a sexually polymorphic plant. *Journal of Evolutionary Biology*, **27**, 1454–1466.

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 (λ) 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.

	Fixed effects				Random effects	
Response	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) 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) Extinct_{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 (λ), 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.

	Fixed effects		Random effects	
Plot A	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(λ+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_A versus Log(λ_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 (λ) 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.

	Fixed effects				Random effects	
Response	Intercept	Δ_{Soil}	Δ_{Annuals}	$\Delta_{\text{Perennials}}$	Year	Transect[Year]
a) Log(λ_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) 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 ~2.5 km over the first 5 km and ~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).