

INVASION GENETICS: THE BAKER AND STEBBINS LEGACY

Evolution of the mating system in colonizing plants

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Abstract

Colonization is likely to be more successful for species with an ability to self-fertilize and thus to establish new populations as single individuals. As a result, self-compatibility should be common among colonizing species. This idea, labelled 'Baker's law', has been influential in discussions of sexual-system and mating-system evolution. However, its generality has been questioned, because models of the evolution of dispersal and the mating system predict an association between high dispersal rates and outcrossing rather than selfing, and because of many apparent counter examples to the law. The contrasting predictions made by models invoking Baker's law versus those for the evolution of the mating system and dispersal urges a reassessment of how we should view both these traits. Here, I review the literature on the evolution of mating and dispersal in colonizing species, with a focus on conceptual issues. I argue for the importance of distinguishing between the selfing or outcrossing rate and a simple ability to self-fertilize, as well as for the need for a more nuanced consideration of dispersal. Colonizing species will be characterized by different phases in their life pattern: dispersal to new habitat, implying an ecological sieve on dispersal traits; establishment and a phase of growth following colonization, implying a sieve on reproductive traits; and a phase of demographic stasis at high density, during which new trait associations can evolve through local adaptation. This dynamic means that the sorting of mating-system and dispersal traits should change over time, making simple predictions difficult.

Keywords: Baker's law, dioecy, metapopulation, outcrossing, pollen limitation, range expansion, reproductive assurance, self-fertilization, sex allocation

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Introduction

Colonization involves the establishment of a new population in habitat unoccupied by its species, usually by a small number of colonizers. On the one hand, reduced crowding in the new habitat may allow an increase in per-individual reproductive success that could compensate against the loss of local adaptation; on the other hand, it means that sexual individuals will have fewer potential mates. In the extreme, where colonization has been effected by a single individual, mating opportunities will have been lost entirely – unless that individual is able to mate with itself via self-fertilization, or await the later arrival of compatible mates. Where dispersal

events are rare, as might be the case for dispersal over large distances, an ability to self-fertilize will usually represent the only basis on which a new sexual population might become successfully established. If colonization by long-distance dispersal typically involves single or small numbers of individuals, we should expect populations that then become established to comprise self-fertile individuals.

This simple and intuitive line of reasoning was exposed by Herbert Baker (1955) to explain his observation that populations that had been established by putatively long-distance dispersal indeed showed a capacity for self-fertilization (and uniparental reproduction in general). Baker (1955) had been thinking mainly about plants, but it was the publication of similar patterns found in animals by Longhurst (1955) that prompted his paper; the pattern seemed to be general to both

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plants and animals. Two years later, reflecting on just how general the pattern seemed to be, G. Ledyard Stebbins (1957) suggested that the idea should be labelled 'Baker's law'.

By elevating Baker's idea to the status of 'law', Stebbins' (1957) paper was bound to attract debate and disagreement. Indeed, almost immediately the generality of Baker's law was questioned by the botanist Carlquist (1966), who drew attention to examples of obligate outcrossers on oceanic islands, notably dioecious plants that seemed to be even more common than one should expect on the basis of their frequency elsewhere. Carlquist (1966) suggested abandoning the idea altogether. The idea has not (yet) been abandoned, but discussion about the appropriateness of its label has rumbled on to the present, 50 years later (Baker 1967; Carr *et al.* 1986; Mackiewicz *et al.* 2006). The proposition that long-distance dispersal might influence the distribution of mating system and reproductive traits has inspired both theoretical analysis and empirical tests in biological contexts that go beyond Baker's initial articulation of his idea. The notions implied in Baker's idea, for example, have been discussed and analysed not only in the context of long-distance dispersal to oceanic islands (McMullen 1987; Barrett 1996; Bernardello *et al.* 2006), but also of dispersal in range expansions (Barrett & Husband 1990; Randle *et al.* 2009; Wright *et al.* 2013), species invasions (Van Kleunen & Johnson 2007; Van Kleunen *et al.* 2008; Barrett 2011; Ward *et al.* 2012; Rodger *et al.* 2013) and metapopulation dynamics (Pannell 1997a; Pannell & Barrett 1998; Dornier *et al.* 2008; Schoen & Busch 2008).

That colonization might act as a selective sieve on the trait combinations displayed by a population (or ensemble of populations) is an important idea, but it has been profitable to consider it more broadly than in the terms initially discussed by Baker (1955). Whereas Baker focused his attention specifically on the effect that the selective sieve imposed by long-distance colonization should have on the *capacity* of successful colonizers to self-fertilize, colonization might affect the geographical distribution of reproductive traits for other reasons, too. These include effects of changes in pollinator availability, the evolution of inbreeding depression and dispersal, and affects that the mating system might have on a capacity for local adaptation. Such effects take place in a sequence of phases that all follow from colonization, but which should have different implications for the traits we ought to see. Specifically, it may be useful to conceptualize these various aspects of colonization in terms of three separate phases, which encompass dispersal and colonization, initial establishment following colonization, and the longer term evolution of trait combinations after establishment. This conceptuali-

zation highlights the fact some trait combinations can be a direct result of dispersal and reproductive sieves on pre-existing trait variation, which we might thus view as exaptations, while others will be the result of new adaptations (see Box 1).

Baker (1955) focussed his discussion on the colonization of oceanic islands, but the extension of his explanation to contexts that were not explicitly envisaged by him, particularly recurrent dispersal in metapopulations and range expansions, have both yielded important new insights and raised new questions. Here, I review these advances and address questions that remain. I first consider the evolution of colonizing species under selection for reproductive assurance and then explore in turn the importance of the joint evolution of the mating system and inbreeding depression and that of the mating system and dispersal. I go on to emphasize the distinction between selection on the mating system in terms of a selfing rate and a simple capacity for occasional self-fertilization. I ask to what extent is it appropriate to consider (e.g. in a modelling context) the impact of a single event of colonization of an oceanic island, for example, within the context of a scenario where colonization is repeated and ongoing, such as in range expansions or metapopulations of ruderal weeds. Finally, I end by reflecting on the contributions made on these issues by authors of the landmark book 'The Genetics of Colonizing Species' (Baker & Stebbins 1965), which we are here commemorating.

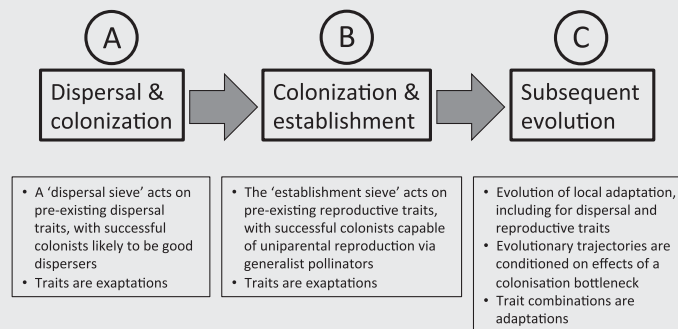
Colonization and the benefits of reproductive assurance

A striking feature of plant reproduction is the extent to which the mating system (in particular, the selfing or outcrossing rate) varies among species and even among populations of the same species (Barrett 2002; Harder & Barrett 2006). To a large extent, research has focused on understanding the apparent enigma of intermediate selfing rates, where self-compatible plants both outcross and self-fertilize their progeny (Goodwillie *et al.* 2005). Most of this work has considered selection within demographically stable populations, but intermediate selfing rates could also be the result of selection in habitually colonizing species, in which selfing rates might fluctuate from high values during colony establishment and lower values when mates (or pollinators) are more abundant in large established populations. The consideration of how dispersal and fluctuating pollinator availability might select for intermediate selfing rates has been considered by Cheptou & Massol (2009) and Massol & Cheptou (2011a), and metapopulation models such as those of Pannell (1997a), Pannell &

Box 1. Why should colonization affect plant mating?

Baker (1955) drew attention to the evolution of a capacity to self-fertilize in organisms prone to long-distance dispersal, but we might expect selection during and after colonization to influence plant mating for a number of reasons. Baker drew attention to one of these reasons in his initial study: the likelihood that colonization would not only take populations through a severe demographic bottleneck (of a single individual), but that it would also likely disrupt the native association with pollinators, with concomitant effects on the evolution of the mating system (Cheptou & Massol 2009). Other potential causes of an association between the mating system and colonization include: the loss of genetic diversity at loci that affect levels of inbreeding depression (Pujol *et al.* 2009; Peischl *et al.* 2013), a variable known to be important for the evolution of self-fertilization (Lande & Schemske 1985; Goodwillie *et al.* 2005); the loss of self-incompatibility alleles, otherwise maintained in large populations by negative frequency-dependent selection, with a resulting decrease in mate availability even after populations have grown (Vekemans *et al.* 1998; Brennan *et al.* 2003, 2006; Busch & Schoen 2008; Young & Pickup 2010); the effect that (repeated) colonization might have on the joint evolution of the mating system and dispersal – as opposed to the evolution of the mating system within the context of a particular (fixed) syndrome of dispersal (Cheptou & Massol 2009; Massol & Cheptou 2011a); the interactive effect that bottlenecks and the mating system have on levels of genetic diversity and linkage disequilibrium for loci that might be important in local adaptation to novel environments (Stebbins 1957; Allard 1965); and the extent to which self-fertilization tends to isolate populations from gene flow that might compromise local adaptation at range margins, thereby preventing further range expansion. The diverse ways in which colonization might affect the evolution of the mating system and dispersal traits might be conceptualized in terms of three phases of colonization in its broad sense, as depicted in the figure below.

- Phase A concerns the fact that colonization requires dispersal. There will thus be an ecological sieve on variation among and within species that selects on dispersal and reproductive traits already represented in the pool from which potential colonists are drawn. Traits that confer success on colonization are thus best viewed as exaptations.
- Phase B concerns establishment immediately upon dispersal. Here, success will be favoured for lineages with exaptations in terms of their reproductive system (e.g. perenniality, a capacity for self-fertilization or uniparental reproduction in general, or a capacity to be pollinated by generalist pollinators). The sieves associated with phases A and B may thus fashion combinations of dispersal and reproductive exaptations, but such associations do not require the joint evolution of these traits as adaptations.
- Phase C concerns evolution of traits subsequent to establishment, in the new ecological setting (with, for example, new and generalist pollinators and seed dispersers). How populations respond to selection will depend on genetic diversity that survives the colonization bottleneck (in the short term) or on new mutations (in the longer term). An immediate consequence of a genetic bottleneck will be a decline in inbreeding depression, which can set up conditions for the evolution of selfing. See text for details.



Barrett (2001) and Schoen & Busch (2008), reviewed below, point to this possibility, although more work is needed on mixed mating in metapopulation models (see review by Barrett & Pannell 1999).

At the extremes, the variation in the mating system observed among species and populations likely reflects transitions between predominant outcrossing, often secured by way of molecular self-incompatibility (SI)

systems (Hiscock & McInnis 2003; Takayama & Isogai 2005), and predominant self-fertilization, which may evolve via the spread of mutations that cause a breakdown of the SI system (Barrett 1988; Uyenoyama *et al.* 2001; Busch & Schoen 2008). Indeed, the shift from outcrossing to selfing has been perhaps the most common major evolutionary transition to have taken place during the course of plant evolution (Stebbins 1950, 1974), with two main explanations advanced to explain it (Goodwillie *et al.* 2005; Busch & Delph 2012). Fisher's 'automatic transmission hypothesis' posits that mutations that increase the selfing rate should enjoy an automatic and immediate selective advantage, because they should be transmitted not only through the ovules of affected individuals, but also by the pollen grains (Fisher 1941). Such mutations might be expected to spread particularly rapidly if they affect the male component of self-rejection, that is if genes expressed in or on pollen grains fail to be recognized as self, because such pollen grains not only benefit by siring the ovules on the plant that produces them, but will be compatible with all other individuals in the population so that they quickly become expressed in the progeny of other individuals. Empirical evidence supports this logic: in those cases for which the mutation causing self-compatibility (SC) has been found in natural populations, all are in the male-acting component of the self-incompatibility locus (S-locus) (Tsuchimatsu *et al.* 2012). (Interestingly, in crops, where self-fertility will presumably have been favoured by humans choosing the more highly fertile selfing variants in populations that produce more seed, mutations in the female-acting component are more common (Tsuchimatsu *et al.* 2010)).

The second major hypothesis for the evolution of selfing is the 'reproductive assurance hypothesis' (Darwin 1876; Lloyd 1979, 1992). This hypothesis predicts that selfing will evolve from outcrossing in response to selection for an ability to self-fertilize when mates and/or pollinators are absent. Although it is easy to see the advantage of mechanisms that confer reproductive assurance when opportunities for outcrossing are limited, clear experimental support for the reproductive assurance hypothesis has been surprisingly elusive (Herlihy & Eckert 2002; Busch & Delph 2012). Evidence for it is still largely based on associations between self-fertilization and either life histories for which reproductive assurance would seem likely to be more often important (e.g. annual or ephemeral plants) or a geographical distribution that is marginal to a species' range (e.g. because both mates and pollinators might be scarcer in marginal habitats) (Fausto *et al.* 2001).

The hypothesis encompassed by Baker's law is, in an important respect, an analogue of the reproductive assurance hypothesis (Schoen & Busch 2008) and a potential

example of a strong Allee effect, where population growth is negative below a threshold population size (Allee *et al.* 1949; Stephens *et al.* 1999). Here, an ability to self-fertilize will be strongly favoured over obligate outcrossing in colonizing species, because colonizers will often lack compatible mates and may have to rely on less abundant, unspecialized (and thus less effective) pollinators. In the extreme situation of colonization by a single individual (which Baker (1955) and Stebbins (1957) both emphasized), the benefits of an ability to self are obvious and almost do not need to be tested. For instance, Hesse & Pannell (2011) showed that isolated self-compatible monoecious individuals of the wind-pollinated annual plant *Mercurialis annua* set maximal seed, whereas isolated females of the same species did not (Fig. 1). How often populations are colonized by single as opposed to multiple individuals is not known and unfortunately very difficult to gauge directly, because populations often only become evident when they are already large. Indirect estimates based on genetic diversity do not allow discrimination between a scenario of colonization by multiple individuals and a gradual accumulation of diversity over time as migrants join previously established populations. Mate limitation can also occur in the less severe situation where colonization is by more than one individual that, however, are of the same gender (in dioecious species) or carry the same S-alleles – the so-called S-Allee effect (Wagenius *et al.* 2007) (see Box 2).

Several models have considered various aspects of the benefits of reproductive assurance during colonization, typically in the context of metapopulation models in which stochastic extinction is balanced by frequent recolonization of patches by dispersal. Pannell (1997a) modelled the maintenance of males or females with hermaphrodites and showed that a unisexual (obligate outcrossing) strategy was increasingly disfavoured by selection at the metapopulation level as the rate of population turnover increased and/or the mean number of individuals that colonized available habitat patches decreased. He found that unisexuals were much more quickly lost from a metapopulation with increasing population turnover when the hermaphrodites were SC than when they were SI, in which case unisexuals could be maintained with SI hermaphrodites even to the point of metapopulation extinction (Pannell 1997a). The model made predictions linking the evolution of the sexual and mating system with the proportion of occupied habitat in the landscape, which can potentially be measured (Fig. 2a). In particular, the proportion of occupied sites should increase with the amount of dispersal across the metapopulation (which also limits advantages of reproductive assurance, because populations can be more often colonized by more than one individual) and decrease with the rate of local turnover

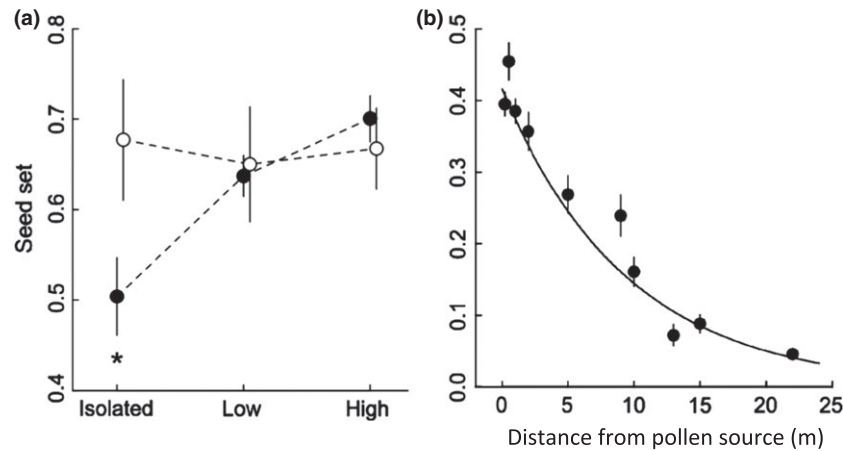


Fig. 1 (a) Mean seed set for females (closed circles) and self-compatible hermaphrodites (open circles) of *Mercurialis annua* from high-density (approx. 70 plants per m²) and low-density populations (approx. 8 plants per m²) and isolated individuals (at least 2 m from the nearest non-self-pollen donor). Only the isolated females set significantly less than what appeared to be maximal seed set. (b) The negative dependence of seed set by females on the distance to the nearest male in an experimental population of *M. annua*. Reproduced from Hesse & Pannell (2011). A similar dependence of seed set on distance to neighbours has recently been found for *Echinacea angustifolia* (Ison & Wagenius 2014).

Box 2. Mate limitation when there is more than one colonizing individual

Baker (1955) emphasized the advantages of an ability to self-fertilize in cases of colonization by a single individual. However, mate limitation can also occur when more than one individual colonizes a new habitat, if the individuals are of the same gender or are self-incompatible with one another, for example by sharing the same self-incompatibility alleles. In large populations of self-incompatible (SI) species, mate availability (i.e. the probability that a given mating partner is cross-compatible) is maintained at high levels by negative frequency-dependent selection on the S-locus (Wright 1964; Schierup 1998). Typically, SI acts such that individuals that share an S-allele will tend to be cross-incompatible (although the details will depend on whether SI is gametophytic or sporophytic). This means that individuals carrying a rare S-allele will be self-incompatible but cross-compatible with a large majority of the rest of the population, whereas those carrying common S-alleles will have greater cross-incompatibility within a population. The result is that rare alleles tend to increase in frequency and are protected from loss through genetic drift. Nevertheless, colonization, especially when it involves repeated genetic bottlenecks that would occur during a protracted range expansion, will strongly increase the effect of drift, and S-alleles can be lost (Wagenius *et al.* 2007). We might thus expect that populations established via long-distance colonization or range expansion to have a small number of more common S-alleles and relatively low mate availability, even after population growth.

It is not known how often SI colonizers have low S-allele diversity, but there is accumulating evidence that S-allele diversity can indeed be much lower in small, isolated populations than in larger ones. In the successful colonizer *Senecio squalidus*, which has spread rapidly throughout much of the United Kingdom following its introduction from Sicily, UK populations appear to harbour fewer S-alleles than their Italian counterparts, even though population sizes are much larger in the introduced range (Brennan *et al.* 2013). In the herbaceous perennial *Rutidosia leptorrhynchoidea*, small populations not only have lower S-allele diversity, but also appear to suffer from the reduced mate availability by producing fewer seeds (Young *et al.* 2000). An experimental manipulation of both population size in the relatedness among individuals within populations of the invasive species *Raphinus sativus* has shown that such effects can be directly attributed to genetic causes (including S-allele interactions) and are not just a by-product of pollination failure in small populations per se (Elam *et al.* 2007). The direct impact on seed production of mate availability as a result of shared S-alleles was also demonstrated for the threatened European species *Biscutella neustriaca* using experimental manipulations (Leducq *et al.* 2010). Computer simulations similarly point to a direct effect of S-allele diversity on mate availability (Young & Pickup 2010). All these studies suggest that diversity at the S-locus could have an important impact on a species' colonization success.

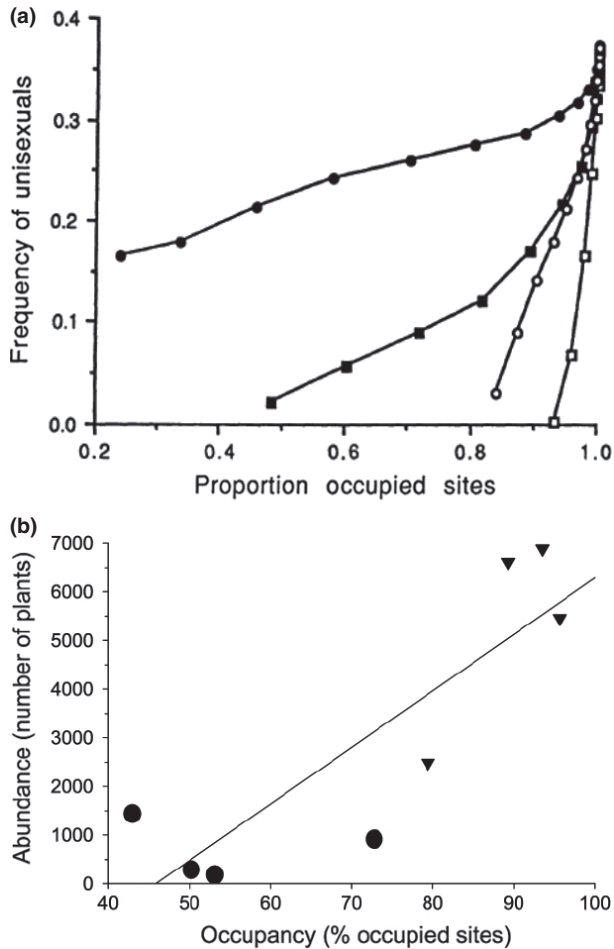


Fig. 2 (a) The frequency of unisexual individuals (males or females) maintained in a metapopulation with either SC hermaphrodites (open symbols) or SI hermaphrodites (closed symbols). Squares and circles denote low (0.05) and high population turnover rates (0.2), respectively. Each point corresponds to simulations with a given mean number of colonizing individuals, with higher values to the right on each curve. Reproduced from Pannell (1997a). (b) Mean population size plotted against the percentage of habitat occupied by *Mercurialis annua* across eight regions (metapopulations) with different sexual systems in the Iberian Peninsula: triangles represent populations that are dioecious or androdioecious (males and hermaphrodites); circles represent populations of self-fertile hermaphrodites. Reproduced from Eppley & Pannell (2007b).

(which also favours a selfing ability). The proportion of occupied sites can thus be used as a useful signature of the underlying metapopulation dynamics, as they affect the evolution of an ability to self. These predictions were corroborated in a test linking high versus low rates of habitat occupancy with the occurrence of dioecy versus monoecy, respectively (Eppley & Pannell 2007b; and Fig. 2b). Here, the predictions depended strongly on the expected number of individuals that founded new colonies.

In a subsequent model, Pannell & Barrett (1998) examined in further detail the persistence of SI vs. SC individuals in a metapopulation as a function of the proportion of occupied habitat (again, assuming stochastic extinction and migration that involved a given number of individuals). A key insight from this model is that although individuals with a selfing ability will often enjoy the expected advantage of reproductive assurance during colonization, the maintenance of SI in some species subject to metapopulation processes, such as ruderal weeds, should not come as a surprise. It was reasonably expected, for example, that the highly successful colonizer of human-disturbed habitat in the UK, *Senecio squalidus*, might have evolved increased levels of SC during its invasive spread (Abbott & Forbes 1993), but its strong SI system has been maintained throughout. The metapopulation models of Pannell (1997a) and Pannell & Barrett (1998) suggest, perhaps counter-intuitively, that it is precisely in good colonizing species such as *S. squalidus* that we might expect to see SI maintained. This is because colonization will often be by more than one individual when abundance and occupancy rates are high. On the basis of a related model, Dornier *et al.* (2008) also concluded that a high number of propagules of SI species can compensate for an incapacity to found new colonies as single individuals. All these models highlight the importance of considering not only population turnover, but also the 'propagule pressure' involved in recolonization. Indeed, Salisbury (1953), cited in Baker (1965), suggested the need for a certain density of propagule production before the explosive spread of *S. squalidus* throughout Britain. Of course, the effect of propagule pressure on mate availability will necessarily be modulated by the dispersal mode (endozoochory, epizoochory, wind-dispersal, etc.), particularly in dioecious or self-incompatible species, because of its influence on the relatedness of individuals within a dispersing propagule and the extent to which they will be mutually compatible with one another.

Effect of colonization on inbreeding depression and the mating system

The most likely reason for the maintenance of outcrossing in hermaphrodites despite the automatic transmission advantage of selfing is that selfed progeny will often express inbreeding depression. Indeed, simple models that account for gene transmission via both seeds and pollen predict that selfing can only invade and spread in a population if the levels of inbreeding depression suffered by selfed progeny are <0.5 (Lande & Schemske 1985; Goodwillie *et al.* 2005). To understand how the mating system should evolve in colonizing

species, it would thus seem important to incorporate notions of inbreeding depression. Relevant models vary substantially in how they have dealt with this issue (Goodwillie *et al.* 2005).

Empirical work has established quite firmly that most inbreeding depression expressed within populations is the result of the expression of deleterious recessive alleles in progeny rendered more homozygous by inbreeding (Charlesworth & Charlesworth 1987; Charlesworth & Willis 2009). We also know from theory (Lande & Schemske 1985; Charlesworth *et al.* 1990; Uyenoyama & Waller 1991; Porcher & Lande 2005), from the observed association between the mating system and levels of inbreeding depression (Byers & Waller 1999), and from experiments (Crnokrak & Barrett 2002) that inbreeding depression due to deleterious recessives will evolve with the mating system and cannot realistically be assumed to be fixed. Specifically, inbreeding allows the deleterious recessive alleles responsible for inbreeding depression to be purged from the popula-

tion, so that inbreeding populations end up with little or no inbreeding depression, even though there may have been substantial inbreeding depression before a transition to self-fertilization began (Crnokrak & Barrett 2002).

Although a great deal has been learned about mating system evolution from single-population models that assume a fixed value of inbreeding depression, it seems difficult to extract meaningful predictions from such models about inbreeding depression and the mating system in metapopulations. Single-population models with fixed inbreeding depression are useful because they can inform us about the boundary conditions for the invasion of a mutant strategy into a population, but they are unable to predict the trajectories that populations will take as they approach a new equilibrium. This is particularly important in the context of metapopulations, because the genetic architecture of each deme or subpopulation is likely to change over the course its existence from the time of its colonization

Box 3. Models of inbreeding depression and the mating system in metapopulations

Models of the evolution of the mating system in metapopulations vary in how they have dealt with the issue of inbreeding depression. The models made by Pannell (1997a) and Pannell & Barrett (1998) did not address the question of how inbreeding depression might affect the maintenance of different mating strategies in a metapopulation. In a sense, Pannell & Barrett (1998) avoided this issue by comparing the fate of self-compatible and self-incompatible species separately, that is their model was not concerned with the evolution of the mating system, but with the conditions under which one or other system might be maintained on its own. The effects of inbreeding depression, should it occur, could thus be seen to be incorporated implicitly into the intrinsic population growth rates of selfers vs. outcrossers. Dornier *et al.* (2008) did incorporate inbreeding depression as a fixed parameter into their metapopulation model and showed that, under their assumptions, inbreeding depression could paradoxically favour the evolution of self-fertilization in a metapopulation by diminishing local population densities sufficiently. Later models by Cheptou and Massol (Cheptou & Massol 2009; Massol & Cheptou 2011a) also incorporated fixed inbreeding depression into their analysis of how variation in the pollination environment might affect the joint evolution of dispersal and the mating system and predicted an association between outcrossing and dispersal, although colonization was not part of their models.

To see why metapopulation models that assume fixed inbreeding depression might be unrealistic in important ways, consider inbreeding depression in a recently colonized population (the argument will apply to any scenario of population growth from a narrow bottleneck). Because individuals in a deme will all tend to be related by descent from the one or few colonizers, selfed progeny will tend to differ genetically very little from locally outcrossed individuals. This has at least two important consequences. First, a population established by one or few self-fertilizing individuals simply cannot express much inbreeding depression in the sense that is usually required in mating system models: outcrossing within such a population does not avoid the cost of inbreeding any more than self-fertilization does. And second, because selfing and local outcrossing will tend to suffer equivalently from the inheritance of locally fixed deleterious alleles (or to benefit equivalently from their local purging), self-fertilization should enjoy the benefits from the automatic transmission advantage without paying the relative costs (Uyenoyama 1986). Any analysis of the evolution of the mating system in a metapopulation as a function of inbreeding depression that does not explicitly allow for the dynamic evolution of inbreeding depression clearly needs to be interpreted critically. More work needs to be done to explore mating-system evolution in metapopulations in which inbreeding depression is maintained in a balance between mutation (or migration into sinks from demographically stable source populations) and its purging by inbreeding and purifying selection.

until its extinction; the genetic architecture of the whole metapopulation will be thus the accumulated outcome of multiple (ongoing) trajectories (see Box 3). The relationship between the selfing rate and the level of inbreeding depression predicted for single populations, as used in the appendix of Dornier *et al.* (2008) model, thus seems unlikely to apply to a metapopulation scenario in a straightforward manner. Rather, models need to account for the fact that inbreeding depression can vary greatly between long-established and recently colonized populations, in a way that might foster the evolution of self-fertilization in the latter (Box 3). Some progress has been made in this direction through the theoretical and empirical population genetic analysis of range expansions, which involve the repeated colonization of available habitat and which thus have much in common with metapopulation scenarios.

Evolution of inbreeding depression and the mating system at range edges

In species range expansions, the wave of colonizations and repeated genetic bottlenecks that establish populations in new habitat are expected to bring about reduced levels of genetic diversity (Petit *et al.* 2002; Eckert *et al.* 2008). This affects not only neutral loci, but also loci subject to selection (Pujol & Pannell 2008; Pujol *et al.* 2009). While the increased levels of inbreeding towards the range edge can potentially allow the purging of deleterious recessive alleles, deleterious alleles can also be taken to high frequency by drift, resulting in a so-called expansion load in these populations (Peischl *et al.* 2013). This additional genetic load carried by colonized populations reduces mean fitness, but the combined effect of purging deleterious mutations at some loci and purging them at others means that inbreeding depression within populations should be lower towards range edges than at the core of a species' distribution. To test this prediction, Pujol *et al.* (2009) measured inbreeding depression in 16 populations of *Mercurialis annua* by comparing fitness components of selfed and outcrossed progeny. They found a sharp decline in inbreeding depression in populations with distance from the putative pre-expansion core of the species range, as predicted (Fig. 3).

It has long been observed that populations on the edge of a species' range are more likely to be self-fertilizing than those towards its core (Randle *et al.* 2009). This pattern has been attributed to potential selection for reproductive assurance, either during colonization at the leading edge of a range expansion (as expected under Baker's law) or because range-edge populations occur in marginal habitat where population densities are low and/or pollinators are scarce (Randle *et al.*

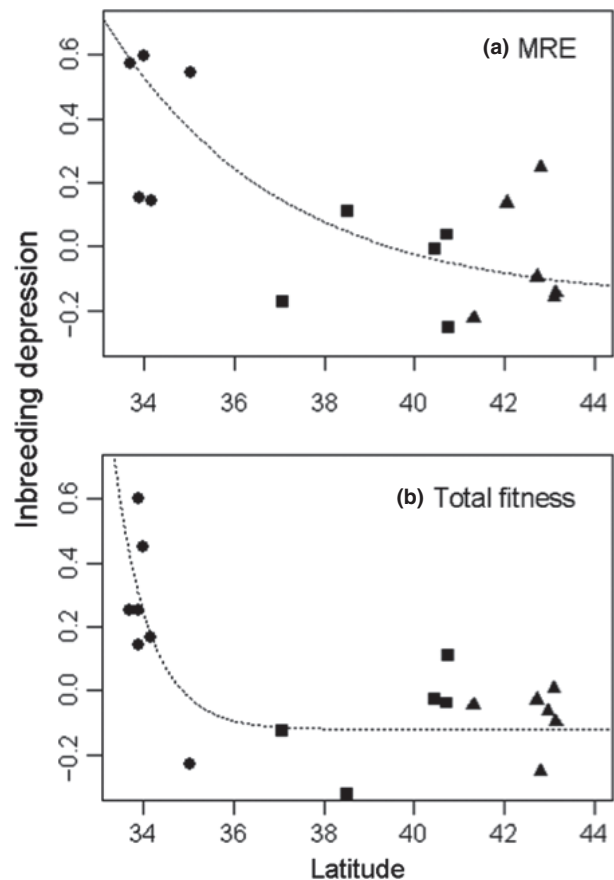


Fig. 3 The reduction in inbreeding depression for (a) male reproductive effort and (b) total fitness in populations of the wind-pollinated annual colonizer *Mercurialis annua* from populations that migrated from southern Spain and northern Morocco, the species' putative refugium (the lowest latitudes shown) into northern Spain (the higher latitudes). Figure taken from Pujol *et al.* (2009).

2009). Another possible reason for an enrichment of selfing towards range margins is that selfing may allow range-edge populations to evolve local adaptation more freely than outcrossing ones, because they will be less affected by the migration load caused by suboptimal alleles dispersing from populations in less marginal populations (Kirkpatrick & Barton 1997; Sexton *et al.* 2009). This perspective is similar to that taken by Allard (1965) in his reflections on the advantages that selfers would have in occupying novel habitats in a heterogeneous environment. Finally, in discussing the results of their study of inbreeding depression, Pujol *et al.* (2009) posed yet another hypothesis: if range-edge populations express lower inbreeding depression, we should expect mutations that increase the selfing rate to spread because of their automatic transmission advantage.

With four distinct hypotheses for an increased incidence of self-fertilization at species range edges, we face

something of an embarrassment of riches. Usefully, however, they differ in their implications for subsequent evolution once selfing has evolved, notably for the likelihood that selfing could spread throughout the species range. If selfing evolves at range edges because their habitats are marginal (Allard 1965), we would predict the maintenance of selfing in marginal habitats and the persistence of outcrossing where populations are denser and pollinators more abundant. This appears to be the case, for example, in *Clarkia xantiana* (Moeller & Geber 2005). If selfing has evolved because only selfing (or asexual) populations are able to continue their expansion without being held back by the effects of gene flow from nonadapted populations towards the species' core, then we might expect that selfing populations come to occupy much larger areas than their outcrossing counterparts, as is the case for the selfing ruderal weed *Capsella rubella* (Foxe *et al.* 2009; Guo *et al.* 2009). In contrast, the benefits of reproductive assurance during the demographic bottlenecks inherent to Baker's law will be transitory and should quickly be lost once populations grow in size. An observation of a strategy that reflects a capacity to self-fertilize in the absence of mates but potentially high outcrossing rates in established populations would be consistent with this explanation, as seems to be the case for metapopulations of the self-compatible *M. annua*, in which outcrossing rates are positively density dependent (Eppley & Pannell 2007a; Dorken & Pannell 2008) and are typically high in established populations (see Fig. 4).

The long-term implications of the evolution of selfing in range-edge populations with depleted inbreeding depression are less clear. On the one hand, the reduction in inbreeding at range margins ought to be transitory, as shown by the simulations of Pujol *et al.* (2009), because genetic load can re-establish itself both through new mutations and migration from the species core. On the other hand, the evolution of selfing in populations with low inbreeding depression would prevent the accumulation of genetic load, thereby further maintaining conditions for the persistence of selfing (Lande & Schemske 1985). The long-term maintenance of selfing at the range margin would thus seem assured. This intuitive prediction was confirmed in simulations conducted by Encinas-Viso *et al.* (F. Encinas-Viso, J.R. Pannell and A.G. Young, unpublished), which assess evolution of the mating system in a range expansion with fully dynamic inbreeding depression. Interestingly, their simulations indicate that the long-term maintenance of outcrossing in the core is also assured as long as there is some recombination between the mating system locus and viability loci causing inbreeding depression, that is the evolved selfing strategy cannot spread back into the core (Fig. 5). This, too, is quite intuitive:

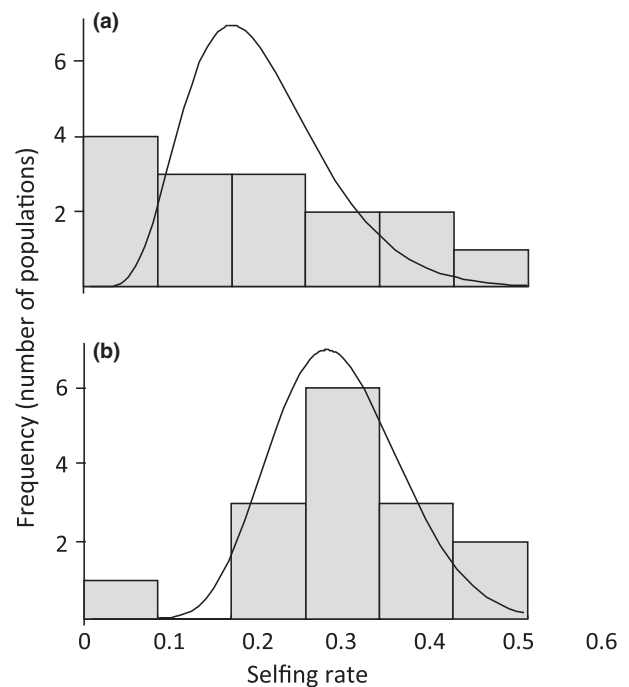


Fig. 4 The distribution of selfing rates in natural populations of the wind-pollinated annual herb *Mercurialis annua* for: (a) androdioecious populations in which males co-occurred with hermaphrodites and (b) hermaphroditic populations in which males were absent. Although *M. annua* hermaphrodites set full seed upon autonomous selfing in the absence of mates, for example during colonization (Pannell 1997b; Eppley & Pannell 2007a), these data indicate that natural established populations have a mixed mating system with outcrossing rates that range from near zero to one. From Korbecka *et al.* (G. Korbecka, J. P. David, J. L. García-Castaño and J. R. Pannell, unpublished).

an allele for increased selfing could only spread into core populations if it were linked to a nonloaded genome; recombination into the background of an outcrossing population would associate it with inbreeding depression, and selection would eliminate it. Encinas-Viso *et al.*'s simulations also confirm this prediction: with sufficiently low recombination rates, selfing spreads into the core and throughout the species range (Fig. 5). Species with a reduced number of chromosomes, as is found in some colonizing species [e.g. genes from 20 chromosomes appear to have been brought together on only four chromosomes in the ruderal *Eupatorium microstemon* (Baker 1965)], would presumably ease the conditions for the spread of selfing throughout the species range.

Joint evolution of dispersal and the mating system

Almost by definition, colonizing species will be those that have evolved some capacity to disperse. Any con-

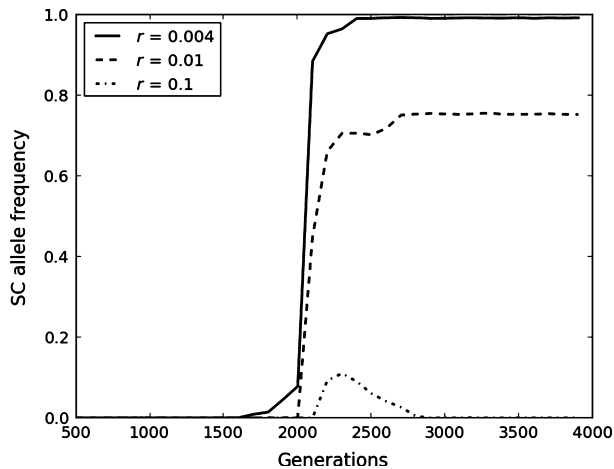


Fig. 5 The spread of self-compatibility in a range expansion as a result of selection for selfing when inbreeding depression is depleted by colonization bottlenecks. The graph shows the trajectory of three different simulations of a range expansion, under different rates of recombination between loci (r , shown). Simulations began as a metapopulation of self-incompatible hermaphrodites at equilibrium between largely recessive deleterious mutations at multiple loci, purifying selection, and drift. The loaded loci were partially linked to a gametophytic self-incompatibility locus at which multiple S -alleles were maintained by negative frequency-dependent selection. Following equilibration in the species core distribution, the metapopulation was allowed to expand its range by stepping-stone migration, a process which gradually purged inbreeding depression, as previously shown by Pujol *et al.* (2009). Initially, recurrent mutations at the S -locus to alleles conferring self-compatibility were always prevented from spreading by selection in a background of high inbreeding depression. But with declining inbreeding depression, the SC allele spread, occupying range-edge populations only. With high recombination between the S -locus and viability loci, the evolution of self-fertilization in range-edge populations was short-lived. However, with increased linkage between the S -locus and viability loci, selfing was either maintained at the edge populations or could even spread into the core of the species' distribution. Results from Encinas-Viso *et al.* (F. Encinas-Viso, J.R. Pannell and A.G. Young, unpublished).

sideration of the mating system of colonizing species would thus seem to require incorporation of the evolution of dispersal, too. Baker's explanation for the high frequency of colonizing species with a capacity to self-fertilize did not account for the evolution of dispersal, and simply took it for granted that long-distance dispersal occasionally took place (or, in some species such as ruderal annuals, is habitual). This absence of any account of the joint evolution of dispersal and the mating system in models or discussions of the biology implied in Baker's law has recently attracted considerable criticism, not least because models that do so make predictions that appear to run counter to the patterns Baker was attempting to explain (Cheptou & Massol

2009; Massol & Cheptou 2011a). It is argued in these models that whereas Baker predicted an association between self-fertilization and dispersal (and thus colonization), we should in fact expect a propensity towards outcrossing and inbreeding avoidance to be associated with dispersal.

It would seem that these arguments take out of context the points that Baker (1955) was attempting to make. For example, in response to criticism by Busch (2011) that Cheptou and Massol had misconstrued the essence of Baker's argument in discussing their models, Massol & Cheptou (2011b) replied that there are two ideas encompassed in Baker's law: the idea that species with a capacity to self-fertilize would be favoured when colonizing new habitats following long-distance dispersal as single individuals; and the idea that newly established populations might often lack appropriate pollinators. It is true that both these points were made by Baker in his original 1955 study. However, Stebbins was referring to the first of these two ideas, which was indeed dominant in Baker's study, when he labelled it 'Baker's law':

The correlation just mentioned [the association between colonization and an ability to self-fertilize] occurs so widely and has such great significance for studies of the origin and migration of genera of flowering plants and probably of other groups, including some animals (Baker 1955), that it deserves recognition as Baker's law. It was logically and reasonably explained by its author on the assumption that accidental long distance dispersal of a single propagule can lead to establishment of a colony only in a species capable of self fertilization.

More interesting than disagreements over emphasis and definition is the question of how one might reconcile Baker's and Stebbins' explanation of an association between a selfing ability and colonization with models that predict that (i) dispersal and outcrossing should be linked and that (ii) a syndrome of self-fertilization should be associated with a stay-at-home strategy (Auld & de Casas 2013). Cheptou and Massol's models (Cheptou & Massol 2009; Massol & Cheptou 2011a), as the authors point out, join a large corpus of theory on the evolution of dispersal. This literature, which has been amply reviewed elsewhere (Clobert *et al.* 2001; Auld & de Casas 2013), emphasizes dispersal as a strategy that evolves in response to selection to avoid inbreeding and inbreeding depression (Perrin & Goudet 2001; Auld & de Casas 2013) and was not motivated by questions relevant to reproductive assurance and colonization *per se*. In other words, the models that might appear to contradict the ideas of Baker (1955, 1967) and Stebbins (1957)

are modelling a different process. To an important extent, the confusion has arisen because similar terms have been used too liberally to refer to fundamentally different things, both in terms of the characterization of the mating system and what authors have meant by an ability to self-fertilize, and in terms of the extent to which metapopulation-like processes are truly able to represent Baker's initial idea. I address these issues in the following two sections.

The mating system versus an ability to self-fertilize

In reconciling models that predict an advantage to selfing in colonizing species with those that predict a syndrome of dispersal with outcrossing, it is important to distinguish between a simple ability to self-fertilize, and the habitual mating system of the species or populations in question. Models linking dispersal with inbreeding avoidance and outcrossing typically refer to the latter concept and are coined in terms of selfing or outcrossing rates, and/or inbreeding coefficients (Perrin & Goudet 2001; Cheptou & Massol 2009; Massol & Cheptou 2011a). In contrast, Baker and Stebbins, in their original studies, were more concerned with a species' *capacity* for self-fertilization. This is explicit in Stebbins' paragraph cited at length above, in which Baker's law was first proposed and where he refers to the 'establishment of a colony only in a species *capable of self fertilization*' (my italics). Stebbins is true to the sense of Baker's original study, whose title refers to self-compatibility rather than self-fertilization. The crucial point that Baker makes in his study is expressed thus:

With self-compatible individuals a single propagule is sufficient to start a sexually-reproducing colony, making its establishment much more likely than if the chance growth of two self-incompatible yet cross-compatible individuals sufficiently close together spatially and temporally is required. In addition, self-compatible flowering plants are usually able to form some seed in the absence of visits from specialized pollinating insects, which may be absent from the new situation.

The second sentence in this passage has been interpreted by Massol & Cheptou (2011b) as a second element to Baker's law, in which selection in large populations facing low pollinator visitation might favour evolution of high selfing rates. Rather, that sentence emphasizes the fact that self-compatible species are 'usually able to form *some* seed' (my italics) under pollinator limitation. There is no sense here of a prediction that long-distance dispersal should be associated with high selfing rates (although that is not ruled out) –

only that species that could produce a few seeds by selfing would be more likely to become successful colonizers than those that are completely self-incompatible.

It may be tiresome to quibble about words, but the distinction between an ability to self-fertilize (simply by being self-compatible) and a strategy of self-fertilization is conceptually important. One of the hallmarks of plant sexuality is its plastic nature, as are minor deviations from otherwise fixed reproductive strategies (Lloyd & Bawa 1984; Ehlers & Bataillon 2007). The phenomenon of pseudo-self-compatibility is a case in point: in some species, individuals that are basically self-incompatible allow a degree of self-seed set, particularly at the end of the flowering period if ovules have not been pollinated (Levin 1996; Stephenson *et al.* 2000). Such behaviour has been interpreted as a reproductive assurance device and might aid colonization. Critically, an ability to self-fertilize in this case does not imply a selfing strategy, and the mating system of such species would properly be characterized as outcrossing.

Incomplete separation of the sexes in dioecious species provides another example of an outcrossing strategy that accommodates an ability to self-fertilize, and indeed one that has been much discussed in the context of Baker's law. It is well known that individuals of dioecious species often display 'leaky' gender expression by producing a few flowers of the opposite sex (Lloyd & Bawa 1984; Delph 2003; Delph & Wolf 2005). Indeed, Baker (1967) himself drew attention to this tendency in a lengthy passage in his response to Carlquist (1966), who had argued that the high frequency of dioecy on oceanic islands such as Hawaii ran counter to the prediction of Baker's law. (The same argument continues to be raised by detractors of Baker's law (Massol & Cheptou 2011b)). Here, Baker (1967) was making the simple point that leakiness in gender would be sufficient to allow colonization by single individuals, particularly in perennial species, as are all Hawaiian plants. In the subsequent paragraphs of his study, he then argued that the high frequency of dioecy on the islands of Hawaii may also be the outcome of repeated instances of selection to maintain outcrossing in taxa that had arrived 'unarmed with any self-incompatibility' (i.e. following the principle of Baker's law). Thus, whether dioecious lineages arrived as such (with colonization aided by leakiness in gender expression) or whether separate sexes evolved subsequent to colonization (from colonizers that lacked self-incompatibility; see Box 1), Baker (1967) did not agree that the high incidence of dioecy on islands provided a counter-example to Baker's law. Critically, he expected the colonizers to have maintained or evolved outcrossing mechanisms, not a selfing syndrome. The interesting tension that results from selection for an ability to self-fertilize in a

Box 4. Selection of an ability to self-fertilize in the context of the maintenance of outcrossing: the case of androdioecious metapopulations

The idea that outcrossing may be maintained alongside an *ability* to self-fertilize applies not only to the once-off colonization by a lineage on an oceanic island, but also to the recurrent colonization that takes place in colonizing species that occupy ephemeral habitats, as might be characterized in terms of a metapopulation. In the wind-pollinated ruderal plant *Mercurialis annua*, for example which colonizes disturbed and ephemeral habitats, self-compatible hermaphroditism has evolved from dioecy (Pannell *et al.* 2008). Interestingly, hermaphrodites of this species often co-occur with males in 'androdioecious' populations (Pannell 1997b). It is known from sexual-system theory that androdioecious populations can only be maintained if outcrossing rates are high (because selfing by hermaphrodites would seriously compromise the siring opportunities of males) (Lloyd 1975; Charlesworth & Charlesworth 1978; Charlesworth 1984). Recent estimates of the mating system in wild populations of *M. annua* (G. Korbecka, J. P. David, J. L. García-Castaño and J. R. Pannell, unpublished results; Fig. 4) have indeed confirmed that outcrossing rates are often high, consistent with this prediction. Yet isolated hermaphrodites of *M. annua* set abundant seed through selfing (Pannell 1997b; Eppley & Pannell 2007a; Hesse & Pannell 2011), allowing them to colonize available habitat as single individuals. Here, it would seem that an ability to self-fertilize has been selected in hermaphrodites, but that males can persist in the metapopulation by migrating into established populations in which outcrossing rates are in fact high (Pannell 2001).

The metapopulation model for the maintenance of sexual-system variation in *M. annua* seems to apply to other androdioecious species, too (Pannell 2002). The plants *Datisca glomerata* and *Schizopepon bryoniaefolius* are both colonizers of disturbed and ephemeral habitats and comprise males that coexist with self-compatible hermaphrodites populations that are largely outcrossing (Fritsch & Rieseberg 1992; Akimoto *et al.* 1999). A particularly interesting example is provided by the Branchiopod crustacean genus *Eulimnadia*, in which self-compatible hermaphrodites have evolved from gonochoristic (i.e. dioecious) ancestors more than once (Sassaman & Weeks 1985; Weeks *et al.* 2006). Indeed, Baker was inspired to write his original 1955 study by reading about the evolution of hermaphroditism from gonochory in freshwater crustaceans. Here, the animals colonize ephemeral freshwater ponds that frequently dry out during drought. Their ability to self-fertilize almost certainly improves their colonization abilities, but they tend preferentially to outcross with males when males are present (Hollenbeck *et al.* 2002). This example is especially revealing for the current discussion, because hermaphrodites in populations that lack males are incapable of outcrossing at all and thus display complete self-fertilization.

species otherwise selected for outcrossing is well illustrated by the maintenance of males with hermaphrodites in androdioecious metapopulations (see Box 4).

Single-event versus recurrent long-distance colonization

Just as a plant's mating system might encompass both its ability to self-fertilize and its selfing rate, so the term 'dispersal' can refer to different phenomena. For instance, dispersal scenarios can vary in terms of the frequency or probability with which organisms disperse from their natal patch, the mean distance over which they do so, the full distribution of dispersal distances, and the composition of the dispersing propagule or group of individuals (Ronce *et al.* 2001). This diversity of perspectives on dispersal is also relevant for discussions of models of colonization. To what extent does selection acting on dispersal traits influence long-distance colonization? Can traits for long-distance colonization be selected directly? Despite substantial effort

spent in modelling the evolution of dispersal and, to some extent, its links with the mating system, there is still a dearth of theory on selection directly on colonization, and there is surely scope for more work here. In a stimulating article, Ronce *et al.* (2001) has laid out a wide range of questions that still need to be addressed, some of which are directly relevant to colonization. A particularly important question, for example, concerns the extent to which selection favouring increased dispersal at short spatial scales will affect the frequency and success of long-distance dispersal. Another question concerns whether rare long-distance dispersal, of the sort that establishes new species on oceanic islands, can be related to, and even modelled by, recurrent dispersal in a metapopulation (Ronce *et al.* 2001).

From a conceptual point of view, there are at least two factors that distinguish dispersal that leads to colonization from dispersal over short distances. First, an important facet of dispersal is that it leads to an immediate rupture from genetic exchange and any possibilities of mating with individuals that have not dispersed.

Depending on the organisms involved, such a rupture could take place over distances that are, in absolute terms, quite small. And second, because dispersal kernels are inevitably leptokurtic, with long thin tails, long-distance dispersal will be rare (Nathan & Muller-Landau 2000). Thus, we might expect selection to act overwhelmingly on the basis of the fate of short-distance events.

The importance of a continuing connection to a gene pool under selection is nicely illustrated by the contrast between the expected evolution of dispersal traits on oceanic islands and metapopulations. On oceanic islands, selection on dispersal is, in a sense, entirely negative: because dispersers leave the island and are unlikely to return (even as descendants of the dispersers), oceanic island populations should lose the very dispersal traits that allowed them to colonize the island when they first arrived. This is presumably one reason for the evolution of flightlessness in many animal island inhabitants (Darwin 1859; Slikas *et al.* 2002), and the evolution of traits associated with reduced seed dispersal in island plants (Carlquist 1966; Cody & Overton 1996). In the context of a subdivided population with colonization of empty habitat patches, this notion has been labelled the 'metapopulation effect' (Olivieri *et al.* 1997; Ronce & Olivieri 1997): it explains why the initial colonists of a patch are likely to possess dispersal traits, and why, over time, patch residents gradually lose those traits. The observed decline with patch age in the proportion of dispersing achenes in Asteraceae inflorescences illustrates this phenomenon well (Olivieri *et al.* 1990). The predicted and observed evolution of dispersal traits following colonization of both oceanic islands and demes or patches in a metapopulation show that models that seek a single dispersal rate will mislead us. Significantly, just as we might find that populations established via long-distance colonization will end up as (almost) obligate outcrossers with a (residual) ability to self-fertilize, so traits that allow colonization by long-distance dispersal may soon become lost.

Because some mating system and dispersal traits will evolve more quickly after colonization than others, careful thought is required when choosing traits for tests of Baker's law. The most revealing trait variation is probably that which Baker (1955) first focussed on: self-incompatibility and its loss. First, although SI can be leaky, typically it is strong, and SI individuals are thus likely to be poor colonizers as single individuals in comparison with SC individuals. And second, the loss of SI tends to be definitive; once lost, SI systems are very unlikely to re-evolve (Igic *et al.* 2006; Goldberg & Igic 2012). This means that subsequent evolution of reproductive traits will not obscure the relationship predicted by Baker's law, irrespective of whether a syn-

drome of near complete selfing evolves (e.g. with the loss of inbreeding depression), or whether some other mechanism of outcrossing evolves (e.g. dioecy). The frequency of self-compatibility among colonizers relative to their noncolonizer relatives should therefore be a clearer indication of a selective sieve for a selfing ability than measures of the mating system (i.e. selfing or outcrossing rates).

Although metapopulation models seem able to reflect certain aspects of once-off colonization of islands (the selective advantage of a selfing ability is one of them; the metapopulation effect and the evolution of reduced dispersal on islands is another), they also differ in an important respect: a genetic connection is potentially maintained between the demes of a metapopulation by migration, whereas oceanic island colonization disrupts all ongoing connection with other populations. The connection among demes of a metapopulation by migrants effectively allows selection to act on individuals or strategies at the metapopulation level, whereas selection on newly established populations on oceanic islands will be able to act only on the island. This difference will not always be critical: the selective advantage of a selfing ability seems to apply to both scenarios, and the metapopulation effect, cited above, is to some extent analogous to the loss of dispersal traits on oceanic islands. However, from other points of view the difference probably matters, and metapopulation models will then be poor analogues for once-off dispersal. This probably applies to the joint selection of the mating system and dispersal, because its outcome is contingent on the structure and dynamics of the metapopulation as a whole. The evolution of conditional altruism, phenotypic plasticity and sex allocation would be other cases in which it is probably important to distinguish between single-event and recurrent dispersal and colonization. In the present context, the evolution of sex allocation is of particular note, because sex allocation is known to be selected differently in outcrossing vs. inbreeding species, and because colonization gives rise to high levels of inbreeding at the metapopulation level, even where mating in each local population is random (see Box 5).

Perspectives from 'The Genetics of Colonizing Species'

Before concluding, it is worth reflecting on the extent to which the ideas presented and discussed above were featured in the chapters of 'The Genetics of Colonising Species' and in the discussions that took place at Asilomar in 1964, which the current volume is commemorating. Both Baker and Stebbins, the book's editors, contributed chapters to the book. Although neither chapter focused specifically on questions concerning

Box 5. Evolution of sex allocation under the influence of recurrent colonization in a metapopulation

The genetic bottlenecks brought about by colonization in a metapopulation cause recurrent bouts of local inbreeding, even in otherwise outcrossing species. Hamilton (1967) first showed that selection under inbreeding will favour female-biased sex allocation, because of 'local mate competition', a phenomenon that explains the low pollen:ovule ratios in selfing populations of hermaphroditic plants (Cruden 1977). Theory thus predicts a positive association between the inbreeding coefficient within populations, typically F_{IS} , and the proportion of reproductive resources allocated to female function (West 2009). As we have discussed, although metapopulation dynamics are expected to favour a capacity for self-fertilization, outcrossing within populations following colonization is often likely to be high; in this case, the local inbreeding coefficient F_{IS} will on average tend to be close to zero. But inbreeding may nevertheless continue to be high across the metapopulation if most mating takes place among the descendants of the single (or few) colonists of each deme. This type of metapopulation-wide inbreeding is measured as F_{ST} .

It is well known that population turnover in a metapopulation gives rise to elevated F_{ST} (Wade & McCauley 1988; Pannell & Charlesworth 2000) – unless demes are colonized by more than one colonist drawn from more than one source deme (Slatkin 1977; Whitlock & McCauley 1990). The relationship between F_{ST} and sex allocation in a metapopulation has to my knowledge hitherto not been explored, but simulations investigating the evolution of sex allocation in hermaphroditic metapopulations have indeed found the expected relationship (J.R. Pannell and C. Roux, unpublished): population turnover selects for female-biased sex allocation across the metapopulation, the level of which is well predicted by F_{ST} (but not by F_{IS} ; see Fig. 7). This is of course not something we would expect to find in the context of oceanic island colonization, because selection on the sex allocation of the colonized population will occur only locally. We should thus be cautious when using metapopulation models to explore processes that occur at spatial and/or temporal scales that do not correspond.

Baker's law, both authors made comments and observations relevant to it. Baker (1965) devoted his chapter to comparisons of the characteristics of ruderals and 'agrastals' (weeds that colonize disturbed waste places and agricultural fields, respectively), with several examples taken from the Asteraceae, a large family comprising both species with strong sporophytic self-incompatibility and highly self-fertile species. He reported that the evolution of weediness in this family (the ability to be a successful colonizer of disturbed, ephemeral habitats) frequently coincided with a shift away from self-incompatible perenniality towards a life history typified by rapid development, rapid flowering, increased plasticity and self-compatibility. In describing the colonizing weed *Ageratum conyzoides*, it is noteworthy that he typified its breeding system as 'thoroughly self-compatible, even self-fertilizing', revealing Baker's view that self-compatibility was the critical trait, not necessarily a syndrome of self-fertilization, common though that appeared to be in many weeds, too. Yet, later in his chapter (p. 165), Baker (1965) stated 'self-pollination or even apomixis is likely to be important for establishment after long-distance dispersal'. We see here, in his reference to 'self-pollination' (rather than a capacity to self-fertilize), germs of the confusion that has plagued recent discussion of Baker's law.

In his chapter, Stebbins (1965) in turn directed his attention towards an analysis of the weeds of the Cali-

fornian flora, searching for generalizations that might be made about what makes certain species successful colonizers of human-disturbed habitats. On the basis of his survey, in which he found an equal frequency of self-fertility among annual weeds as in their nonweedy annual relatives, Stebbins (1965) concluded (p. 181) that 'no particular type of mating system or chromosomal condition is either necessary or generally favourable for preadapting a group of species to evolve in the direction of weediness'. Here, Stebbins distinguished between annual and perennial species, arguing that 'the most adaptive condition for an annual is self-fertilization and in a perennial obligate outcrossing is most often favoured by selection'. The importance of distinguishing between annual and perennial colonizers is a theme running through several of the other chapters of the volume. For instance, Ehrendorfer (1965) felt that it is sensible to look for the hallmarks of colonizing species particularly in annuals, notably because a perennial habit removes some of the urgency with which plants must self-fertilize to reproduce. In an interesting analysis of variation in dispersal, chromosomal and breeding system traits in Mediterranean Dipsacaceae species, he picked up the familiar theme regarding the importance of an ability to self-fertilize. Thus, Ehrendorfer (1965) noted that in selfing species, 'seed production is safeguarded by autogamy making possible reproduction even of single founder individuals'. In predominantly

outbreeding species, he observed, 'self-incompatibility very rarely seems to be complete, so that at least occasionally self-fertilization is nearly always possible' (p. 348–349).

The flexibility shown by plants in their reproductive systems was discussed at some length by delegates of the Asilomar meeting, not only the ability of outcrossers to set occasional seed, as just noted, but also the tendency of habitual selfers towards occasional outcrossing. Allard (1965) noted, for example, that 'although barley is commonly considered to be one of the most highly self-pollinated among the cereal grasses, [...] some outcrossing appears almost every generation' – as is the case for many other selfing species, including the much studied *Arabidopsis thaliana* (Abbott & Gomes 1989; Platt *et al.* 2010). Although this mixed strategy seems unlikely to have evolved in response to selection within populations and is more likely a residue from a history of greater outcrossing prior to a transition to selfing, Allard (1965) argued that it allowed colonizers to enjoy the best of both worlds. On the one hand, predominant selfing conferred not only the advantage of reproductive assurance, but also benefits of high homozygosity, which allows 'the perpetuation of the presently best adapted genotypes for various specific microenvironments'; on the other hand, occasional outcrossing and recombination among the otherwise selfing populations should maintain substantial variation among subpopulations that inhabit different microenvironments (Allard 1965). The idea that selfing allows adaptation to local microsites by avoiding the contaminating effects of massive gene flow from non-adapted populations is perhaps one reason for which selfing lineages have been able to expand their species' range limits to end up with geographically marginal distributions.

Finally, although expressed in very general terms, the model presented by Lewontin (1965) provides a helpful perspective for discussing the evolution of the mating system in colonizing species and conceptually formalizes some of the points made in the preceding sections here. Lewontin (1965, p. 78) made the valuable point that instead of referring to 'colonizing species', it would be more generally interesting to consider 'colonizing episodes' for any species. Ultimately, as Lewontin (1965) observed, all species are colonizers – in the sense that, at some point, they will have colonized the site they currently occupy. But roadside weeds are colonizers in a sense that giant redwood forests are not, because the former represent species 'whose entire life pattern is one of colonization', characterized by relative time spent in a phase of density-independent (or log-phase) growth, whereas the life pattern of the latter is characterized by demographic stability (at a density-dependent carrying capacity). Lewontin's (1965) empha-

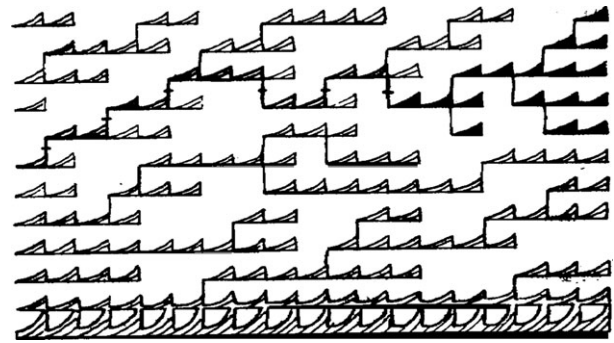


Fig. 6 Sewell Wright's (1940) cartoon depicting the dynamics of a subdivided population with frequent extinctions and recolonizations. Each row of 'saw-teeth' represents the dynamics of the subpopulation (deme) occupying a single habitat patch; the horizontal axis represents the passage of time; and the vertical axis represents population size for each deme. The cartoon emphasizes the fact that, for most of the time, lineages will find themselves in a population during density-independent (log-phase) growth. Wright's sketch was intended to illustrate the effect of population turnover on a species' effective population size. However, it also illustrates the repeated phases during which selection on the mating system and sex allocation will differ from that in populations maintained at carrying capacity. Reproduced with permission.

sis on the relative importance of colonizing episodes brings to mind Sewell Wright's cartoon (Fig. 6) of a subdivided population with frequent population turnover, which we would now recognize as a metapopulation.

In establishing his case for the importance of considering colonizing episodes, Lewontin (1965) drew attention to three aspects of selection that might characterize colonizers. First, selection shaping colonizers should take place predominantly during the exponential colonization phase, that is from the point of colonization to the point where population density begins to slow growth. This is where an ability to self-fertilize might be favoured, where inbreeding depression might be purged, and it is where selection on traits such as sex allocation will tend to differ most from that expected in populations at (perhaps outcrossing) demographic stability. Second, selection during the growth phase may actually be in a direction opposite to that on a population at demographic equilibrium. For example, while an ability to self-fertilize (and a female-biased sex allocation, Fig. 7) might be favoured during colony growth, outcrossing (and an equal sex allocation) might subsequently be favoured. And third, it is the peculiarity of differential local population growth after colonization that makes most likely the possibility of interdeme selection. The role of group selection in the evolution of metapopulations has been controversial, but similarities

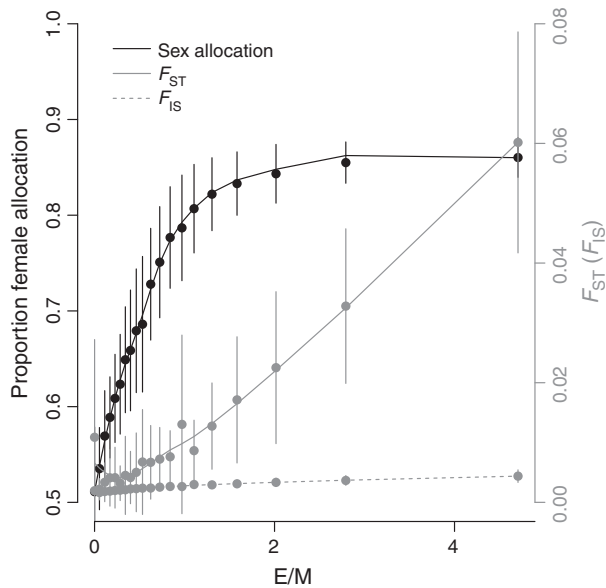


Fig. 7 The effect of ratio of population turnover (the extinction rate, E) to propagule pressure (the migration rate, M) on the selection of female-biased sex allocation in a metapopulation (left axis) and on the corresponding values of F_{ST} and F_{IS} (right axis). Points and bars are the means and standard deviations over 3000 independent simulations of each scenario; lines are the loess regression fits for each relationships. We assumed a metapopulation of 200 demes, each with a carrying capacity of 500 individuals. Migration and colonization followed an island model. We assumed that extinction was followed immediately by recolonization by a single individual, with migration into extant patches that varied among simulations. From Pannell *et al.* (J.R. Pannell and C. Roux, unpublished).

between kin selection in subdivided populations (put into terms of relatedness coefficients) and group selection render this controversy partially semantic (Grafen 1984; West *et al.* 2007).

Lewontin's (1965) analysis, although highlighting the fact that colonizing species will typically not remain in a colonizing phase for long, captures the essence of the implications of demographic fluctuations through a single colonization event, but it misses the importance of gene flow among demes of a metapopulation. We may retain the useful perspective of two phases, but incorporation of the notion of migration splits them somewhat differently. In a metapopulation of demes connected by gene flow, colonization establishes a pattern of tight genetic relationships among individuals that will persist during population growth (and potentially continue into Lewontin's phase of density-dependent stasis). It is thus not demographic stasis that ends the phase, but rather the erosion of patterns of relatedness by migration from other demes. Ultimately, the extent to which population turnover will matter in a genetic sense must

depend of the rate of extinction and colonizations relative to that of migration. This intuition is supported by formal metapopulation models (Slatkin 1977; Pannell & Charlesworth 1999).

Concluding remarks

The overwhelming feeling one gets from the literature on the evolution of reproductive and dispersal traits in colonizing species is one of cryptic complexity. Terms such as colonization, self-fertilization and dispersal roll easily off the tongue (or pen), but each of these terms encompasses a hazardedly broad range of possible meanings. The simplest of them is perhaps colonization, or what we mean by a colonizing species. Lewontin (1965) made a helpful observation that what probably matters most in discussions about the evolution of traits of colonizing species is the extent to which such species actually find themselves in a state of colonization (the colonization bottleneck and the period of log-phase growth) as opposed to a state of demographic status following colonization. This perspective is heuristically useful both for repeated colonization in metapopulations or range expansions as well as for single-event colonization of oceanic islands, as it prompts the question: how much trait evolution might have occurred to erase the mark left by colonization? The answer will depend on the trait involved. The loss of self-incompatibility is unlikely to be reversed, whereas species on islands may evolve both reduced dispersal and increased outcrossing following their arrival.

In this study, I have stressed importance of clarifying what we mean by the mating system in the context of colonizing species, but the same applies to dispersal. The complexity of the mating system is due largely to the fact that plants are often plastic in their sex expression, so that outcrossers and selfers may self or outcross, respectively, from time to time. It is also due to the fact that outcrossing rates are often density-dependent, so that the mating system during the colonization phase may differ from that in established populations. An ability to self-fertilize is likely to be a substantial advantage to many species establishing new populations following long-distance dispersal, as noted by Baker (1955), but this does not imply an association between colonization and a mating system characterized by high selfing rates generally.

Dispersal, too, is a term loaded with complexity that encompasses a distribution of distances moved as well as rates of proportions of individuals that leave their natal patch. Critically, there is no necessarily clear link between dispersal and colonization rates or distances. Explorations of the links between dispersal and the mating system have been valuable, not least in exposing

possible reasons for which organisms have evolved to take on the risk of leaving the safety of their natal patch. However, the sort of dispersal that leads to long-distance colonization may be an incidental outcome of selection for dispersal over much smaller distances, so we may ask how relevant models for the evolution of dispersal rates are for colonization; this relationship deserves attention. Stebbins' (1957) view, in coining Baker's law, was that colonization is essentially 'accidental'. This would suggest that species that have evolved towards a syndrome of low dispersal may, occasionally (but significantly), be subject to the accidents of colonization that establish the patterns Baker (1955) sought to explain. Of course, many plants possess no clear dispersal mechanisms, but they may nevertheless be good colonizers.

Despite the complexities of mating and dispersal, new insights have been gained by models that consider their joint evolution, but, to date, no models address questions concerning dispersal as part of a process of colonization through genetic and demographic bottlenecks. This would seem to be an obvious direction for future theoretical work. Another obvious direction to take would be the incorporation of dynamic inbreeding depression into such models. Ultimately, though, the crucial questions are empirical. Despite substantial effort, we still have a poor understanding of the distribution of reproductive and dispersal traits in colonizing species, and further tests based on reliable data will be valuable. Nevertheless, Baker's (1955) observation of a paucity of self-incompatible species in island situations would seem to have withstood the test of time so far (Igic & Busch 2013).

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