Tansley review

The scope of Baker's law

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Summary

Baker's law refers to the tendency for species that establish on islands by long-distance dispersal to show an increased capacity for self-fertilization because of the advantage of self-compatibility when colonizing new habitat. Despite its intuitive appeal and broad empirical support, it has received substantial criticism over the years since it was proclaimed in the 1950s, not least because

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it seemed to be contradicted by the high frequency of dioecy on islands. Recent theoretical work has again questioned the generality and scope of Baker's law. Here, we attempt to discern where the idea is useful to apply and where it is not. We conclude that several of the perceived problems with Baker's law fall away when a narrower perspective is adopted on how it should be circumscribed. We emphasize that Baker's law should be read in terms of an enrichment of a capacity for uniparental reproduction in colonizing situations, rather than of high selfing rates. We suggest that Baker's law might be tested in four different contexts, which set the breadth of its scope: the colonization of oceanic islands, metapopulation dynamics with recurrent colonization, range expansions with recurrent colonization, and colonization through species invasions.

I. Introduction

The startling diversity in the form of flowers and inflorescences reflects the numerous innovations that plants have evolved to receive and disperse their pollen. Viewed in a phylogenetic context, this diversity often reflects evolutionary transitions that have taken place between different reproductive strategies, such as biotic versus abiotic pollination, resource allocation to combined versus separate sexes (i.e. hermaphroditism versus dioecy), or outcrossing versus inbreeding (Barrett, 2002). Similarly, plants have evolved a wonderful variety of ways to disperse their seeds over distances that range from the very local (with seeds remaining in the same habitat as their parents and siblings) to journeys that cross continents and oceans (with seeds transported to new habitats well beyond the reach of their immediate ancestors) (Nathan, 2006). Because plants typically mate with nearby individuals, evolution of seed dispersal distance (hereafter referred to as dispersal distance) should influence their patterns of mating.

Theoretical modeling confirms this intuitive expectation of an association between reproduction and dispersal. For example, it has been argued that the propensity to disperse may be associated with the propensity to outbreed in animals (Clobert *et al.*, 2001; Perrin & Goudet, 2001). However, recent discussions of such models have emphasized that these predictions appear to differ from an old idea attributable to Herbert Baker (1955) (Fig. 1), who explained an association between the ability to self-fertilize and long-distance dispersal. Baker's idea was simple: because the haphazard nature of long-distance dispersal should tend to remove individuals from their potential mates, colonization success should be more likely for individuals capable of self-fertilizing. The strength of this idea to explain observed patterns in the geographic distribution of selfing ability in both plants and animals attracted the attention of Stebbins (Stebbins, 1957) (Fig. 1), who labeled it 'Baker's law' in an article published 2 yr later. In a passage that emphasizes the significance of mate limitation as the selective force central to Baker's law, Stebbins (1957, p. 344) wrote:

> The correlation just mentioned [between a capacity for uniparental reproduction and establishment following long-distance dispersal] 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.

This statement was the birth of 'Baker's law'. By labeling Baker's idea a 'law', Stebbins probably drew more attention to it than it might otherwise have received, and citations of Baker's paper have accumulated exponentially with the passage of time (Fig. 2). Inevitably, the generality of Baker's law was soon questioned, particularly by the botanist Carlquist (1966), who went so far as to suggest that 'Baker's law must, in part, be abandoned'. Carlquist's reservations were based largely on the observation of a high proportion of dioecious taxa on oceanic islands, particularly Hawaii, from which he deduced that the advantage conferred on long-distance colonizers by an ability to self-fertilize 'must be more imaginary than real'. Baker immediately demurred, replying that Carlquist's interpretation of the law was too rigid and defending his idea 'as a rule' (Baker, 1967). He restated his hypothesis, citing his original text and emphasizing the point that long-distance dispersal should favor a capacity for uniparental reproduction, whether through self-fertilization or through asexual reproduction (Baker, 1967, p. 853):

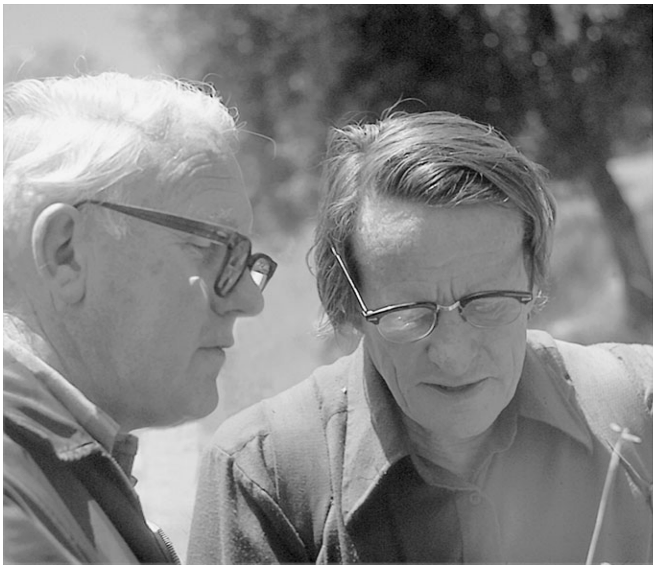

Fig. 1 Photograph of Herbert Baker (left) and Ledyard Stebbins (right) together in the field in Napa County, California, in 1973. Image courtesy of Spencer C. H. Barrett.

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> 'With self-compatible individuals a single propagule is sufficient to start a sexually-reproducing colony (after long-distance dispersal), making its establishment much more likely than if the chance of two self-incompatible yet cross-compatible individuals sufficiently close together spatially and temporally is required. . .. [while] with plants apomixis and purely vegetative reproduction are also available to replace self-incompatible hermaphroditism (and monoecism) or dioecism.' There is nothing so absolute here that the occasional successful establishment of a dioecious stock in Hawaii should cause the abandonment of any part of the principle.

In defending his law 'as a rule', Baker dwelt at length on the question of dioecy in Hawaii. On the one hand, he noted that only species that had arrived in Hawaii as dioecious immigrants 'would be offenders against the spirit of "Baker's Law"' (p. 854), arguing that those that evolved dioecy subsequently would potentially count in its favor if they reflected the evolution of an outcrossing strategy following the loss of self-incompatibility (e.g. through colonization or subsequent change). On the other hand, he attempted to downplay the extent to which the successful colonization of dioecious immigrants should count against the law, citing ameliorating factors such as perenniality (which would allow the accumulation of more than one immigrant of the species over an extended period of time) or the arrival of multi-seeded fruits (which would immediately allow biparental reproduction). The implication of Baker's rebuttal here is that his law should be read as a probabilistic statement, not one that disallows exceptions. To the mind of an evolutionary or comparative biologist, this defense would seem to be entirely reasonable. But fundamental questions about the scope and applicability of Baker's law still persist nearly 50 yr later.

In this Tansley review, we revisit Baker's law with two key aims in mind. First, we re-ask the questions: what is Baker's law, and how is it accommodated within the set of models of the evolution of reproductive and dispersal traits more generally? And second, we ask how generally Baker's and Stebbins' ideas apply to plant reproduction and colonization. Baker's law was originally articulated in terms of an enrichment of self-fertility in species that established on islands following long-distance dispersal. However, the idea has been widely cited in a number of general contexts in which colonization plays a role (Cheptou, 2012), including metapopulations, biological invasions, and range expansion (Table 1; Figs 2–4). We comment on the weight of evidence for and against Baker's law in each of these four biological contexts. Finally, we consider the effects of pollinator limitation as opposed to mate limitation as a driver in shaping reproductive evolution in colonizing species – not least because Baker (1955) also referred to pollinator limitation in his seminal note, but also because its importance has been discussed and debated in the recent literature (Cheptou & Massol, 2009; Busch, 2011; Massol & Cheptou, 2011b; Cheptou, 2012; Pannell, 2015). Throughout, we attempt to provide an overview of both conceptual and theoretical work; while we refer to several important empirical studies that bear on the predictions, a comprehensive literature review is beyond the scope of this paper. We emphasize from the outset that, while Baker's idea has immediate intuitive appeal, reliance on that intuition can result in a lack of clarity. Our aim is therefore to seek greater clarity for the idea by tracing the development of interest in Baker's law since it was named, and by attempting to formulate a perspective that will allow it to be tested unambiguously.

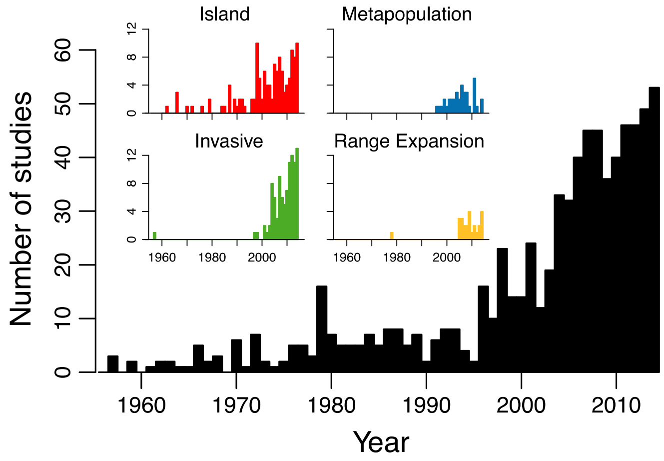

Fig. 2 The number of papers citing Baker's (1955) paper plotted for the years following its publication. Data were gleaned from a simple citation search on WebOfScience. Inset panel: the number of studies per year that include the following keywords in the title or abstract: island, metapop*, invas*, and range expansion.

II. What is Baker's law, and how did it originate?

As cited above, Baker's law was originally articulated in terms of an enrichment of self-fertility in species that established on islands following long-distance dispersal. The focus was on a demographic sieve favoring colonists capable of establishing a population from a single individual after rare colonization events, not on the outcome of selection on dispersal or reproductive traits in situations where colonization was habitual (as opposed to rare). In this sense, 'long-distance dispersal' is meant to describe the situation where the colonizer and the source population are linked by minimal to no gene flow. Over the last two decades, however, ideas surrounding selection on dispersal and reproductive traits have been explicitly linked to Baker's law, notably in the context of the evolution of invasive species, range expansions, and metapopulations (Fig. 2). At least superficially, the links with Baker's law in these ideas and models are fairly evident: they all deal with scenarios in which dispersal and colonization are important.

The concept underlying Baker's law centers on the association between the reproductive system (specifically uniparental versus biparental reproduction) and long-distance dispersal. But both the reproductive system and dispersal are vague concepts. There are important differences, for example, between a *capacity* for uniparental reproduction and the *habitual mating system* of individuals in a population. These distinctions have recently been discussed at length by Pannell (2015), who argued that it is a capacity for self-fertilization that lies at the heart of Baker's law, not the mating system in general. Indeed, Pannell (2015) emphasized reasons to expect the maintenance of high outcrossing rates in species that, by virtue of an ability to set a few seeds by self-fertilization, are able to colonize new

Table 1 The scope of Baker's law (BL) (the contexts in which it might apply), with notes about potential mechanisms favoring a capacity for uniparental reproduction, patterns that might appear to contradict BL, why contradictory patterns may still be consistent with BL, hypotheses for testing BL, and alternative explanations for the patterns observed

Context in which BL may apply	Mechanism whereby a demographic sieve favors a capacity for uniparental reproduction	Patterns that appear to contradict BL	Why contradictory patterns may be consistent with BL	Hypotheses for testing BL	Alternative explanations for enrichment of a capacity for uniparental reproduction
Oceanic island–mainland	Long-distance 'accidental' dispersal results in mate limitation	High frequency of dioecy on oceanic islands	Dioecy is often incomplete, or may have evolved after establishment	Enrichment of a capacity for uniparental reproduction on oceanic islands relative to mainland communities	Selection under pollinator limitation, or under low inbreeding depression
Metapopulation	High population turnover and/or low propagule pressure results in mate limitation during (re)colonization of empty patches	High outcrossing rates after establishment and the maintenance of obligate outcrossers (e.g. males in andromoneecious populations)	Under conditions of high turnover and low migration (e.g. low propagule pressure), hermaphrodites with a capacity for self-fertilization are favored during colonization in a metapopulation. However, outcrossing may be selected and maintained in established populations	Enrichment of a capacity for uniparental production in metapopulations characterized by low propagule pressure and high extinction rates	Selection under pollinator limitation, or under low inbreeding depression
Species invasions	Geographic disjunction of a species from its native range results in mate limitation	The occurrence of invasive obligate outcrossers	Multiple introductions, or the simultaneous introduction of many individuals, relieves mate limitation; persistence may be achieved by vegetative reproduction	Enrichment of a capacity for uniparental reproduction in an introduced flora relative to a native floral or source region	Selection under pollinator limitation, or under low inbreeding depression
Range expansion	Mate limitation at the range edge during range expansion, particularly after long-distance dispersal	A link between outcrossing and high dispersal capacity; the occurrence of outcrossers at the range margins	A link between dispersal traits and outcrossing is predicted to occur only in the absence of mate limitation. High propagule pressure, or the establishment of a population at the range margin, can result in high outcrossing rates	Enrichment of a capacity for uniparental reproduction at species range margins	Low inbreeding depression at the range edge; maintenance of locally adapted gene complexes; selection favors traits correlated with uniparental reproduction (i.e. rapid life cycle)

habitats. To a large extent, this perspective relaxes the apparent tension between predictions that colonization should favor the evolution of selfing and that dispersal should be associated with outcrossing. The observed high frequency of dioecy on oceanic islands (Carlquist, 1966; Sakai *et al.*, 1995; Barrett, 1996) is a telling case in point: dioecy represents an outcrossing strategy in which, nonetheless, occasional bisexual individuals self-fertilize (Delph & Wolf, 2005; Ehlers & Bataillon, 2007). The maintenance of self-fertile hermaphrodites in androdioecious metapopulations (where males persist by outcrossing with hermaphrodites) is another good example (see below).

In his seminal paper, Baker (1955) discussed two somewhat different ideas that have both influenced theorizing about how long-distance dispersal might affect the evolution of reproductive traits. First, as we have emphasized, Baker considered the effects of a demographic sieve caused by mate limitation during colonization. Here, he argued that a capacity for uniparental reproduction would confer an advantage on individuals that happened to disperse to a new location away from potential mates. Second, noting that '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' (Baker, 1955, p. 348), Baker suggested that this pollinator limitation might also favor a capacity for uniparental reproduction. It has been argued (Cheptou & Massol, 2009; Massol & Cheptou, 2011a,b; Cheptou, 2012) that Baker's law can be read to encompass both these ideas, that is, both mate and pollinator limitation. This view can be defended, but it has the major drawback of leading to contradictory predictions (see section VII 'Pollinator limitation, the evolution of dispersal, and the scope of Baker's law'). We therefore find it sensible to adopt the narrower perspective on Baker's law that reflects the spirit of Stebbins' (1957) paper where Baker's law was first named, with its clear focus on mate limitation. This by no means discounts the potential importance of pollinator limitation in shaping associations between dispersal and the reproductive system (see last section below).

Taken together, the above arguments allow us to formulate the essential components of Baker's law: Baker's law refers to the enrichment of a **capacity** for **uniparental reproduction** in species for which colonization brings about **mate limitation** during their **establishment phase** as new populations following **long-distance dispersal**. The important features of the terms in bold would seem to be as follows.

- Capacity. It is strictly speaking a *capacity* for uniparental reproduction that is crucial for successful colonization following long-distance dispersal. Baker's law does not predict a syndrome of self-fertilization in species that conform to his idea. This is clear from his own response to skepticism of Baker's law, and from empirical examples where outcrossing species manage to be good colonizers because they can self-fertilize when needed (Petanidou *et al*., 2012), for example, *Centaurea solstitialis* (Sun & Ritland, 1998).
- Uniparental reproduction. Baker (1955) referred mainly to self-fertilization as a trait that would confer reproductive assurance during colonization, but he also discussed a capacity for asexual reproduction as conforming to his idea. This should of course include vegetative spread and apomictic seed production or parthenogenesis, so long as such apomictic reproduction does not require pollination by a genetically distinct individual. For a test of Baker's law, it is important to recognize that a capacity for asexual reproduction should render advantages of a capacity for selfing less important: vegetative asexual reproduction and clonality will allow obligate outcrossers to establish populations following long-distance dispersal (Baker, 1955, 1967).
- Mate limitation. Baker discussed the fact that long-distance dispersal may disrupt connections between plants and their adequate pollinators, so that seed production by colonizing populations may come to suffer from pollinator limitation. However, it is fairly clear that Stebbins (1957), in coining 'Baker's law', took the essential feature of the idea to encompass mate limitation (see section VII 'Pollinator limitation, the evolution of dispersal and the scope of Baker's law').
- Establishment phase. Although it was not made explicit by Baker (1955, 1967) or Stebbins (1957), implicit in Baker's law is the idea that the demographic sieve that brings about an association between colonization and reproductive traits occurs during colonization and establishment itself. Following establishment, there is nothing in the idea to rule out subsequent evolution, given adequate time and suitable genetic variation, of trait combinations that would appear to contradict the law, for example, the evolution of dioecy on islands. Because the demographic sieve acts on individuals, almost by definition it may be responsible for an evolutionary transition in reproductive traits within a species across its range. However, inasmuch as species differ in terms of the capacity of their individuals for uniparental reproduction, the demographic sieve may be responsible for the geographic sorting of species, too.
- Long-distance dispersal. Baker (1955) referred both to long-distance dispersal over oceans in the colonization of islands and to the colonization one sees in ruderal species that might be viewed as metapopulations. Clearly, the absolute distances over which colonization occurs in these two scenarios differ. The crucial issue concerns the extent to which colonization brings about mate limitation. It is conceivable that mate limitation can occur for some species at scales of just a few meters (Hesse & Pannell, 2011). The distances over which dispersal occurs in scenarios that might be relevant to Baker's law are thus relative; they need to be measured against probabilities of mating across them.

III. Mate limitation during mainland–island colonization

The colonization of oceanic islands by plants represents the canonical context for Baker's law. In articulating and defending his idea, Baker (1955, 1967) drew specifically on examples from island floras, noting the extent to which they were populated by species with a capacity for uniparental reproduction. Conceptually, his idea makes much sense in the context of island colonization: colonists must necessarily arrive by dispersal over great distances, and most likely in small numbers into a situation in which mates are limited. However, there are good reasons to think that, in fact, testing Baker's idea in the context of the colonization of oceanic islands might be particularly difficult.

As noted above, the empirical basis of Baker's law was quickly questioned precisely because of patterns in the distribution of reproductive systems across oceanic island floras. Although we still have a very incomplete picture of the distribution of mating and sexual systems on islands, it is clear that habitually outcrossing systems are found at appreciable frequencies on oceanic islands (Bawa, 1982; Barrett, 1996). Of particular note is the frequency on islands of dioecy, which is a seemingly obligate outcrossing system; rather than being less common on islands, as Baker's law might have it, islands are strikingly enriched for dioecious species (Carlquist, 1966; Baker & Cox, 1984; Webb *et al*., 1999). Interestingly, a recent study comparing the composition of recently colonized and older forest patches found an enrichment of dioecious species, too (Réjou-Méchain & Cheptou, 2015). What should we conclude from these patterns in the context of colonization following long-distance dispersal? Certainly, the enrichment of dioecy on islands can hardly be interpreted just as an exception to Baker's law drawn from a statistical distribution with a tendency towards a selfing ability. But the enrichment of dioecy on both islands and young successional forest patches

(Réjou-Méchain & Cheptou, 2015) would seem to point towards important processes underlying a connection between dispersal and establishment success.

Tests for Baker's law in the context of the colonization of oceanic islands will be difficult for some traits because of the many temporal scales over which colonization may occur, and the potential for subsequent trait evolution. As emphasized in Fig. 3, Baker's law applies specifically to the outcome of a demographic sieve operating during the establishment phase on individuals arriving in new habitat following long-distance dispersal. Many lineages on oceanic islands will have established long ago and may thus have had time to evolve adaptations to their new setting (Sakai *et al.*, 1995). Importantly, selection during the long persistence phase subsequent to establishment (Fig. 4) is less likely to be characterized by mate limitation, so that mechanisms for outcrossing may then be favored. Adaptive evolution subsequent to colonization and establishment may therefore obscure signatures of Baker's law, in some cases generating patterns that apparently contradict its predictions. We therefore articulate specific traits that will allow for robust tests of Baker's law, even if post-colonization evolution should occur.

In the case of the high frequency of dioecy on islands, tests for Baker's law would need to distinguish between lineages that arrived in a dioecious state and those that evolved dioecy subsequently, for example, as an outcrossing mechanism to replace a lost self-incompatibility system. Given the high frequency with which dioecy evolves relative to self-incompatibility, this latter possibility is quite likely and has been well appreciated, for example, in the analysis and interpretation of the high frequency of dioecy in Hawaii (Sakai *et al.*, 1995). Such evolutionary transitions to dioecy in self-compatible (SC) colonists are perhaps analogous to the evolution of dioecy following the loss of self-incompatibility in previously hermaphrodite lineages upon polyploidization (Miller & Venable, 2000; Pannell *et al.*, 2004; Yeung *et al.*, 2005; Blank *et al.*, 2014). Indeed, both the origin of a new island lineage following long-distance dispersal and the origin of a new ploidy level can be viewed as 'accidental' events that break a connection with a parental population and facilitate adaptive evolution within a new (genetic or ecological) context.

We would argue that studies setting out to test Baker's law need to focus on traits for which signatures of a demographic sieve during colony establishment are most likely to be retained to the present day. Webb *et al.* (1999) concluded that 80% of the dioecious species in New Zealand evolved separate sexes elsewhere, but he noted a strong correlation with fleshy fruits and woody habit-factors that might overcome the demographic sieve through increasing propagule pressure and perenniality, respectively (Vamosi *et al.*, 2007). In lineages where other traits might be held constant, the reproductive trait of greatest utility is the trait Baker originally invoked: the SC versus self-incompatible (SI) status of the populations concerned.

Importantly, the evolution of self-compatibility from self-incompatibility is known to have lasting durability through evolutionary time, given its infrequent reversal (Igic *et al.*, 2008; Goldberg *et al.*, 2010, although see Newstrom & Robertson, 2005 for counter-examples). The evolution of other traits following establishment, which can favor any number of adaptations discouraging close inbreeding (e.g. dichogamy or dioecy), is therefore secondary in nature. While efforts to determine the SI or SC status of species require relatively large amounts of crossing and careful analysis (McMullen, 1987; Crawford *et al.*, 2008; Raduski *et al.*, 2012), these data are invaluable. While many have noted that establishment may select for transient self-compatibility or leaky self-incompatibility, which may be later obscured, outright loss of SI during the evolution of self-compatibility is not subject to this complication (Crawford *et al.*, 2008). Given appreciable evolution along both of these avenues, strong empirical tests of Baker's law should scrutinize the distribution of SI and SC breeding systems on mainlands and islands (Baker, 1955).

IV. Mate limitation in metapopulations

Although Baker (1955) drew particular attention to a tendency towards self-compatibility in the floras of oceanic islands, his paper was in fact inspired by observations published in the same year (Longhurst, 1955), of an association between the sexual system displayed by freshwater crustaceans (Notostraca) and colonization in the context of what we would now recognize as a metapopulation. The crustaceans to which Longhurst (1955) referred occupy freshwater ponds that periodically become dry, and the animals are able to survive the drought as eggs, which may be dispersed by wind. Dioecy is the ancestral sexual system of these organisms (Weeks *et al.*, 2006), but hermaphroditism evidently evolved with the acquisition of ovotestes by females, probably in response to selection for reproductive assurance when new ponds were colonized by single individuals. Thus, even though the recurrent local extinctions and recolonizations that characterize metapopulations differ in many respects from single-event colonizations of an oceanic island, the idea inherent in Baker's law encompassed both scenarios from the outset, in that it provided a general explanation for the benefit of uniparental reproduction upon colonization of an unoccupied patch.

A metapopulation perspective of Baker's law was first modeled by Pannell (1997) in the context of the maintenance of males or females with hermaphrodites. With a high rate of population turnover in the model, males and females were selected against by a demographic sieve during colonization, ultimately leading to the evolution of purely hermaphroditic metapopulations. With an intermediate rate of turnover, males could be maintained with self-fertile hermaphrodites in 'androdioecious' metapopulations (Pannell, 1997). Many of the freshwater crustacean metapopulations to which Longhurst (1955) had referred in fact show the maintenance of males and hermaphrodites, and androdioecy appears to be maintained by similar dynamics in several plant species (Pannell, 2002). Importantly, sexual-system theory (Lloyd, 1975; Charlesworth & Charlesworth, 1978; Charlesworth, 1984) shows that males can only be maintained with hermaphrodites that are largely outcrossing (because self-fertilization would remove mating opportunities from the males), and indeed outcrossing rates in androdioecious plant populations are relatively high. Thus, both theory and empirical studies (Pannell *et al.*, 2014) demonstrate that colonization in a metapopulation

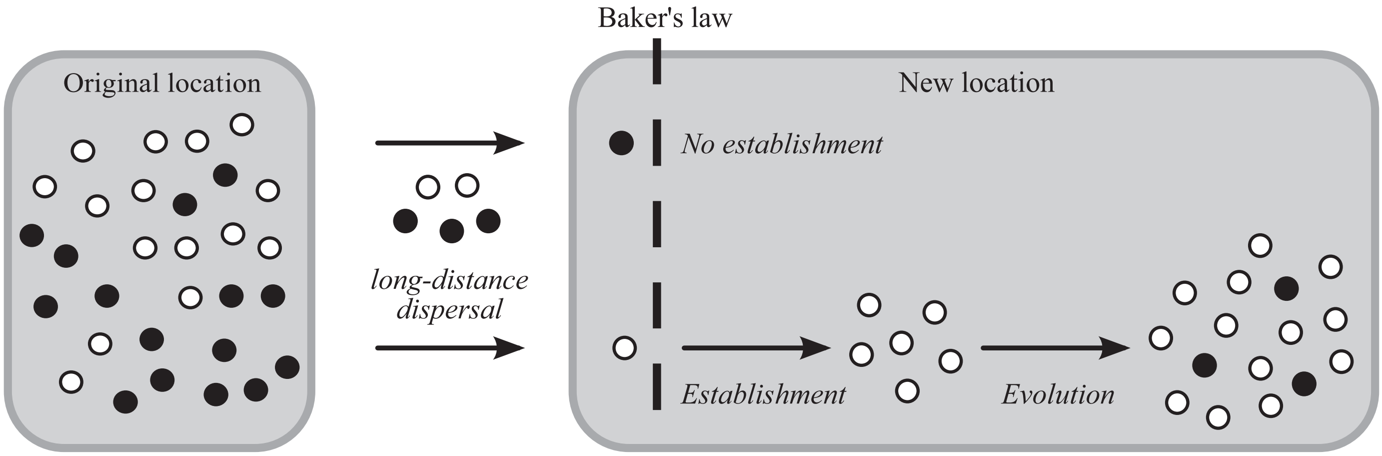

Fig. 3 Baker's law. When a single individual arrives in a location that lacks mates, population establishment requires the capacity for uniparental reproduction. Open circles denote individuals with this capacity, and the dashed line represents the demographic sieve envisioned by Baker. Subsequent evolution in the new habitat may reduce the frequency of uniparental reproduction, diminishing the signal of Baker's law; e.g. closed symbols may denote individuals that evolve an outcrossing mechanism.

may select for a capacity for self-fertilization while simultaneously maintaining a syndrome of outcrossing in established populations. The maintenance of males in androdioecious metapopulations therefore nicely illustrates the fact that Baker's law does not necessitate an association between dispersal and a selfing syndrome.

The impact of metapopulation dynamics on the mating system has been modeled in a number of other papers. Pannell & Barrett (1998) investigated the conditions under which either SC or SI strategies alone could be maintained at equilibrium in a metapopulation. Their model showed that, when population sizes and patch occupancy rates were low, a metapopulation of selfers – but not of outcrossers – could avoid extinction. This condition is equivalent to low propagule pressure, so the conclusion is consistent with Baker's law, and it is supported by empirical observations. For example, in explaining the rapid spread of the invasive SI *Senecio squalidus*, Salisbury (1953) noted that the lag between the species' introduction to the UK in 1799 and its spread after World War II could be explained if it were 'necessary for a certain density of propagule production to be achieved before the explosive spread of this species could occur' (Baker, 1965, p. 164). Baker (1965) also cited high propagule pressure to explain the successful invasion and spread of dioecious *Silene alba* (*S. latifolia*) in North America. Thus, one perspective (it was certainly Baker's view) is that excellent colonizers that are SI obligate outcrossers do not constitute refutations of his principle, because high propagule pressure means the establishing populations are not mate-limited.

Another idea relating mate limitation to mating-system evolution in a metapopulation framework is that the advantage of reproductive assurance provided by selfing may be offset by the cost of inbreeding depression. Dornier *et al.* (2008) considered density dependence in these forces during the evolution of the mating system within a metapopulation. Their model accounts for the possible influence of inbreeding depression on population densities, which, when low, can bring about the selection of selfing for reproductive assurance under mate limitation. The model is heuristically valuable in that it connects demographic processes to density-dependent selfing and inbreeding depression (Dornier *et al.*, 2008). How inbreeding depression might affect the evolution of the mating system in a metapopulation in general, however, is a question that deserves further study. The issue is complicated because inbreeding depression within individual populations will be affected by their recent colonization history, so that, for example, populations that are outcrossing might nevertheless have no genetic variation at viability loci and therefore no inbreeding depression (Pujol *et al.*, 2009).

Several case studies reflect the principles of Baker's law in a metapopulation. *Sagittaria latifolia* (Alismataceae) is a clonal, perennial aquatic herb with variation in gender expression. Some populations are composed of self-compatible monoecious hermaphrodites, which inhabit more ephemeral habitats in streams and ditches and appear to exhibit metapopulation dynamics (Sarkissian *et al.*, 2001; Dorken & Barrett, 2003; Yakimowski & Barrett, 2014). Other populations are dioecious; these are larger, are found in and adapted to more permanent wetlands, and do not function as metapopulations (Sarkissian *et al.*, 2001; Dorken & Barrett, 2003). Thus, self-compatibility is associated with frequent colonization. Another example is provided by *Eichhornia paniculata*, an insect-pollinated aquatic annual colonizer. *Eichhornia paniculata* is tristylous and outcrossing through much of its range, but in parts of its distribution selfing variants have evolved (Glover & Barrett, 1986; Barrett *et al.*, 1989); these areas are characterized by smaller population sizes and higher rates of population turnover (Husband & Barrett, 1998). It is thus possible that the shift to self-fertilization in *E. paniculata* was brought about by selection under strong mate limitation. As a final example, the plant *Mercurialis annua* is a dioecious wind-pollinated herb that has evolved towards self-fertile monoecy in regions of its range where populations are subject to increased rates of extinctions and, presumably, colonizations (reviewed in Pannell *et al.*, 2008).

Although monoecious individuals have high selfing rates in the absence of mates, established populations are sufficiently highly outcrossing to allow the invasion of males (Eppley & Pannell, 2007; Dorken & Pannell, 2008). In *M. annua*, it is thus the capacity for selfing in the absence of mates that conforms to Baker's law rather than its habitual mating system, which is largely outcrossing.

V. Mate limitation during species introductions and invasions

Within the context of introduced species, there are two phases of invasion where Baker's law might apply. First, Baker's law applies to the establishment of a population in an introduced range, analogous to establishing a population originating from the mainland in an island habitat. Later, Baker's law may apply as a species expands its initial range into unoccupied habitats. The key difference from the mainland–island case is the anthropogenic rather than natural dispersal of the species. This has an important implication for the applicability of Baker's law to the study of introduced species. Baker's law arises through the effects of a sieve acting on single colonizers, but invasive and weedy species are often repeatedly introduced or introduced as groups of colonists. With multiple colonists introduced within the lifespan of the colonizer, including dormant seeds, uniparental reproduction is not necessary.

Despite Baker's early acknowledgment that his ideas would apply to introduced weedy species (Baker, 1955), there are few explicit tests of Baker's law in the invasion literature. In a recent review of pollen limitation studies, Burns *et al.* (2011) report higher rates of uniparental reproduction in introduced compared with native species, but no differences between invasive and noninvasive introduced species. These results are consistent with processes underlying Baker's law at the colonization stage but not in the range expansion phase (see next section). Similarly, in South African Iridaceae that were introduced globally for horticulture, species that became naturalized had increased uniparental reproduction compared with those that failed to naturalize (Van Kleunen *et al.*, 2008). In addition, a high representation of uniparental reproduction has been reported in South African invasive species (Rambuda & Johnson, 2004), Asteraceae species invasive to China (Hao *et al.*, 2011) and Canadian weeds (Mulligan & Findlay, 1970). Finally, some within-species comparisons have shown higher rates of self-compatibility in the introduced range compared with the native range (Petanidou *et al.*, 2012; Ward *et al.*, 2012).

VI. Mate limitation during range expansions and evolution at range margins

Populations at the edge of species' ranges may be more likely to be self-fertilizing, or to have lost mechanisms that prevent selfing, than populations in the core of the distribution. Similarly, in species whose geographic distributions span wide latitudinal ranges, it is especially high-latitude populations that tend to be enriched for asexual reproduction, a pattern that has been labeled 'geographic parthenogenesis' (Vandel, 1928; Bell, 1982; Bierzychudek, 1985). A number of hypotheses have been advanced to account for these patterns (Peck *et al.*, 1998). One of these invokes processes underlying Baker's law. Specifically, because range-edge habitats will often have been colonized during a range expansion, a capacity for unisexual reproduction will have been selected at the colonization front, particularly where colonization dynamics at the leading edge correspond to 'jump dispersal' (when range-edge populations repeatedly become occupied by relatively long-distance dispersal, leading to mate limitation) as opposed to dispersal by diffusion (where individuals occupying range-edge habitat may continue to mate with individuals closer to the core).

It should be noted that a number of processes unrelated to Baker's law can also result in the enrichment of selfing within a species' geographic range margins, so that inferring evidence for Baker's law can be difficult. For example, declines in inbreeding depression that accompany the potential decline in population heterozygosity at the range edge provide one such potential mechanism (Pujol *et al.*, 2009). Similar patterns may also be found after dispersal to islands or in a metapopulation context. If declines in inbreeding depression are sufficiently strong, populations immediately become susceptible to the invasion of selfing variants, even in the absence of mate limitation, because the primary cost of selfing is diminished (Pannell, 2015). Ecological marginality provides another explanation for an enrichment of uniparental reproduction in geographically marginal populations. If range-edge (particularly high-latitude) populations are less likely to be affected by antagonistic biotic interactions such as those with pests and pathogens, one possible benefit of recombination and sex through outcrossing will be diminished (Bell, 1982), which may therefore tip the balance in favor of inbreeding. Alternatively, if range-edge populations occupy environmental extremes with respect to latitude, elevation, or water availability, selection may favor a rapid life cycle that might indirectly lead to autonomous self-fertilization independent of selection for reproductive assurance (Arroyo, 1973; Aarssen, 2000; Mazer *et al.*, 2004; Dudley *et al.*, 2007; Elle *et al.*, 2010). Likewise, local adaptation in environmentally extreme habitats may favor selfing as a means of preventing maladaptive gene flow from the source population (Antonovics, 1968) and help to fix genotypes that are tolerant of the conditions in the novel habitat (Mather, 1943; Mayr, 1963). Support for this idea is provided by the many studies showing reduced gene flow and the evolution of selfing on mine tailings or other sites with heavy metal-laced soils as a result of strong selection for high selfing (reviewed in Antonovics, 2006; Widmer *et al.*, 2009). Recently, Levin (2010) suggested that phenotypically plastic selfing can provide a rapid response to preserve tolerant genotypes in novel environments, and Peterson & Kay (2015) have shown that plasticity in the mating system can contribute to the persistence of colonizing species.

Distinguishing between a scenario of selection under mate limitation, consistent with Baker's law, and other hypotheses for mating-system shifts in geographically marginal populations will be difficult when the shift has been from outcrossing to habitual self-fertilization. By contrast, a simple increase in a species' capacity for self-fertilization in its geographically marginal populations, with outcrossing largely maintained, would be consistent only with Baker's law, as all the other explanations cited above predict a transition towards habitual self-fertilization or asexuality. In the context of range expansion, then, we see again the utility of focusing on a species' capacity for self-fertilization over its habitual selfing rate for formulating tests of Baker's law.

VII. Pollinator limitation, the evolution of dispersal, and the scope of Baker's law

A somewhat different perspective on traits relevant to Baker's law has emerged in the literature over the last few years based on predictions of models that deal with stochastic variation among patches in pollinator availability (Cheptou & Massol, 2009; Massol & Cheptou, 2011a). Baker (1955) did recognize pollinator limitation as a hurdle that plants face after long-distance dispersal, but its implications differ somewhat from those of mate limitation. As Baker pointed out, mate limitation can be overcome by asexual reproduction or self-compatibility (whether in the absence or presence of suitable pollinators, via autonomous or geitonogamous selfing, respectively). However, whereas a paucity of suitable animal pollinators can similarly be overcome by uniparental reproduction, it can also be overcome when mates are present by floral adaptations that allow pollination by multiple pollinators or through pollen transfer by wind.

While it is possible to defend a concept of Baker's law that encompasses both mate limitation and pollinator limitation (Micheneau *et al.*, 2008; Massol & Cheptou, 2011b), we feel that this breadth allows so broad a range of predictions that the concept becomes vague – essentially because 'anything goes'. A narrower circumscription of Baker's law focussing specifically on the consequences of mate limitation would seem to be more workable and to stick more closely to the spirit of Baker's (1955) paper. Indeed, it is fairly clear that Stebbins (1957) was thinking about the consequences of mate limitation when he named Baker's law, not pollinator limitation.

The models of Cheptou and Massol (Cheptou & Massol, 2009; Massol & Cheptou, 2011a) address the interesting question of how the mating system (the selfing versus outcrossing rate) co-evolves with the dispersal rate (the proportion of individuals leaving a natal patch). Their models predict an association between the evolution of a population towards a syndrome of self-fertilization and reduced dispersal when pollinator services frequently fail; when pollinators are more frequently abundant, populations evolve towards a syndrome of outcrossing and increased dispersal. Such predictions are consistent with a broad class of theory on the evolution of dispersal: dispersal should evolve when there is selection for inbreeding avoidance and among-patch pollination heterogeneity, which also selects for outcrossing (Clobert *et al.*, 2001; Perrin & Goudet, 2001; Auld & de Casas, 2013). Their predictions are also largely congruent with empirical findings (Moeller, 2006). Although Cheptou and Massol concluded that their predictions were at odds with Baker's law, this conclusion becomes unnecessary when the Baker's law is interpreted in terms solely of mate limitation.

As interesting as the joint evolution of dispersal and the mating system is, Baker's law is principally about the effects of a sieve on the mating system in the context of accidental dispersal rather than about how dispersal might evolve under a scenario of repeated colonization. It is likely that dispersal traits will have been under selection in the ancestral populations from which colonists originate, but it is more likely that such selection will have acted principally on short-distance events that lead to the avoidance of mating with relatives, for example. Long-distance dispersal might thus be viewed as an incidental process, representing the potentially long tail of a dispersal kernel that has been shaped by selection at smaller scales (Ronce *et al.*, 2001; Nathan, 2006). One might imagine sampling for eventual long-distance colonization from a pool of species or individuals in a source community or population that represent all four of the states represented in Fig. 4 (i.e. dispersive and nondispersive selfers and outcrossers). In this case, the logical expectation, and one consistent with Baker's idea, would be enrichment of dispersive or nondispersive selfers among the successfully established populations.

We argue that Baker's law is ultimately a stronger scientific notion if it leads to a single and coherent set of predictions. Including both mate limitation as a result of demographic bottlenecks associated with colonization *and* the evolution of both the mating system and dispersal under pollinator limitation in the absence of colonization bottlenecks naturally leads to too broad a range of predictions to be useful. The discussions and debates that were prompted by Cheptou and Massol's papers (Cheptou & Massol, 2009; Massol & Cheptou, 2011a) were instrumental in precipitating a reassessment of the scope of Baker's law and have been useful in that context, as well as in helping to form an understanding of plant–pollinator interactions in fluctuating environments. However, that reassessment seems now to necessitate a narrowing of the scope of Baker's law.

VIII. Conclusions and future perspectives

Despite Stebbins' (1957) early enthusiasm for the law that he named after his friend and colleague, long-distance colonization acts as a demographic sieve favoring species with a capacity for uniparental reproduction – has met repeated skepticism. Some of this skepticism has been based on the large number of apparent empirical contradictions to the law, with many successful colonists displaying obligate outcrossing. Reservations about the law have also been expressed on the basis of theoretical analysis that links dispersal with outcrossing rather than selfing syndromes. From an empirical viewpoint, numerous examples appear to provide support for Baker's idea, and many of the countervailing examples will probably fall away with a focus on the capacity for uniparental reproduction. However, there are inevitably exceptions to the pattern predicted by Baker, even with this narrower focus, and more will no doubt accumulate with further study. Given these exceptions, it might be argued that 'Baker's law' is a misnomer, and that Baker's idea should be relabeled a 'rule' or a 'contention'. We

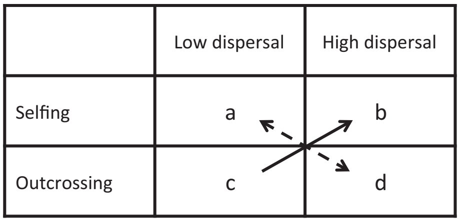

Fig. 4 A two-dimensional conception of the relationship between the mating system and dispersal. Under certain assumptions, modeling of the joint evolution of selfing and dispersal predicts the occupation of quadrants a and d, with high selfing rates associated with low dispersal rates (a) and highly dispersing lineages tending towards outcrossing (d). These models predict shifts from one extreme to the other in response to changed environmental conditions, for example, pollinator availability (here represented by the dashed arrows linking a and d). By contrast, Baker's law might rather imply an association between a capacity for dispersal and for self-fertilization, as indicated by the arrow linking quadrants c and b – although note that dispersal under Baker's law is best seen as accidental rather than necessarily selected.

have some sympathy for such a position, but we have elected to retain the usage 'Baker's law' because it is so well established in the literature.

From a conceptual or theoretical perspective, we have attempted to clarify what Baker's law necessitates, and what might better be regarded as incidental. Importantly, we have argued that Baker's idea, whether regarded as a law, a rule, or a contention, can only be a useful element in evolutionary biology if it makes coherent predictions that could, in principle, be unambiguously falsified. For this and other important reasons, it makes sense to regard Baker's law within the context of mate limitation rather than pollinator limitation. While pollinator availability will no doubt influence the evolution of reproductive traits expressed by colonizing species, it is mate limitation brought about by colonization bottlenecks that should select for a capacity for uniparental reproduction, not pollinator limitation.

We have seen that certain interpretations of the patterns described by Baker's law can be brought about not only by the demographic sieve of mate limitation during colonization, but also by several other processes. This is an important shortcoming of the hypothesis, as a number of processes could be responsible for an enrichment of high rates of self-fertilization in colonizing species. By contrast, we argue that an enrichment of the *capacity* for self-fertilization in colonizing species on its own is more narrowly predicted by processes inherent to Baker's law. Indeed, the least ambiguous evidence consistent with Baker's law would be an increased capacity for selfing (or uniparental reproduction in general) in otherwise habitually outcrossing species. The loss of self-incompatibility in species that maintain other outcrossing mechanisms (such as temporal or spatial separation of male and female functions) or evolve new outcrossing devices (such as dioecy) is a prime example of such a scenario.

Finally, we have attempted to accommodate both the enrichment of a capacity for uniparental reproduction on islands and the subsequent evolution of outcrossing mechanisms within a single conceptual framework that recognizes two distinct phases in the colonization of new habitat: the establishment of new lineages immediately following long-distance dispersal, and their subsequent evolution during their persistence in the novel abiotic or biotic context of their new habitat. Baker's law is really an explanation of trait variation resulting from the sorting of pre-existing variants by a demographic sieve during an establishment phase that will usually be too short for meaningful adaptive evolution (Fig. 3). By contrast, many of the trait combinations that might appear to contradict Baker's law will often be the result of adaptive evolution during the long-term persistence of populations after their successful establishment. It will probably often be difficult to draw clear empirical distinctions between these two phases or classes of trait variant, but focusing on slowly evolving or effectively irreversible evolutionary steps, such as the loss of self-incompatibility, will make such distinctions easier. Either way, the distinction is important to make and should be borne in mind when evaluating evidence for Baker's law.

Although we argue for a narrowing of the perspective on Baker's law, we also propose that the scope of Baker's law encompasses at least four broadly important biological scenarios within which evidence for or against it might be sought (Table 1). These are: colonization of islands by single-event long-distance dispersal; repeated colonization in metapopulations as a balance to local extinctions; colonization in the context of species invasions; and repeated colonization in range expansions. A full review of evidence within these four contexts is beyond the scope of this article, but much appropriate data have already been published that bear on the issues we have discussed, and it would be timely to draw these data together in a synthetic way. It seems that further empirical and theoretical work would be most revealing if it focused on assessing the capacity for uniparental reproduction of colonizing species rather than on estimating their habitual mating system.

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References

Aarssen LW. 2000. Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing. *Oikos* **89**: 606–612.

Antonovics J. 1968. Evolution in closely adjacent plant populations: V Evolution of self-fertility. *Heredity* **23**: 219–238.

Antonovics J. 2006. Evolution in closely adjacent plant populations: X long-term persistence of prereproductive isolation at a mine boundary. *Heredity* **97**: 33–37.

Arroyo MTK. 1973. Chiasma frequency evidence on the evolution of autogamy in *Limnanthes floccosa* (Limnanthaceae). *Evolution* **27**: 679.

Auld JR, de Casas RR. 2013. The correlated evolution of dispersal and mating-system traits. *Evolutionary Biology* **40**: 185–193.

Baker HG. 1955. Self-compatibility and establishment after "long-distance" dispersal. *Evolution* **9**: 347–348.

Baker HG. 1965. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL, eds. *The genetics of colonising species*. London, UK: Academic Press, 141–172.

Baker HG. 1967. Support for Baker's Law – as a rule. *Evolution* **21**: 853–856.

Baker HG, Cox PA. 1984. Further thoughts on dioecism and islands. *Annals of the Missouri Botanical Garden* **71**: 244–253.

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

Barrett SCH. 2002. The evolution of plant sexual diversity. *Nature Reviews Genetics* **3**: 274–284.

Barrett SCH, Morgan MT, Husband BC. 1989. The dissolution of a complex genetic polymorphism: the evolution of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae). *Evolution* **43**: 1398–1416.

Bawa KS. 1982. Outcrossing and the incidence of dioecism in island floras. *American Naturalist* **119**: 866–871.

Bell G. 1982. *The masterpiece of nature: the evolution and genetics of sexuality*. Berkeley, CA, USA: University of California Press.

Bierzychudek P. 1985. Patterns in plant parthenogenesis. *Experientia* **41**: 1255–1264.

Blank CM, Levin RA, Miller JS. 2014. Intraspecific variation in gender strategies in *Lycium* (Solanaceae): associations with ploidy and changes in floral form following the evolution of gender dimorphism. *American Journal of Botany* **101**: 2160–2168.

Burns JH, Ashman TL, Steets JA, Harmon-Threatt A, Knight TM. 2011. A phylogenetically controlled analysis of the roles of reproductive traits in plant invasions. *Oecologia* **166**: 1009–1017.

Busch JW. 2011. Demography, pollination and Baker's law. *Evolution* **65**: 1511–1513.

Carlquist S. 1966. The biota of long distance dispersal. *Evolution* **20**: 30–48.

Charlesworth D. 1984. Androdioecy and the evolution of dioecy. *Biological Journal of the Linnean Society* **23**: 333–348.

Charlesworth D, Charlesworth B. 1978. A model for the evolution of dioecy and gynodioecy. *American Naturalist* **112**: 975–997.

Cheptou PO. 2012. Clarifying Baker's Law. *Annals of Botany* **109**: 633–641.

Cheptou PO, Massol F. 2009. Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *American Naturalist* **174**: 46–55.

Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. 2001. *Dispersal*. Oxford, UK: Oxford University Press.

Crawford DJ, Archibald JK, Stoermer D, Mort ME, Kelly JK, Santos-Guerra A. 2008. A test of Baker's law: breeding systems and the radiation of *Tolpis* (Asteraceae) in the Canary Islands. *International Journal of Plant Sciences* **169**: 782–791.

Delph LF, Wolf DE. 2005. Evolutionary consequences of gender plasticity in genetically dimorphic breeding systems. *New Phytologist* **166**: 119–128.

Dorken ME, Barrett SCH. 2003. Life-history differentiation and the maintenance of monoecy and dioecy in *Sagittaria latifolia* (Alismataceae). *Evolution* **57**: 1973–1988.

Dorken ME, Pannell JR. 2008. Density-dependent regulation of the sex ratio in an annual plant. *American Naturalist* **171**: 824–830.

Dornier A, Munoz F, Cheptou P-O. 2008. Allee effect and self-fertilizationn in hermaphrodites: reproductive assurance in a structured metapopulation. *Evolution* **62**: 2558–2569.

Dudley LS, Mazer SJ, Galusky P. 2007. The joint evolution of mating system, floral traits and life history in *Clarkia* (Onagraceae): genetic constraints vs. independent evolution. *Journal of Evolutionary Biology* **20**: 2200–2218.

Ehlers BK, Bataillon T. 2007. 'Inconstant males' and the maintenance of labile sex expression in subdioecious plants. *New Phytologist* **174**: 194–211.

Elle E, Gillespie S, Guindre-Parker S, Parachnowitsch AL. 2010. Variation in the timing of autonomous selfing among populations that differ in flower size, time to reproductive maturity, and climate. *American Journal of Botany* **97**: 1894–1902.

Eppley SM, Pannell JR. 2007. Density-dependent self-fertilization and male versus hermaphrodite siring success in an androdioecious plant. *Evolution* **61**: 2349–2359.

Glover DE, Barrett SCH. 1986. Variation in the mating system of *Eichhornia paniculata* (Spreng.) Solms. (Pontederiaceae). *Evolution* **40**: 1122–1131.

Goldberg EE, Kohn JR, Lande R, Robertson KA, Smith SA, Igic B. 2010. Species selection maintains self-incompatibility. *Science* **330**: 493–495.

Hao JH, Qiang S, Chrobock T, van Kleunen M, Liu QQ. 2011. A test of baker's law: breeding systems of invasive species of Asteraceae in China. *Biological Invasions* **13**: 571–580.

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

Husband BC, Barrett SCH. 1998. Spatial and temporal variation in population size of *Eichhornia paniculata* in ephemeral habitats: implications for metapopulation dynamics. *Journal of Ecology* **86**: 1021–1031.

Igic B, Lande R, Kohn JR. 2008. Loss of self-incompatibility and its evolutionary consequences. *International Journal of Plant Sciences* **169**: 93–104.

Levin DA. 2010. Environment-enhanced self-fertilization: implications for niche shifts in adjacent populations. *Journal of Ecology* **98**: 1276–1283.

Lloyd DG. 1975. The maintenance of gynodioecy and androdioecy in angiosperms. *Genetica* **45**: 325–339.

Longhurst AR. 1955. Evolution in the Notostraca. *Evolution* **9**: 84–86.

Massol F, Cheptou P-O. 2011a. Evolutionary syndromes linking dispersal and mating system: the effect of autocorrelation in pollination conditions. *Evolution* **65**: 591–598.

Massol F, Cheptou P-O. 2011b. When should we expect the evolutionary association of self-fertilization and dispersal? *Evolution* **65**: 1217–1220.

Mather K. 1943. Polygenic inheritance and natural selection. *Biological Reviews* **18**: 32–64.

Mayr E. 1963. *Animal species and evolution*. Cambridge, MA, USA: The Belknap Press of Harvard University Press.

Mazer SJ, Paz H, Bell MD. 2004. Life history, floral development, and mating system in *Clarkia xantiana* (Onagraceae): do floral and whole-plant rates of development evolve independently? *American Journal of Botany* **91**: 2041–2050.

McMullen CK. 1987. Breeding systems of selected Galapagos-island angiosperms. *American Journal of Botany* **74**: 1694–1705.

Micheneau C, Fournel J, Gauvin-Bialecki A, Pailler T. 2008. Autopollination in a long-spurred endemic orchid (*Jumellea stenophylla*) on Reunion Island (Mascarene Archipelago, Indian Ocean). *Plant Systematics and Evolution* **272**: 11–22.

Miller JS, Venable DL. 2000. Polyploidy and the evolution of gender dimorphism in plants. *Science* **289**: 2335–2338.

Moeller DA. 2006. Geographic structure of pollinator communities, reproductive assurance, and the evolution of self-pollination. *Ecology* **87**: 1510–1522.

Mulligan GA, Findlay JN. 1970. Reproductive systems and colonization in Canadian weeds. *Canadian Journal of Botany* **48**: 859–860.

Nathan R. 2006. Long-distance dispersal of plants. *Science* **313**: 786–788.

Newstrom L, Robertson A. 2005. Progress in understanding pollination systems in New Zealand. *New Zealand Journal of Botany* **43**: 1–59.

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

Pannell JR. 2002. The evolution and maintenance of androdioecy. *Annual Review of Ecology and Systematics* **33**: 397–425.

Pannell JR. 2015. Evolution of the mating system in colonizing plants. *Molecular Ecology* **24**: 2018–2037.

Pannell JR, Barrett SCH. 1998. Baker's Law revisited: reproductive assurance in a metapopulation. *Evolution* **52**: 657–668.

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

Pannell JR, Eppley SM, Dorken ME, Berjano R. 2014. Regional variation in sex ratios and sex allocation in androdioecious *Mercurialis annua*. *Journal of Evolutionary Biology* **27**: 1467–1477.

Pannell JR, Obbard DJ, Buggs RJA. 2004. Polyploidy and the sexual system: what can we learn from *Mercurialis annua*? *Biological Journal of the Linnean Society* **82**: 547–560.

Peck JR, Yearsley JM, Waxman D. 1998. Explaining the geographic distributions of sexual and asexual populations. *Nature* **391**: 889–892.

Perrin N, Goudet J. 2001. Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. *Dispersal.* Oxford, UK: Oxford University Press, 123–142.

Petanidou T, Godfree RC, Song DS, Kantsa A, Dupont YL, Waser NM. 2012. Self-compatibility and plant invasiveness: comparing species in native and invasive ranges. *Perspectives in Plant Ecology Evolution and Systematics* **14**: 3–12.

Peterson ML, Kay KM. 2015. Mating system plasticity promotes persistence and adaptation of colonizing populations of hermaphroditic angiosperms. *American Naturalist* **185**: 28–43.

Pujol B, Zhou SR, Sahchez-Vilas J, Pannell JR. 2009. Reduced inbreeding depression after species range expansion. *Proceeding of the National Academy of Sciences, USA* **106**: 15379–15383.

Raduski AR, Haney EB, Igic B. 2012. The expression of self-incompatibility in angiosperms is bimodal. *Evolution* **66**: 1275–1283.

Rambuda TD, Johnson SD. 2004. Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? *Diversity and Distributions* **10**: 409–416.

Réjou-Méchain M, Cheptou P-O. 2015. High incidence of dioecy in young successional tropical forests. *Journal of Ecology* **103**: 725–732.

Ronce O, Olivieri I, Cobert J, Danchin E. 2001. Perspectives on the study of dispersal evolution. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. *Dispersal.* Oxford, UK: Oxford University Press, 123–142.

Sakai AK, Wagner WL, Ferguson DM, Herbst DR. 1995. Origins of dioecy in the Hawaiian flora. *Ecology* **76**: 2517–2529.

Salisbury EJ. 1953. A changing flora as shown in the study of weeds of arable lands and waste places. In: Lousley JE, ed. *The changing flora of Britain.* Oxford, UK: Botanical Society of the British Isles, 130–139.

Sarkissian TS, Barrett SCH, Harder LD. 2001. Gender variation in *Sagittaria latifolia* (Alismataceae): is size all that matters? *Ecology* **82**: 360–373.

Stebbins GL. 1957. Self-fertilization and population variability in the higher plants. *American Naturalist* **91**: 337–354.

Sun M, Ritland K. 1998. Mating system of yellow starthistle (*Centaurea solstitialis*), a successful colonizer in North America. *Heredity* **80**: 225–232.

Vamosi JC, Zhang Y, Wilson WG. 2007. Animal dispersal dynamics promoting dioecy over hermaphroditism. *American Naturalist* **170**: 485–491.

Van Kleunen M, Manning JC, Pasqualetto V, Johnson SD. 2008. Phylogenetically independent associations between autonomous self-fertilization and plant invasiveness. *American Naturalist* **171**: 195–201.

Vandel A. 1928. La parthéngénèse géographique: contribution l'étude biologique et cytologique de la parthénogénèse naturelle. *Bulletin Biologique Belgique* **62**: 164–281.

Ward M, Johnson SD, Zalucki MP. 2012. Modes of reproduction in three invasive milkweeds are consistent with Baker's Rule. *Biological Invasions* **14**: 1237–1250.

Webb CJ, Lloyd DG, Delph LF. 1999. Gender dimorphism in indigenous New Zealand seed plants. *New Zealand Journal of Botany* **37**: 119–130.

Weeks SC, Sanderson TF, Reed SK, Zofkova M, Knott B, Balaraman U, Pereira G, Senyo DM, Hoeh WR. 2006. Ancient androdioecy in the freshwater crustacean *Eulimnadia. Proceedings of the Royal Society B: Biological Sciences* **273**: 725–734.

Widmer A, Lexer C, Cozzolino S. 2009. Evolution of reproductive isolation in plants. *Heredity* **102**: 31–38.

Yakimowski SB, Barrett SCH. 2014. Variation and evolution of sex ratios at the northern range limit of a sexually polymorphic plant. *Journal of Evolutionary Biology* **27**: 1454–1466.

Yeung K, Miller JS, Savage AE, Husband BC, Igic B, Kohn JR. 2005. Association of ploidy and sexual system in *Lycium californicum* (Solanaceae). *Evolution* **59**: 2048–2055.