

Metapopulation dynamics and mating-system evolution in plants

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ABSTRACT

Patterns of plant mating are strongly influenced by genetically determined factors such as floral design, display and phenology, self-incompatibility mechanisms, and levels of inbreeding depression. They also depend on the ecological context in which mating takes place. While the importance of pollination biology for mating-system evolution is increasingly being recognised, the demographic context of mating has received relatively little attention to date. Here, we outline metapopulation models which assess the effect of recurrent local extinction and re-colonization on the evolution and maintenance of mating-system alleles. Such metapopulation processes can alter selective pressures on patterns of sex allocation, modes of self-fertilization and the maintenance of outcrossing. Our results suggest that for species with ephemeral populations, broadscale studies of plants at the landscape level are needed. We review studies of several taxa (*Eichhornia paniculata*, *Lythrum salicaria* and *Mercurialis annua*) which display striking patterns of geographical variation in their sexual systems. Such intraspecific studies lead to insights that are not evident from the analysis of local populations alone. Moreover, we suggest that research at the metapopulation level may form a bridge between microevolutionary investigations within local populations and historical reconstruction of the evolution of reproductive traits using phylogenetic methods.

5.1 Introduction

Flowering plants display unrivalled structural diversity in their reproductive traits, which function to promote reproductive success through their influence on pollination and mating. A particularly striking feature of flowering plants is that patterns of mating vary considerably, often among closely related species. The mode of transmission of genes from one generation to the next can range from predominant self-fertilisation, through mixed mating involving different amounts of self- and cross-fertilisation, to complete outcrossing, sometimes among populations of a single species (Barrett and Eckert, 1990). Variation in mating systems has a direct influence on population genetic structure, quantitative and molecular variation and rates of evolution (Brown, 1979; Hamrick and Godt, 1990; Charlesworth, 1992; Charlesworth and Charlesworth, 1995; Liu *et al.*, 1998). A major task of evolutionary biology is to determine which selective mechanisms are responsible for

specific changes in plant mating systems. The way plants mate is also relevant to plant systematics. This is because mating systems have a strong influence on patterns of group variability, and evolutionary changes in reproductive mode are often closely associated with the development of reproductive isolation and speciation (Stebbins, 1957; Baker, 1959). Indeed, systematists were among the first biologists to recognise that variation in 'breeding systems' have both important micro- and macroevolutionary consequences (Davis and Heywood, 1963; Ornduff, 1969; Briggs and Walters, 1984).

Current research on the evolution of plant mating systems involves three complementary approaches. Ecological and genetic studies of local populations focus on the selective mechanisms responsible for the evolution and maintenance of particular patterns of mating. Such microevolutionary studies employ experimental manipulations and the use of genetic markers as tools for investigating the proximate ecological factors that influence mating success and the fitness consequences of different mating patterns (reviewed by Barrett and Harder, 1996). Much of this empirical work has been motivated by the development of a rich theoretical literature on mating-system evolution in plants (reviewed by Morgan and Schoen, 1997a). A variety of population genetic and sex allocation models have been developed to explore the conditions that favour different levels of selfing and outcrossing, as well as the evolution of sexual systems (e.g. Charlesworth and Charlesworth, 1981; Charnov, 1982; Lande and Schemske, 1985; Holsinger, 1991; Uyenoyama *et al.*, 1993). These two approaches have dominated the field of mating-system biology for the past two decades, and both focus on the local population as the most relevant evolutionary unit. More recently, a broader perspective has begun to emerge as the comparative biology of reproductive traits is investigated through advances in phylogeny reconstruction and molecular systematics (Donoghue, 1989; Barrett *et al.*, 1996; Hodges, 1997; Sakai *et al.*, 1997; Schoen *et al.*, 1997). Using these methods it is possible to address historical questions concerned with the origin of particular mating systems. Evolutionary models that make predictions about the functional associations of traits can be tested by examining the sequence in which they appear in a phylogeny. A major issue when using these different approaches is whether the macroevolutionary patterns of interest to systematists can be satisfactorily explained by microevolutionary processes evident within local populations. A potential link between these two levels in the genealogical hierarchy is the study of geographical variation in mating systems within species (Barrett, 1995).

Most theoretical models of mating-system evolution in plants involve single populations of infinite size. Within such populations selection usually proceeds to a particular deterministic equilibrium that is governed by fitness differences among genotypes or phenotypes. However, real populations are often short-lived because demographic or environmental stochasticity results in local extinction before any deterministic equilibrium has been reached (Schaffer, 1987; Barrett and Husband, 1997). Among plants with annual or short-lived perennial life histories the longevity of single populations may often be insufficient for significant evolutionary changes in mating patterns to occur. Yet much of the strongest empirical evidence for intraspecific variation in mating systems involves short-lived species, particularly annuals that typically exhibit frequent colonisation and extinction cycles (e.g. *Amsinckia* – Ganders *et al.*, 1985; *Clarkia* – Holtsford and Ellstrand, 1989;

Eichhornia – Barrett and Husband, 1990; *Gilia* – Schoen, 1982; *Ipomoea* – Clegg and Epperson, 1988; *Leavenworthia* – Lloyd, 1965; *Limnanthes* – McNeill and Jain, 1983; *Lupinus* – Harding *et al.*, 1974; *Mercurialis* – Pannell, 1997a; *Mimulus* – Ritland and Ritland, 1989; *Senecio* – Abbott, 1985). This association raises the question as to whether the local population is the most appropriate evolutionary unit for investigating the evolution of mating systems in these species. Here we propose that, for species with ephemeral populations, it may often be more appropriate to consider processes at the landscape level using a metapopulation approach, rather than to focus exclusively on those occurring within single populations. A similar argument based on the ephemeral nature of the local population has been made by Levin (1995) for studies of speciation.

Metapopulations are assemblages of interconnected populations existing in a balance between extinction (or more correctly local extirpation) and colonisation (Levins, 1969). The metapopulation approach provides a means of investigating ecological and evolutionary processes at a spatial scale above the local population at both landscape and regional levels. Metapopulation models depict species occupying an array of habitat patches linked by migration. The longevity of a metapopulation will depend on the relative rates of population extinction and colonisation. Since metapopulations will greatly outlive local populations, they provide greater opportunities for significant evolutionary changes, to establish within their boundaries. Despite a rapidly growing literature on metapopulation dynamics (reviewed by Hanski and Gilpin, 1997), relatively few studies have involved plant populations and even fewer have addressed issues of mating-system evolution (Husband and Barrett, 1996). Here, we ask whether application of a metapopulation perspective can provide novel insights into ecological processes governing changes in reproductive traits that are not evident from studies of local populations alone.

In this chapter we apply a metapopulation approach to two central topics in plant reproductive biology: the selection of self- versus cross-fertilisation and the evolution of combined versus separate sexes. Both problems were studied extensively by Darwin (1876, 1877) and a large literature has accumulated on these topics this century (reviewed by Richards, 1997). Here we summarise several recent empirical studies that indicate the importance of metapopulation perspectives for understanding the ecological factors responsible for regional variation in mating systems. We also outline several theoretical models of metapopulation dynamics that provide insights into these empirical observations. However, before we discuss these topics, we first consider general principles involved in plant reproduction within a metapopulation framework and ask whether the levels and direction of selection might differ between local populations and metapopulations.

5.2 General principles and levels of selection

The implications of metapopulation dynamics for mating-system evolution can be distilled into three general principles (Table 5.1). Because individual plants incapable of producing seeds by selfing cannot establish colonies on their own, metapopulation processes (i.e. local colony extinction and recolonisation) will tend to select against unisexuality and self-incompatibility. This first principle is essentially Baker's Law (Baker, 1955, 1967), considered in the context of a metapopulation (Pannell

Table 5.1 Some general principles concerning the influence of metapopulation dynamics on plant reproductive traits and their evolutionary implications.

Principle	Implication
(1) Single seeds incapable of selfing cannot found new colonies	Unisexual and self-incompatible individuals selected against
(2) Seeds but not pollen can found new colonies	Female allocation selected
(3) Ecological processes within versus among populations are distinct	Direction of selection at population and metapopulation levels may differ

and Barrett, 1998a). Traditionally, Baker's Law has been invoked to explain the higher frequency of self-compatible relative to self-incompatible species on oceanic islands (e.g. McMullen, 1987; Webb and Kelly, 1993; Barrett, 1996), but the concept applies to any situation where dispersal to a new site results in potential reproductive failure through reduced opportunities for cross-fertilisation. Baker (1955) himself drew upon observations of what we would now term metapopulation dynamics in notostracan clam shrimps to support his hypothesis, noting that cosexuality had evolved from unisexuality where populations were ephemeral and frequent recolonisation was necessary.

The second principle linking metapopulation dynamics to plant reproduction implicates selective effects on sex allocation. Although plants transmit genes to their progeny through both pollen and seeds, the recolonisation of sites in a metapopulation after local population extinction will favour increased allocation to female function, because seeds, not pollen, can found new colonies (Table 5.1). Such increased female allocation can be manifest either in the provisioning of seeds with structures for better dispersal (Olivieri *et al.*, 1990), by producing better quality seeds (Holsinger, 1986), or by simply producing more seeds (Pannell and Barrett, 1998b). As discussed below, selection on the sex allocation of cosexuals has implications for the differential success in metapopulations of selfing versus outcrossing phenotypes, cosexual versus unisexual phenotypes, and of quantitative variation in sex allocation of cosexual plants generally.

The third principle concerning the effects of metapopulation dynamics on plant reproductive traits involves the consequences of contrasting selective pressures at the population and metapopulation levels. For example, in a metapopulation there will be a trade-off between resource allocation to growth and competition versus that to reproduction and dispersal (Hamilton and May, 1977). This antagonism between selective forces acting during colonisation and population growth was termed the 'metapopulation effect' by Olivieri and Gouyon (1997). They reviewed several cases where such an effect has influenced the evolution of plant life history traits, including those affecting reproduction. For example, in *Thymus vulgaris* (Lamiaceae), cytoplasmic male-sterility is thought to be maintained at the metapopulation level even though nuclear fertility restorers might have checked its spread within local populations (Gouyon and Couvet, 1987). A recent theoretical model has shown that a joint nuclear-cytoplasmic polymorphism for male sterility can be maintained in a metapopulation with recurrent local extinction as a result of the tendency of females to disperse more seeds to surrounding populations than

hermaphrodites (Couvét *et al.*, 1998). In this chapter we present several additional examples that demonstrate how selection on mating-system traits may differ within versus between populations.

Our second general principle indicates that metapopulation dynamics may select for increased seed production. This suggests that we might reconsider arguments for mating-system evolution that invoke 'reproductive efficiency' and, by implication, group selection. Such ideas were common currency in the early literature on plant evolution (Darlington and Mather, 1949; Stebbins, 1950) and have continued to hold sway (e.g. Cruden, 1977; Anderson and Stebbins, 1984; Richards, 1997; Karoly, 1994), though they seldom stand the test of rigorous analysis (Lloyd, 1965; Charlesworth, 1980). Arguments for the importance of reproductive efficiency have tended to consider fitness as a population quantity measured in terms of seed productivity (e.g. Mulcahy, 1967; Putwain and Harper, 1972). This view has largely been discredited by sex allocation theory, which recognises the equal importance of pollen and ovules as vehicles for gene transmission and which predicts the selection of equal allocation of resources to both male and female functions in outcrossing populations (Charnov, 1982; Lloyd, 1987). According to sex allocation theory, deviations from equal sex allocation are selected when marginal fitness gains through investment to either sexual function are reduced by such factors as local mate competition (Hamilton, 1967) or local resource competition (Lloyd, 1984).

In stable populations, biased sex allocation is unlikely to arise through an inefficiency of resource use rendering some populations fitter (i.e. more productive) than others. However, for species characterised by metapopulation dynamics, the concept of differential population fitness and selection between groups may appear to be more applicable. Populations comprising individuals with a greater capacity to disperse seeds will make a disproportionate contribution to the composition of a metapopulation before they eventually go extinct. Nevertheless, unless populations suffer non-random extinction probabilities as a result of traits shared by their component individuals, arguments invoking group selection are unnecessary. Couvét *et al.* (1998) explained the maintenance of a nuclear-cytoplasmic polymorphism for male sterility by appealing to group selection, because populations with mainly females grow more rapidly and disperse more seeds than those with lower female frequencies. However, we suggest that metapopulation dynamics are better regarded simply as another component of a species' ecology by which the characteristics of its constituent individuals, including the mating system, are selected. Metapopulation dynamics may thus confer fitness dividends on individuals with a female-biased sex allocation because the availability of vacant habitat patches across the landscape effectively accelerates fitness gains through female function.

The greater premium on seed (as opposed to pollen) production in a metapopulation has implications for the selection of alleles for increased selfing if selfed seeds suffer from inbreeding depression and are reduced in either quality or number. Because individuals with greater outcrossing rates may produce more seeds compared with selfers, the populations in which they occur will have a faster growth rate and hence a greater potential to export seeds to other sites in the metapopulation. This is illustrated in Fig. 5.1 which plots the expected growth rate of a population comprising predominant selfers and predominant outcrossers against the frequency of an allele for increased selfing (see legend for details). Differences in

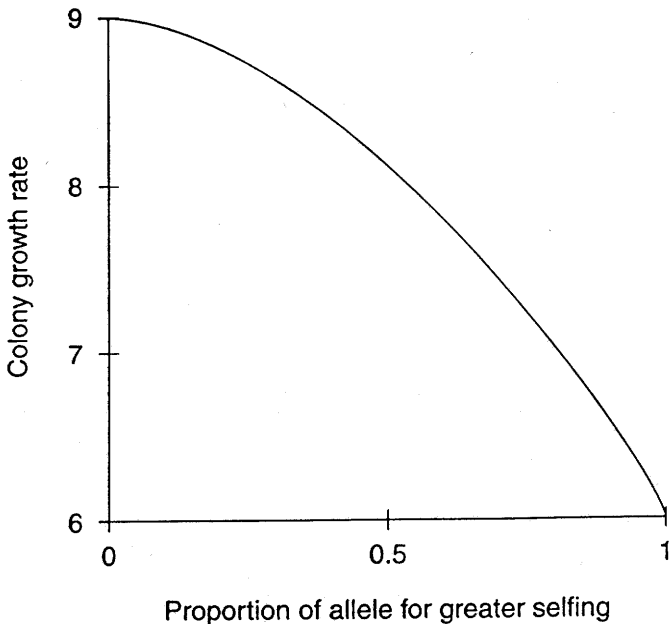


Figure 5.1 The intrinsic rate of population growth as a function of the frequency of the allele for greater selfing. Colonies with a higher frequency of the allele for greater outcrossing grow more rapidly than those for greater selfing, because the progeny of outcrossers do not suffer from inbreeding depression. In the model, inbreeding depression was 0.5. The allele for greater selfing and outcrossing caused selfing rates of 0.8 and 0.2, respectively, and plants produced 10 progeny before inbreeding depression was expressed. Populations were sufficiently large for competing self-fertilisation to be ignored. (After Pannell and Barrett, 1998b).

growth rate between colonies comprising mainly selfers and those comprising mainly outcrossers can therefore cause selection to favour outcrossing at the level of the metapopulation, even where selfing might tend to spread within individual populations (see below). Thus, the direction of selection at a mating-system locus may differ between these two levels of the ecological hierarchy.

5.3 Self- and cross-fertilisation

The comparison of self and cross-fertilisation has been considered the central topic of floral biology (Lloyd and Schoen, 1992). This is because different rates of selfing and outcrossing have profound genetic and evolutionary consequences. The effects of selfing and outcrossing on fitness through inbreeding depression and heterosis are well established (Charlesworth and Charlesworth, 1987; Ritland, 1996), and extensive data on their influence in determining patterns of genetic diversity within and among plant populations exist (Hamrick and Godt, 1990). Selection for self- versus cross-pollination often involves evolutionary modifications to aspects of floral design and display, so that shifts in mating pattern are also accompanied by changes in sex allocation (Charnov, 1982). Since resource allocation, pollination

and mating determine reproductive success in an integrated manner, changes in mating system can also have important ecological and life-history consequences. Functional associations between different plant life histories and contrasting rates of self-fertilisation indicate that changes in mating patterns are usually driven by altered ecological and demographic circumstances (Barrett *et al.*, 1996; Morgan and Schoen, 1997b).

5.3.1 Theoretical background

Early models of the evolution of self- and cross-fertilisation focused mainly on genetic factors, particularly inbreeding depression resulting from the expression of deleterious recessive alleles and the transmission advantage of alleles governing the selfing rate (Fisher, 1941; Lande and Schemske, 1985). Most genetic models predicted that predominant selfing and predominant outcrossing should be alternative stable outcomes of mating-system evolution. Whereas survey data on the distribution of outcrossing rates generally supports this prediction (reviewed by Barrett and Harder, 1996), many species exhibit intermediate selfing rates, and stable mixed mating can occur when additional genetic factors are considered in theoretical models. These include biparental inbreeding, inbreeding depression caused by overdominance, and the association between mating-system alleles and viability genes (reviewed by Uyenoyama *et al.*, 1993). The evolutionary dynamics of selfing and outcrossing are also influenced by a range of ecological factors associated with pollination biology (Harder and Barrett, 1996; Holsinger, 1996). These include pollen and seed discounting, reproductive assurance and the mode of self-pollination. More recent models have explored their effects on selfing rates and have shown that these factors modify the threshold values of inbreeding depression above which selfing cannot evolve (Lloyd, 1992; Holsinger, 1996; Schoen *et al.*, 1996; Harder and Wilson, 1998).

Theories on mating-system evolution have become increasingly sophisticated through attempts to build more ecological realism into models. However, a noticeable feature of most models, whether they are primarily genetical in emphasis or involve ecological factors, is that they ignore aspects of population structure and do not consider the influence that stochastic processes might have on mating-system evolution (though see Ronfort and Couvet, 1995). Since the majority of species with wide variation in selfing rates have colonising life histories it seems likely that ecological and demographic influences on population structure are important in the evolution of their reproductive systems. Lloyd (1980) identified a range of demographic factors that might influence frequencies of self- versus cross-fertilisation, but there have been surprisingly few attempts to relate the evolution of mating systems to such ecological factors. What evidence is there that population structure is relevant to plant reproduction, and how might altered demographic circumstances influence mating-system evolution?

5.3.2 Population structure in tristylous species

Tristylous species provide convenient model systems for investigating the influence of ecological and demographic factors on the maintenance of outcrossing (Barrett,

1993). These sexual polymorphisms possess simple inheritance, and theoretical models indicate that frequency-dependent selection due to disassortative mating between the three style morphs should give rise to equal frequencies in large ideal populations (Heuch and Lie, 1985). However, real populations of tristylous plants are often small, and in species with colonising life histories frequent colonisation and extinction cycles provide opportunities for destabilisation of the polymorphism, leading to the evolution of alternate mating systems. Geographical surveys of population structure provide opportunities to investigate the maintenance of these polymorphisms under varying ecological and demographic circumstances at the landscape level. In particular, the spatial dispersion of populations across the landscape and their mutual isolation are likely to be critical in determining the local stability of the polymorphism.

Comparisons of style-morph frequency variation between native and introduced populations of tristylous *Lythrum salicaria* (Lythraceae) have provided valuable insights into the role of population structure and stochastic forces in governing the maintenance of the polymorphism (Eckert and Barrett, 1992; Eckert *et al.*, 1996). A sample of 102 populations from south-western France revealed few populations (5%) that did not contain the three style morphs. In contrast, in the introduced range in southern Ontario, Canada, where the species is rapidly invading wetlands, 23% of 102 populations sampled were missing style morphs. In both areas there was a greater likelihood that small rather than large populations were missing style morphs, implying a role for stochastic forces in morph loss. Despite the lower frequency of morph loss in France, native population sizes were significantly smaller than those in Ontario. How can this observation be reconciled with data on the relation between morph loss and population size? The answer appears to lie in differences in ecology and population structure between the two regions. French populations of *L. salicaria* occur primarily in roadside ditches associated with the agricultural landscapes of the region. The distribution of populations implies a high level of connectivity which provides opportunities for gene flow among populations. Metapopulation models indicate that levels of gene flow on the order of $m \geq 0.05$ can account for the maintenance of tristily in small French populations (Eckert *et al.*, 1996). In contrast, populations in Ontario are more isolated from one another, and opportunities for missing morphs to establish in non-trimorphic populations are thus restricted. Founder effects associated with colonisation of new territory appear to be largely responsible for the higher incidence of morph loss in this region.

Similar demographic processes leading to stochastic morph loss have played a crucial role in destabilising tristily in the annual emergent aquatic *Eichhornia paniculata* (Pontederiaceae) in northeastern Brazil (Barrett *et al.*, 1989). As in *L. salicaria*, large-scale geographical surveys of style-morph frequencies indicate that morph loss is associated with small population size. Of 167 populations sampled, 29% had at least one style morph missing, larger populations were more likely to be trimorphic than smaller ones, and there was a significant positive correlation between style-morph evenness and the harmonic mean of population size. Moreover, populations missing style morphs were significantly more vulnerable to local extinction than trimorphic populations (Husband and Barrett, 1992; Barrett and Husband, 1997). These patterns strongly implicate ecological factors associated

with colonization-extinction cycles as the primary mechanism leading to the stochastic loss of style morphs from local populations. Unlike *L. salicaria*, a self-incompatible perennial, *E. paniculata* is annual and self-compatible, thus providing greater opportunities for demographic changes to exert their influence on mating patterns. Indeed, there is good evidence that the loss of style morphs from populations is accompanied by increases in selfing rate (Barrett and Husband, 1990). Self-pollinating variants occur rarely in trimorphic populations, are common in dimorphic populations, and are frequently fixed in monomorphic populations.

What evidence is there that metapopulation processes may be important in the dissolution of tristily and the evolution of self-fertilisation in *E. paniculata*? Estimates of gene flow among 44 populations from seven spatially separated areas in northeastern Brazil indicate significant variation among areas (Husband and Barrett, 1995). Estimates of gene flow were highest among areas in which populations were exclusively trimorphic. In contrast, reduced estimates of gene flow were evident in the part of the range in which selfing populations dominate (Fig. 5.2). In this area demographic conditions differ. Populations are smaller in size, less dense and more isolated from one another than elsewhere in the range. The precise ecological factors responsible for these differences in population structure are not known, but they may be related to rainfall patterns and the availability of habitats suitable for *E. paniculata* in the zone of selfing. Nevertheless, under these altered demographic conditions populations appear to be more vulnerable to the stochastic loss of style morphs, and restricted gene flow due to population isolation restricts opportunities for the re-invasion of missing style morphs. These patterns are consistent with the view that metapopulation dynamics play a role in destabilising outcrossing and precipitating the evolution of self-fertilisation. Importantly, they could not have been revealed by focusing on a few local populations of *E. paniculata*, and it is clear that in these studies a metapopulation perspective has provided valuable new insights.

Microevolutionary forces operating at the metapopulation level may ultimately be expressed at higher taxonomic levels. This appears to be the case in *Lythrum* and *Eichhornia*, as stochastic loss of the short-styled morph has influenced pathways of floral evolution in both genera. New World members of the genus *Lythrum* (section *Euhyssopifolia*) are uniformly distylous and likely derived from a tristylous Eurasian ancestor. Comparative morphological evidence indicates that the morphs in distylous taxa correspond to the long- and mid-styled morphs of a tristylous species (Ornduff, 1979), implying loss of the short-styled morph during migration to North America. In *Eichhornia* phylogenetic reconstructions indicate multiple breakdown of tristily, giving rise to several predominantly selfing species (Graham and Barrett, 1995; Kohn *et al.*, 1996). These small flowered homostylous species are composed of self-pollinating long- and mid-styled morphs. This pattern is evident at both the inter- and intra-specific levels, since each of the tristylous species displays predominantly selfing populations that typically lack the short-styled morph (Barrett, 1988). As discussed above, metapopulation processes resulting in stochastic loss of the short-styled morph appear to have played a key role in eliciting these patterns within the constraints imposed by the inheritance of tristily.

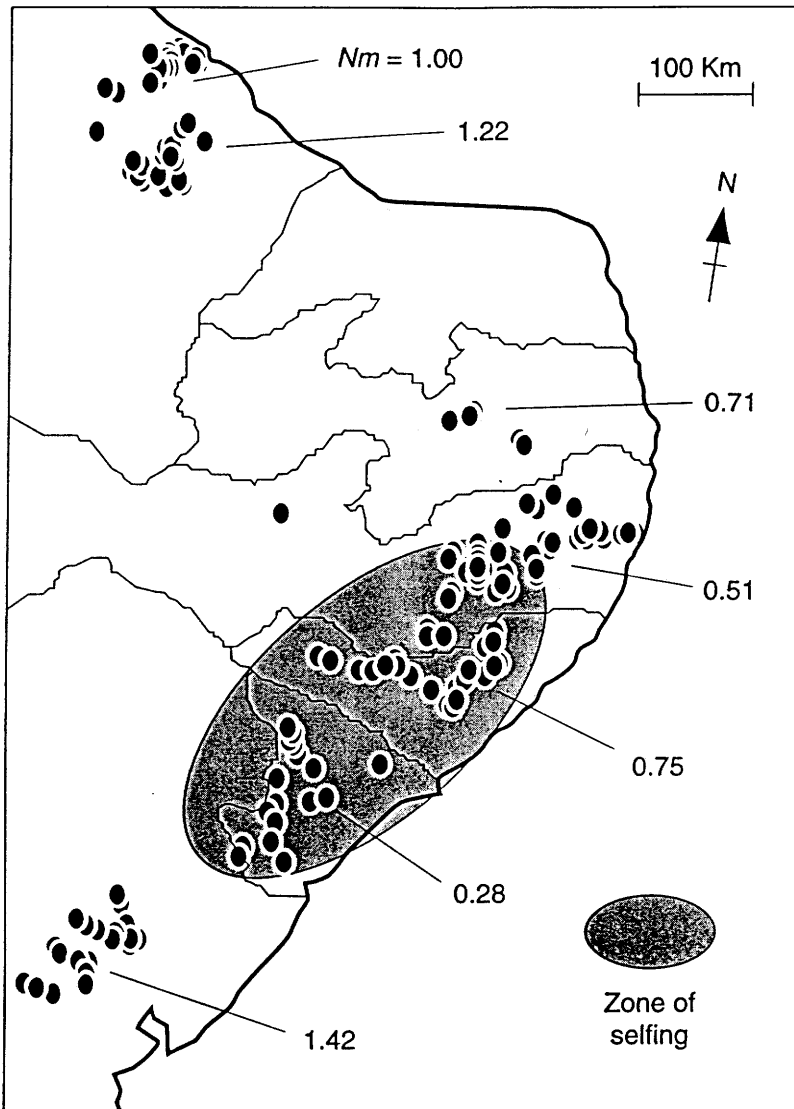


Figure 5.2 Estimates of gene flow based on polymorphism at allozyme loci among populations of *Eichhornia paniculata* from different states in northeastern Brazil. Values of Nm were lowest in the zone in which selfing populations occur. (After Husband and Barrett, 1995).

5.3.3 Polymorphisms for selfing and outcrossing

Populations of *E. paniculata* in the zone of selfing indicated in Fig. 5.2 are frequently dimorphic for style morph and they possess a selfing–outcrossing polymorphism. Long-styled plants exhibit high outcrossing rates whereas mid-styled plants experience considerable self-fertilisation because of genetic modifications to their stamen

position. Selfing-outcrossing polymorphisms are known in other heterostylous plants (e.g. *Amsinckia* – Ganders *et al.*, 1985; *Oxalis* – Ornduff, 1972; *Primula* – Charlesworth and Charlesworth, 1979), as well as non-heterostylous taxa such as *Senecio vulgaris* (Abbott, 1985). An important question concerning these mating-system polymorphisms is whether they are evolutionarily stable, or whether selection inevitably drives one of the mating morphs to fixation. To address this problem, we have recently developed a computer simulation model that examines the effects of genetic drift and selection at various levels of the ecological hierarchy on the maintenance of a selfing-outcrossing polymorphism (Pannell and Barrett, 1998b).

In our model, we assume that there are two mating phenotypes: one that self-fertilises 80% of its ovules (the selfer); and one that selfs only 20% of its ovules (the outcrosser). Selfing occurs autonomously prior to opportunities for outcrossing; this mode of selfing is termed 'prior self-fertilisation' (Lloyd, 1992). Following prior-selfing, pollen grains dispersed in the population compete for the remaining unfertilised ovules. In large populations, almost all these ovules are outcrossed, but in small populations some are selfed through 'competing selfing' (Lloyd, 1992). This is because pollen dispersed into the population pollen pool is more likely to return to the plant that dispersed it. The mating system in our model is thus context-dependent, varying with population size and the frequency of selfing and outcrossing phenotypes (Fig. 5.3). Because of this context dependence, recently founded colonies will have higher selfing rates than larger and older colonies. Context-dependent mating has been demonstrated experimentally in bee-pollinated *E. paniculata* (Kohn and Barrett, 1994) and is likely to be particularly common in wind-pollinated species where selfing rates are sensitive to plant density (Farris and Mitton, 1984; Holsinger, 1992; and see below).

In our simulations, it was difficult to find conditions under which a selfing-outcrossing polymorphism could be maintained indefinitely, although with certain parameter values the loss of one or other of the mating-system phenotypes was very protracted. These results help to explain the overall rarity of selfing-outcrossing polymorphisms in plants, and it is possible that the known mixed-mating polymorphisms cited above represent transitional states from predominant outcrossing to selfing. Another important outcome of our model was that with high colony turnover in a metapopulation, the allele for predominant outcrossing was fixed more often than that for selfing, even though the mating-system locus was neutral (Fig. 5.4). This lends further support for the 'metapopulation effect' discussed above (i.e. Principle 3 in Table 5.1), where selection at the metapopulation level acts in a direction not evident within single component populations. This outcome is due to the relatively greater seed output of colonies with a high frequency of outcrossers, the seeds from which did not suffer from inbreeding depression (Fig. 5.1). Thus, because only seeds can found new colonies, selection at the metapopulation level acts in favour of increased seed fertility (Principles 1 and 2, respectively, in Table 5.1).

A third finding of our simulations was that when selfed progeny suffered inbreeding depression, selfers became fixed within finite populations more often than expected. This 'fixation bias' was due to the fact that predominant outcrossers selfed more of their seeds by competing selfing than did selfers; this is analogous to the finding that geitonogamous selfing (often an important component of

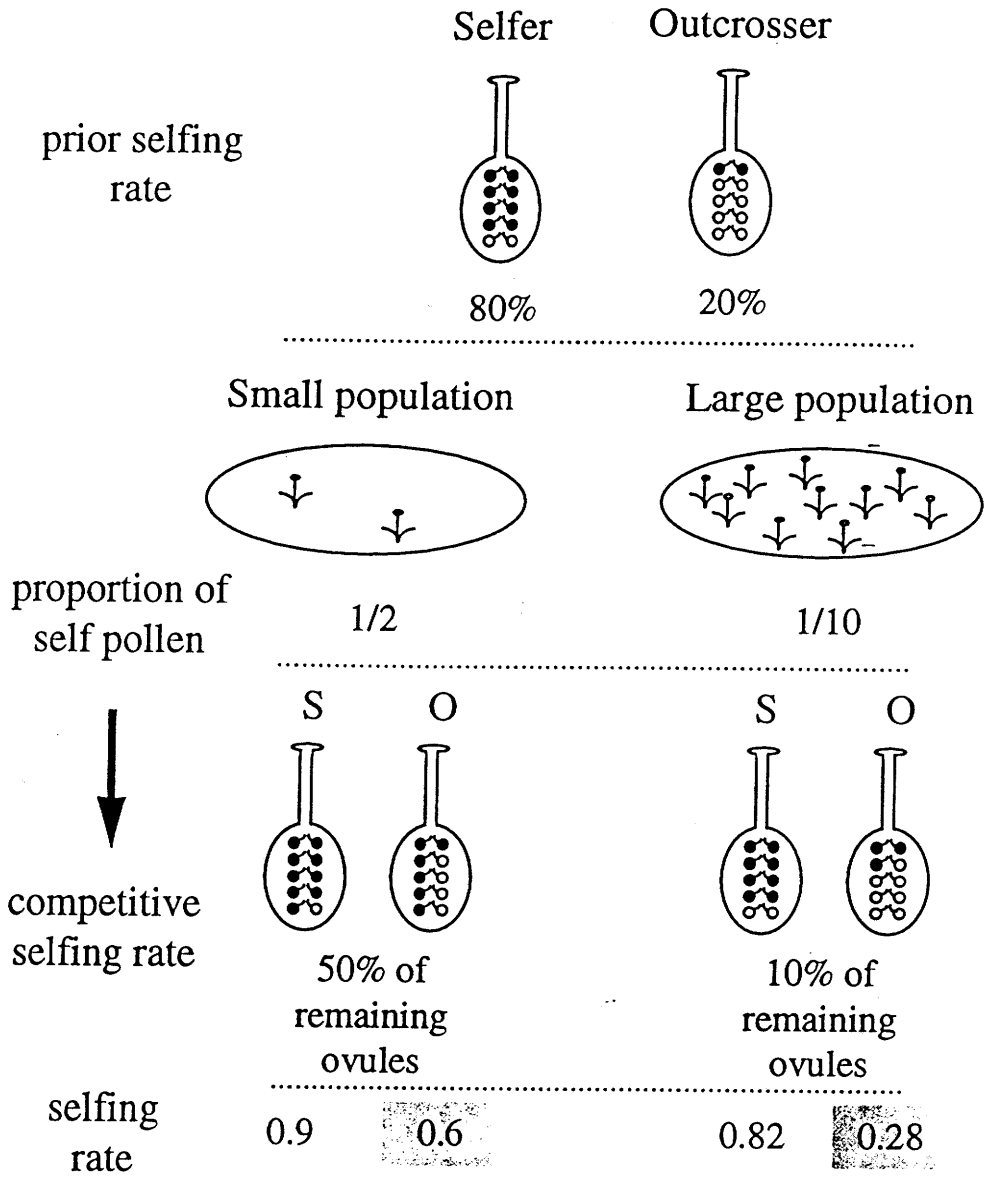


Figure 5.3 A graphic depiction of context-dependent mating for selfers and outcrossers with different prior selfing rates. In small populations, self pollen accounted for an appreciable amount of the pollen dispersed to the pollen pool, while in large populations negligible self pollen was dispersed. In small populations the rate of competing selfing is greater than in large populations. As a result, the difference in selfing rate between selfers and outcrossers is smaller than in large populations.

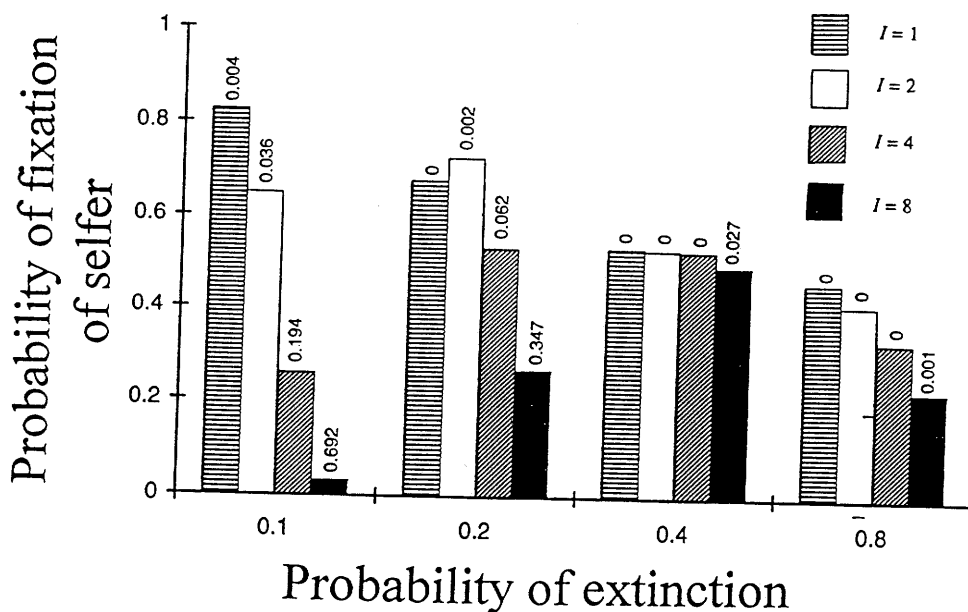


Figure 5.4 Model of a selfing-outcrossing polymorphism in a metapopulation. The probability of fixation of an allele for greater selfing in a metapopulation of 20 sites, in relation to the colony extinction rate and the mean number of immigrants into each site per generation, l . The number of immigrants followed a clumped distribution, such that seeds arrived at sites in groups of $5l$ with a probability of 0.2. The genotypic composition of the immigrants was determined probabilistically according to their frequency in the metapopulation. Numbers given over bars are the probability that a selfing-outcrossing polymorphism was maintained after 2000 generations. (After Pannell and Barrett, 1998b).

competing selfing) can never be selected (Lloyd, 1992). These results highlight the need to consider the context in which mating occurs (i.e. population size, density and composition) as well as the mode of self-fertilisation. Both these aspects can be influenced by population structure and metapopulation dynamics and it is clear that empirical studies of the ecological context in which mating occurs are badly needed.

5.3.4 Reproductive assurance in a metapopulation

Darwin (1876) was of the opinion that reproductive assurance was the main selective force in the evolution of selfing from outcrossing in flowering plants, and this view is supported by recent theoretical models (Schoen *et al.*, 1996). Most authors have invoked pollinator scarcity as the ecological mechanism responsible for the advantage of reproductive assurance within single populations (reviewed by Lloyd, 1980). However, in a metapopulation, phenotypes with assured reproduction are likely to be selected because they can found new colonies as single seeds. In contrast, outcrossers will fail to reproduce, irrespective of the presence or absence of pollinators, unless compatible partners reach a site concurrently (Principle 1).

As discussed earlier, Baker's Law can be viewed as a generalisation concerning the selective advantage of reproductive assurance when colonisation is frequent. Whereas it has most often been invoked to explain the high frequency of self-fertilisation in species which have undergone long-distance dispersal, the principle applies equally to the process of colonisation in a metapopulation. Although examples illustrating the principle of Baker's Law have been drawn from both plants and animals, many counter examples have been identified and its generality has been questioned (Carlquist, 1966; Carr *et al.*, 1986; Sakai *et al.*, 1995b). We might ask, for example, to what extent the success of self-incompatible colonising species vitiates the hypothesis. In an attempt to answer this question, and to quantify the selective pressure for reproductive assurance invoked by Baker's Law, we have used a metapopulation model that reframes the question in terms of colony turnover rates and plant life history traits (Pannell and Barrett, 1998a).

Our model considers the maintenance of a single phenotype in a metapopulation in which individual colonies go extinct at a rate E per year and are recolonised at a rate B . If a proportion p of the sites in the metapopulation is occupied at any point in time, then it follows that the relation $Ep = (1 - p)B$ describes the state of the metapopulation at equilibrium. Thus, for any given extinction rate we can find the colonisation rate at which a proportion p of the sites in the metapopulation remains occupied. The model assumes that B will be some function of the mean number of seeds immigrating to a site per year, and this will depend on particular aspects of demography and life history (e.g. perenniality, seed dormancy, dispersal dynamics).

As an example, consider the contrast between the maintenance of a selfer and an outcrosser in a metapopulation. Whereas only a single selfing individual is required for the founding of a new colony, at least two obligate outcrossers are needed. Thus, for outcrossers to be maintained in a metapopulation, they will have to be more proficient at dispersing seeds to vacant sites than selfers. Fig. 5.5 indicates that with greater extinction rates the seed fecundity of outcrossers required for their maintenance in a metapopulation must increase relative to that of selfers. This difference in requisite fecundities between selfers and outcrossers can be viewed as an index of the selective pressure for reproductive assurance and will depend on the site occupancy levels within the metapopulation (Fig. 5.5). In particular, as p falls towards zero, reproductive assurance becomes increasingly important and the relative fecundity tends towards infinity. This result provides an explanation for the otherwise puzzling observation that several successful sexual colonising species are in fact self-incompatible (e.g. *Centaurea solstitialis* – Sun and Ritland, 1998; *Papaver rhoeas* – Campbell and Lawrence, 1981; *Senecio squalidus* – Abbott and Forbes, 1993; *Turnera ulmifolia* – Barrett, 1978) or dioecious (e.g. *Ecballium elaterium* – Costich, 1995; *Mercurialis annua* – Pannell, 1997a; and see below), in apparent contradiction to Baker's Law. Our model indicates that selection for reproductive assurance will be weak when most of the available sites in the metapopulation are occupied, even for high colony extinction rates (Fig. 5.5). It will be strongest in situations where a species is not common across the landscape (e.g. on the periphery of its geographic distribution), and this accords well with empirical observations of the geographical distribution of selfing (reviewed by Lloyd, 1980).

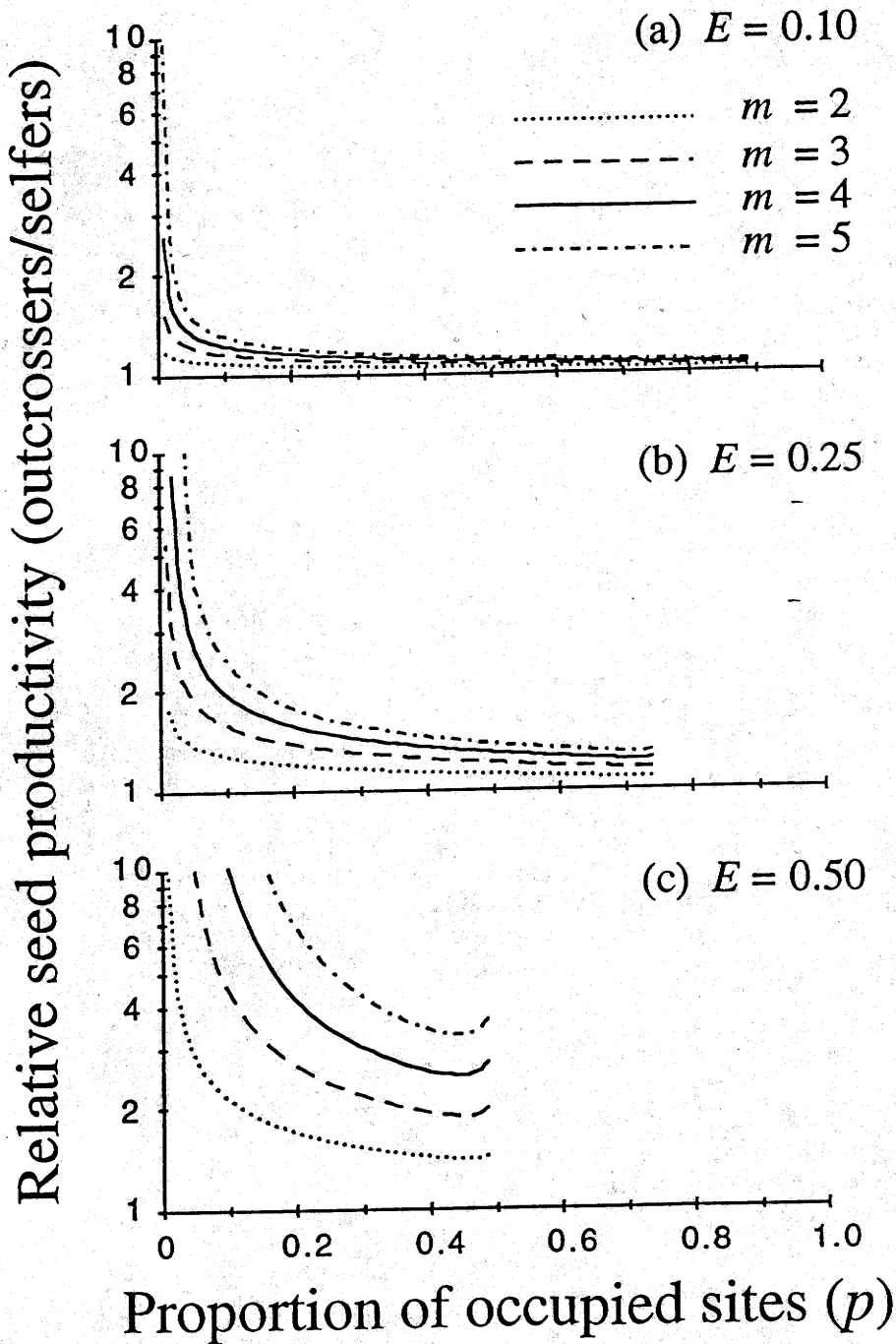


Figure 5.5 Model of reproductive assurance in a metapopulation. The number of seeds that outcrossers must produce relative to selfers to be maintained in a metapopulation in which a proportion p sites are occupied at equilibrium. Extinction rates for graphs a, b and c, are $E = 0.10, 0.25$ and 0.50 , respectively. Different curves correspond to cases where at least m seeds are required for successful colonisation. Thus, selfers need only a single seed to colonise a new site ($m = 1$), whereas outcrossers require $m > 1$ seeds. Curves are truncated at the maximum possible colony site occupancy levels for the respective extinction rate. (After Pannell and Barrett, 1998a).

5.4 Combined versus separate sexes

Darwin (1877) raised the question of why some plants have evolved unisexuality. The overwhelming majority of plant species are cosexual (hermaphroditic or monoecious), and this no doubt reflects the advantages of combined versus separate sexes. Because animal-pollinated species must invest resources towards attracting and rewarding pollinators, the ability of cosexuals to share these fixed costs between male and female functions can amount to significant advantages over unisexuals, which incur the same costs for only one sexual function (Heath, 1977). Saturating male or female fitness-gain curves (or both) are also disadvantageous to unisexual plants because marginal gains in fitness are reduced when allocation to each sexual function is high. As a result, cosexuals, which divide their resources between two sexes, are more likely to be selected (Charnov, 1982)

5.4.1 Ecological and demographic associations

The evolution of combined versus separate sexes is closely associated with plant life histories. For example, dioecy is particularly common in long-lived, woody species but is rare in annuals (Renner and Ricklefs, 1995; Sakai *et al.*, 1995a). This pattern presumably reflects, in part, the risks associated with reproductive failure for annual life histories and the costs of geitonogamy in perennials with large floral displays. Evidence for associations between life history and sexual systems are evident in the few taxa showing gender monomorphism and dimorphism at the species level. For example, in the Australian geophyte, *Wurmbea dioica* (Colchicaceae), plants in dioecious populations are longer lived than those in cosexual populations, even where the two sexual systems co-occur in sympatry (A. L. Case and S. C. H. Barrett, unpublished). Similar patterns occur in the emergent aquatic, *Sagittaria latifolia* (Alismataceae), in Ontario, Canada (S. C. H. Barrett, unpublished). Monoecious populations are commonly found in drainage ditches, stream edges and other disturbed aquatic environments and are short-lived, whereas dioecious populations are restricted to extensive marshes and more stable wetland habitats and are both long-lived and highly clonal. A particularly striking example of intraspecific variation in sexual systems occurs in *Mercurialis annua* (Euphorbiaceae), an annual ruderal distributed across western and central Europe and around the Mediterranean (Durand, 1963). Recent microevolutionary investigations of this species have revealed associations between ecology, demography and sexual system (Pannell, 1997a, b, c).

Throughout most of its range, *M. annua* is dioecious; however, its western Mediterranean populations are largely monoecious. Whereas dioecious populations tend to persist throughout the year, monoecious populations are winter annuals. In southern Spain, southern Portugal and northern Morocco, males co-occur with monoecious individuals in androdioecious populations. Monoecy has been selected in the drier, less predictable parts of the species' range, presumably as a result of selection for reproductive assurance. In contrast, males have been able to persist with cosexuals in the moister regions where populations are longer lived and more densely distributed across the landscape (Pannell, 1997a).

A theoretical model has produced results supporting a metapopulation interpretation of mating-system variation in *M. annua* (Pannell, 1997d). The model consists

of an array of equivalent sites that suffer constant extinction rates and exchange seeds according to an island model of dispersal. As in *M. annua* (Pannell, 1997a, b), unisexuality is determined by a dominant allele, and unisexual individuals produce five times as many seeds or as much pollen as their cosexual counterparts. Simulations indicated that when rates of colony extinction were low and immigration rates high, unisexuals could be maintained at high frequencies in the metapopulation. By contrast, when colony turnover was rapid, cosexuality spreads to fixation in the metapopulation, which could not be invaded by unisexuals (Fig. 5.6). In this model, unisexuality always spreads locally on its invasion into a cosexual population, but extinction and colonisation dynamics selected against males and females at the metapopulation level. As illustrated above for the contrast between selfing and outcrossing, these results highlight the fact that selection on mating-system alleles can act in opposing directions at the metapopulation and population levels. This implies that an important component of selection on mating systems may be invisible within local populations where biologists have concentrated their efforts in estimating selection parameters. Although rates of colony extinction and recolonisation can be difficult to measure in the field, it is important to realise that processes not readily apparent in local populations may have shaped the course of mating-system evolution in significant ways.

5.4.2 Sex allocation

The theory of sex allocation (Charnov, 1982) has been a powerful tool for understanding gender variation in plants. However, most models have focused exclusively on selection acting within local populations (but see Lloyd, 1982; Ronce and Olivieri, 1997). As we have seen above, processes occurring at the metapopulation level can influence the evolutionary stability of mating systems, but the models and data we have discussed thus far have confined themselves to discrete variation: self-compatibility versus self-incompatibility; selfing versus outcrossing in general; and cosexuality versus unisexuality. Whilst each of these issues is intimately linked with questions regarding sex allocation, we now consider briefly the influence of metapopulation dynamics on quantitative variation in the allocation of resources to male and female functions.

The model we summarise here (Pannell, 1995) is similar to that described in the previous section, except that cosexuals are assumed to vary in their sex allocation rather than to have a single phenotype. For brevity, we describe the model only for an androdioecious species, though it can be applied equally to nuclear-inherited gynodioecy, which yielded similar simulation results. Sex allocation is determined by the additive interaction of co-dominant alleles at a locus unlinked to the one that determines unisexuality. The model assumes that males are more than twice as successful at fertilising ovules than cosexuals, which divide their resources equally between sexual functions. This might occur in a wind-pollinated species in which males are taller and possess inflorescences better suited to pollen dispersal than cosexuals, as found in *M. annua* (Pannell, 1997a). Simulations were conducted for an array of 500 sites interconnected by seed dispersal, with varying colony extinction and recolonisation rates.

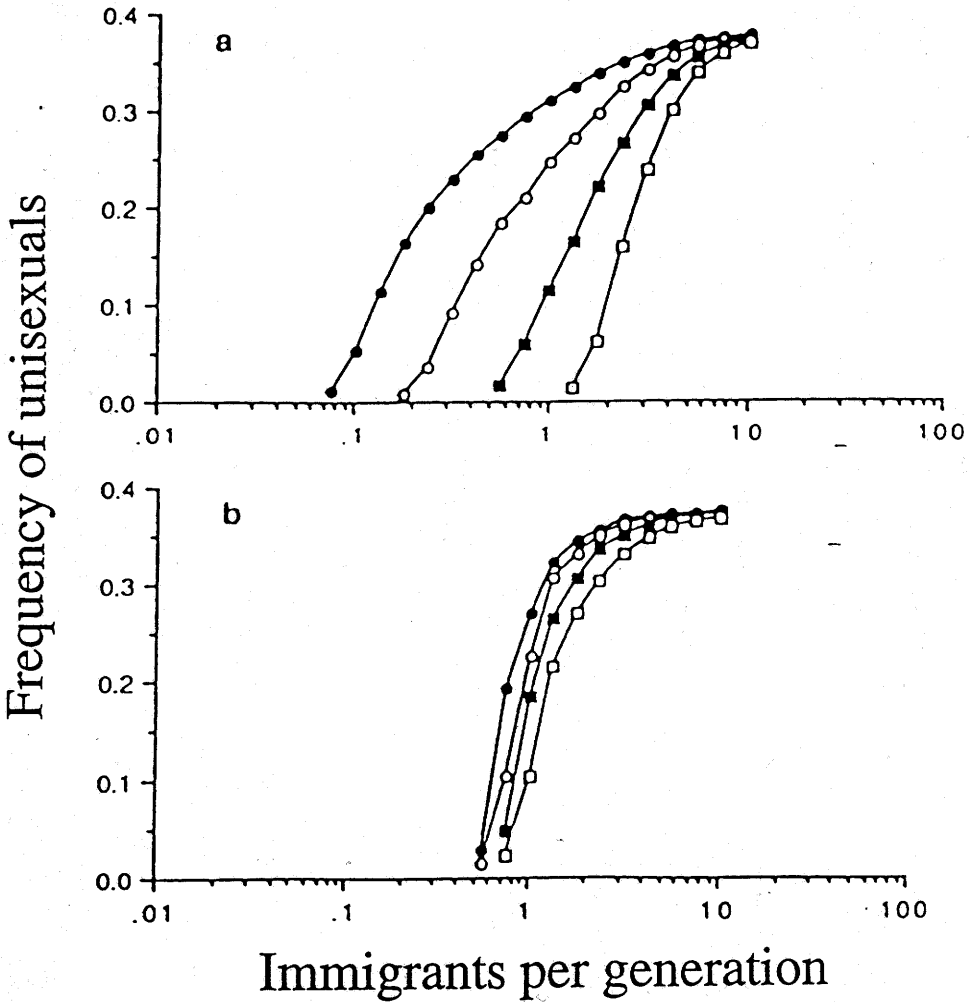


Figure 5.6 Model of combined versus separate sexes in a metapopulation. The frequency of unisexuals at equilibrium in a metapopulation of 2500 sites, plotted against the mean number of immigrants into each site per generation. Curves for four extinction rates are given: 0.05 (closed circles); 0.10 (open circles); 0.20 (closed squares); and 0.40 (open squares). Plots are given for the case of a dominant (a) and a recessive (b) allele for unisexuality. Unisexuals were assumed to produce five times as many seeds (females) or five times as much pollen (males) as cosexuals. (After Pannell, 1997d).

Simulation results differed from those for which cosexuals were assumed to have a single allocation phenotype. In particular, for any given extinction rate, males and cosexuals could be maintained together in the metapopulation only within a relatively narrow range of immigration rates. This is illustrated in Fig. 5.7 for an androdioecious metapopulation with an extinction rate of 0.5. When the mean number of immigrants to a site per generation was high, males occurred at a frequency that approached 0.5 and cosexuals were almost completely female

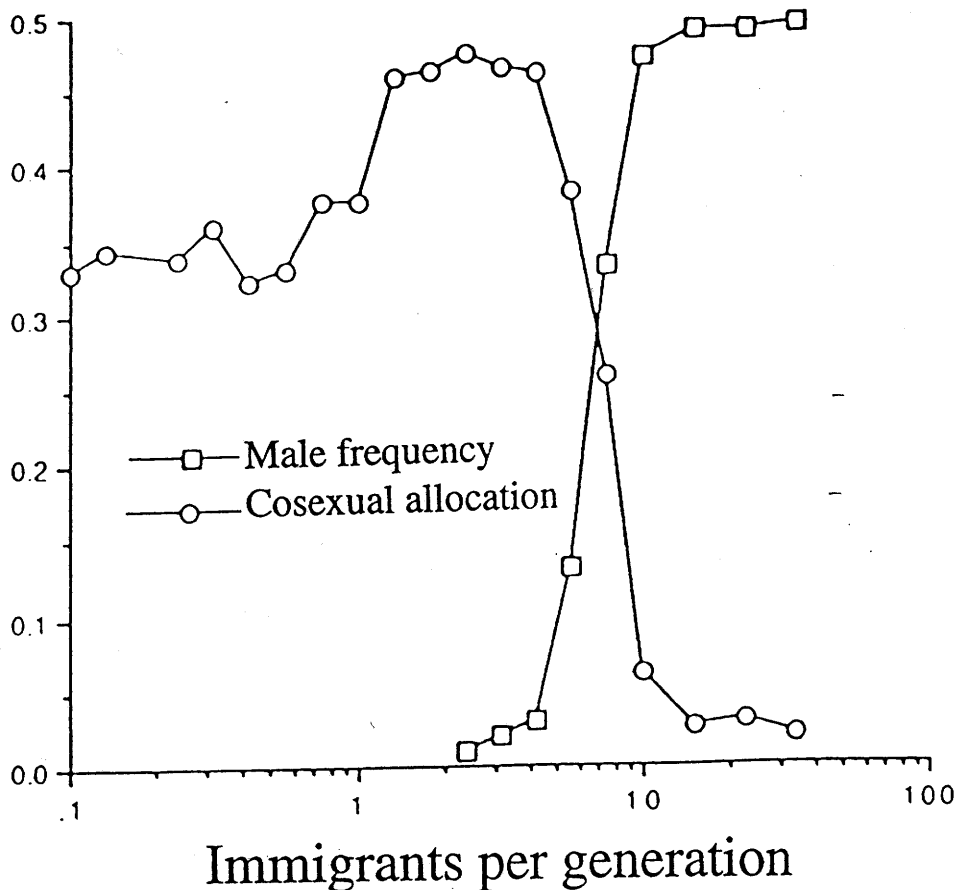


Figure 5.7 Model of sex allocation in a metapopulation. The male frequency (squares) and the relative allocation of resources to female function by cosexuals (circles) in a metapopulation of 500 sites at equilibrium, plotted against the mean number of immigrants into each site per generation, l . At low and high values of l , cosexuality and dioecy, respectively, are selected. (After Pannell, 1995).

(i.e. dioecy was stable). At intermediate immigration rates, the frequency of males fell towards zero, and cosexuals became equisexual. As long as males persisted in the metapopulation, the mean sex allocation, averaged across males and cosexuals, was approximately equal. However, when the immigration rate was low, males were lost from the metapopulation entirely, and cosexual sex allocation became strongly female biased (Fig. 5.7). As discussed above, this is because metapopulation dynamics with a high colony turnover rate favour phenotypes with increased seed productivity, because only seeds are able to found new colonies.

These results provide a further instance of the metapopulation effect, where selection acts in different directions at the local colony and metapopulation levels. Within individual populations, frequency-dependent selection favours equal sex allocation through dioecy with a sex ratio of 0.5. In contrast, at the metapopulation level,

female-biased cosexuality is selected when colony turnover is rapid. This is because males and females lack reproductive assurance, and high seed productivity in cosexuals carries a premium when colonisation of vacant sites is important. The model provides a plausible explanation for the distribution of sexual systems in *Mercurialis*. All seven species of the genus are dioecious and wind-pollinated, and all but *M. annua* are perennial (Tutin *et al.*, 1968). Inflorescence architecture is highly conserved throughout *Mercurialis*, with males bearing their flowers on erect peduncles above the plant and female flowers axillary in position (Pannell, 1997a). This sexual dimorphism is probably the result of selection for optimal dispersal and receipt of pollen (Niklas, 1985), and the convex fitness-gain curves implied by it are most likely the basis for the evolutionary stability of dioecy in the genus. In western Mediterranean populations of *M. annua*, however, it appears that increased population turnover rates have led to the destabilisation of dioecy at the metapopulation level and the evolution of cosexuality. In this region, androdioecy is likely the outcome of selection for cosexuality at the landscape level, opposed by selection for dioecy in established populations due to morphological constraints in inflorescence design and the syndrome of wind-pollination.

5.5 Conclusions

The empirical data reviewed for *Lythrum*, *Eichhornia* and *Mercurialis* indicate that the intraspecific variation in mating systems displayed in these taxa is best understood by considering ecological processes operating at a landscape level. Moreover, our metapopulation models provide plausible explanations for the patterns of variation observed. These results are encouraging and argue for an increased focus on broad-scale spatial variation in ecological and demographic factors as important determinants of evolutionary changes in reproductive mode. Future work on plants will benefit if workers abandon the view of the local population as the only relevant evolutionary unit for studies of mating-system evolution and replace this by a more inclusive perspective that considers the demography and connectivity of populations and their distribution across the landscape.

Metapopulations are likely to have properties more conducive to evolutionary diversification than local populations, because of their greater longevity and the typically broader range of ecological conditions that they encompass. A considerable literature, tracing back to Sewall Wright's 'shifting balance' hypothesis, has considered the importance of population subdivision and metapopulation structure on speciation and the evolution of adaptations (e.g. Wright, 1931; Lande, 1985; Barton and Whitlock, 1997). However, little of this literature has been applied to problems in plant evolution, despite the fact that many plants have small effective population sizes and exhibit strong spatial population structure. Because gene flow, and genetic transmission generally, are governed directly by the mating system, metapopulation processes that influence reproductive mode will also affect processes of adaptive divergence and speciation. In this sense, studies at the metapopulation level may act as a conceptual bridge in the genealogical hierarchy linking micro- and macro-evolutionary enquiry.

What are the prospects that metapopulation studies will help inform systematic and evolutionary studies of plants? At the present time few workers have used these

approaches presumably because of the difficulty in measuring extinction, colonisation and migration (Husband and Barrett, 1996). However, the increased availability of a broader range of genetic markers and the development of phylogeographic methods provide exciting new opportunities to examine the history of genetic exchange among populations (Awise, 1998; Schaal, 1998; Templeton, 1998). Mating system studies will undoubtedly benefit from advances in genetic-marker technology and new statistical models that enable pollen- versus seed-mediated gene flow to be measured at both local and landscape levels (Ennos 1994; Ennos *et al.*, 1999 – this volume; McCauley, 1997; Sork *et al.*, 1999). For species in which populations experience high colonisation and extinction rates, studies of metapopulation dynamics are likely to provide novel insights into the evolution of plant reproductive traits.

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