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Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.de/ppees



Research article

Self-compatibility and plant invasiveness: Comparing species in native and invasive ranges

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ARTICLE INFO

Article history:

Received 1 February 2011

Received in revised form 27 July 2011

Accepted 27 August 2011

Keywords:

Baker's rule

Mating system

Pollination

Self compatibility index

Variation in self compatibility

Echium plantagineum

Centaurea solstitialis

Solanum elaeagnifolium

ABSTRACT

A longstanding hypothesis (“Baker’s rule”) is that plant invasiveness is facilitated by floral self compatibility rather than self incompatibility. Extending this idea, invasive species whose individuals vary in degree of self compatibility within the native range might be self compatible in invading or weedy populations, due to natural selection on the mating system. We compared mating system between native and invasive ranges for two major world invasives, one annual (*Echium plantagineum*) and one perennial (*Solanum elaeagnifolium*). For an additional annual species (*Centaurea solstitialis*) we compared non-weedy and weedy populations in the native range. No species was strongly spontaneously self pollinating, but the degree of self compatibility after hand pollination varied dramatically. Both annuals were self incompatible in native or non-weedy populations but self compatible in invasive or weedy ones; the reverse was true for the perennial. Individuals within populations of all three species also varied in their degree of self compatibility, suggesting a basis for natural selection, and populations of the same species sharing a status (native/non-weedy, invading/weedy) varied in average self compatibility. These results support the hypothesis that differential selection of progeny during invasion can result in self-compatible populations derived from ancestrally self-incompatible ones, but that this process may be less important in perennial species, which experience multiple opportunities for sexual reproduction. Overall, however, mating system may not operate alone and its contributions to invasiveness may be conditional on other attributes of a species including physiology, morphology, and life history.

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Introduction

Invasive plant species are a major contemporary driver of ecological change worldwide, with implications for nature conservation and for ecosystem services such as primary production (Millenium Ecosystem Assessment, 2005; Schweiger et al., 2010). An immense literature has developed aiming to understand factors that turn a seemingly harmless plant into a troublesome, even noxious one (Vilà et al., 2006; Pyšek and Richardson, 2007; Küster et al., 2008; Tylianakis et al., 2008; van Kleunen et al., 2010). Many studies have attempted to link invasiveness to

physiological and ecological traits (Rejmánek and Richardson, 1996; Williamson and Fitter, 1996; Radosevich et al., 2003), and whereas it is rare to find such traits that are consistent across species and geography (Pyšek and Richardson, 2007; Hayes and Barry, 2008), recent meta-analyses suggest some physiological and vegetative characteristics that are strongly associated with invasiveness (Pyšek and Richardson, 2007; van Kleunen et al., 2010).

Since the 1950s several authors have also proposed that colonizing ability, a key factor in invasiveness, is related to mating system (Baker, 1955, 1965, 1974; Allard, 1965). In particular, the idea that plants capable of uniparental reproduction (i.e., apomixis or autogamy) are most likely to be successful long-distance colonists, known as Baker’s rule, is based on the argument that high levels of self fertility will decrease demographic stochasticity arising

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from dependence on ancestral pollinators and on conspecifics to serve as mates. Reproductive assurance, which has long been proposed to be the main cause of the evolution of self fertility (Darwin, 1876), will thereby be increased. According to Baker (1974) the above would also apply to plant weeds, which can “be native to the area in which they take advantage of human-induced disturbance”. To be self compatible is an ideal characteristic for a weed, especially if it is not a perennial species (Baker, 1974).

Since Baker's (1955) initial observation that colonists of oceanic islands tend to be self compatible (see also McMullen, 1987; Webb and Kelly, 1993; Barrett, 1996; Igic et al., 2008), a large body of empirical evidence has developed in support of the hypothesis that self-compatible (SC) species are more likely to be more successful invaders than self-incompatible (SI) species. For example, all 17 invasive species tested in their invaded territories by Rambuda and Johnson (2004) were either SC (15) or apomictic (2); and 83.3% of the 12 invasive species of Asteraceae in China were capable of autonomous seed set, i.e. SC or apomictic (Hao et al., 2011). Similar high frequencies of SC taxa within a variety of invaded areas and among arrays of invasive plants have been documented by van Kleunen and Johnson (2007), van Kleunen et al. (2008), and Harmon-Threatt et al. (2009). Baker's ideas on weeds (1955, 1965, 1974) were also supported by Mulligan and Findlay (1970), who found all annual and 91% of biennial Canadian weeds to be SC (even self-pollinating), whereas all rhizomatous and stoloniferous perennials are SI. At the same time, the compatibility status of invasive and weedy plants often seems to vary in more complex ways. Some repeated studies on the same species suggest that these species can also be SI in some or all invasive populations (Maddox et al., 1996; Sun and Ritland, 1998; Gerlach and Rice, 2003; López-García and Maillet, 2005), and analysis of a random selection of the entire flora of the USA (3121 out of 19,960 species) suggests that invasive exotics are more likely to be SI than non-invasive exotics (Sutherland, 2004).

One possibility is that the mating system of successful invaders may vary between populations in the native geographic range and in invaded areas, or between populations in undisturbed and disturbed locations within the native range. A simple expectation is that species characterized by incomplete SI in the undisturbed native range might eventually invade when genotypes that are more strongly SC arrive in a new area or at a disturbed site. Here one would expect to find SI species giving rise to invading or weedy populations that are SC, with the frequency of such conversions depending on the strength of selection for reproductive assurance (Pannell and Barrett, 1998; Porcher and Lande, 2005; Willi, 2009). In this regard, perennial species, which enjoy enhanced reproductive assurance through a longer lifetime of opportunities for sexual reproduction and the possibility of vegetative spread, might be less likely to convert from SI to SC. Self incompatibility might also be favored in colonizing perennials insofar as this minimizes inbreeding depression (Böhle et al., 1996), or allows more allocation to vegetative spread at the expense of seed production when vegetative spread is a superior means of colonizing. Collectively, therefore, we might expect development of SC to be less pervasive among perennial species than among annuals. Finally, it is also possible that a self-compatible mating system is not as critical for invasion as once thought, in which case we would expect little overall pattern.

In this paper we investigate mating system shifts in three extremely successful invasive species (i.e., fulfilling the criteria of Richardson et al., 2000). We included two annuals and one perennial to capture key variation in life history suspected to be linked with SI to SC conversion (Pannell and Barrett, 1998). Novel aspects of our approach are that we measured compatibility

status in populations of each species both inside and outside the native range, or both in undisturbed and disturbed sites within the native range, and that we combined two different approaches to assess the mating system. We ask (1) whether native and invasive or weedy populations of each species can self pollinate either spontaneously or when assisted by hand; (2) whether the degree of self compatibility varies among populations in native and invasive or weedy populations; and (3) whether the degree to which individual plants express self compatibility varies within single populations, suggesting a basis for natural selection on the mating system. We discuss our findings in comparison to those reported for several other invasive species in which self incompatibility has been determined in the area of origin, area of invasion, or both.

Materials and methods

Study species and populations

Centaurea solstitialis L. (yellow star thistle) is a spiny annual to biennial species native to the entire Mediterranean basin, but with many subspecies in the eastern and central parts (Dostál, 1976). It is one of the few wild plants flowering there in the summer, which is probably made possible by a taproot that can reach a meter deep into the soil and so can access moisture in hot, dry seasons. Yellow star thistle is versatile in growth pattern, and varies greatly in stature (20 cm up to >1 m tall). By massively flowering in summer in the absence of co-flowering competitors it takes advantage of bee pollinators, mainly leaf cutters (Megachilidae), that are numerous in this season (Petanidou, 1991, 2004). The species is a large-scale noxious weed in several states of the USA, with heavy impacts on California (Maddox et al., 1985, 1996; Joley et al., 1992; Barthell et al., 2001; Roché and Thill, 2001). Although *C. solstitialis* normally does not dominate the flora in the eastern Mediterranean, it can temporarily form large and dense populations in its native range. Following Table 1 of Richardson et al. (2000) we refer to these as “weedy” populations, i.e. those resembling invasive populations outside of the native range but occurring within the native range, apparently as a result of human-induced changes in land use such as agriculture or other disturbance (Uygur et al., 2004; T. Petanidou, personal observations). We compared such a weedy population with three non-weedy native populations in undisturbed settings, all on the Greek island of Lesvos in the northeastern Aegean Sea (see Uygur et al., 2004 for a similar comparison). Non-weedy and weedy populations differed in size (Table 1), plant stature and density (much larger and higher in the weedy population), habitat (semi-natural phrygana scrub for non-weedy populations; a cultivated farm for the weedy one), homogeneity in coverage (*C. solstitialis* was the only flowering species in the weedy population, whereas it shared the same habitat with other species in the non-weedy ones), and persistence (non-weedy populations persisted without changing in size for >10 years; the weedy population is ephemeral depending on land management).

Echium plantagineum L. (purple viper's bugloss) is a spring-flowering annual plant 20–60 cm tall in its native environment (southeastern Europe and the Mediterranean). It is highly invasive in Australia where it often expands to form huge populations, a moderate and recent invader in the Canary Islands (Burdon et al., 1983; Forcella et al., 1986; Burdon et al., 1988; Grigulis et al., 2001; Sheppard et al., 2001; Gerlach and Rice, 2003; Dupont and Skov, 2004), and a mild invasive in California (R.W. Thorp, personal communication). We studied three native populations on the island of Lesvos, three invasive populations around the city of Canberra, Australia, and two invasive populations from Tenerife, Canary Islands (Table 1). Populations were separated by 2 km minimally and varied in size from small to very large (Table 1).

Table 1

Study plant species and populations. We chose study populations that represent the existing populations as to their size, ranging from small to immense.

Plant species and populations	Population locations and traits		
	Location; year of fieldwork	Size (# plants)	Status
<i>Centaurea solstitialis</i>			
Mystegna	Lesvos, Greece; 2008	200	Native, non-weedy
Oikos	Lesvos, Greece; 2008	40	Native, non-weedy
Achladeri bridge	Lesvos, Greece; 2008	300	Native, non-weedy
Vassilika farm	Lesvos, Greece; 2008	>5000	Native weedy
<i>Echium plantagineum</i>			
Katarraktes	Lesvos, Greece; 2008	300	Native
Pedi	Lesvos, Greece; 2005	>3000	Native
Agra	Lesvos, Greece; 2008	>4000	Native
Black Mountain	Canberra, E. Australia; 2010	500–1000	Invasive
Urambi	Canberra, E. Australia; 2010	25,000–50,000	Invasive
Mugga	Canberra, E. Australia; 2010	5,000,000–25,000,000	Invasive
NE Tenerife	Canary Islands; 2008–2009	>2000	Invasive
NW Tenerife	Canary Islands; 2008–2009	>1000	Invasive
<i>Solanum elaeagnifolium</i>			
Santa Rita	Arizona, USA; 2006	>500	Native
Arisvi	Lesvos, Greece; 2006	300	Exotic, naturalized
Atlanta cultivated field	E. Thessaloniki, N. Greece; 2007	>100,000	Invasive
Ioannou wasteland	W. Thessaloniki, N. Greece; 2007	>100,000	Invasive

Constraints of time and funding did not allow us to travel to Tenerife for an extended period, so we instead grew seed offspring from those populations in a greenhouse at Aarhus University, Denmark, and assessed self compatibility of the resulting adults. Greenhouse-grown plants are commonly used in studies of plant mating systems (e.g., Davis, 2005).

Both of the above annual species are mostly reported as SI and obligatory seeders either in their native environment (*E. plantagineum*: Dauber et al., 2010) or in invaded areas (*C. solstitialis*: Maddox et al., 1996; Sun and Ritland, 1998; Gerlach and Rice, 2003), although see Burdon et al. (1988) and Davis (1992) for evidence of self compatibility for an Australian population of *E. plantagineum*. For both species seed set is guaranteed by a diversity of pollinators both in native and invaded areas. On Lesvos alone, more than 120 bee species have been identified as flower visitors to *E. plantagineum* (Dauber et al., 2010; T. Petanidou et al., unpublished data) and at least 60 species to *C. solstitialis* (Barthell et al., 2009, Petanidou et al., unpublished data; D.S. Song et al., unpublished data). In invaded areas the flowers of both species are also visited by many bee species (Davis, 1992; Barthell et al., 2001; Dupont and Skov, 2004).

The third study species, *Solanum elaeagnifolium* Cav. (silver-leaf, nightshade), is an herbaceous perennial native to South and Central America and the southwestern USA (Boyd et al., 1984), and is highly invasive in many other areas of the world including Mediterranean-climate areas (for references see Tscheulin et al., 2009a). In Greece it is widespread especially on the northern part of the mainland, and is locally extremely abundant (Boratynski et al., 1992; Tscheulin et al., 2008; Vilà et al., 2009). Flowers are buzz-pollinated by different groups of bees throughout the native and invasive range, and plants also spread vegetatively (Cooley and Smith, 1971; Buchmann and Cane, 1989; Tscheulin et al., 2009a,b). Because it lowers quantity and quality of many crops with which it grows, and is toxic to livestock, *S. elaeagnifolium* is considered a noxious weed in most invaded areas of the world. We studied one native population on the Santa Rita Experimental Range south of Tucson, Arizona, USA, one exotic naturalized (i.e., mildly invasive) population on the island of Lesvos, and two aggressively invasive populations near the city of Thessaloniki on the northern Greek mainland (Table 1). The naturalized Lesvian population is known to have not changed substantially after its establishment more than 30 years ago, whereas the two invasive populations are

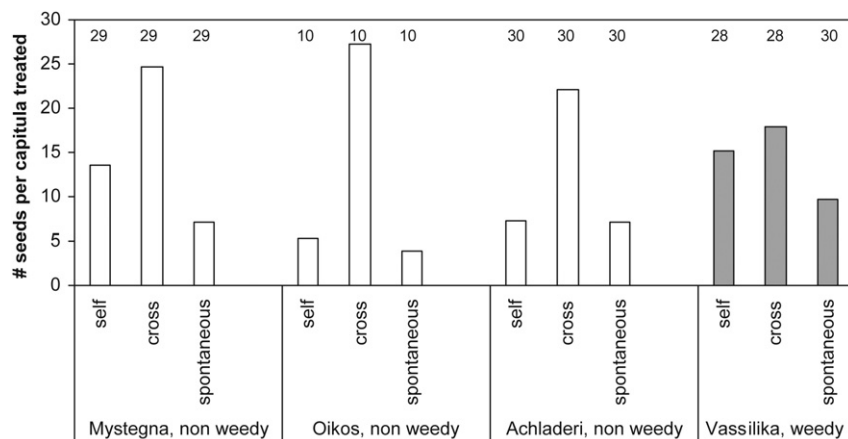


Fig. 1. Seed set results after three pollination treatments (hand self and cross pollination, spontaneous self pollination) for study populations of *Centaurea solstitialis* shown in Table 1 (open bars for non-weedy populations, grey bars for the weedy). Sample numbers are given at the top of the bars and statistical results in Table 2.

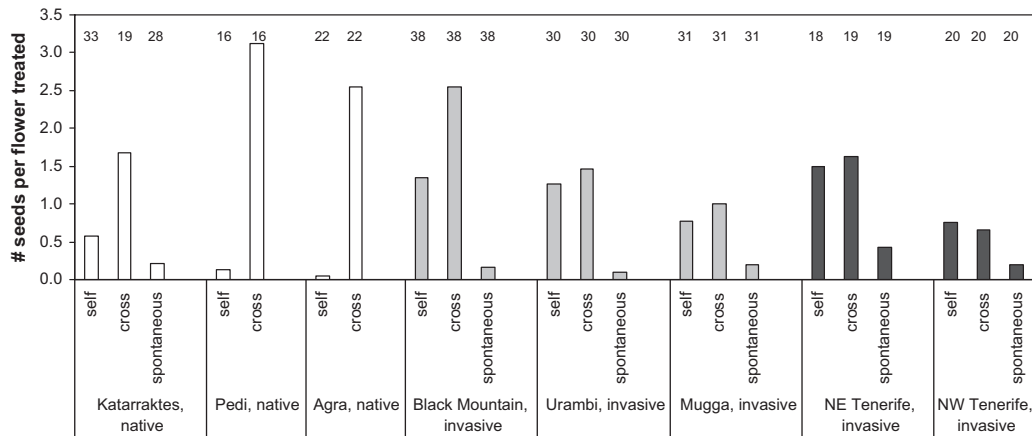


Fig. 2. Seed set results after different pollination treatments (hand self and cross pollination, spontaneous self pollination) for study populations of *Echium plantagineum* shown in Table 1 (open bars for native populations from Lesvos, Greece; grey bars for invasive populations in Australia; and black bars for invasive populations in the Canary Islands). Sample numbers are given at the top of the bars and statistical results in Tables 2 and 3 (the latter for Pedi and Agra).

huge and continuing to expand around the metropolitan area of Thessaloniki.

Mating systems

We assessed the mating system for plants from each of the 16 study populations by applying self and cross pollen by hand, leaving some flowers unpollinated in one native and one invasive or weedy population of each species (Table 1) to test for spontaneous selfing. Except for the Canary Island populations, all hand pollinations were carried out in the field during peak flowering of the population in question on relatively warm days. All treatments were carried out under favorable growing conditions both in the field and in the glasshouse.

We used the same protocol across all populations. To minimize among-plant effects all the above three treatments were carried out on the same individual plants. The plants used were a sample chosen at random within each population (n = 10–30 per population for *C. solstitialis*, n = 16–38 for *E. plantagineum*, n = 29–60 for *S. elaeagnifolium*). On each individual chosen we marked 1–2 triplets of flower buds (or capitula in bud stage for *C. solstitialis*) with waterproof paint, and covered each flower or capitulum separately with fine netting to prevent insect access. When flowers or capitula in each

triplet were female-receptive, one was pollinated by hand with pollen from freshly open flowers on the same plant, another was similarly cross-pollinated with pollen from plants 2–5 m from the recipient, and the third was left untouched. After treatment hand-pollinated flowers were covered again with netting. Treatments to each triplet of *E. plantagineum* and *S. elaeagnifolium* flowers were applied in sequence on a single day, whereas they were applied over successive days (as many as 7) on *C. solstitialis*, depending on the number of flowers per capitulum. We harvested mature fruits of *C. solstitialis* after 2–3 wk., of *E. plantagineum* after 2–4 wk., and of *S. elaeagnifolium* after 5–6 wk., and counted viable seeds per fruit or per capitulum under a dissecting microscope, excluding any shrivelled or unfilled seeds. The achenes of *C. solstitialis* and capsules of *S. elaeagnifolium* in particular had many undeveloped or aborted seeds. In the case of *C. solstitialis* we counted hairy and non-hairy achenes as a single group (Maddox et al., 1996).

To calculate seed set for each treatment we took the mean value across all flowers receiving the treatment within a population. In order to calculate the mating system variability among plants within a population (i.e. seed set after self and cross pollination) we took the mean value of seed set for each treatment per individual plant. Because of many zero values, especially in the tests for spontaneous self pollination in all three species and

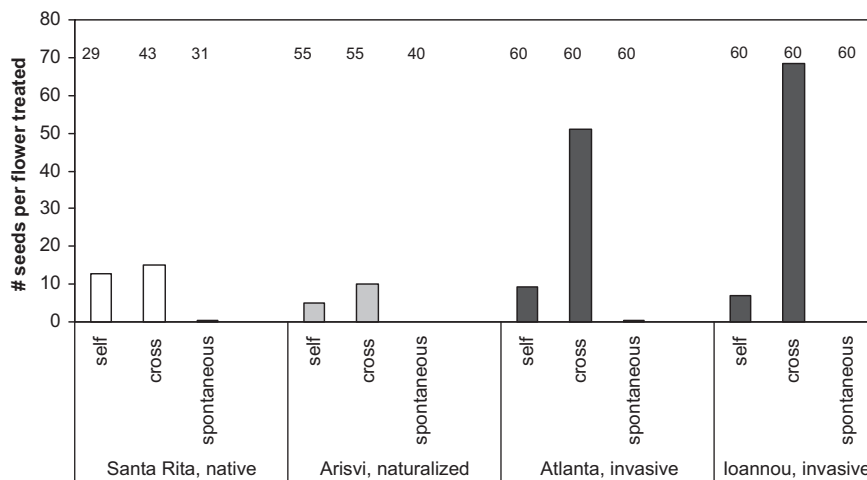


Fig. 3. Seed set results after three pollination treatments (hand self and cross pollination, spontaneous self pollination) for study populations of *Solanum elaeagnifolium* shown in Table 1 (open bars for the native population in Arizona, grey bars for the exotic naturalized population on Lesvos, and black bars for invasive populations in northern Greece). Sample numbers are given at the top of the bars and statistical results in Table 2.

in all of the *S. elaeagnifolium* treatments, for comparisons of seed set we used Kruskal–Wallis *H* tests (nonparametric alternative to the one-way independent-samples ANOVA) and Mann–Whitney *U* tests (nonparametric alternative to the two-sample *t* test for post hoc comparisons). In all post hoc comparisons we applied a conservative Bonferroni correction.

To judge the mating system we used two approaches. First, we calculated self-compatibility indices (SCI) following Lloyd and Schoen (1992), where

$$SCI = \frac{\text{seed set after hand selfing}}{\text{seed set after hand outcrossing}}$$

SCI ranges from zero to ≥ 1 , with 1 representing full self compatibility. Apart from providing a value that is relative to the outcrossed seed set, the advantage of this method is that it allows comparisons of populations grown under different environments (e.g., in different habitats, including the greenhouse). Second, we compared the absolute values of seed set after selfing and outcrossing. This approach is critical in cases of low seed set, where small numbers can give misleading SCI values. We took the two measures of mating system at the level of entire populations. In order to assess the basis for selection on the mating system, we also took them at the level of individual plants within 12 populations overall (four Lesvian populations for *C. solstitialis*; two native populations on Lesvos and three invasive ones in Australia for *E. plantagineum*; and one native population in Arizona and two invasive ones near Thessaloniki for *S. elaeagnifolium*). A population or plant was considered SC if SCI exceeded 0.75 (as proposed by Lloyd and Schoen, 1992) and if at the same time no statistically significant difference was detected between seed set after hand selfing and hand outcrossing; otherwise it was considered SI.

Results

Mean population-level seed sets following the different pollination treatments are shown for *C. solstitialis* in Fig. 1, *E. plantagineum* in Fig. 2, and *S. elaeagnifolium* in Fig. 3, and statistical comparisons are summarized in Tables 2 and 3. In all populations of *C. solstitialis* spontaneous self pollination produced fewer seeds on average than outcross pollination by hand, although it differed less from self pollination by hand. Spontaneous selfing was rare or absent in the other two species. Self pollination by hand yielded at least somewhat lower seed set on average in populations of all three species than cross pollination (Table 3), although the reductions were not always statistically significant.

We detected substantial variation in self compatibility among different native populations or different invasive and weedy populations within a species (Table 3). A more remarkable finding was that native populations of each species differed greatly in their compatibility status compared to invasive or weedy populations (Table 3). However, the direction of difference varied among species. Native populations of *E. plantagineum* were SI (i.e., had a low SCI value as well as significantly lower seed sets after hand selfing than after outcrossing), whereas invasive ones were strongly SC (except one Australian population that did not fulfil the criteria despite its relatively high SCI value), and the same applies to *C. solstitialis* non-weedy vs. weedy populations. For the perennial *S. elaeagnifolium* the situation was reversed; invasive populations were SI whereas the native population was SC, and the exotic naturalized mildly invasive population on Lesvos had a mating system intermediate between the two, although still judged by our strict criteria as SI.

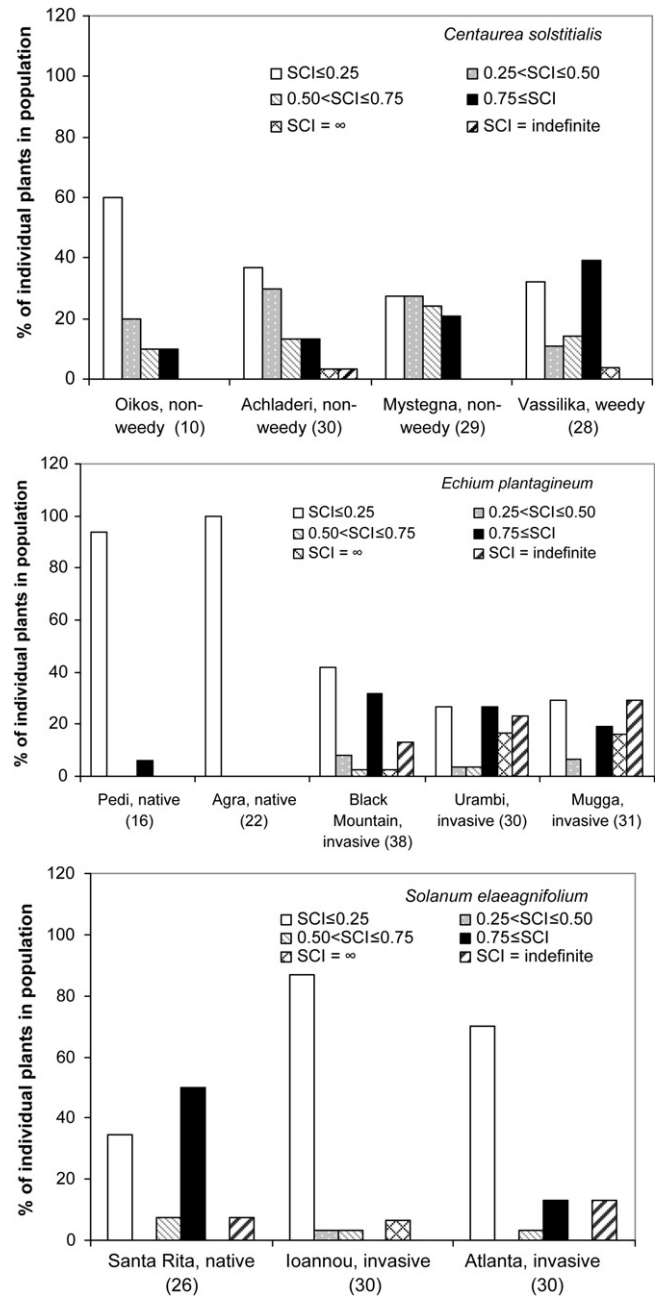


Fig. 4. Variation in mating system among plants within native and invasive populations of the three study species. Categorization within populations was based on the value of self-compatibility index (SCI) calculated per individual plant. Numbers on the x-axis show the number of individual plants examined per population. Infinite SCI values apply in cases where the numbers of seeds set after hand cross and self pollination were 0 and ≥ 1 , respectively. Similarly, indefinite SCI values apply in cases where 0 seeds were set after both cross and self pollination.

Finally, individual plants within all but one of the 12 populations for which this was measured, regardless of their status as native or invasive, also varied in mating system expression (Fig. 4). In the majority of these populations we detected individuals expressing everything from strong self compatibility to strong self incompatibility, although not necessarily in equal percentages. In a number of populations, although by no means all, there was a suggestion of bimodality, with relatively large percentages of individuals either SI ($SCI \leq 0.25$) or SC ($SCI \geq 0.75$), and smaller percentages with intermediate self-compatibility status.

Table 2
Summary statistics for the results after three pollination treatments (hand selfing, hand crossing, and spontaneous selfing) of the study species. All study populations are described in Table 1 and the results illustrated in Figs. 1–3. We compare seed sets among the 3 treatments with Kruskal–Wallis H tests (“K–W H ”), followed by post hoc comparisons with Mann–Whitney U tests (“M–W U ”) and Bonferroni corrections.

Plant species and populations	Statistical results	
	K–W H test	M–W U test
<i>Centaurea solstitialis</i>		
Mystegna, non-weedy	$H_{(2,87)} = 36.528; P < 0.0000$	HS vs. HC***; HS vs. SP*; HC vs. SP***
Oikos, non-weedy	$H_{(2,30)} = 13.697; P = 0.0011$	HS vs. HC*; HC vs. SP**
Achladeri, non-weedy	$H_{(2,90)} = 29.802; P < 0.0000$	HS vs. HC***; HC vs. SP***
Vassilika, weedy	$H_{(2,86)} = 6.796; P = 0.0334$	HC vs. SP*
<i>Echium plantagineum</i>		
Katarraktes, native	$H_{(2,80)} = 33.050; P < 0.0000$	HS vs. HC**; HC vs. SP***
Black Mountain, invasive	$H_{(2,114)} = 42.161; P < 0.0000$	HS vs. HC*; HS vs. SP*; HC vs. SP***
Urambi, invasive	$H_{(2,90)} = 19.853; P < 0.0000$	HS vs. SP*; HC vs. SP**
Mugga, invasive	$H_{(2,93)} = 11.568; P = 0.0031$	HC vs. SP*
NE Tenerife, invasive	$H_{(2,56)} = 13.441; P = 0.0012$	HS vs. SP*; HC vs. SP**
NW Tenerife, invasive	$H_{(2,60)} = 4.421; P = 0.1096$	–
<i>Solanum elaeagnifolium</i>		
Santa Rita, native	$H_{(2,103)} = 32.879; P < 0.0000$	HS vs. SP***; HC vs. SP***
Arisvi, naturalized	$H_{(2,150)} = 13.191; P = 0.0014$	–
Atlanta, invasive	$H_{(2,180)} = 66.897; P < 0.0000$	HS vs. HC***; HC vs. SP***
Ioannou, invasive	$H_{(2,180)} = 93.375; P < 0.0000$	HS vs. HC***; HC vs. SP***

HS, hand self-pollination; HC, hand cross pollination; SP, spontaneous self pollination. Numbers in parentheses separated by comma under K–W H test column are df and total sample size. Non-significant results are not shown.

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Discussion

Our pollination studies indicate that visits to flowers by animal pollinators will strongly enhance fecundity in virtually all populations of the three species, but that the exact expression of the mating system was far from a fixed trait. We instead detected variation in the average degree of self incompatibility or self compatibility among populations of the same species within the native range (*E. plantagineum*, *C. solstitialis*) and within the invasive range (*E. plantagineum*, *S. elaeagnifolium*), as well as between native and invasive or weedy populations of the same species (all species). Furthermore, all but one of 16 populations exhibited a mean SCI between 0 and 1, that is, were neither perfectly SI nor SC. Closer examination within non-weedy populations (*C. solstitialis*) and within invasive

or weedy ones (all species) suggests that this finding of intermediate mean values derives from variable (and usually widely variable) compatibility values across individual plants. These are not surprising findings. Although self compatibility is often discussed as if it were fixed and absolute, evidence against such a view is widespread (e.g., Waser, 1993; Levin, 1996; Stone et al., 2006). Even obligately outcrossed species have been reported to have variable proportions of SC individuals in different populations (*Senecio inaequidens*: López-García and Maillet, 2005; *Arabidopsis lyrata*: Mable et al., 2005), and indeed *C. solstitialis* has been reported previously to vary in this regard as well (Maddox et al., 1996). Such variation suggests that a population of a species in a novel area or habitat might commonly express a different compatibility phenotype or range of phenotypes than its parent population,

Table 3
Seed set after hand selfing and outcrossing in all study populations. Mann–Whitney U test results differ from those in Table 2 due to the application of Bonferroni correction (Table 2).

Plant species and populations	Seed set				
	Hand crossing (# seeds \pm SE)	Hand selfing (# seeds \pm SE)	M–W U test	SCI	Self compatibility
<i>Centaurea solstitialis</i>					
Mystegna, non-weedy	24.7 \pm 0.31	13.5 \pm 0.87	$U_{(29,29)} = 169.5; P < 0.0000$	0.55	SI
Oikos, non-weedy	27.2 \pm 0.60	5.3 \pm 1.15	$U_{(10,10)} = 8.5; P = 0.0007$	0.19	SI
Achladeri, non-weedy	22.1 \pm 0.54	7.3 \pm 0.89	$U_{(30,30)} = 133.5; P < 0.0000$	0.33	SI
Vassilika, weedy	17.9 \pm 0.69	15.2 \pm 0.90	$U_{(28,28)} = 332.0; P = 0.3250$	0.85	SC
<i>Echium plantagineum</i>					
Katarraktes, native	1.7 \pm 0.22	0.6 \pm 0.17	$U_{(33,19)} = 114.0; P < 0.0000$	0.34	SI
Pedi, native	3.1 \pm 0.18	0.1 \pm 0.13	$U_{(16,16)} = 1.5; P < 0.0000$	0.04	SI
Agra, native	2.5 \pm 0.17	0.0 \pm 0.05	$U_{(22,22)} = 1.0; P < 0.0000$	0.02	SI
Black Mountain, invasive	2.6 \pm 0.25	1.3 \pm 0.26	$U_{(38,38)} = 425.5; P = 0.0014$	0.53	SI
Urambi, invasive	1.5 \pm 0.27	1.3 \pm 0.26	$U_{(30,30)} = 414.0; P = 0.5761$	0.86	SC
Mugga, invasive	1.0 \pm 0.21	0.8 \pm 0.19	$U_{(31,31)} = 428.5; P = 0.4286$	0.77	SC
NE Tenerife, invasive	1.6 \pm 0.29	1.5 \pm 0.32	$U_{(18,19)} = 158.5; P = 0.7041$	0.92	SC
NW Tenerife, invasive	0.7 \pm 0.22	0.8 \pm 0.29	$U_{(20,20)} = 196.5; P = 0.9246$	1.15	SC
<i>Solanum elaeagnifolium</i>					
Santa Rita, native	14.9 \pm 1.67	12.9 \pm 2.18	$U_{(43,29)} = 569.5; P = 0.5271$	0.87	SC
Arisvi, naturalized	10.1 \pm 2.60	5.0 \pm 1.99	$U_{(55,55)} = 1316.5; P = 0.0993$	0.50	SI
Atlanta, invasive	51.0 \pm 5.60	9.1 \pm 2.92	$U_{(60,60)} = 806.5; P < 0.0000$	0.18	SI
Ioannou, invasive	68.6 \pm 5.31	7.1 \pm 3.04	$U_{(60,60)} = 521.0; P < 0.0000$	0.10	SI

M–W U , Mann–Whitney U ; SCI, self-compatibility index; SC, self compatible; SI, self incompatible. Conclusions as to self compatibility are based on two criteria (see text).

Table 4
Literature review of self-compatibility traits for species that are invasive in different parts of the world and for which data from both the areas of origin (AoO) and invasion (Aol) are available. Comparative data on our study species are also included.

Species	Notes	Life form	Area of origin (AoO)	Area of invasion (Aol)	Compatibility in AoO	Compatibility in Aol	Reference
Studies with data from both native and invaded areas							
<i>Cyrtopodium polyphyllum</i>		p	Brazil		SC		Pansarin et al. (2008)
<i>C. polyphyllum</i>		p	Brazil	Florida		SC	Liu and Pemberton (2010)
<i>Onopordum illyricum</i>	ga	p	Mediterranean, France	Australia	Outcrossing rate: $t = 0.52$; mixed	Outcrossing rate: $t = 0.57$; mixed	Michalakakis et al. (1993)
<i>Opuntia stricta</i>		p	N. America	W. Mediterranean	SC (both on near and far islands)		Spears (1987)
<i>O. stricta</i>		p	N. America	W. Mediterranean		Rel. SC	Bartomeus and Vilà (2009)
<i>Rhododendron ponticum</i>		p		Ireland	SC, not fully (seed set based)		Stout (2007)
<i>R. ponticum</i>		p	Spain			Fully SC (fruit set based)	Mejias et al. (2002)
<i>Senecio inaequidens</i>		hp	S. Africa	E. Pyrennees, France		SI; some plants highly SC	López-García and Maillet (2005)
<i>S. inaequidens</i>		hp	S. Africa	The Netherlands		SC (but no evidence given)	Ernst (1998)
<i>S. inaequidens</i>		hp	S. Africa	S. France		SI; some plants were 30–50% SC	Breton (2000) cit. López-García and Maillet (2005)
<i>S. inaequidens</i>	1 native and 4 invasive pop	hp	S. Africa	Continental Europe	SI	SI	Lafuma and Maurice (2007)
<i>S. pterophorus</i>		hp	S. Africa	Spain	SI	SI	Cano et al. (2008)
<i>Spartina alterniflora</i>	Several pop	p grass	Atlantic and Gulf coasts (US)	Pacific coast (US)	Lower SC	Greater SC	Davis (2005)
<i>Carduus acanthoides</i>	20 pop; ga	b	Europe, Czech Republic	America, N. Zealand	SI		Mandák et al. (2009)
<i>C. acanthoides</i>	3 pop; ga	b	Europe	Ontario, Canada		SI	Warwick and Thompson (1989)
Studies from different areas invaded at different times							
<i>Lythrum salicaria</i>	12 pop along an invasion gradient	p	Europe	N. America	No evidence of SC change as a result of the invasion process		Colautti et al. (2010)
<i>Nicotiana glauca</i>		p	S. America	Channel Islands and mainland California	SC higher in islands (especially the recently colonized ones) than in mainland		Schueler (2004)
Studies on species dealt with in the present study							
<i>Centaurea solstitialis</i>	Highly invasive	a	Mediterranean	California and Sierra Nevada		SI; with variability in SI levels	Maddox et al. (1996)
<i>C. solstitialis</i>	8 pop; ga	a	Mediterranean	California		Predominantly SI	Sun and Ritland (1998)
<i>C. solstitialis</i>	Highly invasive	a	Mediterranean	California		Highly SI	Gerlach and Rice (2003)
<i>Echium plantagineum</i>	Highly invasive	a	Mediterranean	Australia		Highly SC	Burdon et al. (1988)

Abbreviations: a, annual; b, biennial; hp, herbaceous perennial; p, perennial; mixed, mixed or versatile regime of self and cross pollination; pop, populations; ga, results from genetic analysis.

either through stochasticity in the phenotypes of vegetative fragments or seeds that form the pool of colonists, as a result of natural selection acting at the time of dispersal (see also van Kleunen et al., 2008; Whitney and Gabler, 2008), or even as a result of phenotypic plasticity in the reproductive system itself (Levin, 2010).

The question that next arises is whether shifts in compatibility status are predictable during an invasion event. Our results, and others in the literature, suggest two possible predictions. The first is that an invasive originating from a SI ancestor shifts to a SC mating system. This follows from Baker's rule, since self compatibility would facilitate establishment and subsequent expansion of invasive populations by removing the need for nearby flowering conspecifics as mates and for ancestral pollinators. The fact that native pollinators commonly visit alien plant species (Memmott and Waser, 2002; Olesen et al., 2002; Vilà et al., 2009) suggests that reproductive assurance in the face of mate limitation is the stronger mechanism of selection for self compatibility. Mechanistically, SI to SC conversion, including the development of partial or quantitative SI, can follow the invasion of mutant SC alleles into gametophytic SI systems (Charlesworth and Charlesworth, 1979) or changes in modifier genes or polygenes that lie beyond the S-locus (Levin, 1996; Stone et al., 2006). The nature of this change can depend on the magnitude of inbreeding depression, of selection favoring reproductive assurance (Willi, 2009), of pollen discounting (Barrett, 2002; Igic et al., 2008), and on the potential for purging of deleterious mutations (Porcher and Lande, 2005). When inbreeding depression is significant, partial SC may even be a superior strategy to obligate SC (Pannell and Barrett, 1998; Willi, 2009). Large-scale studies support the conclusion that SI to SC conversion is a common evolutionary process in angiosperms worldwide (Stebbins, 1974; Igic et al., 2008).

The theoretical expectation of SI to SC conversion in invasive plant populations is certainly consistent with our results for *E. plantagineum* in particular. This species was highly SI in all native and SC in all invasive populations (except for the Black Mountain population which was partially SC), and previous studies also documented self compatibility in invasive Australian populations (Burdon et al., 1988; Davis, 1992). The high level of SC is also compatible with an expectation that annual species are likely to experience stronger selection for reproductive assurance than perennial species (Pannell and Barrett, 1998). The situation appears analogous for *C. solstitialis*, which our studies suggest is SI in non-weedy populations but SC in weedy ones (although previous studies of invasive populations in California inferred a highly SI condition, albeit with some variation among individuals; Maddox et al., 1996; Sun and Ritland, 1998; Gerlach and Rice, 2003). Interestingly, it has been recently suggested that when colonizing or invasive plant populations are exposed to inhospitable environments or altered abiotic conditions, phenotypic plasticity in flower architecture, age and phenology can also result in elevated levels of SC relative to source populations (Levin, 2010). Since our data for *E. plantagineum* and *C. solstitialis* were collected under favorable growing conditions (including some under glasshouse conditions), and are consistent with past estimates of SC (e.g., Burdon et al., 1988), there is little evidence that reproductive system plasticity explains the observed SI to SC shift in these species. However, further investigation of the potential role of plasticity in adaptation of these and other species to new environments would be a fruitful area for future research.

The second possible prediction is that a SC ancestor gives rise to a SI invasive. On both theoretical and empirical grounds, this transition is usually considered unlikely. First, transition of an SI system to SC is predicted to result in selective neutrality for alleles at the S-locus, leading to rapid convergence towards selfing (Igic et al., 2008). Further genomic changes (Wright et al., 2008), including

loss of functional coordination of genes both linked and unlinked to the S-locus (Igic et al., 2008), might reinforce this change. Second, empirical evidence argues that rates of SI loss far exceed those of SI gain across many plant families (Stebbins, 1974), and that SI loss may be effectively irreversible (Igic et al., 2006). On the other hand, it is possible that predominantly SI populations could arise from partially SI populations if the cost of inbreeding depression in seed offspring (a cost which may be persistent; Byers and Waller, 1999) exceeds fitness gain from reproductive assurance (Barrett, 1988). As Pannell and Barrett (1998) show, the relative advantage of reproductive assurance is predicted to be lower in perennials than in annuals, and in species for which vegetative reproduction is a superior means of colonization, self incompatibility might be favored if this allowed reduced allocation to sexual reproduction and increased allocation to vegetative spread. Perhaps these factors explain the reduced SCI that we detected in the invasive populations of *S. elaeagnifolium*—the species certainly spreads vegetatively via detached root fragments, for example (Cooley and Smith, 1971; Buchmann and Cane, 1989; Tscheulin et al., 2009a,b)—but an obvious first step with this species is to sample additional native populations to see if a pattern of high SCI persists.

While any comparisons of breeding system across three species is obviously insufficient to demonstrate an adaptive explanation for shifts in compatibility status, much less two opposing explanations, our study suggests that shifts from SI to SC do not always characterize successful invasions. We are aware of only a few other invasive species whose mating system expression has been characterized in both native and invaded ranges, and these results are also mixed. Of eight such species studied in both native and invaded areas, three were SI in all populations, two were either SC or partially SC in all populations, two were described as fully SC in their native range and relatively SC in the invaded range, and only *Spartina alterniflora* exhibited greater self compatibility in the invaded vs. native range (Table 4). In another two invasive species studied only in invaded areas, *Lythrum salicaria* and *Nicotiana glauca*, the results of self compatibility along the invasion gradient were contrasting (Table 4). Thus the implication from Baker's rule that reproductive assurance should drive a shift from SI to SC in invasive populations was not usually supported.

Overall it does seem likely, then, that invasiveness does not depend primarily on the ability of a species to self pollinate with or without pollinator support, and that species may become successful invaders regardless of their self-compatibility status. This conclusion is consistent with several recent studies that have identified other traits as associated with invasiveness. These include plant height, vigorous vegetative growth, long flowering period, and attractiveness to humans (Pyšek and Richardson, 2007). A meta-analysis by van Kleunen et al. (2010) also suggested associations with performance-related traits such as physiology, leaf area, shoot allocation, growth rate, size, and reproductive fitness. In another recent study Fenesi and Botta-Dukát (2010) suggest that invasive plant species are aided by traits that enhance competitive abilities, such as height (e.g., in short-lived species) and tolerance for a wide range of anthropogenic disturbance and dispersal abilities (e.g., in long-lived species). Such explanations for invasiveness certainly are consistent with traits exhibited by the species we studied.

Acknowledgements

The Fulbright Foundation funded the study of TP in Arizona (2006–2007) and the study of DSS on Lesvos (2008–2009). We also were supported by the European Commission Framework Programme 6 (Integrated Project ALARM; GOCE-CT-2003-506675;

Settele et al., 2005) and the Danish Natural Sciences Research Council. Many people assisted in pollination experiments in Greece (C. Zografou, D. Vivarelli, E. Lamborn, N. Kantsas, and E. Petanidou), Denmark (J. Genini), and Australia (D. Marshall and B. Robertson); collected and counted seeds (S. Allen, C. Alexiou, M. Candelaria-Rodriguez, K. Georghiou, A. González-Castro, and A. Karatza); tended plants in the greenhouse (staff of the experimental farm of Aarhus University); and helped with finding experimental populations (S. Buchmann, N. Krigas, and R.W. Thorp). TP is especially grateful to J. Bronstein for hosting her at the University of Arizona, to A. Young and J. Burdon for providing fruitful connections, to the Santa Rita Experimental Range for permission to work there, and to M. Price for stimulating discussions. We also thank J. Nason, the subject editor, and two anonymous reviewers for their insightful suggestions.

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