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A phylogenetic comparative study of preadaptation for invasiveness in the genus *Silene* (Caryophyllaceae)

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Abstract The role of preadaptation in ecology and evolution is determined by how the traits evolved by a species in one environment allow it to be successful in novel environments. This concept bears directly on modern biological invasions, as species are introduced to new locations beyond their historical borders. In this study, we used a phylogenetically-controlled analysis of the flowering plant genus *Silene* (Caryophyllaceae) to show that native geographic range size, along with a suite of life history traits affecting plant growth and reproduction, have preadapted some species for the invasion of new ranges. Using a path analytic approach, we further show that some of the covariance between life history traits and invasiveness is indirect, caused by mutual associations with native range size. Specifically, we found that reproductive traits such as the number of flowers per inflorescence and length of the flowering season directly preadapt species for invasion, while plant height is indirectly associated with invasion through a correlation with native range size. Other traits such as ovule number and leaf size are both directly and indirectly associated with invasion success. Our results reveal the importance of accounting for correlations among plant traits and geographic range size when predicting preadaptation for invasiveness. We also highlight that the traits predictive of invasion success among species of *Silene* are often those found to be rapidly evolving within introduced populations, suggesting common forces of selection operating at these different biological scales of organization during invasion.

Keywords Invasive species · Preadaptation · Geographic range · Comparative method · Phylogeny · Supertree · *Silene*

Introduction

Understanding the ecological and evolutionary mechanisms by which species maintain self-sustaining populations in response to abrupt changes in environment has become a pressing question for conservation and invasion biologists (Lee 2002; Stockwell et al. 2003; Bell and Collins 2008; Keller and Taylor 2008). Which of the traits possessed by a species in

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one environment will enable its success upon encountering a novel environment? Ultimately, this concerns the role of preadaptation in evolution (Gould and Vrba 1982; Futuyma 1998), and has direct consequences for persistence and extinction during periods of rapid environmental change. A prime example of such change is during biological invasion, when a species is introduced to and rapidly spreads throughout a new biogeographic range (Williamson 1996). Since an invasive species must successfully disperse and then survive to reproduce in a region where it has no prior history of adaptation, some degree of preadaptation must be prerequisite for successful invasion (Elton 1958; Baker 1974; Sakai et al. 2001; Suarez and Tsutsui 2008).

A substantial amount of research has been focused on attempting to find sets of physiological and life history traits that predict invasiveness across broad taxonomic scales (e.g., Baker 1974; Rejmanek and Richardson 1996; Williamson and Fitter 1996; Kolar and Lodge 2001; Hamilton et al. 2005; Pyšek and Richardson 2007; Hayes and Barry 2008). To date, one of the best established predictors of invasion success across a diverse set of taxa is the breadth of a species' native geographic range (Blackburn and Duncan 2001; Prinzing et al. 2001a; Pysek et al. 2009). Yet interpreting the contributions of native range size to invasion can be complicated because geographic range is itself an emergent trait that integrates components of individual-level traits such as dispersal ability, environmental tolerance, growth rate, size, mating system, and reproductive potential, among others (Brown et al. 1996; Holt 2003; Ricklefs et al. 2008; Randle et al. 2009). These individual-level traits likely exert direct effects on the probability of establishing self-sustaining populations and thus on the distributional area occupied in native and/or introduced regions. Obvious parallels then emerge between the evolution of traits that promote colonization and range expansion where a species is native, and the traits that preadapt some species to becoming invasive in other ranges. However, it remains unclear what the direct and indirect contributions of native range size and life history traits are to invasion success, and few studies have explicitly attempted to separate these factors (but see Goodwin et al. 1999; Pysek et al. 2009).

A promising way to start answering these questions is to use a comparative approach involving a large sample of both invasive and not invasive taxa (Williamson 1996; Sutherland 2004; Pyšek and Richardson 2007; Hayes and Barry 2008). In plants, a common approach is to compare species invasive to a particular region with the native flora of that same region (e.g., Williamson and Fitter 1996). This has the advantage of demonstrating which traits may permit introduced species to become numerically dominant over native species in a specific ecological area, but fails to identify traits of general importance prior to establishment. Other studies compare species that originate from the same biogeographical native range but contrast in their history of becoming invasive elsewhere (e.g., Goodwin et al. 1999; Prinzing et al. 2001a). This is better suited for identifying traits that distinguish invaders from non-invaders across the full spectrum of the invasion process, but is subject to the wide variance that arises when comparing traits across large groups of taxa. An alternative approach is to focus on a particular taxonomic group, often at the family or genus level, and compare closely related taxa to test for associations between traits and the propensity to become invasive (e.g., Muth and Pigliucci 2006). Provided there is sufficient variance in the degree of invasiveness, this last approach has perhaps the greatest potential to reveal meaningful causal relationships. However, related species tend to have similar trait values, making it necessary to control for phylogeny when analyzing associations between traits (Harvey and Pagel 1991; Pyšek and Richardson 2007). Such phylogenetically controlled studies of invasiveness in a focal taxonomic group remain relatively uncommon (but see Rejmanek and Richardson 1996; Burns 2006; van Kleunen et al. 2008).

In this paper we address the importance of preadaptation during the invasion of new ranges using a phylogenetic comparative analysis of the flowering plant genus *Silene* and closely related taxa (family Caryophyllaceae). After controlling for phylogenetic history using the method of independent contrasts, we employed a path analysis to examine the correlation structure between life history traits that affect colonization, native geographic range size, and invasiveness. The idea behind this use of path analysis is to explore the influence that life history traits have on predicting invasiveness, either directly through a causal relationship, and/or indirectly through a correlation with native range size. Such an approach is well suited to reveal novel insights into predicting invasiveness, since previous studies give us the a priori expectation that strong correlations exist between life history and geographic range size (Brown et al. 1996; Johnson et al. 2010), life history and invasiveness (Pyšek and Richardson 2007), and geographic range size and invasiveness (Goodwin et al. 1999; Kolar and Lodge 2001; Pysek et al. 2009). Based on this expectation, we predicted that life history traits and native range size would be strong determinants of invasiveness in *Silene*, but that the effect of individual life history traits would involve both direct and/or indirect correlations, mediated by the enormous variation in geographic range size in this diverse genus. By explicitly considering how traits contribute to species becoming widespread versus invasive, we begin to characterize the different pathways of preadaptation for invasion success.

Materials and methods

Study group

Silene L. (Caryophyllaceae) is a diverse plant genus comprising over 700 species, *sensu lato* (Rabeler and Hartman 2005; Hood et al. 2010). Most species are herbaceous, and exhibit great phenotypic diversity especially with regard to life history, pollination syndromes, and breeding systems (Desfeux et al. 1996; Kephart et al. 2006; Bernasconi et al. 2009). While the genus exhibits a primarily Holarctic distribution, it occurs globally as either native or introduced species on every continent except for Antarctica. Many species are narrowly endemic, especially in the Mediterranean region where taxa are often restricted in distribution to particular geographical features (e.g., islands) or habitat types (Greuter 1995; Oxelman and Liden 1995; Trigas et al. 2007). In contrast, other members of the genus possess widespread, often trans-continental distributions across much of Europe, Asia, and North America (Hitchcock and Maguire 1947; Jalas and Suominen 1986). These include several ruderals and weeds of human disturbance and agriculture that have emerged as cosmopolitan invaders since being introduced worldwide with the assistance of humans. These latter species include *S. latifolia* and *S. vulgaris*, two species which have become model systems in ecology and evolutionary biology (Bernasconi et al. 2009), including the study of plant weediness/invasiveness (Keller et al. 2000; Runyeon-Lager and Prentice 2000; Wolfe 2002; Blair and Wolfe 2004; Wolfe et al. 2004; Taylor and Keller 2007; Andersson et al. 2008; Keller et al. 2009).

For this study, we attempted to gather a broad sample of *Silene* species that had information on both phylogenetic relationships and available trait data for comparative analysis. We restricted our search to taxa that had available phylogenetic information from molecular sources, to minimize any confounding of a morphological based taxonomy with the analysis of trait variation. In total, we gathered phylogenetic and trait data on 157 species, including taxa native to Europe, Africa, Asia, and North America. These included 141 species of *Silene* (*sensu stricto*) as well as several species previously shown to be phylogenetically closely related to *Silene* but assigned to other genera (Oxelman and Liden 1995). These included four species in *Atocion*, two species in *Eudianthe,* six species in *Lychnis,* one species in *Petrocoptis,* and 1 species in *Viscaria*. However, these are all regarded as part of tribe *Sileneae*, which is under ongoing taxonomic investigation (Oxelman and Liden 1995; Oxelman et al. 1997; Oxelman et al. 2000). We also included several more distantly related outgroup taxa within the Caryophyllaceae, subfamily *Silenoideae*: *Agrostemma githago*, *Dianthus seguieri*, and *Saponaria ocymoides*.

Source phylogenies and supertree construction

No comprehensive phylogeny currently exists for conducting comparative studies in *Silene,* although multiple studies have addressed the phylogenetic relationships among taxa in certain sections of the genus. Thus, we chose to combine relationships from individual source trees into a phylogenetic supertree to control for shared ancestry in our comparative analysis (Bininda-Emonds 2004). A benefit of the supertree approach is that it permits the assessment of relationships that have not previously been analyzed by combining the topologies of multiple overlapping trees into a single phylogenetic hypothesis (Sanderson et al. 1998).

We searched the primary literature and obtained 23 DNA-based source phylogenies containing multiple species of *Silene* or closely related genera (Table S1 in Online Resource 1). Much of the available phylogenetic data was gathered by B. Oxelman and colleagues, based on DNA sequences from the chloroplast genome (*rps16* intron), nuclear ribosomal DNA (the internal transcribed spacer regions 1 and 2), and several regions of nuclear autosomal DNA. Most species were represented by >1 source tree, with an average 6 source trees per species. For taxonomic clarity, data from sources listing alternative names for the same taxon, based on the International Plant Names Index (IPNI: http://www.ipni.org/), were treated as synonymous. One exception was *Silene andersonii*, which is considered by some authorities to be a subspecies of *Silene verecunda* (Hitchcock and Maguire 1947); however, in the source trees they were well supported as distinctly different taxa. Therefore, we also considered them as separate taxa in our analyses.

Tree topologies were converted into NEXUS format using the 'build tree' function within the software SUPERTREE 0.85beta (Salamin et al. 2002). Bootstrap percentages from the source phylogenies were included when available as character weights for the nodes they supported, using an exponential transformation (Salamin et al. 2002). When bootstrap percentages were unavailable for particular nodes (most studies don't report values <50%), a default value of one was assigned. We then used SUPERTREE to calculate a Matrix Representation with Parsimony (MRP) binary matrix representing the nodal membership of each taxon among the source trees. When taxa were not included in a particular tree, they were assigned a missing value for those nodes.

We conducted heuristic searches on the MRP matrix for optimal topologies using maximum parsimony in PAUP* 4.05b (Swofford 1998). We ran two separate heuristic searches, one that constrained all characters to be equally weighted and another that weighted each node in proportion to its bootstrap support in the source tree. We observed very few differences between these two approaches, and here just report analyses based on the weighted search. All MRP characters were treated as irreversible (once a taxon has membership in a source node, it cannot be "lost"). Heuristic searches were conducted in two stages. First, we used 1000 replicates of random addition sequence, swapping among trees using nearest neighbor interchange, and keeping 20 trees at each replicate. We then conducted a second search where we swapped among the trees from the first search using the TBR algorithm, keeping the 1,000 best trees. A majority rule (50%) consensus tree was then computed among the most parsimonious trees. The supertree topology is available in standard newick format (Online Resource 1).

Trait selection and analysis of independent contrasts

The invasive status of each taxon was estimated using two different indices. First, we quantified a continuous index of worldwide invasiveness using the number of citations in the Global Compendium of Weeds, hereafter abbreviated GCW (Randall 2002). This database summarizes a worldwide list of primary literature, floras, and government reports that cite observations of a species behaving as a weed in a given locality. While using species prevalence in the GCW does not measure invasiveness directly and may be subject to reporting bias in certain geographic regions, it is regarded as indicative of a species' history of invasive expansion outside its native range and has been used by previous studies to successfully predict associations among traits and invasiveness (e.g., Pysek et al. 2009). As a second measure, we used the exotic status of species in North America, as reported in the USDA plants database (http://plants.usda.gov), hereafter abbreviated as USDA. Species were given an ordinal ranking based on their status in the database (not introduced = 0, introduced = 1, invasive = 2). Introduced status is defined as whether a species was naturally occurring at the time of Columbus, while invasive status was based on species inclusion in the compiled "Weeds of the U.S." database (http://plants.usda.gov/java/invasiveOne), an aggregated set of state and federal lists of invasive and noxious plant species non-native to North America. Species listed as native to North America were omitted from the USDA index because here the focus was on discriminating between non-indigenous species that either did nor did not invade, using North America as a focal region. Use of the USDA index of invasiveness is probably not independent of the GCW database, as 32.5% of the 706 species lists used by the GCW to assess invasive status come from North American species lists (Randall 2002, Pysek et al. 2009). Nevertheless, these two indices provide complimentary assessments of a species' history of establishing as a weed, as recognized by local and regional authorities, and both have been used by previous studies as indicators of invasive status (e.g., Frappier and Eckert 2003; Pysek et al. 2009).

Trait data were obtained from a combination of published floras, primary literature, and on-line databases (Online Resource 2). We selected traits for analysis that quantify different aspects of growth, reproductive capacity, life history, sexual system, and biotic interactions (enemies, mutualists). Many of these traits have been investigated in other studies of plant invasiveness or have been hypothesized as components of an overall phenotype causing weediness among plants (Baker 1974; Blossey and Notzold 1995; Rejmanek and Richardson 1996; Kolar and Lodge 2001; Pyšek and Richardson 2007; Hayes and Barry 2008; Keller and Taylor 2008). Growth potential was quantified using two measurements of maximum plant size: stem height (cm) and leaf size (= length, in cm). Reproductive capacity was estimated using measures of fecundity and length of reproductive period, which included number of flowers per inflorescence, ovule number, seed size, and number of months spent flowering. Life history schedule was categorized into two groups; annuals/biennials (semelparous), and perennials (iteroparous). We also included two germination-related traits as measures of early life history schedule: time to germination (days) and the temperature range (°C) over which seeds successfully germinate. Sexual system traits summarized a species' capacity for reproduction in the absence of available mates. These included two traits, pollen/ovule ratio, which is inversely proportional to a plant's selfing rate, and breeding system, which contrasts species with unisexual morphs (dioecious and gynodioecious) versus strictly hermaphroditic species. We also examined the effect of two biotic interactions: pollination syndrome, categorized as nocturnal or diurnal, and enemy attack by the sterilizing fungal pathogen *Microbotryum violaceum*, categorized as not attacked or attacked. Disease status was determined from an extensive herbarium survey of *Silene* and related genera (Hood et al. 2010). To avoid bias arising from sampling effort (number of herbarium sheets examined) and whether a species was observed infected with *Microbotryum*, we restricted our analysis to species that were examined by Hood et al. (2010) for at least 100 specimens (t test of mean number of sheets for non-diseased vs. diseased specimens: $t = -0.93$, $P = 0.18$). All size and reproductive traits were taken as maximum observed values reported in published floras, except for ovule number and pollen-ovule ratio, which was reported as means for each taxon (Jurgens et al. 2002). When possible, collection of trait values was constrained to those published from the native range of each species to avoid confounding with post-invasion trait evolution.

We estimated the native geographic range size of each species using published range maps. For species native to Europe, we used the Atlas Florae Europaeae (Jalas and Suominen 1986), which maps the distributions of each species in units of gridded squares measuring approximately 50 × 50 km. For North American native species, we utilized range maps published in a taxonomic treatment of native North American *Silene* species based on herbarium distributional records (Hitchcock and Maguire 1947). For distribution maps from each source, we used the program ImageJ to manually circumscribe a minimum area polygon around the species' occurrence points, calculate the resulting area, and scale to units of ln(km^2).

Statistical analysis

To estimate the degree of phylogenetic inertia in invasiveness and native geographic range size, we calculated Blomberg's K statistic (Blomberg et al. 2009), using the R-package Picante (Kembel et al. 2010). Values of K close to 1 indicate a high degree of trait similarity between relatives, as predicted by a Brownian motion model of evolution, while values near zero indicate little correlation among relatives. Significance of K values was tested with a randomization test using 1,000 permutations of the trait values across the tips of the phylogeny.

We controlled for phylogeny in our assessment of trait correlations with invasiveness by conducting all statistical analyses on phylogenetic independent contrasts (PICs) implemented using CAIC v2.6.9 (Purvis and Rambaut 1995). Calculating PICs requires an estimate of topology and branch lengths from a phylogeny, along with trait values for the taxa at the tips. We used the majority-rule consensus supertree from the weighted MRP matrix as our input topology, and used two different approaches to assign branch lengths. First, we treated all branch lengths in the phylogeny as equal, which corresponds to an evolutionary model of punctual trait divergence occurring at speciation events (i.e., at the nodes). Second, we used divergence-time scaled branch lengths, which corresponds to gradual trait divergence under Brownian motion. Branch lengths scaled to approximate divergence times among taxa were obtained using the *bladj* algorithm implemented in Phylocom (Webb et al. 2008). Divergence times (in millions of years) were estimated by *bladj* for each node in the supertree using 5 dated nodes as calibration points (Frajman et al. 2009), corresponding to splits between major lineages in *Sileneae* that were topologically congruent between our supertree and the chloroplast DNA analysis of divergence times by Frajman et al. (2009). Standardized PICs were then calculated in CAIC based on the equal and divergence-time scaled branch lengths.

We conducted two sets of analyses corresponding to each measure of invasiveness (GCW and USDA). In each analysis, invasiveness was the dependent variable regressed against an individual predictor trait. CAIC requires that the dependent variable be continuous, but allows calculation of contrasts in two different types of analysis for different types of predictor variables: *crunch* (for continuous traits) or *brunch* (for categorical traits). We used *crunch* and *brunch* for our continuous and categorical predictor traits, respectively, and treated both GCW and USDA as continuous variables. We also examined how traits predicted how widely species were distributed in their native range, using geographic range size as the continuous response variable. All contrasts from *crunch* were tested for significance using linear regression through the origin (PROC REG: SAS 2004). Contrasts from *brunch* were analyzed with a Wilcoxon signed-rank test under a two-tailed null hypothesis that the mean of the standardized contrasts was equal to zero.

After running the initial univariate analyses, we retained the traits found to be significant predictors of invasiveness based on the GCW index and analyzed each focal trait in a path-analytic framework using simple and multiple linear regression. The aim of this analysis was to investigate which of our life history traits identified as significant in the univariate analyses were directly predictive of invasiveness and which were indirectly predictive through their relationship with native geographic range size. We used CAIC to calculate a set of contrasts that specified invasiveness as the dependent variable, and included a predictor trait as well as native geographic range size as a continuous covariate. These contrasts were then used in a multiple regression analysis through the origin to test the relative importance of the life history trait and range size to invasiveness, while controlling for potential covariance among the predictors. Using the same set of contrasts, we then conducted two simple linear regressions that used the life history trait to predict either invasiveness or range size. All regression analyses were forced through the origin and the relative contribution of each predictor estimated using standardized partial regression coefficients.

Analysis of PICs using linear regression carries an evolutionary assumption that the pattern of trait divergence conforms to a random walk process represented by a Brownian motion model of evolution, and uses this assumption to justify scaling raw contrasts by their expected variances given by the branch lengths. Analyses based on equal or scaled branch lengths both resulted in contrasts for many traits that violated the prediction of independence between the nodal value of a trait and its standardized contrast (Online Resource 1). This likely reflects some combination of trait measurement error at the tips of the tree and an evolutionary model in our taxa that differs from the extremes of punctualism or gradualism. Comparative analysis using PICs is still preferable to treating species as independent units, even in the presence of such assumption violations (Harvey and Pagel 1991). However, to assess the sensitivity of our results, we report both sets of analyses based on equal and scaled branch lengths and examine where they are in agreement. Hypothesis testing also requires the usual statistical assumptions of normality and homogeneity of variance made during regression analysis of contrasts generated from *crunch*. Treating the three-state USDA index as continuous violates the assumption of normality, but we retain the USDA index for its value as a comparison with the continuous GCW index against the more difficult problem of quantifying invasiveness. Finally, several traits showed a positive relationship with the residual variance from the regression model, and could not be fixed by variable transformation. The correlation arises because few taxa with small traits values had high indices of invasiveness, while among the taxa with large trait values, some are invasive and others are not. This likely reflects real biological stochasticity inherent in which species become invasive, and will be present in most efforts to predict invasiveness from trait information. Regression is known to be robust to deviations from normality and homogeneity of variance, and it is only the hypothesis tests and not the estimation of regression coefficients that are affected (Zar 1999). However, to provide a conservative assessment of significance, we calculated contrasts for continuous traits using the *brunch* algorithm and tested for association with invasiveness using the non-parametric Wilcoxon signed-rank test. This combination of *brunch* plus non-parametric statistical tests makes no evolutionary or statistical assumptions about the data and is thus conservative with regard to the above assumptions (CAIC user's manual), but also carries the disadvantage of possessing considerably less statistical power than using *crunch* and linear regression.

Results

The MRP matrix consisted of 157 taxa scored for 709 characters (nodes in the source trees), of which 613 were parsimony informative. The phylognetic relationships among these taxa are summarized by the majority-rule consensus tree retained from a heuristic search of the weighted MRP matrix (Figure S1 in Online Resource 1). The supertree recovered several well-established taxonomic relationships known from the individual source phylogenies, including the distinctiveness of the *Lychnis* and *Atocion/Eudianthe/Viscaria* groups outside of the core *Silene* (Oxelman and Liden 1995; Oxelman et al. 2000), and the division within *Silene* into subgenera *Silene* and *Behen* (Desfeux et al. 1996; Oxelman et al. 1997; Popp and Oxelman 2004).

Invasiveness was well represented among the outgroup taxa (*Agrostemma, Dianthus,* and *Saponaria* all contain globally distributed weeds), and among several of the early-branching groups (*Lychnis, Eudianthe*). Overall, there was only weak phylogenetic signal for native range size (K = 0.022; 95% confidence interval of randomized data: 0.012–0.022) and global invasiveness (K = 0.033; 0.008–0.038). Only a few areas of the phylogeny tended to cluster invasive taxa, for example sections *Elisanthe* and *Conomorpha* in subgenus *Behen*, which include the well-known weeds *S. conica, S. dioica, S. noctiflora,* and *S. latifolia* (Figure S1). Interestingly, several groupings included one species that is widespread in its native range and highly invasive elsewhere, and another close relative with a more restricted and endemic distribution (for ex., *S. vulgaris* and *S. uniflora*; *S. diclinis* and *S. latifolia*).

Univariate analyses of phylogenetically independent contrasts based on a model of punctual evolution revealed that invasiveness was significantly predicted by a suite of traits that reflect large native range size and a weedy life history syndrome (Table 1). Invasive species possessed larger ranges, greater potential for reproduction (ovule number, flower number, number of months flowering) and growth (leaf size and height) compared to related non-invasive species (Fig. 1). When comparing species with a large (>10) vs. small ($\leq$10) values for the GCW index, invasive species were 7.1 times larger in native range size, produced 4.4 times as many flowers, and had between 1.28 and 1.39 times greater values for leaf size, months flowering, height, and ovule number. Regressions using the two different indices of invasiveness (GCW and USDA) and the two different estimates of branch lengths were generally congruent, although a few differences were apparent (Tables 1 and 2). One exception was that breeding system was negatively associated with invasiveness (unisexual species more likely to be invasive than hermaphroditic species), but only when comparing species not native to North America using the USDA index. Models with and without branch lengths were mostly in agreement about which traits were associated with invasiveness, though leaf size became non-significant in the branch length model (Table 2). Wilcoxon signed-rank tests further supported the significance of trait associations identified by regression (Table S2 in Online Resource 1). The exceptions were ovule number, which was only significant for the USDA index, and months flowering was only marginally significant ($P = 0.0574$ for USDA; $P = 0.1511$ for GCW), probably reflecting the lower statistical power. Thus across different evolutionary and statistical assumptions, there was broad support for preadaptation for invasiveness caused by native range size, flowering traits, and growth/size traits.

Table 1 Regression analysis of phylogenetic independent contrasts without branch lengths (punctual model) for traits predicting invasiveness

Continuous traits	Global compendium of weeds					USDA plants database				
	N	R^2	β	*F*	*P*	*N*	R^2	β	*F*	*P*
Pollen: ovule ratio	38	0.07	−4.798	2.64	0.1130	37	0.00	−0.000	0.02	0.8923
Ovule number	38	0.26	4.941	**13.27**	**0.0008**	37	0.13	0.002	**5.37**	**0.0263**
Stem height	130	0.11	1.205	**15.06**	**0.0002**	87	0.16	0.007	**15.94**	**0.0001**
Leaf size	106	0.07	0.141	**7.31**	**0.0080**	63	0.13	0.041	**9.05**	**0.0038**
Seed size	103	0.01	0.006	1.05	0.3069	63	0.04	0.244	2.56	0.1148
Germination time	17	0.00	0.011	0.01	0.9366	16	0.10	0.075	1.72	0.2090
Germination temperature range	15	0.07	−0.761	1.06	0.3200	15	0.11	−0.046	1.72	0.2109
Number of months flowering	95	0.14	3.969	**15.86**	**0.0001**	69	0.10	0.195	**7.90**	**0.0065**
Flower number	71	0.40	0.412	**45.61**	**<0.0001**	43	0.29	0.030	**17.01**	**0.0002**
Native geographic range size	100	0.30	2.344	**42.55**	**<0.0001**	68	0.38	0.174	**39.89**	**<0.0001**
Categorical traits	*N*	*n*	Sign	*T*	*P*	*N*	*n*	Sign	*T*	*P*
Breeding system[a]	16	15	Neg	38.0	0.2078	14	8	Neg	**2.0**	**0.0156**
Life history[b]	25	22	Pos	75.0	0.0984	24	14	Neg	49.0	0.8077
Pollination syndrome[c]	13	12	Pos	33.0	0.6772	12	8	Neg	8.0	0.1484
Microbotryum infection[d]	20	13	Neg	31.0	0.3054	13	10	Neg	12.0	0.1309

N refers to the number of contrasts in the model, β is the regression slope, and *F*/*T* are the test statistics from simple linear regressions and non-parametric Wilcoxon signed-rank tests, respectively, *n* is the number of non-zero contrasts (i.e., differences), and "Sign" is the direction of the association in the Wilcoxon test. Values in bold indicate a significant relationship between invasiveness and the trait

[a] Unisexual morphs = 0, hermaphroditic = 1

[b] Annual/biennial = 0, perennial = 1

[c] Nocturnal = 0, diurnal = 1

[d] Not diseased = 0, diseased = 1

Many of the traits predictive of invasiveness were also associated with the size of a species' native geographic range, with the notable exception of flower number and length of flowering period (Table 3). Breeding system was again significant, with unisexual species having larger ranges on average than hermaphroditic species. Interestingly, infection by the fungal pathogen *Microbotryum* was also related to native range size; species known to be susceptible to infection had larger ranges on average than those known not to experience infection (Table 3).

We examined the direct and indirect correlations between life history, native range size, and invasiveness using path analysis on phylogenetic independent contrasts. Number of flowers and number of months flowering retained strong direct relationships with invasiveness while showing no associations with native range size (Fig. 2), indicating that these traits are preadaptive for successful invasion abroad but have not promoted a widespread distribution during the species' evolutionary history. In contrast, stem height showed a highly significant positive relationship with native range size ($P < 0.0001$), but was no longer directly associated with invasion success ($P = 0.3661$). This was in contrast to the univariate analysis, where height was a strong and consistent predictor of invasiveness (Tables 1, 2 and S2). Number of ovules and leaf size were also significant predictors of invasiveness, both directly through their association with the GCW index, and indirectly through their correlations with native range size (Fig. 2).

Discussion

During rapid environmental change, a species' short-term probability of success will largely be determined

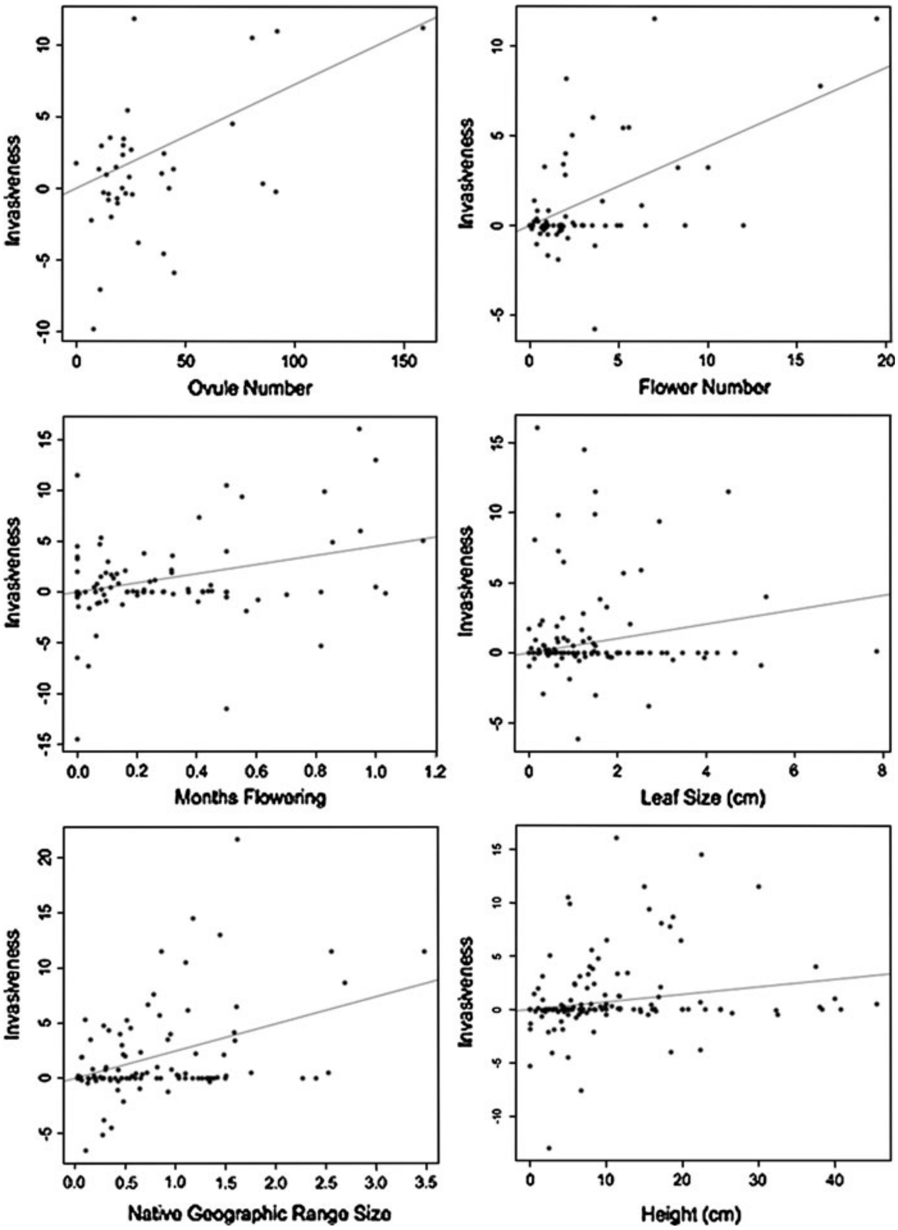

Fig. 1 Scatterplots of traits identified by univariate regression analyses to be significant predictors of invasiveness. All points are standardized phylogenetically independent contrasts. Regression *lines* are the best linear fit through the origin

by whether the life history traits essential for growth and reproduction are a sufficient pre-adaptive match for the new environment. In this study, we used a phylogenetically controlled analysis, focused on a well-known plant genus comprised of both weedy colonizers and local endemics. We identified a suite of life history traits that have preadapted some species to establish and spread beyond their native ranges, and demonstrated that many of these traits correlate strongly with native range size as well. Our results provide clear evidence that certain traits directly preadapt species for invasion while other traits preadapt invaders indirectly by increasing the breadth of a species' native distribution.

Widespread and invasive versus restricted and endemic

Native geographic range size was one of the best single predictors of invasiveness in our analysis, explaining between 24 and 38% of the variance in invasiveness across indices and branch length models

Table 2 Regression analysis of contrasts for continuous variables using branch lengths scaled by estimated divergence times

Continuous traits	Global compendium of weeds					USDA plants database				
	N	R^2	β	F	P	N	R^2	β	F	P
Pollen: ovule ratio	38	0.03	−0.005	1.02	0.3193	37	0.02	−0.000	0.60	0.4427
Ovule number	38	0.17	0.046	**7.55**	**0.0092**	37	0.07	0.002	2.70	0.109
Stem height	130	0.04	0.037	**4.62**	**0.0335**	87	0.17	0.006	**17.60**	**0.0001**
Leaf size	106	0.02	0.244	2.51	0.1159	63	0.04	0.022	2.51	0.1184
Seed size	103	0.00	0.666	0.20	0.6539	63	0.02	0.198	1.56	0.2159
Germination time	17	0.00	−0.085	0.07	0.7974	16	0.07	0.082	1.17	0.3073
Germination temperature range	15	0.02	−0.399	0.32	0.582	15	0.03	−0.025	0.44	0.5187
Number of months flowering	95	0.11	2.747	**11.089**	**0.0012**	69	0.04	0.100	3.17	0.0795
Flower number	71	0.20	0.243	**17.438**	**0.0001**	43	0.24	0.034	**13.60**	**0.0006**
Native geographic range size	100	0.24	1.755	**30.458**	**<0.00011**	68	0.36	0.151	**36.902**	**0.0002**

Legend as in Table 1

Table 3 Regression analysis of phylogenetic independent contrasts predicting native geographic range size

Continuous traits	N	R^2	β	F	P
Pollen: ovule ratio	37	0.01	−0.001	0.20	0.6581
Ovule number	37	0.12	0.006	**5.05**	**0.0309**
Stem height	95	0.19	0.032	**22.65**	**<0.0001**
Leaf size	75	0.12	0.192	**9.70**	**0.0026**
Seed size	83	0.00	−0.305	0.34	0.5616
Germination time	16	0.03	0.085	0.43	0.5212
Germination temperature range	15	0.00	0.028	0.07	0.7960
Number of months flowering	68	0.05	0.568	3.71	0.0582
Flower number	56	0.03	0.040	1.91	0.1722
Categorical traits	N	n	Sign	T	P
Breeding system	15	15	Neg	**24.0**	**0.0353**
Life history	18	18	Pos	67.0	0.4423
Pollination syndrome	13	13	Neg	27.0	0.1909
Microbotryum infection	15	15	Pos	**18.0**	**0.0151**

Legend and footnotes as in Table 1

(Tables 1 and 2). This result corroborates previous studies that have also found strong associations between native range size and invasion success, suggesting that this trait is of especially broad importance across taxonomic groups, focal study regions, and analysis approaches (Goodwin et al. 1999; Blackburn and Duncan 2001; Kolar and Lodge 2001; Prinzing et al. 2001a; Hayes and Barry 2008; Pysek et al. 2009). Phylogenetic signal for both range size and invasiveness was low compared to morphological or life history traits in other taxa (Blomberg et al. 2009). Cadotte et al. (2009) found significant phylogenetic signal for invasiveness at large spatial scales (e.g., continental), but none at finer regional scales. However, their study encompassed broad taxonomic levels (across plant families), while our study was primarily within a single genus. It would be interesting to address how phylogenetic signal of invasiveness varies across taxonomic levels.

There was considerable variation in range size among the *Sileneae*, spanning eight orders of magnitude, including several closely related species that differed dramatically in native range size. This lability in range size is somewhat unexpected, given other evidence that range sizes are phylogenetically conserved (Brown et al. 1996; Peterson et al. 1999; Wiens and Graham 2005), including in herbaceous plants (Ricklefs and Latham 1992; Prinzing et al. 2001b). Some of the range size variation observed in *Silene* is probably attributable to historical biogeography, such as availability of dispersal corridors following ice-age range restrictions (Svenning and Skov 2007; Taylor and Keller 2007; Prentice et al. 2008; Keller et al. 2009), but the correlations between several life history traits and range size suggest this may have a deterministic component as well (Table 3).

The role of native geographic range size in promoting invasion success is likely to be multifaceted, involving several non-exclusive processes.

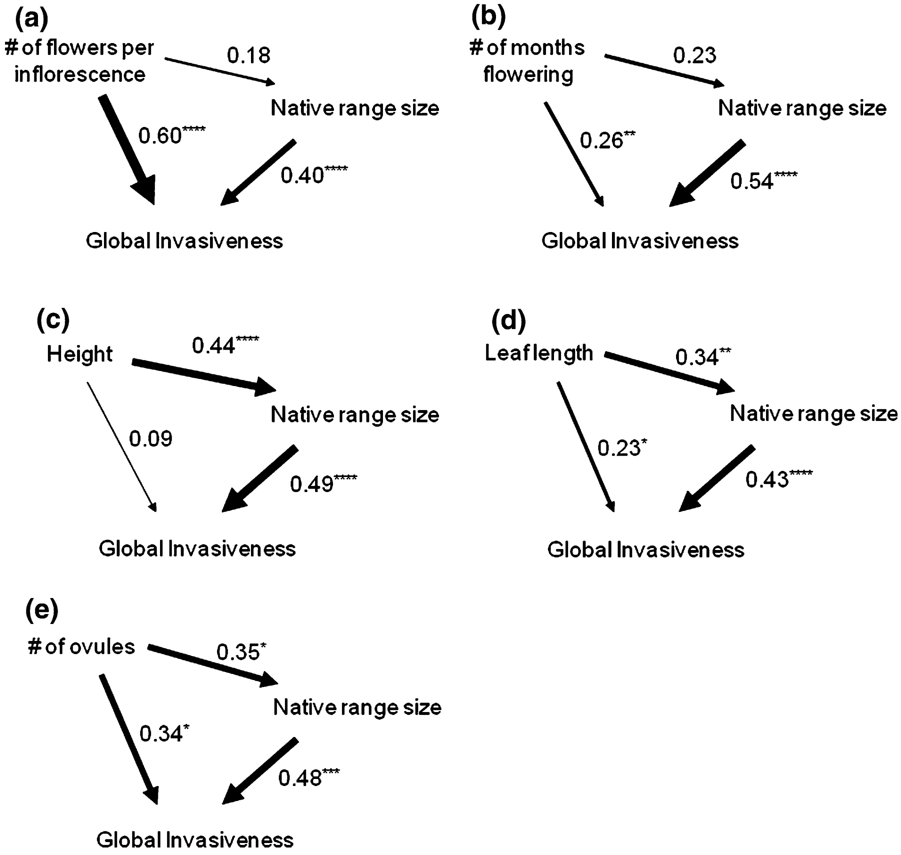

Fig. 2 Path analysis of preadaptation for invasion. *Arrows* represent direct and indirect paths between traits, geographic range, and invasiveness. Numbers are partial regression coefficients, with arrow thickness proportional to the magnitude of the estimate. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.0001$

Probabilistically, widespread species have more opportunities for contact with human dispersal vectors (Baker 1974; Goodwin et al. 1999; Blackburn and Duncan 2001; Pysek et al. 2009). While some human-mediated introductions are deliberate (Mack et al. 2000), many others are unintentional byproducts of human passage, and thus will likely increase in frequency as the contact rate with humans goes up. In *Silene,* most indications are that exotic introductions were largely unintentional (Martindale 1876; Baker 1948; McNeill 1977). Of course, once a species has been introduced, there are successive "filters" to overcome (establishment of self-sustaining populations, range expansion into new sites), but the initial uptake from the native range is a transition that must be met by all successful invaders (Williamson and Fitter 1996), and is likely to be facilitated by geographic ranges that increase contact rates with humans.

We also observed several strong correlations between native range size and life history traits, especially those related to fecundity (ovule number) and growth (height, leaf size) (Table 3, Fig. 2). These traits affect reproductive rate and competitive ability in plants, and may contribute to the ability to establish new populations. Thus, species with life history traits adapted for colonization may be widespread in their native range and preadapted for expansion within new ranges.

Finally, large geographic range size may indicate wide ecological tolerance to abiotic climate conditions or biotic interactions (Brown 1984; Brown et al. 1996; Hayes and Barry 2008; Pysek et al. 2009). Lack of requirements for specific habitats or mutualistic relationships may be preadaptive for colonizing species in both their native ranges and where they have been introduced. Such a syndrome of ecological generalization describes some *Silene* species which lack strong pollinator mutualisms and are capable of establishing populations across a wide range of climate conditions (Pettersson 1991; Keller et al. 2009). Range size may also increase exposure to plant pathogens, which invaders may escape from during introduction to a new range (Keane and

Crawley 2002). We found a positive association between range size and susceptibility to the sterilizing fungal pathogen *Microbotryum* (Table 3), although this did not translate into differences in invasiveness (Table 1). It is also important to consider that wide-ranging species may not be generalists at all, but rather specialists on certain habitats that are in high frequency across the landscape. Nevertheless, these species still must cope with many environmental variables that are not constant in space, such as climate, photoperiod, and biotic interactions. Widespread native geographic ranges reflect such ecological breadth, and thus serve as good predictors of a species' ability to survive introduction to a new range.

Life history traits and invasiveness

Multiple life history and morphological traits showed consistent correlations with invasiveness. These included major components of growth (height, leaf size) and reproductive potential (ovule number, flower number, number of months flowering), in accordance with the findings of previous studies on other taxa (Hamilton et al. 2005; Pyšek and Richardson 2007; Hayes and Barry 2008). These results may not be fully independent, as trait correlations were present at the species-level, especially between leaf size, height, and ovule number (Table S3). Nevertheless, the overall picture strongly supports a life history syndrome involving large size and allocation to reproduction as key preadaptations for plant invasiveness.

Our understanding of the pathways by which traits preadapt species for invasion improved after controlling for native range size (Fig. 2). Reproductive traits such as the number of flowers and months flowering were directly predictive of invasiveness, but neither were correlated with native range size. This suggests that maximizing reproductive potential may be advantageous during invasion of a new range, but may otherwise confer little benefit once a species has reached equilibrium with its new environment. It is also possible that flowering traits increase invasion success through attractiveness to pollinators or humans. While most of our study taxa are not known to be intentionally propagated, several are sometimes used as ornamentals and escape from cultivation, particularly members in the genus *Lychnis* (*L. chalcedonica, L. coronaria, L. flos-cuculi*) and several *Silene* species (*S. armeria*, *S. nutans, S. pendula,* and *S. uniflora*) (Gleason and Cronquist 1991). These species also tended to have high value of GCW invasiveness, with the exception of *S. uniflora.* Cultivation by humans may contribute to invasiveness by increasing propagule pressure of ornamental species in new ranges, as well as selecting on life history traits that are simultaneously attractive to humans and increase the reproductive success of plants that escape cultivation.

Interestingly, traits that were more strongly associated with native geographic range size than invasiveness tended to represent a species' growth potential. Stem height significantly predicted invasiveness in univariate analyses (Table 1, 2, and S2), but this relationship disappeared after controlling for native range size, indicating species with taller stature are not preadapted towards invasiveness per se. Similarly, leaf size had a stronger correlation with native range size than invasiveness.

The absence of a direct association between height and invasiveness after controlling for range size is intriguing, since height is often found to be significant in comparative studies of invasiveness. Primary stem height in plants reflects the ability to compete with neighbors for access to limiting light resources for carbon fixation and growth (Westoby et al. 2003), and this competitive ability has been implicated in the emergence of invasiveness (Blossey and Notzold 1995). However, other studies have also challenged the basis of the association between height and invasiveness in plants (Thebaud and Simberloff 2001), and at least two other studies found the effect of height became non-significant after controlling for native range size (Goodwin et al. 1999; Pysek et al. 2009). It is not obvious why height would contribute to range size where a species is native, but not invasiveness where it is introduced. One possible reason is if species experience a higher average density of competitors in the native range compared to their areas of introduction, perhaps because of less frequent disturbance in native communities. In this case, taller species may have been more successful at colonizing a broad range of ecological communities in the native range, and hence be more likely to be exported (e.g., an indirect association with invasiveness through range size), but experience little direct competitive advantage under low density conditions where they've been introduced (no direct effect on invasiveness).

We used two different indices of invasiveness and two different branch length models to test the robustness of our results to different assumptions about quantifying invasiveness and the evolutionary process underlying trait evolution. In general, we found consistent support across these approaches for growth and reproductive traits as predictors of invasiveness, with few exceptions. One involved the role of breeding system. Species containing unisexual morphs were more likely to be invasive, but only in the North American analysis (Table 1 and S2). This is in contradiction to the notion that self-compatibility provides reproductive assurance ("Baker's law": Baker 1955; van Kleunen et al. 2008; Randle et al. 2009), but is consistent with an outcrossing advantage of unisexuals when pollen is not limiting.

Preadaptation among species and rapid evolution within species occurs at many of the same traits in Silene

Synthesis across comparative and microevolutionary studies of which traits are important to invasion are infrequent in the literature, yet they have important implications for the ability of comparative models to predict invasion success, as well as their efficacy in deriving accurate risk assessments (Whitney and Gabler 2008). In our study of *Silene* species, we identified fecundity (ovule number), growth (height, leaf size), and reproductive effort (number of flowers, months flowering) as preadaptive for invasion at the species level. Many of these same traits were previously shown to be rapidly evolving between introduced and native range populations of *S. latifolia* and *S. vulgaris* (Blair and Wolfe 2004; Wolfe et al. 2004; Keller et al. 2009, Keller and Taylor unpublished data). For example, common garden studies in *S. latifolia* have shown that introduced North American populations have evolved increased growth and reproduction; specifically, invasive genotypes germinated earlier, grew larger, flowered earlier (resulting in a longer flowering period), and produced more flowers than native range genotypes (Blair and Wolfe 2004; Wolfe et al. 2004). In similar experiments with *S. vulgaris*, introduced North American populations have rapidly evolved germination time, height, leaf size, flower production, and length of the flowering period (Keller et al. 2009; Keller and Taylor, unpublished data). Thus, there is good evidence that within the *Silene* genus, plant size, flower production, and flowering period are preadaptations that act to filter which species initially become invasive, and are simultaneously the targets of contemporary selection within introduced populations, showing evidence of rapid evolution.

The association between traits at comparative and microevolutionary scales is revealing about how natural selection contributes to the emergence of invasiveness. In particular, we propose that the same selective processes may be acting on traits at multiple levels of biological organization, both at the species level through a non-random selection of taxa, and at the population level, through a non-random selection of genotypes. This echoes a classic prediction from ecological genetics that the forces structuring species diversity and genetic diversity are fundamentally similar (Antonovics 1976). Thus, to understand how invasiveness emerges, we should strive for a mechanistic understanding of how certain traits confer fitness across different stages of invasion. Likewise, we should expect that the greatest response to selection during invasion will occur at the level of organization that shows the greatest amount of heritable variance for these key traits. Future studies that have the goal of predicting invasiveness would do well to consider not only the variance among taxa for preadaptive traits, but also the magnitude of within-species variance for these same traits, as indicative of future evolutionary potential.

Conclusions

Invasive species continue to be a worldwide problem for biodiversity and conservation. Our results show that native geographic range size, along with a suite of life history traits associated with growth and reproduction, can preadapt species for invasion success either directly (number of flowers, months flowering), indirectly through correlations with native range size (height), or through both direct and indirect paths (leaf size, number of ovules). Thus identifying the traits that underlie variance among species in native range size may lead to an improved understanding of how traits preadapt certain species for successful invasion abroad. We also suggest that possession of key preadaptations at the species level may act in parallel with rapid post-invasion evolution within species to increase invasion success, and in fact may represent a similar selective process operating at different biological levels of organization. These results from *Silene* may be representative of many herbaceous invasive plant species, given the large variation in life history and range size captured by this diverse genus. Understanding the origins of invasiveness will continue to benefit from an evolutionary perspective, including a better understanding of historical divergence between widespread and restricted taxa in the native range, the forces driving the evolution of trait differences during this process, and the causal mechanisms generating relationships between traits, native range size, fitness, and invasiveness.

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