

Plant reproductive systems and evolution during biological invasion

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Abstract

Recent biological invasions provide opportunities to investigate microevolution during contemporary timescales. The tempo and scope of local adaptation will be determined by the intensity of natural selection and the amounts and kinds of genetic variation within populations. In flowering plants, genetic diversity is strongly affected by interactions between reproductive systems and stochastic forces associated with immigration history and range expansion. Here, we explore the significance of reproductive system diversity for contemporary evolution during plant invasion. We focus in particular on how reproductive modes influence the genetic consequences of long-distance colonization and determine the likelihood of adaptive responses during invasion. In many clonal invaders, strong founder effects and restrictions on sexual reproduction limit opportunities for local adaptation. In contrast, adaptive changes to life-history traits should be a general expectation in both outbreeding and inbreeding species. We provide evidence that evolutionary modifications to reproductive systems promote the colonizing ability of invading populations and that reproductive timing is an important target of selection during range expansion. Knowledge of the likelihood and speed at which local adaptation evolves in invasive plants will be particularly important for management practices when evolutionary changes enhance ecological opportunities and invasive spread.

Keywords: founder effect, genetic variation, invasive plants, local adaptation, microevolution, reproductive systems, sex

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Introduction

Biological invasion involves the long-distance dispersal of species to regions where they have not previously occurred, followed by rapid multiplication and range expansion. Because the key ingredients for successful establishment and spread involve reproduction, invasion success is strongly influenced by the production, dispersal and genetic constitution of propagules (García-Ramos & Rodríguez 2002; Kinlan & Hastings 2005). These features of life history are largely governed by the reproductive system of populations. Flowering plants exhibit enormous diversity in reproductive systems including extensive variation in the relative importance of sexual vs. asexual reproduction, the degree to which sex involves mating among

unrelated individuals (outcrossing) vs. self-fertilization (selfing), the vectors used to transmit pollen between mates and disperse seeds, and the timing of reproduction during the life cycle. These axes of variation have the potential to influence diverse aspects of invasion dynamics and therefore knowledge of the reproductive system is critical for understanding the biology of plant invasions, and for predicting microevolutionary change in human-altered environments.

Microevolutionary change during biological invasion can occur over contemporary timescales. This 'contemporary' or 'rapid' evolution may influence the rate and pattern of invasion, although evidence for a direct role of adaptive evolution in promoting invasion success is still quite limited (Sakai *et al.* 2001; Stockwell *et al.* 2003; Cox 2004; Lambrinos 2004). The reproductive system determines opportunities for adaptive evolution because it influences important population-genetic parameters

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including genetic recombination, effective population size, gene flow and the partitioning of genetic diversity within and among populations. Extensive surveys of allozyme diversity in plant populations have clearly demonstrated the important role of reproductive systems in governing the organization and levels of genetic diversity within species (Hamrick & Godt 1996). These genetic markers have also provided insights into the relations between reproductive systems and population genetic structure in invasive plants (Barrett & Shore 1989; Lee *et al.* 2004; Bossdorf *et al.* 2005; Novak & Mack 2005). However, the precise role of genetic diversity in invasion success is still poorly understood and future comparative and experimental studies are desirable (Lambrinos 2001).

Large-scale range expansion during biological invasion may demand that invading species adapt to geographical variation in climatic and local ecological conditions, although phenotypic plasticity (Baker 1965; Parker *et al.* 2003) and pre-adaptation through climate matching (i.e. long-distance dispersal between climatically similar regions, Welk *et al.* 2002; Thuiller *et al.* 2005) can also play important roles. For plants in particular, the amount of sexual reproduction and patterns of mating will be crucial for determining the tempo of local adaptation. Because environmental and demographic conditions under which reproduction occur may also change during geographical spread, the reproductive system may be subject to evolutionary modification during invasion (Brown & Marshall 1981). Changes in reproductive traits may then influence the rate and pattern of migration potentially causing evolutionary and ecological timescales to converge during invasion (Hairston *et al.* 2005).

Here, we explore the role of reproductive systems in contemporary evolution during plant invasion. We focus on how reproductive modes influence the genetic consequences of long-distance colonization and the likelihood of microevolutionary change during invasive spread. Our review highlights results from our own research on plant invaders and contrasts taxa with strikingly different reproductive strategies. There has been little synthetic work on the consequences of reproductive diversity for plant invasion and the goal of our review is to illustrate, using three case studies, what may become general principles with continued empirical testing. We begin by exploring the complex interplay between stochastic forces and clonal reproduction in *Butomus umbellatus* (flowering rush). We argue that in this species, strong founder effects and restrictions on sexual reproduction limit opportunities for local adaptation in the introduced range. We then provide evidence that in populations of *Eichhornia* spp. (water hyacinth) with regular sexual recruitment, selection on the reproductive system itself can increase the colonizing potential of invading populations. Finally, we illustrate that reproductive timing is a crucial target of selection

during geographical range expansion in the outbreeding species *Lythrum salicaria* (purple loosestrife) and provide evidence for rapid adaptive evolution in life-history traits. We conclude our review by discussing the implications of reproductive diversity and local adaptation for the management of invasive plants.

Stochastic processes during invasion

Long-distance dispersal is commonly associated with founder events followed by periods of small population size, both of which can result in the stochastic loss of genetic diversity. The frequency of stochastic events and the extent to which their genetic consequences affect the microevolutionary potential of introduced populations are important questions in invasion biology (Barrett 1992; Novak & Mack 2005; Wares *et al.* 2005). Reproductive systems play a key role in determining whether introduced populations experience the stochastic loss of genetic diversity during the invasion process. In contrast to animal groups that rely on outbreeding, the prevalence of self-compatible hermaphroditism and the capacity for asexual reproduction in many invasive plants increase the likelihood for stochastic processes to influence the genetic diversity of populations.

Reproductive assurance provided by uniparental reproduction (e.g. selfing or asexual reproduction by clonal propagation and apomixis) allows establishment after dispersal when founder group sizes are very small. In principle, a single individual can initiate an invasion and severe genetic bottlenecks are reported in invasive plants (e.g. selfing *Echinochloa microstachya* in Australia, Barrett & Husband 1990; clonal *Fallopia japonica* in the United Kingdom, Hollingsworth & Bailey 2000; clonal *Eichhornia crassipes* in China, Li *et al.* 2006). However, by providing reproductive assurance, uniparental reproduction can allow small populations to grow faster than if they were obligately outcrossing (Cheptou 2004; Morgan *et al.* 2005). Such an effect may reduce the duration of post-introduction demographic bottlenecks. Throughout the invasion process, uniparental reproduction restricts recombination and preserves multilocus associations. Reduced recombination also decreases the effective size (N_e) of introduced populations making them more susceptible to genetic drift.

Recent genetic evidence suggests that many large-scale invasions involve multiple introductions from the native range. This may serve to ameliorate founder effects, especially in outcrossing species (Novak & Mack 2005). In contrast, reproduction via predominant self-fertilization or clonal propagation can limit or entirely prevent opportunities for the admixture of genetically differentiated founder stocks. Both types of uniparental reproduction reduce gene dispersal via pollen, which, in outcrossing populations, can be more extensive than gene flow via seed

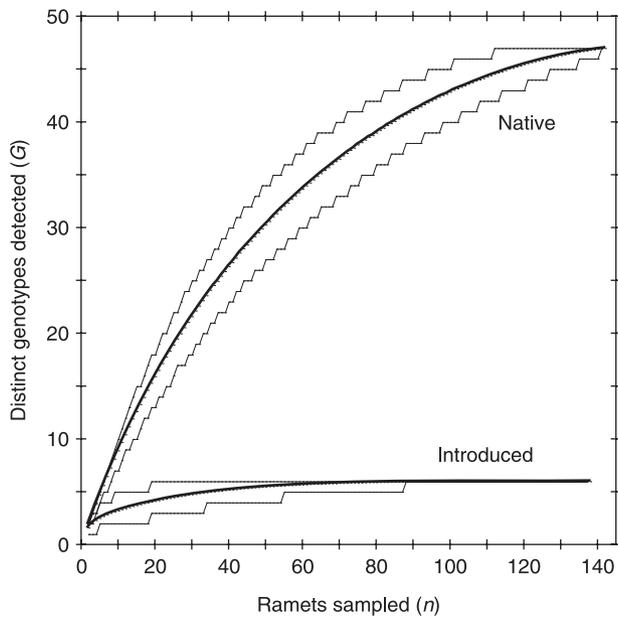


Fig. 1 Evidence of severe founder effect associated with the invasion of North America by the clonal aquatic plant *Butomus umbellatus*. The number of distinct multilocus RAPD genotypes detected (G) increases with the number of ramets sampled (n) much faster and to a much higher level for native than introduced populations. For each region, mean G and 95% confidence limits around G (thin lines) were estimated for each possible n by randomly drawing 10 000 replicates samples of n from the full data set. Figure taken with permission from Klüber & Eckert (2005).

(Levin 2000). Gene flow is severely reduced in many clonally propagated species, limiting recombination and opportunities for microevolution (Eckert 2002).

A stochastic reduction in genetic diversity associated with invasion is well illustrated by the clonal aquatic *Butomus umbellatus* (Butomaceae). Like many aquatic plants, this species has the capacity to reproduce sexually through seed and clonally through rhizome fragmentation, and more importantly, pea-sized, vegetative bulbils produced on rhizomes and inflorescences (Lui *et al.* 2005). Widespread throughout its native range in Eurasia, although often uncommon, the species was introduced to eastern North America in the late 1800s and has since spread across southern Canada and the northern USA. Recent increase in spread, especially in the Great Lakes region, has brought this species to the attention of resource management agencies (White *et al.* 1993).

Klüber & Eckert (2005) compared range-wide patterns of genetic diversity in *B. umbellatus* by assaying random amplified polymorphic DNA (RAPD) variation at 28 loci for pairs of plants from 71 native and 69 introduced populations throughout Europe and North America, respectively. Genetic variation within native and intro-

duced populations indicated predominant clonal reproduction. Only three of 140 paired samples drawn from the same population included more than one multilocus genotype, indicating that genotypic diversity within populations was remarkably low, even for a clonal plant (Widén *et al.* 1994). In contrast, range-wide genotypic diversity differed markedly between Europe and North America (Fig. 1). In both regions, the number of genotypes detected (G) increased with sampling effort (n), as expected for an asexual species. For native populations, however, G increased steadily with n , reaching a plateau only as the final sample size was approached. For introduced populations, G exhibited almost no increase after an n of 40. Overall, 47 genotypes were detected among 142 plants from European populations compared to only 6 genotypes from 138 plants from North American populations. There was also a major difference between regions in how genotypic diversity was structured geographically. European populations exhibited substantial differentiation and a pattern of isolation by distance, whereas two very widespread but divergent genotypes predominated among North American populations, and there was little difference in their geographical distributions.

A common-garden glasshouse experiment involving eight clonal populations of *B. umbellatus* sampled across 8° of latitude and 20° of longitude in North America revealed virtually no population differentiation in life-history traits including flowering time (C.G. Eckert, unpublished data). Based on field observations, there is likely a strong correlation between early flowering and total seed production in *B. umbellatus*. If so, there are two distinct but not mutually exclusive hypotheses for the lack of a latitudinal differentiation in flowering time in introduced *B. umbellatus*. First, genetic uniformity of introduced populations at neutral markers (Klüber & Eckert 2005) may also be associated with low additive genetic variation and reduced response to climatic selection. This could be tested by artificial selection on flowering time. The second hypothesis is that covariation between flowering time and seed production does not affect fitness because most natural recruitment involves clonal progeny rather than seed.

To address the second hypothesis, the relative importance of sexual vs. asexual reproduction was estimated by comparing genotypic diversity between plants in introduced populations with their sexual progeny grown from seed in a glasshouse (Klüber & Eckert 2005). Segregation of RAPD markers occurred among seed progeny despite almost no genotypic variation among their parents. This indicates that very little recruitment in invasive populations involves sexual progeny and is therefore consistent with relaxed selection on traits associated with sexual reproduction such as flowering time. However, latitudinal variation for traits associated with vegetative growth, clonal reproduction and resource allocation was also very

low (C. G. Eckert, unpublished data), suggesting that since introduction, there may have been little or no adaptive evolutionary change for any trait in *B. umbellatus*.

Invasive North American populations of *B. umbellatus* exhibit substantially higher plant vigour than native populations, including strikingly higher allocation to both sexual and clonal reproduction (Brown & Eckert 2004). Without our genetic evidence for a near total lack of sexual reproduction in North American populations, such a difference could be interpreted as the evolution of traits that enhance invasiveness during range expansion (Bossdorf *et al.* 2005). Instead, it is clear that these differences must have arisen from either founder effect or extreme selective sieving of clonal genotypes at introduction (Simons 2003).

We suspect that these findings for *B. umbellatus* may not be atypical and that many clonal invasive plants have the ability to spread extensively over vast geographical regions in the absence of local adaptation as a result of well-developed phenotypic plasticity. Clonal populations should show less adaptive differentiation during range expansion owing to bottlenecks, reduced recombination and limited opportunities for genetic admixture of founding stocks. Unfortunately, there are few comparative studies of clonal and sexual plant invaders that address this prediction (but see Lambrinos 2001).

Evolutionary changes to reproductive systems during invasion

Evolutionary changes to life-history traits during invasion may be most significant when they involve aspects of the reproductive system itself. This is because changes to reproductive strategy feed back on demographic and genetic parameters, which in turn affect the course of evolution. The frequent occurrence in plants of inter- and intraspecific variation in reproductive characters indicates that many traits influencing reproductive mode are evolutionarily labile, and hence could potentially respond to stochastic and selective forces during invasion. There are several examples of reproductive shifts associated with founder events due to the stochastic loss of mating types in species with polymorphic sexual systems (e.g. self-incompatibility, dioecy, heterostyly). These often involve a shift to obligate asexuality through clonal propagation (e.g. *Elodea canadensis*, Sculthorpe 1967; *Fallopia japonica*, Hollingsworth & Bailey 2000; *Oxalis pes-caprae*, Ornduff 1987) and evolutionary modifications to reproductive traits are therefore generally absent in these species.

During immigration, founding individuals usually occur at low density, thus restricting mating opportunities. For plants that rely on animals for cross-pollination, this situation may be exacerbated if pollinators avoid visiting small, sparse populations. Low-density conditions

can therefore persist for a considerable time after the initial founder event resulting in 'allee effects'. Repeated cycles of colonization and low-density may favour uniparental reproduction because selfing and asexuality provide reproductive assurance (Eckert *et al.* 2006). This is supported by a preponderance of selfing or asexual species under conditions of low density or during frequent episodes of colonization (Baker 1967; Price & Jain 1981; Pannell & Barrett 1998). A recent analysis of 17 invasive species in South Africa indicated that all were capable of uniparental reproduction. This is unusual given the low frequency of this condition among long-lived woody plants, which comprised 13 of the species studied (Rambuda & Johnson 2004).

Whether allee effects play a role in limiting the spread of invaders has received some theoretical (Kinlan & Hastings 2005) and empirical investigation (Parker 1997; Davis *et al.* 2004; van Kleunen & Johnson 2005; Elam *et al.* 2007). Yet, to what extent allee effects exert selection on the mating systems of invading populations, and whether selective and stochastic forces interact to modify reproductive systems has been largely unexplored by invasion biologists. The limited data available provide mixed results with the outcomes depending largely on the spatial and temporal scale of colonization and the particular reproductive mode involved (Michalakis *et al.* 1993; Amsellem *et al.* 2001; Brennan *et al.* 2005; Cheptou & Avendaño 2006; Lafuma & Maurice 2007). Heterostylous colonizers are likely to be especially vulnerable to evolutionary destabilization of their reproductive systems because of the limited number of mating groups within populations (Barrett & Shore 1987; see below).

One of the most comprehensive analyses of a shift from outcrossing to selfing involves *Eichhornia paniculata* (Pontederiaceae), a tristylous aquatic plant common in ephemeral wetland habitats in northern Brazil that has colonized Central America and the Caribbean, where it is a weed of rice fields and flooded pastures. Populations are largely annual and therefore depend on seed production for persistence (Barrett & Husband 1997). Stochastic processes during colonization are implicated in the evolution of selfing from outcrossing in *E. paniculata*. The colonization of Caribbean islands and Central America from Brazil is coincident with the loss of floral morphs from populations. Self-fertilization has evolved in geographically marginal populations because selfing facilitates establishment following long-distance dispersal in regions where the species' Brazilian pollinators are absent (Barrett *et al.* 1989). Evidence from allozymes and DNA sequence variation indicates that selfing has evolved on multiple occasions in *E. paniculata* in different geographical regions (Husband & Barrett 1993; R.W. Ness, S.I. Wright & S.C.H. Barrett, unpublished data). Recessive modifiers are responsible for the morphological changes to flowers that promote

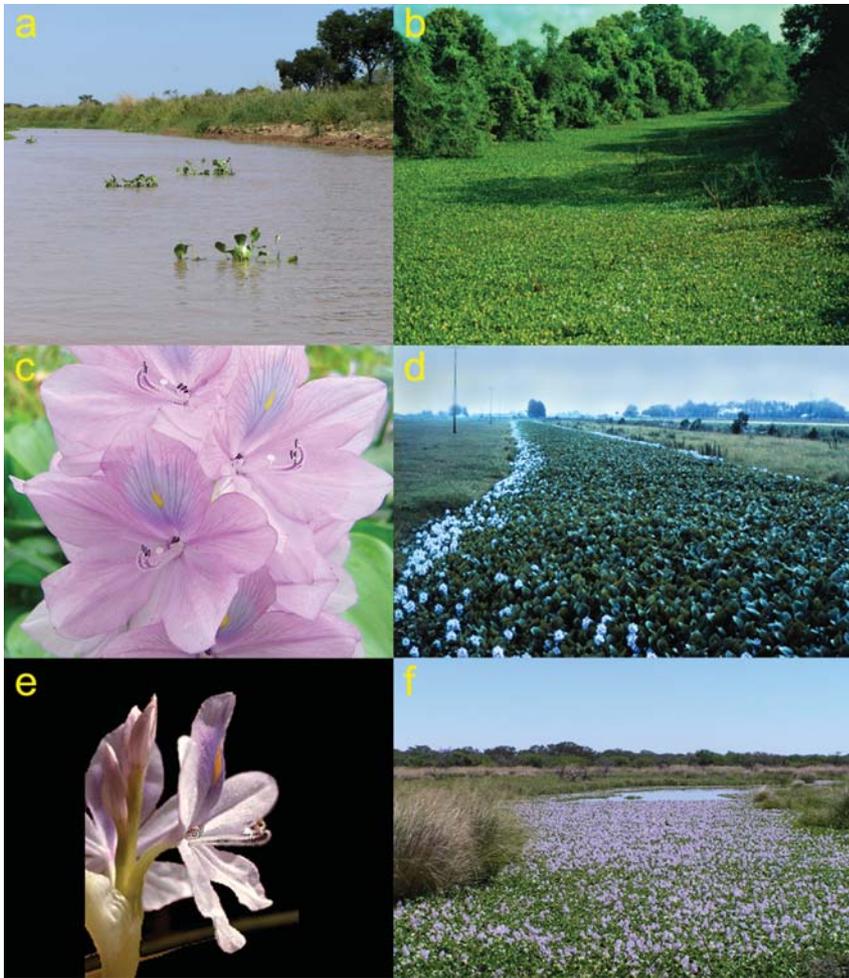


Fig. 2 Biological invasion by water hyacinth (*Eichhornia crassipes*). (a) water-dispersed floating plants along tributaries of the Rio Parana, Rosario, Argentina. In the introduced range, these initiate new invasions and also function in 'mate-finding', particularly in the native range where all three floral morphs occur; (b) severe river infestation resulting from prolific clonal propagation near Louisiana, USA. Flowering can be infrequent in these primarily clonal populations; (c) the mid-styled morph illustrating the physical separation between female and male sexual organs, which limits the autonomous self-pollination of flowers. This morph dominates throughout the introduced range; (d) blockage of a canal in Florida, USA by clonal propagation. Note the band of flowering at the colony edge, which is probably stimulated by contact with the substrate. Although seed is often produced in these circumstances it rarely germinates owing to an absence of safe sites; (e) selfing variant of the mid-styled morph from Palo Verde Marsh, Guanacaste Province, Costa Rica. Stigmas and long-level anthers are adjacent resulting in autonomous self-pollination of flowers; (f) mass flowering in Argentina stimulated by receding water levels. Under these circumstances sexual reproduction is common, especially if clones are destroyed by desiccation. Sexual populations in the native range often contain mixtures of floral morphs.

self-pollination, indicating that adaptation can result from relatively simple genetic changes (Fenster & Barrett 1994).

How often adaptation results from new mutations rather than from standing genetic variation is currently a central question in evolutionary biology (Orr & Bettancourt 2001; Hermisson & Pennings 2005). Because invasive species frequently confront novel environmental conditions, it is possible that adaptive change could be fuelled by alleles with neutral or even deleterious effects in source populations, but which become favoured in new ecological contexts. This appears to be the case in *E. paniculata*. Selfing modifiers commonly occur at low frequency in outcrossing, tristylous populations in Brazil but they probably fail to spread because reliable pollinator service maintains fertility and selfing involves genetic costs resulting from inbreeding depression and pollen discounting.

Pronounced founder effects are also evident in the widespread biological invasion by *Eichhornia crassipes* (Pontederiaceae; water hyacinth). This species is a tristylous floating aquatic, native to lowland South America, with a prodigious capacity for clonal propagation (Fig. 2).

Founder effects have played a major role in governing the geographical distribution of style morphs in the introduced range. Indeed, in common with *E. paniculata*, these have compromised the functioning of the species' tristylous outcrossing system. Tristylous populations are restricted to lowland South America; whereas throughout the introduced New and Old World ranges, the mid-styled morph predominates, the long-styled morph is less common, and the short-styled morph is absent (Barrett 1989). Most invasive populations only contain the mid-styled morph (Fig. 2c), which strongly indicates that these populations are exclusively clonal, even though plants can produce viable seed if pollinated. In common with *Butomus umbellatus*, clonal reproduction predominates in invasive populations of *E. crassipes* because ecological conditions strongly favour recruitment of clonal progeny over seed. In *E. crassipes*, this occurs because of an absence of suitable ecological conditions for seed germination and establishment. Geographical variation in opportunities for seed recruitment may be common in clonal plants producing corresponding geographical variation in the

evolutionary potential of populations (Eckert 2002). Occasionally, *E. crassipes* invades habitats where seasonal fluctuations in water level encourage mass flowering and sexual reproduction (Fig. 2f). Under these conditions, there is good evidence for evolutionary changes to floral morphology that promote self-pollination, similar to those that occur in *E. paniculata* (Fig. 2e; Barrett 1979; Ren *et al.* 2004).

Reproductive transitions in both *Eichhornia* species are triggered by dispersal associated with range expansion. Stochastic processes result in the loss of floral morphs from populations and this sets the stage for the evolution of adaptations that promote selfing in populations suffering from unreliable pollinator service. The main difference between *E. crassipes* and *E. paniculata* is the tempo of evolutionary change, and this is undoubtedly linked to the contrasting life histories of the two species (perennial vs. annual, respectively) and the degree of sexuality of populations. However, the effect of these differences on the rate of microevolutionary change is contingent on ecological conditions. Global climate change scenarios predict more frequent droughts and floods in certain regions. These environmental extremes simulate the dramatic water level fluctuations that characterize the native wetland habitats that *E. crassipes* inhabits in lowland South America and where seasonal episodes of sexual recruitment commonly occur (Barrett 2000). Future global environmental change could provide opportunities for frequent bursts of sexual reproduction in the introduced ranges of water hyacinth and other clonal aquatic plants resulting in microevolutionary responses and the development of local adaptation.

Adaptive evolution of flowering time during invasion

Quantitative genetic variation in life-history traits within and between plant populations is near ubiquitous (Mazer & Leubhn 1999). Given that invasive populations of sexual and outcrossing species usually maintain genetic variation following long-distance dispersal (Novak & Mack 2005), it is expected that invasive species will undergo adaptive evolutionary change as they encounter novel selective pressures during range expansion. Large-scale range expansion exposes invaders to geographical variation in climate, and successful invasion requires that populations sustain a positive growth rate in the face of this variation. Hence, adaptive differentiation of life-history traits associated with variation in temperature, rainfall and seasonality should occur commonly. Climatic adaptation often produces clinal variation and several studies of invasive plants have detected latitudinal clines in life-history traits (Weber & Schmid 1998; Kollmann & Bañuelos 2004; Maron *et al.* 2004; Leger & Rice 2007). The timing of flowering, in particular, is considered to be one of the most important

traits likely to influence range expansion (Griffith & Watson 2006).

We are investigating variation in flowering time in tristylous *Lythrum salicaria* (Lythraceae; purple loosestrife) to obtain evidence for contemporary evolution in reproductive traits during its invasive spread in eastern North America (J.L. Montague, S.C.H. Barrett & C.G. Eckert, unpublished manuscript; R.I. Colautti, C.G. Eckert & S.C.H. Barrett, unpublished data). Native to Eurasia, this species was introduced ~200 years ago to the eastern seaboard of North America, and has since spread to many parts of the continent (Thompson *et al.* 1987). The first phase of our study was aimed at determining whether *L. salicaria* has re-developed the clinal patterns in flowering time reported from the native range (Olsson & Ågren 2002). Evidence for clinal variation among introduced populations of *L. salicaria* depends on the amount of heritable variation in flowering time and the relative strength of deterministic vs. stochastic forces acting on this variation. Our earlier studies of *L. salicaria* indicated that stochastic forces were strong enough to affect the frequency and representation of mating types in invasive populations, despite negative frequency-dependent selection (Eckert *et al.* 1996a, b). Therefore, it was plausible that stochastic processes during migration could impede adaptive evolution.

We selected 25 populations across most of the latitudinal range of *L. salicaria* in eastern North America representing the full range of invaded habitats. Our transect spanned ~1400 km, with the length of the growing season varying from 138 to 256 days based on an 8 °C growth threshold for *L. salicaria*. First, we monitored all populations throughout an entire reproductive season and measured a range of life-history traits including flowering time, size at flowering and reproductive output. We then sampled open-pollinated half-sib seed families from each population and grew these to flowering in different common glasshouse environments, and in field plots over several seasons. Because we used family structured comparisons in our glasshouse experiments, we were able to estimate the heritable component of phenotypic variation.

Among natural populations of *L. salicaria*, we detected a strong latitudinal cline in the time from the beginning of the growth season to the mean date of first flowering (Fig. 3a). Plants in populations at higher latitudes flowered earlier in the season than those at lower latitudes. This pattern was associated with a trade-off between time to flowering and reproductive output mediated by size. Plants in the most northern populations were much smaller at flowering and produced only ~10% of the seeds per season compared with the most southern populations, indicating a potentially severe demographic cost to early flowering. Almost identical clines in time to flowering and size at flowering were observed in both glasshouse

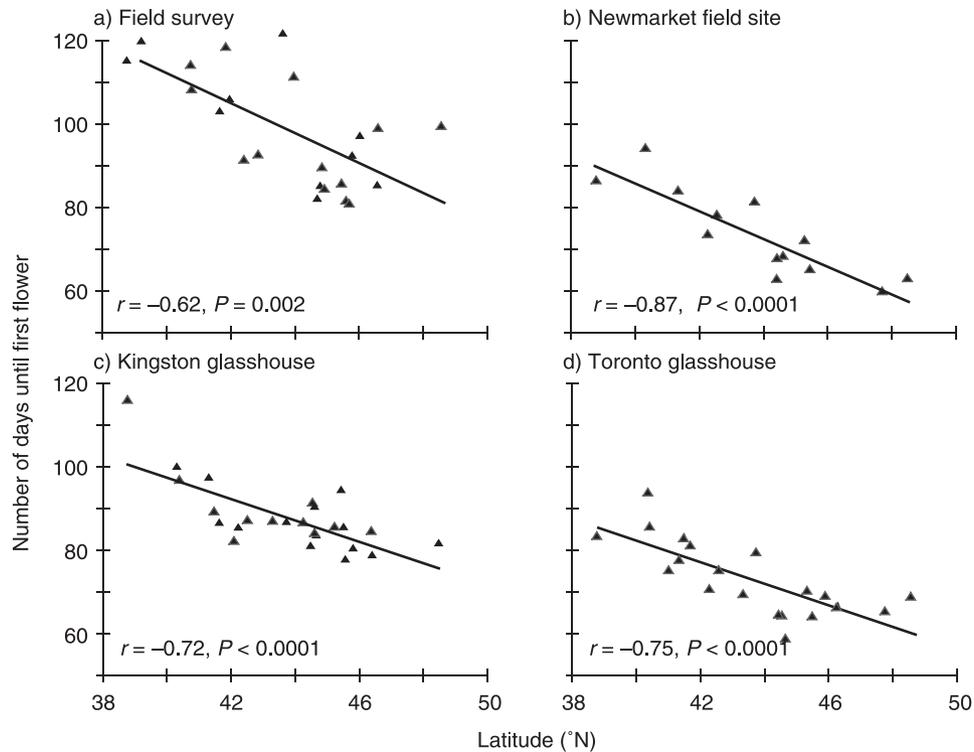


Fig. 3 Latitudinal cline for flowering time among introduced populations of *Lythrum salicaria* in eastern North America (J.L. Montague, S.C.H. Barrett & C.G. Eckert, unpublished manuscript; R.I. Colautti, C.G. Eckert and S.C.H. Barrett, unpublished data). Points are population means. (a) 23 natural populations along a latitudinal transect for days to flower from the beginning of the growing season (i.e. when the mean temperature exceeded 8 °C); (b) 13 populations (planted the previous year and over-wintered in the field) for number of days from the beginning of the growing season to first flower, based on 20 families per population each represented by four progeny grown in a common garden at Newmarket, Ontario, Canada; (c) 25 populations for the number of days from sowing to first flower based on 30 families each represented by two progeny grown in a common glasshouse environment at Kingston, Ontario, Canada; (d) 20 populations for the number of days from germination to first flowering, based on 17 families each represented by eight progeny, grown in a common glasshouse environment at Toronto, Ontario, Canada. For each data set, there is a strong significant negative Pearson correlation (r) between time to flowering and latitude.

experiments (Fig. 3c, d), suggesting a strong genetic basis to the geographical variation observed in the field. The cline was also evident when open-pollinated families were grown for several years under field conditions (Fig. 3b), indicating that nongenetic maternal effects on life-history traits in this very small-seeded species are unlikely to explain the marked latitudinal variation in life history. The glasshouse experiments revealed significant broad-sense heritability for a variety of traits including flower time (and see O'Neil 1997). Finally, the distribution of flowering time varied markedly along the cline with populations at the northern limit exhibiting much narrower variation and a truncation of the distribution below ~45 days (Fig. 4). This pattern suggests that there may be a limit to how early plants of *L. salicaria* can flower, with implications for further northward spread.

Our results are consistent with the evolution of clinal variation in flowering time during the invasive spread of *L. salicaria* following introduction to North America.

However, inferences from 'common garden' studies do not constitute definitive evidence of adaptation. This requires reciprocal transplant experiments demonstrating local adaptation and selection gradient analysis providing evidence of selection on the timing of flowering (see O'Neil 1999). Moreover, several alternative explanations for the geographical patterns we observed also need to be evaluated. These alternative hypotheses are particularly relevant to studies of invasive species for which source regions are not well understood, as is the case in *L. salicaria*.

Clinal variation in wide-ranging species can sometimes arise through the joint action of genetic drift and gene flow (Endler 1977). However, in *L. salicaria*, we consider this unlikely since many populations, especially at range limits, are geographically isolated so that gene flow among populations is probably quite limited. Another possibility is that the cline we observed is the result of introductions from source populations in Europe directly to climatically similar regions in North

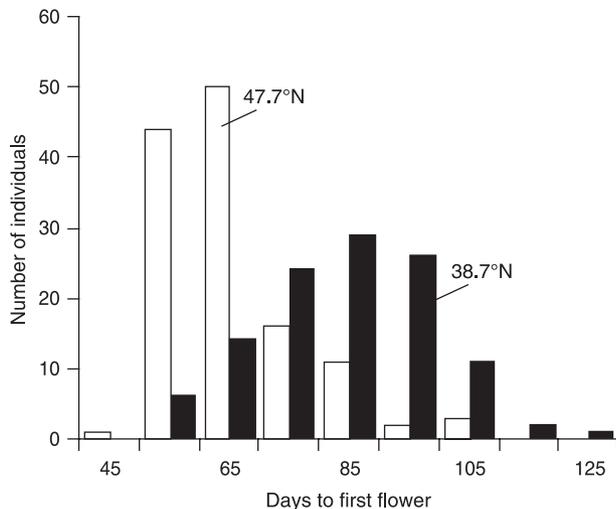


Fig. 4 Latitudinal difference in the distribution of phenotypic variation for flowering time among introduced populations of *Lythrum salicaria* from eastern North America grown in a common glasshouse environment at Toronto, Ontario, Canada. Each distribution involves eight progeny from 17 open-pollinated families sampled from a single population. At the southern end of the species' introduced range (38.7°N), the phenotypic distribution is near-normal, whereas the distribution is highly skewed and truncated at ~45 days at the northern end of the species' range.

America ('climate matching'; see Maron *et al.* 2004; Leger & Rice 2007). We also consider this 'ecological sorting' hypothesis unlikely since it is at odds with what is known about the colonization and spread of *L. salicaria* in North America. Herbarium records indicate introduction to a few ports on the east coast followed by expansion north, south and westwards (Thompson *et al.* 1987). In Ontario, where many of our populations were sampled, *L. salicaria* has only recently spread northwards and newly founded populations are unlikely to have been introduced directly from Europe, pre-adapted to northern conditions.

Phylogeographical analysis of *L. salicaria* would be useful to provide the geographical context for immigration. In common with other plant invaders for which introduction history has been investigated using genetic markers (Novak & Mack 2001; Maron *et al.* 2004; Bossdorf *et al.* 2005; Kliber & Eckert 2005) it seems likely that in *L. salicaria* this would reveal multiple introductions. However, to untangle the complex interplay of history and contemporary selective forces, it may be less important to know how many introductions are involved in a specific invasion, but rather where they came from and where they arrived. This is because recent invasions may be affected as much by historical processes in the source regions as by the number of introductions involved (Taylor & Keller 2007). Unfortunately, for outbreeding species like *L. salicaria*,

identifying source regions may be difficult because of genetic admixture in early immigrant populations before the main phase of invasive spread (Wares *et al.* 2005). It has also been suggested that hybridization with native *Lythrum alatum* has played a role in the spread of *L. salicaria*, although molecular evidence does not clearly support this scenario (Houghton-Thompson *et al.* 2005).

Implications for management of invasives

Many invasive plants colonize a wide range of environmental conditions through phenotypic plasticity (Baker 1965; Parker *et al.* 2003). Indeed, for invaders that rely largely on asexual reproduction (e.g. many aquatic weeds), plasticity represents the principal means by which genotypes cope with environmental heterogeneity. However, for most species that engage in sexual reproduction, prolonged residency in the introduced range should inevitably lead to the adaptation of populations to local environmental conditions. Our review has considered how stochastic forces and natural selection interact in invasive populations and the extent to which both processes are influenced by reproductive mode. We conclude our review by asking how evolution in introduced populations could impact management strategies designed to control invasive plants.

Despite recent literature on the evolutionary dimension of biological invasion (Sakai *et al.* 2001; Lambrinos 2004; Bossdorf *et al.* 2005) there has been much speculation but little quantitative analysis of how local adaptation is likely to influence the spread of invasives (but see García-Ramos & Rodríguez 2002). In obvious cases such as the development of mimetic (Barrett 1983) or herbicide resistant (Le Baron & Gressel 1982) races of agricultural weeds, microevolutionary responses clearly favour spread and complicate attempts to reduce weed infestations. However, does contemporary evolution in other types of invasive plants always represent a threat, and if so, what measures should be taken to limit opportunities for local adaptation?

We conclude by considering these questions in light of our recent work on *L. salicaria*. We focus on this species for two reasons. First, *L. salicaria* is one of the most serious invaders of wetland ecosystems in North America and has been the target of diverse management strategies from simple mechanical eradication through herbicide spraying to biological control. Second, *L. salicaria* is a highly diverse outbreeder, with an exceptionally wide geographical distribution in Europe, ranging from Israel to Finland. This species therefore has the potential physiological and ecological amplitude to spread to diverse climatic regions of North America and other temperate regions of the world. In so doing, *L. salicaria* could serve as a model for studies

of adaptive evolution in other invasive plants, particularly sexual outbreeders.

How might the re-establishment of clinal variation in flowering time affect the spread of *L. salicaria* in eastern North America and influence control? The striking differences in reproductive output that we recorded between northern and southern populations seem likely to influence the rate of spread at a regional scale. This is because seed is particularly important in establishing new populations of *L. salicaria*, even though it may be relatively unimportant for the growth of established populations (C.A. Lacroix & B.C. Husband, unpublished data). Indeed, the regional distribution of *L. salicaria* in North America appears to be largely limited by seed dispersal (Yakimowski *et al.* 2005). Based on our results, we predict that the southern limit of the range of *L. salicaria* will expand more quickly than the northern limit. This could occur for two reasons. First, the much higher seed output ($> 10\times$) of southern populations favours increased dispersal, and second, northern range expansion may be limited by genetic and developmental constraints on early flowering (Fig. 4). Herbarium records, field observations and reports from regional biologists support the prediction of southern range expansion. Therefore, efforts to limit the geographical spread of *L. salicaria* in eastern North America might usefully focus on preventing seed output in populations along the southern boundary. Elsewhere, it has been proposed that concentrating on the management of nascent foci at range limits in invasive plants represents a more effective strategy for limiting spread than focusing effort on eradicating high-density populations in central parts of the introduced range (Moody & Mack 1988).

Burdon & Marshall (1980) reported that outbreeding species might be more difficult than asexual species to eradicate by biological control because of the possibility of host resistance developing in genetically variable populations. Although this conclusion may have been premature (Chaboudez & Sheppard 1995), abundant genetic variation in populations of *L. salicaria* could have important implications for current management strategies based on biological control. Four species of insects have been introduced to North America to control *L. salicaria*, two of which feed on leaves, one on flowers and one on roots (Malecki *et al.* 1993). Temporal matching of growth and reproduction between these specialist herbivores and their host may influence their effectiveness as control agents. The geographical variation in reproductive phenology and growth that we demonstrated may lead to parallel adaptations in insect life history. Direct selection via climatic factors on insect life history may counter or augment selection imposed by phenological variation among host populations. Although effective control agents must be able to adapt as they spread geographically with their host, they must at the same time lack the adaptive

potential to shift on to nontarget hosts. Temporal variation in damage by control agents may ultimately alter the intensity and form of selection on host phenology.

Phenological matching has been considered in the selection of biological control agents (reviewed in Myers & Bazely 2003). However, subsequent geographical co-adaptation between host and control agent has received less attention in the literature on biological control. Evolutionary differentiation in phenology and growth accompanying the spread of introduced populations of *L. salicaria* may provide opportunities to investigate the co-evolutionary dynamics of biological control agents and their hosts. This could lead to new insights into the biological control of invading plant species.

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References

- Amsellem L, Noyer JL, Hossaert-McKey M (2001) Evidence for a switch in the reproductive biology of *Rubus alceifolius* Poir. (Rosaceae) towards apomixis, between its native range and its area of introduction. *American Journal of Botany*, **88**, 2243–2251.
- Baker HG (1965) Characteristics and modes of origins of weeds. In: *The Genetics of Colonizing Species* (eds Baker HG, Stebbins GL), pp. 147–172. Academic Press, New York.
- Baker HG (1967) Support for Baker's Law as a rule. *Evolution*, **21**, 853–856.
- Barrett SCH (1979) The evolutionary breakdown of tristylly in *Eichhornia crassipes* (Mart.) Solms (water hyacinth). *Evolution*, **33**, 499–510.
- Barrett SCH (1983) Crop mimicry in weeds. *Economic Botany*, **37**, 255–282.
- Barrett SCH (1989) Waterweed invasions. *Scientific American*, **260**, 90–97.
- Barrett SCH (1992) Genetics of weed invasions. In: *Applied Population Biology* (eds Jain SK, Botsford L), pp. 91–119. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Barrett SCH (2000) Microevolutionary influences of global change on plant invasions. In: *The Impact of Global Change on Invasive Species* (eds Mooney HA, Hobbs RK), pp. 115–139. Island Press, Covelo, California.
- Barrett SCH, Husband BC (1990) The genetics of plant migration and colonization. In: *Plant Population Genetics, Breeding, and Genetic Resources* (eds Brown AHD, Clegg MT, Kahler AL, Weir BS), pp. 254–277. Sinauer & Associates, Sunderland, Massachusetts.
- Barrett SCH, Husband BC (1997) Ecology and genetics of ephemeral plant populations: *Eichhornia paniculata* (Pontederiaceae) in northeast Brazil. *Heredity*, **88**, 277–284.

- Barrett SCH, Shore JS (1987) Variation and evolution of breeding systems in the *Turnera ulmifolia* L. complex (Turneraceae). *Evolution*, **41**, 340–354.
- Barrett SCH, Shore JS (1989) Isozyme variation in colonizing plants. In: *Isozymes in Plant Biology* (eds Soltis DE, Soltis PE), pp. 106–126. Dioscorides Press, Portland, Oregon.
- Barrett SCH, Morgan MT, Husband BC (1989) The dissolution of a complex genetic polymorphism: the evolution of self-fertilization in tristylous *Eichhornia paniculata*. *Evolution*, **43**, 1398–1416.
- Bossdorf O, Auge H, Lafuma L *et al.* (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.
- Brennan AC, Harris SA, Hiscock SJ (2005) Modes and rates of selfing and associated inbreeding depression in the self-incompatible plant *Senecio squalidus* (Asteraceae): a successful colonizing species in the British Isles. *New Phytologist*, **168**, 475–486.
- Brown JS, Eckert CG (2004) Evolutionary increase in sexual and clonal reproductive capacity during biological invasion in an aquatic plant *Butomus umbellatus* (Butomaceae). *American Journal of Botany*, **92**, 495–502.
- Brown AHD, Marshall DR (1981) Evolutionary changes accompanying colonization in plants. In: *Evolution Today: Proceedings of the Second International Congress of Systematic and Evolutionary Biology* (eds Scudder GE, Reveal JL), pp. 351–363. Hunt Institute for Botanical Documentation, Carnegie-Mellon, Pittsburgh, Pennsylvania.
- Burdon JJ, Marshall DR (1980) Biological control and the reproductive mode of weeds. *Journal of Applied Ecology*, **18**, 649–659.
- Chaboudez P, Sheppard AW (1995) Are particular weeds more amenable to biological control? A reanalysis of mode of reproduction and life history. In: *Proceedings of the Eighth International Symposium on Biological Control* (eds Delfosse ES, Scott RR), pp. 95–102. DSIR/CSIRO, Melbourne, Australia.
- Cheptou PO (2004) Allee effect and self-fertilization in hermaphrodites: reproductive assurance in demographically stable populations. *Evolution*, **58**, 2613–2621.
- Cheptou PO, Avendaño LG (2006) Pollination processes and the allee effect in highly fragmented populations: consequences for the mating system in urban environments. *New Phytologist*, **172**, 774–783.
- Cox GW (2004) *Alien Species and Evolution*. Island Press, Washington, DC.
- Davis HG, Taylor CM, Lambrinos JG, Strong DR (2004) Pollen limitation causes an allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proceedings of the National Academy of Sciences, USA*, **101**, 13804–13807.
- Eckert CG (2002) The loss of sex in clonal plants. *Evolutionary Ecology*, **15**, 501–520.
- Eckert CG, Manicacci D, Barrett SCH (1996a) Frequency-dependent selection on morph ratios in tristylous *Lythrum salicaria*. *Heredity*, **77**, 581–588.
- Eckert CG, Manicacci D, Barrett SCH (1996b) Genetic drift and founder effect in native versus introduced populations of an invading plant, *Lythrum salicaria* (Lythraceae). *Evolution*, **50**, 1512–1519.
- Eckert CG, Samis KE, Dart S (2006) Reproductive assurance and the evolution of uniparental reproduction in flowering plants. In: *Ecology and Evolution of Flowers* (eds Harder LD, Barrett SCH), pp. 183–203. Oxford University Press, Oxford, UK.
- Elam DR, Ridley CE, Goodell K, Ellstrand NC (2007) Population size and relatedness affect fitness of a self-incompatible plant. *Proceedings of the National Academy of Sciences, USA*, **104**, 549–552.
- Endler JA (1977) *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton, New Jersey.
- Fenster CB, Barrett SCH (1994) Inheritance of mating-system modifier genes in *Eichhornia paniculata* (Pontederiaceae). *Heredity*, **72**, 433–445.
- García-Ramos G, Rodríguez D (2002) Evolutionary speed of species invasions. *Evolution*, **56**, 661–667.
- Griffith TM, Watson MA (2006) Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *American Naturalist*, **167**, 153–164.
- Hairston NG, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, **8**, 1114–1127.
- Hamrick JL, Godt MJW (1996) Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **351**, 1291–1298.
- Hermisson J, Pennings PS (2005) Soft sweeps: molecular population genetics of adaptation from standing genetic variation. *Genetics*, **169**, 2335–2352.
- Hollingsworth ML, Bailey JP (2000) Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese knotweed). *Botanical Journal of the Linnean Society*, **133**, 463–472.
- Houghton-Thompson J, Prince HH, Smith JJ, Hancock JF (2005) Evidence for hybridization between *Lythrum salicaria* (purple loosestrife) and *L. alatum* (winged loosestrife) in North America. *Annals of Botany*, **96**, 877–885.
- Husband BC, Barrett SCH (1993) Multiple origins of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae): inferences from style morph and isozyme variation. *Journal of Evolutionary Biology*, **6**, 591–608.
- Kinlan BP, Hastings A (2005) Rates of population spread and geographic expansion. What exotic species tell us. In: *Species Invasions Insights Into Ecology, Evolution and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 381–419. Sinauer & Associates, Sunderland, Massachusetts.
- van Kleunen M, Johnson SD (2005) Testing for ecological and genetic allee effects in the invasive shrub *Senna didymobotrya* (Fabaceae). *American Journal of Botany*, **92**, 1124–1130.
- Kliber A, Eckert CG (2005) Interaction between founder effect and selection during biological invasion in an aquatic plant. *Evolution*, **59**, 1900–1913.
- Kollmann J, Bañuelos MJ (2004) Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). *Diversity and Distributions*, **10**, 377–385.
- Lafuma L, Maurice S (2007) Increase in mate availability without loss of self-incompatibility in the invasive species *Senecio inaequidens* (Asteraceae). *Oikos*, **116**, 201–208.
- Lambrinos JG (2001) The expansion history of a sexual and asexual species of *Cortaderia* in California, USA *Journal of Ecology*, **89**, 88–98.
- Lambrinos JG (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology*, **85**, 2061–2070.
- Le Baron HM, Gressel J (1982) *Herbicide Resistance in Plants*. John Wiley and Sons, New York.
- Lee PLM, Patel RM, Conlan RS, Wainwright SJ, Hipkin CR (2004) Comparison of genetic diversities in native and alien populations of hoary mustard (*Hirschfeldia incana* [L.] Lagreze-Fossat). *International Journal of Plant Science*, **165**, 833–843.
- Leger EA, Rice KJ (2007) Assessing the speed and predictability of local adaptation in invasive poppies (*Eschscholzia californica*). *Journal of Evolutionary Biology*, **20**, 1090–1103.

- Levin DA (2000) *The Origin, Expansion, and Demise of Plant Species*. Oxford University Press, Oxford, UK.
- Li W, Wang B, Wang J (2006) Lack of genetic variation of an invasive clonal plant *Eichhornia crassipes* in China revealed by RAPD and ISSR markers. *Aquatic Botany*, **84**, 176–180.
- Lui K, Thompson FL, Eckert CG (2005) Causes and consequences of extreme variation in reproductive strategy among invasive populations of a clonal aquatic plant, *Butomus umbellatus* (Butomaceae). *Biological Invasions*, **7**, 427–444.
- Malecki RA, Blossley B, Hight SD *et al.* (1993) Biological control of purple loosestrife. *Bioscience*, **43**, 680–686.
- Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecological Monographs*, **74**, 261–280.
- Mazer SJ, Leubhn G (1999) Genetic variation in life-history traits: heritability estimates within and genetic differentiation among populations. In: *Life History Evolution in Plants* (eds Vuorisalo TO, Mutikainen PK), pp. 85–135. Kluwer Academic, Dordrecht, The Netherlands.
- Michalakakis Y, Derancourt F, Noël V, Espiau C (1993) A first estimation of the mating system of *Onopordum illyricum* (L.) and its relevance to the invasion of Australia. *Acta Oecologica*, **14**, 539–545.
- Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.
- Morgan MT, Wilson WG, Knight TM (2005) Plant population dynamics, pollinator foraging, and the selection of self-fertilization. *American Naturalist*, **166**, 169–183.
- Myers JH, Bazely DR (2003) *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge, UK.
- Novak SJ, Mack RN (2001) Tracing plant introduction and spread into naturalized ranges: genetic evidence from *Bromus tectorum* (cheatgrass). *Bioscience*, **51**, 114–122.
- Novak SJ, Mack RN (2005) Genetic bottlenecks in alien plant species. Influence of mating systems and introduction dynamics. In: *Species Invasions Insights Into Ecology, Evolution and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 201–228. Sinauer & Associates, Sunderland, Massachusetts.
- O'Neil P (1997) Natural selection on genetically correlated phenological characters in *Lythrum salicaria* L. (Lythraceae). *Evolution*, **51**, 267–274.
- O'Neil P (1999) Selection on flowering time: an adaptive fitness surface for nonexistent character combinations. *Ecology*, **80**, 806–820.
- Olsson K, Ågren J (2002) Latitudinal population differentiation in phenology, life history and flower morphology in the perennial herb *Lythrum salicaria*. *Journal of Evolutionary Biology*, **15**, 983–996.
- Ornduff R (1987) Reproductive systems and chromosome races of *Oxalis pes-caprae* L. and their bearing on the genesis of a noxious weed. *Annals of the Missouri Botanical Garden*, **74**, 79–84.
- Orr HA, Bettancourt AJ (2001) Haldane's sieve and adaptation from the standing variation. *Genetics*, **157**, 875–884.
- Pannell JR, Barrett SCH (1998) Baker's Law revisited: reproductive assurance in a metapopulation. *Evolution*, **52**, 657–668.
- Parker IM (1997) Pollinator limitation of *Cytisus scoparius* (scotch broom), an invasive exotic shrub. *Ecology*, **78**, 1457–1470.
- Parker IM, Rodriguez J, Loik ME (2003) An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. *Conservation Biology*, **17**, 59–72.
- Price SC, Jain SK (1981) Are inbreeders better colonizers? *Oecologia*, **49**, 283–286.
- Rambuda TD, Johnson SD (2004) Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? *Diversity and Distributions*, **10**, 409–416.
- Ren M-X, Zhang Q-G, Zhang D-Y (2004) Geographical variation in the breeding systems of an invasive plant. *Eichhornia crassipes* in China. *Acta Phytocologica Sinica*, **28**, 753–760.
- Sakai AK, Allendorf FW, Holt JS *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology, Evolution and Systematics*, **32**, 305–332.
- Sculthorpe CD (1967) *The Biology of Aquatic Vascular Plants*. Edward Arnold, London, UK.
- Simons AM (2003) Invasive aliens and sampling bias. *Ecology Letters*, **6**, 278–280.
- Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, **18**, 94–101.
- Taylor DR, Keller SR (2007) Historical range expansion determines the phylogenetic diversity introduced during contemporary species invasion. *Evolution*, **61**, 334–345.
- Thompson DQ, Stuckey RL, Thompson EB (1987) *Spread, Impact, and Control of Purple Loosestrife (Lythrum Salicaria) in North American Wetlands*. US Fish and Wildlife Service, Washington, D.C.
- Thuiller W, Richardson DM, Pyšek P, Midgley GF, Hughes GO, Rouget M (2005) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology*, **11**, 2234–2250.
- Wares JP, Hughes AR, Grosberg RK (2005) Mechanisms that drive evolutionary change. Insights from species introductions and invasions. In: *Species Invasions Insights Into Ecology, Evolution and Biogeography* (eds Sax DF, Stachowicz JJ, Gaines SD), pp. 230–257. Sinauer & Associates, Sunderland, Massachusetts.
- Weber E, Schmid B (1998) Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. *American Journal of Botany*, **85**, 1110–1121.
- Welk E, Schubert K, Hoffman MH (2002) Present and potential distribution of invasive garlic mustard (*Alliaria petiolata*) in North America. *Diversity and Distributions*, **8**, 219–233.
- White DJ, Haber E, Keddy C (1993) *Invasive Plants of Natural Habitats in Canada*. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, Canada.
- Widén B, Cronberg N, Widén M (1994) Genotypic diversity, molecular markers and spatial distribution of genets in clonal plants. In: *Plant Clonality; Biology and Diversity* (eds Soukupová L, Marshall C, Hara T, Herben T), pp. 139–157. Opulus Press, Uppsala, Sweden.
- Yakimowski SB, Hager HA, Eckert CG (2005) Limits and effects of invasion by the non-indigenous plant *Lythrum salicaria* (purple loosestrife): a seed bank analysis. *Biological Invasions*, **7**, 687–698.

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