

Chapter 15

WHY REPRODUCTIVE  
SYSTEMS MATTER  
FOR THE INVASION  
BIOLOGY OF PLANTS

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## 15.1 INTRODUCTION

Human-assisted species introductions and the invasion of newly occupied territory have long fascinated naturalists and biogeographers. In the *Origin of Species*, Charles Darwin (1859) discussed introduced species and considered how their taxonomic relationships might influence competitive interactions and community composition ('Darwin's naturalization hypothesis'; see Hill & Kotanen (2009)). Despite this early interest it was not until almost a century later, with the publication of *The Ecology of Invasions by Animals and Plants* by the Oxford zoologist Charles S. Elton in 1958, that biological invasions were recognized as a distinct phenomenon worthy of study. Today, Elton's volume is still the most cited work in the field of invasion biology and many of the topics he discussed are still active areas of research (Richardson & Pyšek 2008).

Much of Elton's book concerned case histories of animal species and genetic and evolutionary issues were only mentioned occasionally. He briefly considered the role of polyploidy in colonization of mudflats by *Spartina townsendii* (p. 26), speculated on the role of genetics in the decline of Canadian Pondweed (*Elodea canadensis*) in the UK (p. 115) and mentioned the evolution of resistance in insect pests and fungi (p. 141). However, he ignored the evolutionary consequences of biological invasions and the possibility that local adaptation may play a role in the spread of invasive species. In essence, Elton treated species as uniform entities despite the explosive ecological and demographic changes that he documented so well. From a historical viewpoint this is surprising; Oxford was the birthplace of 'ecological genetics' (Ford 1964), evolutionary studies were actively pursued there when his book was written, and Elton's own work was cited in Ford's classic volume.

An evolutionary perspective on biological invasions was not to emerge until the appearance of *The Genetics of Colonizing Species*, edited by the plant evolutionists Herbert G. Baker and G. Ledyard Stebbins (Baker & Stebbins 1965). This influential work arose from a conference in Asilomar, California, the preceding year and among the contributors were many leading evolutionary biologists and several prominent ecologists. The volume focused on the evolutionary changes that occur when plants and animals are introduced to novel environments, although contributors also considered traits promoting colonizing success, and the role of stochastic forces in affecting patterns of genetic variation during colonization. Baker and Stebbins' volume initi-

ated a new branch of invasion biology firmly rooted in population and evolutionary genetics.

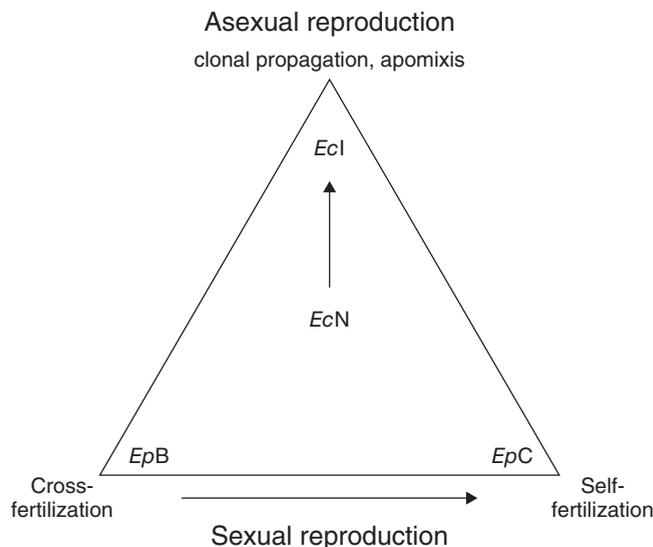
An evolutionary framework for understanding biological invasions has yet to fully emerge and the field still tends to be dominated by case histories despite some attempts at synthesis (Parsons 1983; Williamson 1996; Cox 2004; Sax et al. 2005). One of the difficulties is that invasive species represent a heterogeneous assortment of taxa, with much greater variety in species attributes than is often appreciated. This is especially the case for flowering plants because of their great diversity in life history, reproductive biology and genetic systems. This variation makes attempts at generality a daunting task, even though plants are subject to many of the same ecological and demographic mechanisms that drive evolutionary change in animal populations. Nevertheless, several of the distinctive features of plants including their immobility, hermaphroditism, modularity and clonality, although not unique to plants, influence the character of the invasion process.

In this chapter I consider why reproductive systems matter for the invasion biology of plants. I focus on reproductive systems for two reasons. First, among plant life history traits, modes of reproduction are the most influential in governing evolutionary response to environmental change. This fundamental role arises because reproduction governs genetic transmission between generations, and this in turn affects the organization of genetic variation within and among populations (population genetic structure). Second, plants display enormous diversity in their modes of reproduction, affecting many features of the invasion process including biogeography, demography, and opportunities for the evolution of local adaptation. In this review I pay particular attention to two key topics: (i) plant reproductive diversity and its influence on genetic variation and the evolution of local adaptation; (ii) the role of demographic forces, particularly low density and how this may affect selection on reproductive systems. I conclude by considering future developments in invasion biology and how recent advances in evolutionary genetics may assist in promoting maturity of the field.

## 15.2 PLANT REPRODUCTIVE DIVERSITY

The reproductive system of a population encompasses traits that determine (i) the balance between sexual

**Fig. 15.1** Variation in reproductive systems in flowering plants; the apices (top, left, right) of the triangle represent asexual reproduction (clonal propagation and apomixis), cross-fertilization and self-fertilization, respectively. Species or populations can be located in or on the triangle, depending on their reproductive modes. Arrows indicate shifts in reproductive systems commonly associated with invasion, as discussed in the text for Brazilian (*EpB*) outcrossing and Caribbean (*EpC*) selfing populations of annual *Eichhornia paniculata*, and *E. crassipes* populations from its native (*EcN*) and introduced (*EcI*) range, which differ in the relative importance of clonal versus sexual reproduction. *Eichhornia crassipes* is self-compatible and produces both cross- and self-fertilized seed.



and asexual reproduction, and (ii) the relative amounts of cross-fertilization ('outcrossing') versus self-fertilization ('selfing'). Figure 15.1 illustrates these axes of variation in the form of a triangle in which species or populations can be located, depending on their modes of reproduction (Fryxell 1957). Many angiosperms combine several reproductive modes, and one of the striking features of plant reproductive systems is the diversity that can occur among related species, and among populations within a species. In Fig. 15.1 the location of populations of two *Eichhornia* species featured in this chapter serve to emphasize shifts in reproductive modes that are commonly associated with invasion. Reproductive systems are evolutionary labile and transitions among different modes are commonplace, especially in herbaceous species with widespread distributions (reviewed in Barrett 2008). In this chapter, I consider how invasion fosters such changes and why transitions to uniparental reproduction are a common trend (as indicated in Fig. 15.1). Also, because plants have little direct control over the environments in which they reproduce, ecological and demographic factors play an important role in determining variation in reproductive systems. Much of the observed diversity in modes of reproduction among populations is therefore context dependent.

The reproductive system is an especially important life-history trait for invasive species because the

quantity and genetic quality of propagules influences dispersal and spread to novel environments with both demographic and biogeographical consequences. Reproductive systems also determine opportunities for adaptive evolution because they influence population-genetic parameters including levels of diversity, rates of recombination, effective population size, gene flow and selection response (Schoen & Brown 1991; Charlesworth 1992; Hamrick & Godt 1996). Thus knowledge of the reproductive system is crucial for understanding the demographic and genetic characteristics of populations and for predicting how invasive species are likely to respond to future environmental challenges.

Despite the complexity of plant reproductive systems, a fundamental dichotomy is whether offspring arise from uniparental or biparental reproduction. This distinction is of particular importance for invasive species because mates or pollinators may be limiting during establishment and during subsequent colonizing episodes. Under these circumstances, uniparental reproduction may be favoured over biparental reproduction, especially in species with short life histories. Two axes of quantitative variation are also of significance for invasive populations. First, for species that reproduce both sexually and asexually it is important to establish their relative frequency, as this can influence the clonal diversity of populations (Silvertown 2008). Similarly, determining the fraction

of seeds resulting from cross- versus self-fertilization is relevant for understanding the maintenance of heterozygosity and offspring fitness. Selfing is commonly associated with inbreeding depression and this can have both demographic and evolutionary consequences (Charlesworth & Charlesworth 1987). The use of polymorphic allozyme and microsatellite markers allows measurement of these variables and provides a more quantitative assessment of plant reproductive systems than inferences based on morphology. Much research on plant reproduction (reviewed in Barrett & Eckert 1990; Goodwillie et al. 2005) is concerned with measuring mating patterns in plant populations and evaluating the fitness consequences of outcrossing and selfing.

A recent survey of mating patterns reported that populations occurring in open disturbed habitats on average experienced higher selfing rates than those in undisturbed habitats (Eckert et al. 2010). There is now growing interest in whether anthropogenic changes to environments, including habitat fragmentation, competition between native and introduced species, and various facets of global climate change, influence plant reproduction (Aguilar et al. 2006; Aizen and Vázquez 2006; Traveset & Richardson 2006; Bjerknes et al. 2007; Memmott et al. 2007). Shifts from specialized to generalized pollination and from biparental to uniparental reproduction may characterize future trends in the reproductive biology of populations in human-altered environments.

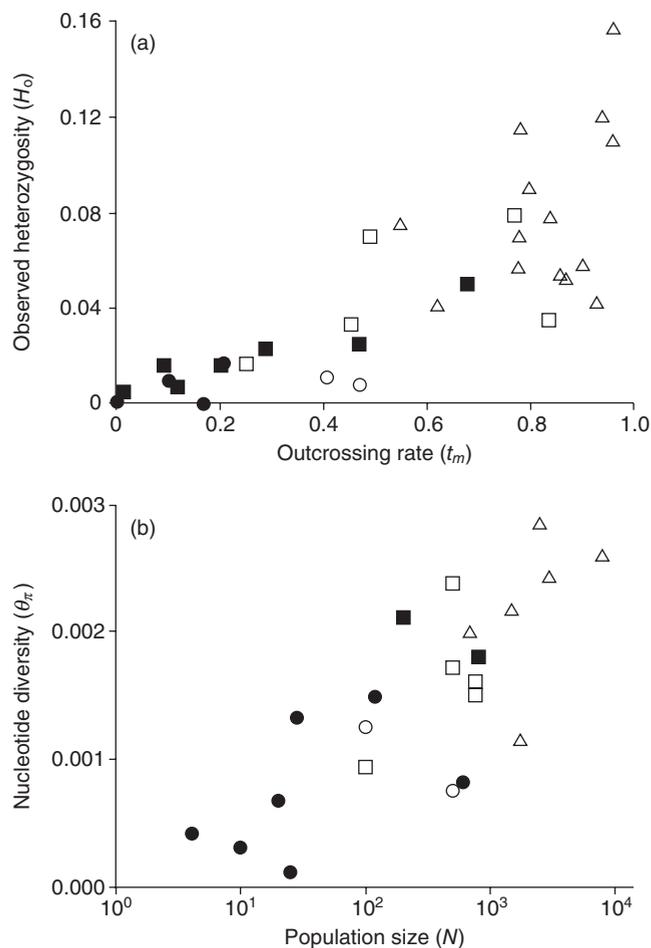
### 15.3 REPRODUCTIVE SYSTEMS AND GENETIC DIVERSITY

Early studies during the biosystematics era established that mating systems were a strong determinant of the patterns of phenotypic variation within and among plant populations (Baker 1953). Inbreeding species generally contained relatively low levels of variation within populations but displayed high differentiation among populations. In contrast, populations of outbreeders maintained more variation but were less differentiated from one another. These early generalizations have now been corroborated theoretically (Charlesworth & Charlesworth 1995) and are supported by surveys of diverse species using allozyme markers (Hamrick & Godt 1996) and, more recently, microsatellites and DNA nucleotide sequences (Charlesworth & Pannell 1999; Baudry et al. 2001;

Ness et al. 2010). Although the total molecular diversity of inbreeders is usually only slightly lower than outbreeders, differences are more dramatic at the population level with inbreeders maintaining, on average, about half of the diversity found in outcrossers. Population structure is more pronounced in inbreeders and this is reflected by significantly higher values of  $G_{st}$  and  $F_{st}$ , both measures of population subdivision. The partitioning of genetic diversity within and among populations is important for invasion biologists, as population differentiation is often associated with ecological differences in the behaviour of populations.

A variety of genetic and demographic factors cause selfing populations to have reduced genome-wide diversity compared with outcrossers (Wright et al. 2008). Homozygosity increases with the selfing rate causing reductions in effective population size ( $N_e$ ) up to twofold with complete selfing (Nordborg 2000). Moreover, because of higher linkage disequilibrium in selfers other processes in the genome, including selective sweeps and background selection, further reduce genetic variation within populations (Charlesworth & Wright 2001). These processes can be augmented by the demographic and life history characteristics of species, especially genetic bottlenecks when a single individual founds a colony. Populations of many annual selfers are characterized by frequent colonization–extinction cycles and these demographic processes can lead to strong population subdivision and erosion of diversity within populations.

The effects of mating patterns and demography on genetic diversity are illustrated by considering the annual *Eichhornia paniculata* (Pontederiaceae), a colonizer of aquatic habitats in the neotropics. This species occurs primarily in northeast Brazil, where populations occupy ephemeral ponds and ditches and are most commonly tristylous, a genetic polymorphism promoting outcrossing. Through long-distance dispersal, *E. paniculata* has also colonized Cuba and Jamaica, where it is a weed of rice fields (see Plate 6a). In contrast to Brazil, populations in the Caribbean are primarily inbreeding because selfing variants capable of setting seed without the requirement of pollinators established after dispersal from South America (Barrett et al. 1989, 2008). Populations in the Caribbean have significantly lower levels of genetic diversity at allozyme loci due to high selfing and bottlenecks associated with island colonization (Barrett & Husband 1990) (Fig. 15.2a). A recent comparison of DNA nucleotide



**Fig. 15.2** Mating patterns and demography are associated with genetic diversity in *Eichhornia paniculata* populations. (a) Relation between multilocus outcrossing rate ( $t_m$ ) and observed heterozygosity ( $H_o$ ) at 19–27 allozyme loci in 32 populations from Brazil and Jamaica. Open and filled symbols are from Brazil and Jamaica, respectively. After Barrett & Husband (1990). (b) Relation between population size ( $N$ ) and nucleotide diversity ( $\theta_\pi$ ) at 10 nuclear loci in 25 populations sampled from Brazil, Cuba and Jamaica. Open symbols are from Brazil, filled symbols are from Cuba and Jamaica. After Ness et al. (2010). In both (a) and (b) the triangles, squares and circles refer to trimorphic (outcrossing), dimorphic (mixed mating) and monomorphic (selfing) populations, respectively.

diversity in populations of varying size and style morph structure from the two regions revealed similar patterns (Ness et al. 2010) (Fig. 15.2b). Low levels of diversity characterized the smallest populations, which were largely composed of selfing variants, whereas larger tristylous populations maintained significantly higher levels of diversity. The association between selfing and small population size in *E. paniculata* highlights the important role that demographic history plays in affecting genetic diversity. The demographic and genetic characteristics of populations are not independent properties and disentangling their joint effects on patterns of diversity is a major challenge.

#### 15.4 GENETIC VARIATION AND RAPID EVOLUTION OF LOCAL ADAPTATION

Biological invasions expose populations to novel selection pressures and the potential for rapid evolution of local adaptation (Prentis et al. 2008). Common garden studies are routinely used to detect differentiation among invasive populations in life-history traits of ecological significance (reviewed in Bossdorf et al. 2005). However, demonstrating that population differentiation results from the evolution of local adaptation is not straightforward because a variety of neutral processes associated with immigration history can also give rise to similar patterns (Maron et al. 2004; Colautti

et al. 2009; Keller et al. 2009). The amount of genetic variation for ecologically relevant traits will determine how rapidly invasive populations respond to natural selection and the rate of response can directly affect the speed of biological invasion (García-Ramos & Rodríguez 2002). Therefore, understanding whether local adaptation is likely to evolve, and how rapidly it will occur, are important questions for invasion biologists and managers.

Evolution during the contemporary timescales typically investigated in studies of invasive species may be constrained by low standing genetic variation within populations and/or the availability of new mutations (Orr & Bettancourt 2001). If adaptation is initiated by new mutations it will depend on the rate at which these arise and whether they are beneficial. In contrast, if a large component of adaptive substitutions results from alleles already present in a population, the rate of change will depend on contemporary selective pressures, the history of selection and the previous environmental conditions that populations encountered (Barrett & Schluter 2008). Given the relatively short timescales involved in most invasions, it is more probable that adaptation will arise from standing genetic variation because beneficial alleles are more likely to be present at low to moderate frequencies.

In some cases, alleles that may be neutral or even deleterious in the native range may become advantageous after introduction to novel environments. This appears to be the case for genes controlling selfing in *E. paniculata* that have enabled colonization of the Caribbean, as discussed above. Selfing modifiers are not uncommon in outcrossing populations in Brazil, but under most circumstances do not spread because they have no advantage because pollinator service is reliable, unlike in the Caribbean (reviewed in Barrett et al. 2008). Understanding the sources and amounts of genetic variation contributing to the evolution of adaptive traits is important because this determines selective outcomes (Hermisson & Pennings 2005). Unfortunately, with the exception of a few well-studied examples of agricultural weeds, for example the evolution of herbicide resistance (reviewed in Neve et al. 2009), little is known about the origin and genetic basis of adaptations in invasive plants.

Most studies of genetic diversity in invasive populations have measured variation at neutral or near neutral genetic markers, usually allozymes (reviewed in Barrett & Shore 1989). Although genetic markers are of use in reconstructing the immigration history of

introduced species (see, for example, Taylor & Keller 2007), they are of less value in predicting the amount of genetic variation for ecologically relevant traits, because the correlation between molecular and quantitative measures of genetic variation is weak at best (Lewontin 1984; Reed & Frankham 2001). The mating system also plays an important role in affecting this relation (Brown & Burdon 1987). In populations of many inbreeding weeds it is not uncommon to find very low levels, or no polymorphism at allozyme loci (see, for example, Schachner et al. 2008). However, genetic uniformity does not necessarily reflect an absence of variation in quantitative characters, and where this has been measured significant amounts of between-family (additive) genetic variation have been revealed in selfing species (Barrett 1988; Warwick 1990). Mutation rates of quantitative characters in selfers are sufficient to generate considerable heritable variation following genetic bottlenecks (Lande 1975, 1977). Adaptive evolution is therefore unlikely to be stalled in most selfing species because of an absence of genetic variation in life-history traits, except where populations have extremely small effective sizes (Schoen & Brown 1991). Indeed, a recent survey of transplant experiments of primarily selfing versus outcrossing species concluded that there was no difference in the likelihood of local adaptation evolving (Hereford 2010).

Reproductive systems mediate the conflicting roles of demographic and historical processes in affecting patterns of genetic variation, with consequences for the evolution of local adaptation. Founder events and genetic bottlenecks result in a loss of diversity, whereas multiple introductions and hybridization can increase diversity. Inbreeding restricts recombination and opportunities for genetic admixture magnifying founder effects and increasing the likelihood that stochastic processes will influence patterns of genetic diversity (Husband & Barrett 1991). In contrast, in outbreeding species hybridization with relatives can boost diversity fostering the evolution of increased invasiveness (Ellstrand & Schierenbeck 2000). Genetic admixture and the origin of genotypic novelty can also occur within invasive species as a result of multiple introductions to the introduced range followed by gene flow between formerly differentiated populations (Kolbe et al. 2004; Lavergne & Molofsky 2007). This process may result in levels of diversity in introduced populations that exceed those generally found in the native range (Novak & Mack 2005; Dlugosch & Parker 2008a). Multiple introductions from source regions

are increasingly reported and the extent to which genetic admixture occurs will be strongly influenced by the mating system of populations. Levels of hybridization should be associated with likelihood of outcrossing, although even highly selfing populations are not immune from occasional outcrossing resulting in genetic admixture (Vaillant et al. 2007).

### 15.5 GENETIC CONSTRAINTS ON THE EVOLUTION OF ADAPTATION

Genetic constraints can restrict opportunities for the evolution of local adaptation, but there is little empirical evidence on how commonly they influence response to selection in natural populations (Antonovics 1976; Blows & Hoffman 2005). Biological invasions provide opportunities for investigating constraints on contemporary evolution because rapid range expansion, especially along climatic gradients, can expose populations to strong selection on traits associated with reproductive phenology. However, fitness trade-offs have the potential to constrain adaptive differentiation across environmental gradients, despite the occurrence of abundant genetic variation for life-history traits within populations (Etterson & Shaw 2001; Griffith & Watson 2006). Genetic constraints may also influence species distributions by preventing local adaptation at range margins, although this has rarely been investigated (reviewed in Eckert et al. 2008). Plant invasions provide experimental systems for understanding the genetic basis of range limits and the role of genetic constraints on responses to selection.

Recent investigations of the invasive spread of the Eurasian wetland plant *Lythrum salicaria* (purple loosestrife, Lythraceae, see Plate 6b) have examined limits to local adaptation associated with northern migration in eastern North America (Montague et al. 2008; Colautti et al. 2010a). This species is highly outcrossing, and molecular evidence suggests that multiple introductions followed by gene flow among introduced populations is responsible for the high levels of diversity within populations (Chun et al. 2009). The showy floral displays of introduced populations attract numerous insect pollinators that mediate pollen transport within and among populations.

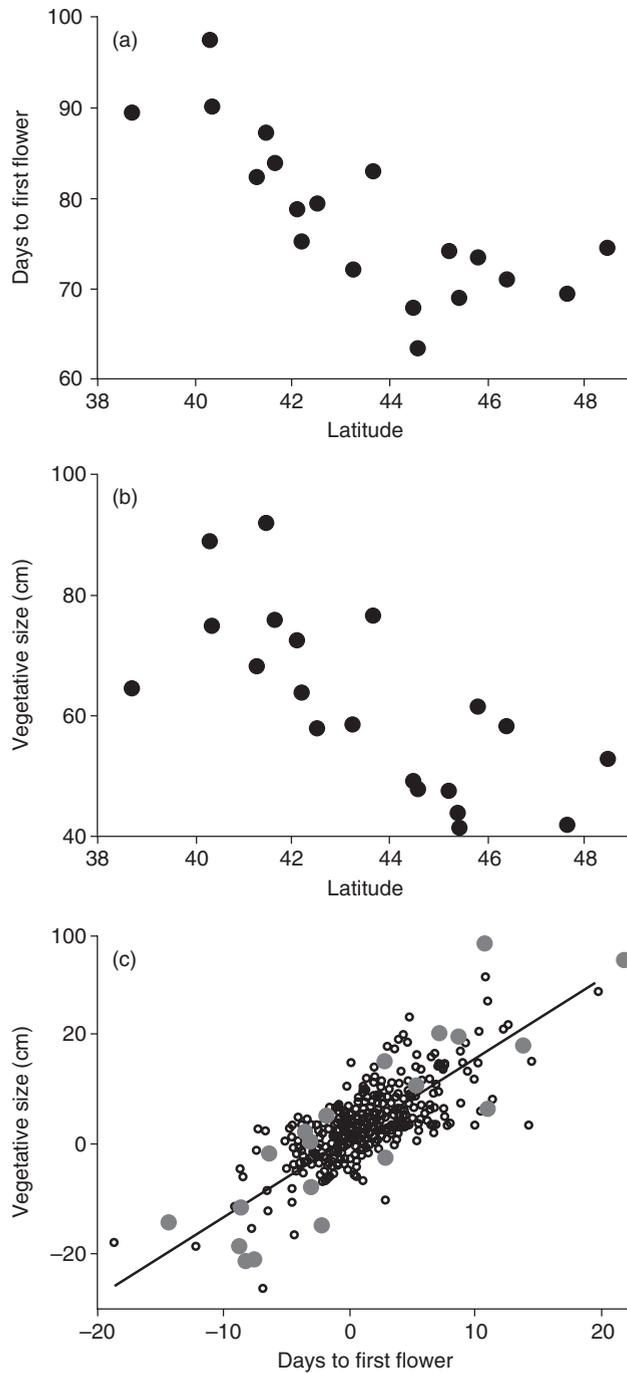
Common garden experiments of *L. salicaria* populations sampled along a latitudinal transect of approximately 1200 km in eastern North America detected large amounts of heritable genetic variation in life-

history traits, of which days to first flower and size were of particular significance (Colautti et al. 2010a). Variation in these two traits formed distinct clines: northern populations flowered more rapidly at a smaller size and those from southern latitudes delayed flowering and were larger (Fig. 15.3a,b; and see Montague et al. 2008). This pattern was associated with a strong genetic correlation between time to first flower and vegetative size. Population means for these traits were distributed along the major axis of covariance of families within populations implicating strong constraints on population divergence (Fig. 15.3c). Northward spread of *L. salicaria* was also associated with a decline in genetic variation of quantitative characters and limited variation for small, early-flowering genotypes. These patterns are consistent with strong selection for local adaptation to shorter growing seasons when there is a trade-off between age and size at reproduction. Striking differences in fecundity distinguished northern and southern populations of *L. salicaria*. Northern populations produced only 4% of the fruit matured by southern populations (Colautti et al. 2010a). Reduced seed production should slow population growth and contribute to reducing rates of spread.

These results suggest that natural selection on reproductive phenology has accompanied the invasive spread of *L. salicaria* in eastern North America. However, genetic constraints and a dearth of early flowering genotypes in northern populations probably contribute to establishing the northern limit of the invasive range, at least over short timescales. Studies at the northern margin of the range of *L. salicaria* in Europe would be valuable to investigate whether genetic factors also play a role in establishing boundaries to the species' native range.

### 15.6 SELECTION ON REPRODUCTIVE SYSTEMS DURING INVASION

Colonization is often associated with low density and/or small population size. These demographic conditions can result in pollen limitation of seed set (Ashman et al. 2004) resulting in 'Allee effects', and a slowing of the invasion process (Allee 1931; Cheptou 2004; Taylor et al. 2004). Empirical efforts to detect Allee effects in invasive species have provided mixed results (Davis et al. 2004; Cheptou & Avendaño 2006; Elam et al. 2007; but see van Kleunen & Johnson 2005; van Kleunen et al. 2007). The vulnerability of populations



**Fig. 15.3** Clinal variation and trade-offs between life-history traits associated with the evolution of local adaptation in invasive populations of *Lythrum salicaria* from eastern North America. Data are from 20 populations, 17 families per population and two individuals per family grown under uniform glasshouse conditions. See Colautti et al. (2010a) for details. (a) Relation between latitude (degrees north) and days to first flower based on population means; (b) relation between latitude (degrees north) and vegetative size based on population means; (c) relation between days to first flower and vegetative size for families (small open symbols) and population means (grey filled symbols). The strong positive relation indicates a genetic trade-off between the two traits.

to Allee effects will be strongly influenced by their mating systems. Self-incompatible species are more susceptible than those that are self-compatible to pollen limitation (Larson & Barrett 2000). Self-compatible plants, particularly those capable of autonomous self-pollination, are more likely to maintain fecundity and establish colonies from a single individual following dispersal. This general principle, known as 'Baker's law' (Baker 1955), was initially used to explain the rarity of self-incompatible species on oceanic islands compared with those that were self-compatible. However, it can be extended to any demographic situation where the reproduction of individuals is limited by an absence of pollinators or mates. This includes conditions at the leading edge of an invasion front or in a metapopulation in which colonization-extinction cycles result in episodes of low density (Pannell & Barrett 1998; Cheptou & Diekmann 2002; Dornier et al. 2008). Uniparental reproduction, by providing reproductive assurance, may allow small populations to grow faster than if they were outcrossing and reduce the duration of post-introduction bottlenecks.

Efforts to investigate the importance of uniparental reproduction for colonization have largely come from surveys of introduced species (Brown & Marshall 1981; Price & Jain 1981; Williamson & Fitter 1996; Rambuda & Johnson 2004). However, interpretation of associations between reproductive systems and colonizing success is complicated by the absence of data on relative rates of introduction (propagule pressure), and by the diverse phylogenetic affinities of species compared. A more powerful method uses paired samples of congeneric introduced species in which one has become invasive, and the other has not. Here, shared ancestry and equivalent opportunity are to some extent controlled. This approach identified the facility for autonomous selfing as an important correlate of invasiveness in South African Iridaceae exported to various regions for horticulture (van Kleunen et al. 2008). More studies of this type using comparative and phylogenetic methods combined with historical information on immigration history would be valuable.

Another way to investigate the reproductive consequences of the invasion process involves looking for direct evidence of evolutionary transitions to uniparental reproduction. Comparisons of conspecific native and introduced populations have been used to explore this question (Brown & Marshall 1981). Shifts to selfing or apomixis are commonly associated with island colonization (see, for example, Barrett et al.

1989; Barrett & Shore 1987; Amsellem et al. 2001). However, at more restricted spatial scales it has proved more difficult to find evidence for genetic changes to reproductive systems, particularly the breakdown in self-incompatibility to self-compatibility (see, for example, Cheptou *et al.* 2002; Brennan et al. 2005; Cheptou & Avendaño 2006; Lafuma and Maurice 2007; Colautti et al. 2010b). Whether recurrent colonization episodes exert selection for uniparental reproductive systems depends on a range of factors including the spatial scale of colonization, gene flow, inbreeding depression, and the availability of genetic modifiers of mating system traits.

Many obligate outbreeders are successful colonizers, especially among introduced woody species where longevity reduces the risk of reproductive failure if mates arrive later in the invasion process. However, outcrossing enforced by self-incompatibility or dioecy should represent a severe liability for annual species because only a single season is available for mating. Not surprisingly in flowering plants as a whole, mating systems are strongly associated with life history, especially longevity, with annual and short-lived species exhibiting, on average, significantly higher selfing rates than long-lived woody species (Barrett et al. 1996). Nevertheless, some self-incompatible annuals have become successful invaders (see, for example, Sun & Ritland 1998; Brennan et al. 2005), raising the question of how these species maintain fecundity during population establishment.

Recent studies of common ragweed (*Ambrosia artemisiifolia*, Asteraceae) are instructive in this regard (Friedman & Barrett 2008). This species is a wind-pollinated annual native to North America but is now invasive in Europe, Asia and Australia. Ragweed had been assumed to be largely selfing, presumably because many annual invaders are selfers. However, Friedman & Barrett (2008) demonstrated high levels of outcrossing enforced by a strong self-incompatibility system using genetic markers. Ragweed possesses several traits that limit opportunities for Allee effects to occur. These include the production of large quantities of windborne pollen reducing the likelihood of pollen limitation, prolific seed production and dormant seed banks. Metapopulation models indicate that high fecundity and seed banks can offset costs associated with low density in self-incompatible colonizing species (Pannell & Barrett 1998). Not all invasive species are equally subject to Allee effects, as the dispersal biology of species plays a crucial role in establishment and

spread. Studies investigating associations between reproductive and dispersal systems of invasive species are long overdue.

### 15.7 INVASION THROUGH ASEQUAL REPRODUCTION

So far, this review has largely considered sexual reproduction, where recombination and gene flow among populations provide the genetic fuel for the evolution of local adaptation. I now turn to species in which sex is infrequent and asexual reproduction predominates through either clonal propagation or apomixis. How likely is the evolution of local adaptation during invasion in these species?

Populations of predominantly clonal plant species are not necessarily genetically depauperate. On the contrary, surveys using genetic markers have demonstrated that populations can maintain considerable amounts of genetic diversity (reviewed in Silvertown 2008). Nevertheless, species that reproduce by asexual means are vulnerable to the influence of founder events, which can become magnified through predominant asexual reproduction, resulting in extensive areas of genetic uniformity. This is a particularly common feature of aquatic invaders through the dispersal of floating vegetative propagules (Barrett et al. 1993; Kliber & Eckert 2005; B. Wang et al. 2005). In some cases, either local or long-distance dispersal events have disabled sexual systems because of the stochastic loss of sexual morphs preventing seed reproduction (e.g. *Fallopia japonica* (Hollingsworth & Bailey 2000); *Nymphoides peltata* (Y. Wang et al. 2005)). When these situations occur, opportunities for local adaptation are curtailed and phenotypic plasticity plays an important role in enabling populations to respond to environmental heterogeneity.

During the past 150 years, water hyacinth (*Eichhornia crassipes*, Pontederiaceae) (see Plate 6c) has become the world's most serious invader of aquatic environments (Gopal & Sharma 1981). It is native to lowland South America but has spread to more than 50 countries, including tropical, subtropical and temperate zones on five continents. Several attributes of *E. crassipes* contribute to its success, including prolific clonal reproduction, the mobility of its free-floating life form and high rates of growth. Interestingly, these features are not represented among the remaining seven species of *Eichhornia*, none of which have become

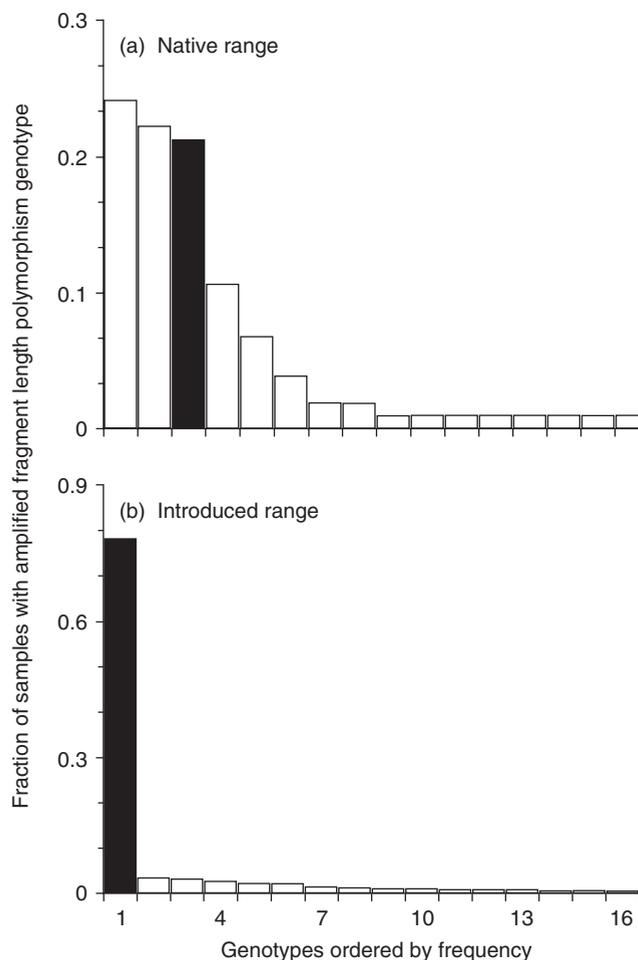
serious weeds (Barrett 1992). This represents a rare case where the traits responsible for invasion success are clear.

Water hyacinth is tristylous, and the geographical distribution of floral morphs indicates that founder events have played a prominent role in the species' worldwide spread (Barrett 1989). Tristylous populations are confined to lowland South America, but in the introduced range the mid-styled morph predominates, with the long-styled morph occurring infrequently. A recent global survey of amplified fragment length polymorphism in ramets sampled from 54 populations has recently confirmed that genetic bottlenecks characterize the species' invasive spread (Zhang et al. 2010). Although 49 clones were detected, introduced populations exhibited very low genetic diversity and little differentiation compared with those from the native range. Eighty per cent of introduced populations were genetically uniform, with one clone dominating in 74.5% of the populations sampled (Fig. 15.4). These patterns of genetic diversity result from extreme bottlenecks during colonization and prolific clonal propagation. This study clearly demonstrates that significant amounts of genetic diversity are not necessarily a prerequisite for global invasive spread over contemporary timescales.

Continent-wide genetic uniformity also occurs in invasive species that reproduce asexually by apomixis (but see Maron et al. (2004) for a counter-example). A recent survey of amplified fragment length polymorphism diversity in *Hieracium aurantiacum* (Asteraceae) revealed almost no genetic variation over much of its introduced range in North America (Loomis & Fishman 2009). *Hieracium* species are particularly interesting because they frequently hybridize, despite being apomictic, providing opportunities for the creation of novel genotypes. In New Zealand reversions from apomixis to obligate sexuality have originated on at least three occasions in populations of *H. pilosella* as a result of hybridization (Chapman et al. 2003). This demonstrates that transitions from uniparental to biparental reproduction can also occur in invasive populations.

### 15.8 FUTURE GENETIC STUDIES ON INVASIVE SPECIES

Invasive species provide opportunities for investigating biological processes over historic timescales. Indeed,



**Fig. 15.4** Genetic bottlenecks and founder events characterize the worldwide invasive spread of *Eichhornia crassipes* (water hyacinth). Comparison of the relative frequency of clones in the native and introduced range based on a survey of amplified fragment length polymorphism. The shaded bar identifies the same clone in the two samples; note the dominance of this clone in the introduced range. Samples size were 104 and 1036 ramets sampled from 7 and 47 populations in the native and introduced range, respectively. A total of 49 clones was detected in the survey; only the most frequent are depicted. From data in Zhang et al. (2010).

this was part of what attracted Charles Elton to the study of introduced species. Elton's focus was primarily ecological; however, because biological invasions are demographic processes, they can have profound genetic consequences of significance for predicting the future evolution of species. Although there is good evidence that reproductive systems of invasive plants play a major role in affecting population genetic structure, it is less clear how important the amounts of genetic diversity are for persistence and spread. In addition, although part of the appeal of studying invasive species is the possibility of integrating historical information into predictions concerning contemporary patterns

and processes, in reality we are only just beginning to use the available tools and approaches for the quantitative analysis of immigration history. I conclude by outlining several future avenues that might be profitably explored on these topics.

Although 45 years have passed since publication of Baker & Stebbins' (1965) seminal volume on the genetics of colonizing species, we still know surprisingly little about the ecological consequences of genetic variation (reviewed in Hughes et al. 2008). As a result, the relations between genetic variation and colonizing success are poorly understood. Long-term field studies are needed to determine the significance of genetic

variation for invasive species. Ideally, these should involve the establishment across environmental gradients of replicated colonies with different genetic inputs of both marker-based polymorphism and quantitative genetic variation for traits relevant to establishment and persistence. Monitoring of population growth and the estimation of demographic parameters of these colonies would help to define the significance of genetic variation for invasive species. Few studies of this type have been conducted on any plant species (although see Martins & Jain 1979; Polans & Allard 1989; Newman & Pilson 1997). It is important to recognize, however, that demonstrating that genetic diversity is associated with colonizing success provides only limited insight into the mechanisms responsible. Experimental manipulations of colonies in which genotype–phenotype relations are identified, combined with phenotypic selection analyses, should help to provide the mechanistic explanations about how and why evolution occurs in invasive populations.

Finally, invasion biology rests on a firmer foundation when information about contemporary patterns of variation can be interpreted using historical information on the source of introductions. Unfortunately, for most invasions we are largely ignorant of immigration history (Marsico et al. 2010). Knowing when, where and how many introductions are responsible for a particular invasion are essential parts of the puzzle of predicting future ecological and evolutionary responses. Recent developments in evolutionary genetics offer some encouragement for more rigorously addressing issues related to migration and demographic history. Phylogeographic methods and the use of coalescence models can reveal novel insights into the evolutionary history of range expansion and the nature of genetic diversity sampled during invasion (Saltonstall 2002; Schaal et al. 2003; Taylor & Keller 2007; Dlugosch & Parker 2008a,b; Rosenthal et al. 2008). This information is of both basic and applied significance and may inform management strategies, such as the choice of geographical areas in the native range sampled for biological control agents of invasive species.

Two recent examples illustrate how evolutionary genetic approaches can aid in providing historical information on invasive species. I begin by returning to the case of *Eichhornia paniculata* and the colonization of Caribbean islands from Brazil. It could be surmised that the occurrence of *E. paniculata* as a weed of rice fields in Cuba and Jamaica resulted from human

assisted migration in historic times, as appears to be the case for the related *E. crassipes*, also native to Brazil (Barrett & Forno 1982). However, coalescent simulations based on nucleotide sequence data firmly reject this hypothesis and show that colonization of the Caribbean by *E. paniculata* probably occurred approximately 125,000 years before present, well before the origins of agriculture (Ness et al. 2010). The second example involves *Arabidopsis thaliana*, an annual selfing weed that is the primary model organism for plant biology. Using Bayesian computations and explicit spatial modelling of molecular variation, François et al. (2008) detected a major wave of migration from east to west about 10,000 years ago in Europe with a westward spread of approximately 0.9 km per year. The spread of *A. thaliana* was associated with a progressive decline in nucleotide diversity probably as a result of repeated bottlenecks. This migration appears to have been associated with spread of agriculture during the Neolithic transition.

These examples demonstrate that gene genealogies and coalescence models can be used to investigate the migration history and demography of species. These approaches have provided unprecedented insights into the global spread of the most successful colonizing species – *Homo sapiens* – (DeGiorgio et al. 2009). It is now time to also apply these approaches to the study of plant invasions so that the value of historical information can be fully realized.

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