

Life-history traits evolution across distribution ranges: how the joint evolution of dispersal and mating system favor the evolutionary stability of range limits?

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Abstract The question of the stability of distribution ranges of species is fundamental in ecology. However, the way in which stable distribution ranges are shaped by natural selection is still poorly studied. For a long time, botanists have studied empirically how self-fertilization and dispersal traits change from the centre to the periphery of species' distribution ranges, but theoretical arguments are lacking. In this commentary, we use a recent evolutionary model by Cheptou and Massol (2009) that analyses the joint evolution of dispersal and the mating system in a metapopulation. Considering that distribution ranges may result in gradients in pollen limitation for plants, habitat availability, or inbreeding depression for plants, we analyse how the association of dispersal and self-fertilization varies across distribution ranges. Interestingly, we show that such gradients result in a change in both traits and may favor evolutionary stable range limits for plant distribution. Based on empirical and theoretical results, we discuss the plausibility of such gradients as a way to explain range limits in plants.

Keywords Range limits · Metapopulation · Mating system · Dispersal

Introduction

Factors determining species range limits include abiotic and biotic factors and are fundamentally related to the ecological niche of species (Sexton et al. 2009). This

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encompasses a variety of factors such as natural enemies, physiological adaptation to climatic conditions (Gaston 2009) or habitat structure conditioning extinction/colonization dynamics (Holt et al. 2005). A variety of theoretical models predicts many ways for range limits to arise, including competitive exclusion, Allee effects, hybridization, and swamping gene flow (Sexton et al. 2009).

In an evolutionary perspective, the question of the stability of species ranges is puzzling. Though rapid adaptation has been documented in many ecological systems (e.g. Cheptou et al. 2008), what can explain that species fail to develop beyond a certain point in space, thus stabilizing distribution ranges at least at a certain timescale? A fundamental question in evolutionary ecology is whether stable species border can be the result of adaptive processes along the species' range. Kirkpatrick and Barton (1997) provided one of the first evolutionary models for a species on a gradient of environmental conditions. They showed that persistent asymmetrical gene flow from central to marginal populations impede local adaptation in peripheral populations which act as sink populations, resulting in stable range limits. Dispersal, being adaptive, is the balance between its benefit (such as finding suitable habitat or avoiding intraspecific competition (Comins et al. 1980; Hamilton and May 1977) and its cost (such as the failure reach a suitable habitat, i.e. the cost of dispersal). In line with this, Dytham (2009) showed that spatially heterogeneous environments along gradients of reduction in patch size or increased habitat turnover could lead to the evolution of longer dispersal distances at the margins.

According to the so-called Baker's law, plant colonizing populations located at the margins of the distribution area tend to be autogamous as a consequence of pollinator scarcity (Baker 1955, 1959). However, empirical data reporting trait variation across distribution ranges are contradictory (see for instance Randle et al. 2009; Miller et al. 2008).

While Baker's law has provided guidelines for analyzing trait variation in the field, we need to go further than verbal arguments and formalize plant traits in heterogeneous environments. The metapopulation framework proposed by Holt et al. (2005) provides a relevant ecological scenario in which the evolution of traits across ranges can be analyzed. Holt et al. (2005) propose that range limits may be shaped by metapopulation processes along gradients, namely gradients in extinction rates, gradients in colonization rates, or gradients in habitat availability. In a metapopulation model, Cheptou and Massol (2009) and Massol and Cheptou (2011a) have analyzed the joint evolution of self-fertilization and dispersal in heterogeneous pollination environments. More specifically, these models studied how extinction caused by pollen limitation stochasticity and the cost of dispersal due to habitat availability condition the evolution of self-fertilization and dispersal. This model revealed that self-fertilization is preferentially associated with the absence of dispersal under uncertain pollination (Cheptou 2011). Though Cheptou and Massol's paper (2009) does not deal with range limits, it is possible to re-analyze the model in relation to gradual changes mimicking metapopulation processes along gradients as suggested by Holt et al. (2005).

Cheptou and Massol model

The model assumes an annual hermaphroditic plant evolving in a metapopulation consisting of a very large number of patches. An individual plant is characterized by the proportion of ovules that are self-fertilized (s). The remaining fraction of ovules ($1 - s$) is devoted to outcrossing, which may be pollinated if pollination conditions are favorable and remains unfertilized if conditions are not favorable. Each patch alternates randomly in time between non-pollinated and pollinated states, with probabilities e and $1 - e$, respectively

($0 < e < 1$). Thus, e defines the intensity of pollination fluctuations. The plant in a non-pollinated patch can only produce seeds by selfing, and cannot deliver pollen to other plants. Offspring produced by selfing suffers from inbreeding depression (δ), as classically envisaged in mating system models (Lloyd 1979). Seeds produced by either selfing or outcrossing are dispersed at a rate d to other patches and a fraction q of dispersing seeds actually survive the dispersal episode, which means that the cost of dispersal is equal to $1 - q$. Pollen can disperse among patches. The full description can be found in Cheptou and Massol (2009).

Model outcomes

Given the model assumptions presented above, Cheptou and Massol (2009) analyzed the joint evolution of seed dispersal (d) and selfing rates (s), that is, when both traits are free to evolve for various sets of parameters for q (seed survival to dispersal), e (probability of pollinator absence), and δ (inbreeding depression). Invasion analysis was performed to define Evolutionarily Stable Strategies (ESSs) for seed dispersal and selfing rates. Technically, such analysis assumes a rare mutant strategy for seed dispersal and selfing rate (Maynard Smith 1978; Dieckmann and Law 1996) and looks for the traits s^* and d^* so that no mutant can invade the populations, that is, the ESS. The invasion analysis was analytically tractable, so that ESS can be easily derived using basic algebraic calculations.

Over the whole range of parameters for q (seed survival to dispersal), e (probability of pollinator absence), and δ (inbreeding depression), the invasion analysis shows that a strong association of traits emerges and that only two evolutionary associations are selected: 1) dispersal associated with full outcrossing (hereafter called “dispersal/outcrossing” syndrome) and 2) absence of dispersal associated with partial or full selfing (hereafter called “no dispersal/selfing” syndrome). The dispersal/outcrossing syndrome is characterized by the following evolutionary equilibria:

$$\begin{aligned} d^* &= \frac{e}{1-q(1-e)} \\ s^* &= 0 \end{aligned} \tag{1}$$

And this association is feasible if $1 - \frac{(1-e)[1-q(1-e)]q}{2[1-q+(2q-1)e]} < \delta \leq 1$. The second association, the no dispersal/selfing syndrome, is characterized by:

$$\begin{aligned} d^* &= 0 \\ s^* &= 2e/(2\delta + e - 1) \end{aligned} \text{ When } 1 - 2\delta < e < 2\delta - 1 \tag{2}$$

or

$$\begin{aligned} d^* &= 0 \\ s^* &= 1 \end{aligned} \text{ When } e > 2\delta - 1$$

The evolutionary syndrome highlights that pollen limitation stochasticity selects for dispersal because it creates among-patch heterogeneity (see Cheptou and Massol 2009 for a more complete explanation). As expected, inbreeding depression selects for outcrossing and thus for the dispersal outcrossing syndrome. Increasing the cost of dispersal counterselects seed dispersal and thus selects for the no dispersal/selfing syndrome.

Evolution of association along gradients

Our aim is to study how these associations of traits change when the parameters vary in a gradual way, mimicking gradients across distribution ranges. This is achieved by plotting

Eqs. [1] and [2] depending on the values of parameters. As mentioned in the Introduction, we considered the gradient in pollen limitation from the centre to the periphery of the distribution (Baker 1959). We also consider the gradient for survival to dispersal which may result from rarefaction of suitable habitat at the periphery of the distribution and gradients for inbreeding depression resulting from environmental changes.

Results and discussion

Evolutionarily stable self-fertilization and dispersal rates along gradients

The analysis of gradients considers the two other parameters fixed but it is important to note that trends in associations of traits are not modified by changes in parameters' values. The results presented here can be considered general in the context of Cheptou and Massol's model (2009). As the pollen limitation (e) increases, dispersal rate of outcrossers increases continuously (Fig. 1a). The positive effect of pollen limitation on dispersal in outcrossers is analogous to the extinction effect on dispersal (Comins et al. 1980). When pollination becomes too low, self-fertilization is selected (reproductive assurance; see Lloyd 1979 for details), which in turn removes selection pressure for dispersal and thus leads to the absence of dispersal. While this effect may appear counterintuitive, it is actually consistent with the fact that once self-fertilization is selected, heterogeneous pollination does not translate into fitness heterogeneity in selfers because of its independence from pollination agents. The same reasoning can be followed for the other two parameters. If habitat availability decreases, it results in a higher cost of dispersal. As a consequence, dispersal rates decrease and even switch to the absence of dispersal when self-fertilization evolves. Also, decreasing inbreeding depression tends to favor self-fertilization (Lloyd 1979) and results in removing fitness heterogeneity due to pollination

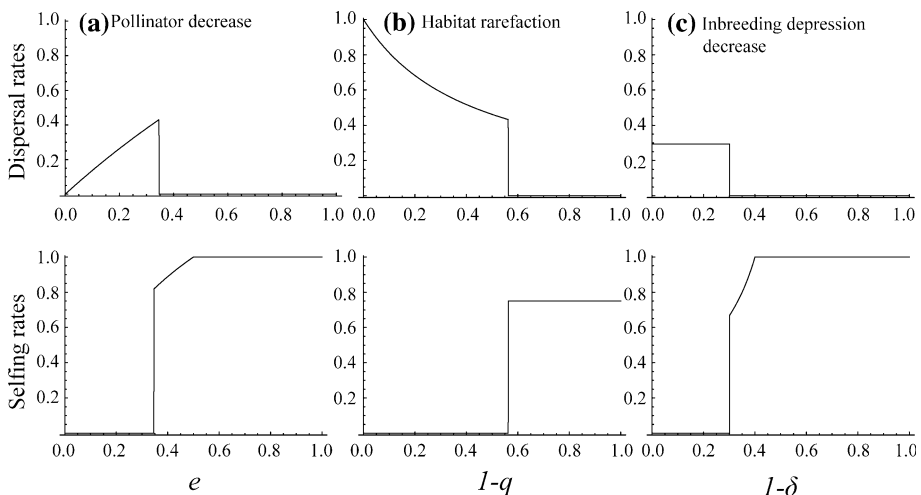


Fig. 1 Evolutionarily stable dispersal rates (*upper*) and selfing rates (*lower*) (given by Eqs. [1] and [2]) are presented as functions of parameters under three scenarios: **a** gradient in pollen limitation (e), **b** gradient in habitat availability (cost of dispersal, $1 - q$), and **c** gradient in inbreeding depression ($1 - \delta$). In **a** $\delta = 0.75$, $q = 0.3$; in **b** $\delta = 0.75$, $e = 0.3$; and in **c** $1 - q = 0.6$, $e = 0.2$

fluctuations. Such associations have not been formally tested in empirical data but several lines of evidence suggest that this association occurs in plants. For instance, Primack (1987) found that large attractive flowers are associated large fruits, more attractive to dispersers. Also, Bawa (1980) reported that dioecy (i.e. complete outcrosser) is preferentially associated to efficient dispersal mechanism, fleshy fruits, an association that has also been reported in gymnosperms (Givnish 1980). Such associations could be tested either among species (comparative analysis) or among populations within a species.

Our results revealed that three types of gradients from the centre to the periphery of a species range can limit dispersal at range limits: (1) an increase in pollen limitation; (2) an increase in the cost of dispersal due to rarity of suitable habitat; and (3) a decrease in inbreeding depression. Our study proposes a new adaptive hypothesis: that adaptive processes can suddenly reduce dispersal on the gradients thanks to the evolution of a syndrome associating self-fertilization and dispersal, which may stabilize distribution ranges.

Gradient of pollen limitation and the stability of range limits

Admittedly, the stability of range limits crucially depends on parameter gradients in the wild. Gradients in pollen limitation could result from reduced visitation by pollinators and/or reduced number or density of available mates from the centre to the periphery. Indeed, pollinator abundance and diversity at range peripheries may differ from those in the centre, thus creating pollen limitation for a focal plant species. In the tristylous species *Eichornia paniculata* (Pontederiaceae), Barrett et al. (1989) found that non-trimorphic populations occur at the margins and tend to be smaller and less dense than trimorphic populations and that the M morph has a higher fruit set relative to the L-morph in dimorphic populations. These results have been explained by the fact that the M-morph has greater capacity for autogamy than the L morph, which is selectively advantageous under low pollinator services (Barrett et al. 1989). This may not always be the case. In *Leavenworthia alabamica* (Brassicaceae), Busch (2005) showed that not only peripheral populations but also central populations were pollen limited. Importantly, the gradient in pollen limitation is more likely when pollination is specialized because it arises from the spatial variation of pollinator distribution. In *Clarkia xantiana* (Onagraceae), there was a close correspondence between specialist abundance and population differentiation in herkogamy, in which geographically peripheral populations had reduced herkogamy, higher autogamy, and lower pollinator abundance compared to central populations (Moeller 2006). In *Aquilegia canadensis* (Ranunculaceae), plants in central populations produced larger flowers with greater herkogamy than plants in northern populations but genetic estimates of the selfing rate between central and marginal populations do not differ (Herlihy and Eckert 2005).

Gradient of habitat availability or inbreeding depression and the stability of range limits

Our results revealed that other parameters which affect dispersal or mating systems but are independent from the classical pollen limitation hypothesis may also create stable range limits, and such parameters are worth considering when analyzing empirical data.

When the increase in the cost of dispersal from the centre to the margins may result from a decline in habitat availability or an increase in habitat fragmentation, our model shows that dispersal traits favor evolutionarily stable range limits through the selection of zero-dispersal at the margins. In line with these results, Dytham (2009) showed that the dispersal ability at the margins depends strongly on the way in which the range limit is

created. In the coastal dune plant *Camissoniopsis cheiranthifolia* (Onagraceae), Samis and Eckert (2009) argued that range limit were not consistent with the fact that fitness and recruitment increased toward the range limits and were relatively high even beyond the northern range limit. As a consequence, the authors argued that the range limits of *C. cheiranthifolia* may result from the reduced rate of dispersal to vacant patches toward the margins. However, some empirical results have not confirmed this pattern. Darling et al. (2008) found an increase in dispersal ability and a shift towards self-fertilizing morphs towards the range limits in *Abronia umbellata* (Nyctaginaceae). Clearly, ecological scenarios at range limit are diverse and we acknowledge that our model do not capture all these scenarios. From another perspective, when pollination does not decrease but fluctuates more at the margins than at the centre, the opposite association of traits may emerge (Massol and Cheptou 2011b).

Finally, our model reveals that a fundamental parameter of mating system evolution, inbreeding depression, may shape the association of traits along distribution range and create stable range limits if inbreeding depression decreases from the centre to the periphery. For instance, there is a possibility that inbreeding depression varies depending on the environmental context of the organisms (Cheptou and Donohue 2011). It has often been considered that stress may increase the magnitude of inbreeding depression (Armbruster and Reed 2005). If species are well adapted to the centre of the distribution, we may expect stress to increase at the range limit. This would increase inbreeding depression at range limits, contrary to our assumptions. However, there are also good reasons to consider the alternative scenario. A recent quantitative genetic model predicted that minimal inbreeding depression is expected in situations of extreme maladaptation, as expected in a new environment, or at range limits in the face of gene swamping from core populations (Ronce et al. 2009). Thus, self-fertilization (and then the absence of dispersal) may be selected at range limits and could result from reduced inbreeding depression. Interestingly, Pujol and Pannell (2008) found that range expansion results in reduced inbreeding depression in *Mercurialis annua* (Euphorbiaceae), potentially selecting for selfing in marginal populations (Pujol et al. 2009). While we have little information on inbreeding depression gradients, it would be worth documenting such variation as a potential driver of mating system and dispersal evolution at range margins.

Conclusion

The association of mating system and dispersal has been studied for a long time in evolutionary ecology (Baker 1955; Williams 1975; Cheplick 1987). While empirical results on various systems have been reported, there are very few models predicting such association. We propose that metapopulation processes along gradients may be the driver of such associations. Our scheme considers only extinction processes linked to mating systems via pollen limitation. In this context, mating system can be viewed as a local adaptation trait where selfing is assimilated to a generalist strategy (able to develop in both pollinated habitat and non-pollinated habitat) and outcrossing can be viewed as a specialist strategy (able to develop only in pollinated habitats). Under the model assumptions, generalists are associated to the absence of dispersal while specialists are associated to dispersal. The predictions presented here can be generalized to any locally adaptive traits (see Cheptou and Massol 2009). We predict that habitat generalist will evolve lower dispersal while habitat specialist will evolve higher dispersal. Moreover, Cheptou and Massol (2009) demonstrated that the associations of traits found in binary habitat (as considered here) can

be generalized to any continuous habitat heterogeneity. Admittedly, other metapopulation processes, such as extinction unlinked local adaptation traits may play a role at range limits. Importantly, we showed that dispersal and the mating system under heterogeneous pollination are inherently intertwined and that gradients in a single parameter may drive the change in association from the centre to the periphery of plant distribution ranges.

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