

# Are Invaders Moving Targets? The Generality and Persistence of Advantages in Size, Reproduction, and Enemy Release in Invasive Plant Species with Time since Introduction

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**ABSTRACT:** Successful plant invasions are often attributed to increased plant size, reproduction, or release from natural enemies, but the generality and persistence of these patterns remains widely debated. Meta-analysis was used to quantitatively assess invasive plant performance and release from enemy damage and how these change with residence time and geographic distribution. Invasive plants were compared either in their introduced and home ranges or with native congeners in the introduced range. Invasive plants in the introduced range were generally larger, allocated more to reproduction, and had lower levels of herbivore damage compared with conspecifics in the home range; pathogen attack, however, varied widely. In congener comparisons, invasive and native plants did not differ in size or herbivory, but invaders did allocate less to reproduction and had lower levels of pathogen damage. Time since introduction was a significant nonlinear predictor of enemy release for both herbivores and pathogens, with initial release in recently arrived species and little to no release after 50 to 200 years. Geographic distribution was also a significant nonlinear predictor of enemy release. The observed nonlinear relationships are consistent with dynamic invasions and may define targets for eradication efforts if these patterns hold up for individual species.

**Keywords:** exotic plants, invasion, congeneric pairs, home versus away, time since introduction, geographic distribution.

Invasions by nonnative plant species are a considerable and costly threat to diversity and ecosystem function

worldwide (Mack et al. 2000; Pimentel et al. 2000, 2001). However, our understanding of why invasive plants (sensu Richardson et al. 2000) are successful is limited and has been focused more on short-term ecological processes rather than long-term evolutionary mechanisms (Lambrinos 2004). Successful invaders often exhibit an advantage over native species. Some of the most-cited putative advantages are size (e.g., Willis and Blossey 1999; Willis et al. 2000; Thebaud and Simberloff 2001; Leger and Rice 2003), competitive ability (Blossey and Notzold 1995; Jonathan and Scott 2001; Bossdorf et al. 2004b), and release from natural enemies (e.g., Elton 1958; Mitchell and Power 2003; Reinhart et al. 2003; Agrawal et al. 2005). The generality of these advantages and whether they are directly responsible for invasion success remains in question (e.g., Thebaud and Simberloff 2001; Colautti et al. 2004). Evidence for advantages in nonnative plants is based on short-term studies, and results frequently differ when plants are followed for more than a single year (e.g., Agrawal et al. 2005). To address long-term patterns of invasion, we must begin to examine both the generality and the persistence of any initial advantages after introduction. The durability of biotic interactions (or their absence), size increases, and other factors with the potential to affect fitness in invaded habitats remains a crucial unresolved gap in our understanding of invasions.

The ecological and evolutionary processes that drive invading species can change over time. How these processes vary may be fundamental to our ability to predict invasion dynamics (Dietz and Edwards 2006). Some introduced species only begin to spread after an initial lag time, which may be attributed to exponential growth, stochastic propagule extinction, or evolutionary change (Sakai et al. 2001). After introduction, rapid evolution can occur in the new range because of new selective pressures, founder effects, or hybridization (Thompson 1998; Lambrinos 2004; Bossdorf et al. 2005). One dramatic example is the apparent recent adaptation of invasive grasses in California to small patches of serpentine soils (Harrison et al. 2001). As res-

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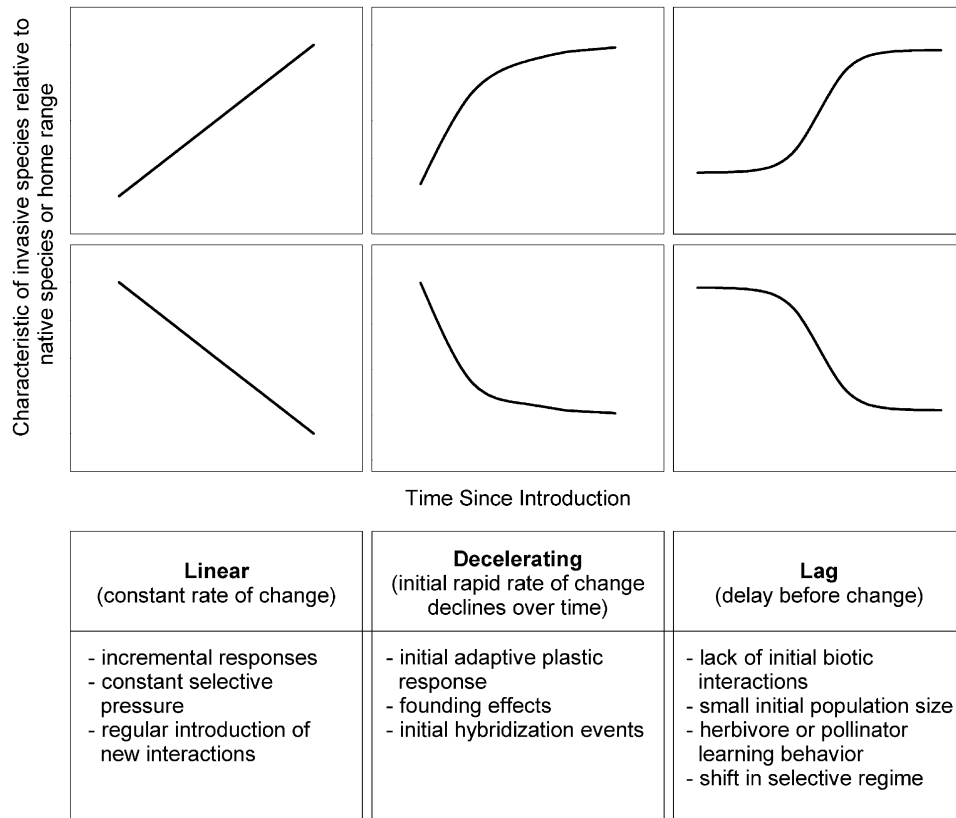
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idence time in the new range increases, Dietz and Edwards (2006) propose that a switch may occur from a primary phase of invasion, in which spread is dependent on species being preadapted for colonizing the new habitat, to a secondary phase, in which additional spread becomes a function of plasticity or adaptation to the environment and biota.

After introduction, patterns of change in traits that confer an advantage to invasive species may be indicative of underlying mechanisms (fig. 1). Most relevant is how the trait changes relative to a baseline to indicate invasion success. For invasive species, the baseline is typically provided by either conspecifics in the home range or native congeners in the introduced range. Linear patterns with time since introduction imply a constant rate of change, either increasing or decreasing depending on the slope, and are consistent with constant or incremental selective pressures. Nonlinear patterns are also possible. A decelerating curve reflects initial rapid changes followed by stasis, potentially the result of founder effects, loss of evo-

lutionary potential, or lack of new selective pressures. A sigmoid curve indicates a lag time, which may be due to similarity of the new range to the home range followed by a shift in selective regime, small initial population size, or the dynamics of learning behavior by or selection on the native biota (e.g., pollinators, herbivores) before interactions begin.

Studies that explicitly address long-term changes in invasive plants with time since introduction often focus on the accumulation of enemy species rather than the effects of those enemies on the plant, but no consistent patterns have emerged. For 23 crop plants in Japan, the proportion of insect-family specialists increased over time, with a 6.6% increase in specialists each century after introduction (Andow and Imura 1994). Other studies have not found an effect of time. For example, in a study of herbivory, Carpenter and Cappuccino (2005) found no overall relationship between time since introduction and leaf damage for 35 nonnative herbs in Canada. Understanding the patterns of change in invasive plants through time would clarify



**Figure 1:** Potential response curves for traits that confer an advantage to invasive plants in their introduced range relative to a baseline (conspecifics in the home range or native congeners in the introduced range). As residence time in the new habitat increases, the trait in invasive plants may increase (*upper graphs*) or decrease (*lower graphs*) at a rate that is constant (*left graphs*), decelerating (*center graphs*), or sigmoid (*right graphs*), relative to the baseline. Potential mechanisms for each pattern are described in the bottom panels.

how invaders continue to be successful and whether “one-time-fits-all” management strategies are sufficient or should be designed to target specific time points of the invasion process.

In some cases, insect or parasite species richness on host plants is better predicted by host species geographic distribution, area occupied, or a combination of distribution and area reflecting host species availability (e.g., Strong et al. 1977; Kennedy and Southwood 1984; Kelly and Southwood 1999; Brändle and Brandl 2001, 2003). The pattern of increasing insect species richness with area or distribution of the host plant has been attributed to three mechanisms: increased encounter rate by colonists, increased habitat heterogeneity, and the equilibrium between immigration and extinction (reviewed by Southwood and Kennedy 1983). It is hypothesized that plants that have been widely introduced experience less enemy release than those that have been narrowly introduced, compared with conspecifics in the native range. These patterns may be confounded, however, by differences in encounters with generalist versus specialist enemies and the degree of taxonomic isolation (e.g., Brändle and Brandl 2001). Because the effects of geographic distribution often outweigh or are correlated with the effects of residence time, it is important to understand both of these potential drivers of invasive species patterns.

We can rarely follow successful invasive species over several centuries (e.g., with herbarium records or aerial photographs; Mack 2005), but we can look for general patterns of change across species introduced to new ranges at different times. I used meta-analysis with the log response ratio as an index of effect size to quantitatively examine invasive plant performance and escape from enemies across published studies. To more broadly understand how invasive species change after introduction, I asked (1) whether invasive plant species are generally larger, allocate more to reproduction, or experience more escape from enemies, (2) how these effects change with increasing residence time in the introduced range, and (3) whether patterns with time are better explained by global geographic distribution.

Studies of plant size, reproduction, herbivory, and pathogen severity were included for the two most common types of comparisons: between invasive species in native “home” versus introduced “away” ranges and between congeners from the introduced range. Each of these analyses speaks to different aspects of successful invasions. Congener comparisons are employed to gauge the demographic success of invasive plants relative to the new community while controlling as much as possible for phylogenetic history. Within a habitat, the presence of related species is often used as an indicator of potential abiotic suitability and biotic resistance. It is this community in

which the invader must be successful. Biogeographic comparisons of conspecifics in native and introduced ranges can provide a window into both ecological and evolutionary mechanisms. How the invader fares in the new range relative to its native range can highlight specific characteristics or biotic interactions that may have shifted to facilitate the invasion. Observed biogeographic differences may be due to composition of the biota (e.g., lack of enemies in the new range), phenotypic plasticity (e.g., altered biomass allocation in response to new light levels), or genetic shifts (e.g., founder effects, postintroduction selection). Comparisons of both congeners and conspecifics are included in this meta-analysis in order to address quantitatively their contributions to understanding invasion success.

This appears to be the first attempt at a quantitative meta-analysis of this topic, as previous reviews have addressed the question only qualitatively, with vote counts, or as a test of enemy species richness (e.g., Thebaud and Simberloff 2001; Mitchell and Power 2003; Colautti et al. 2004; Hinz and Schwarzaender 2004; Bossdorf et al. 2005; Mitchell et al. 2006; but see Agrawal et al. 2005 for an analysis of their own data). Though a meta-analysis will shed light on the broad patterns of invasive species and their changes through time, a pervasive problem in invasion biology is the tendency to focus on the most spectacular plant invaders, which are unlikely to represent all nonnative plant species. Thus, the results of this analysis can be expected to apply only to invasive species and not to casual or benign nonnatives.

## Material and Methods

### *Literature Survey and Criteria for Inclusion*

I conducted a literature survey using keyword searches in ISI Web of Science citation database (Thomson, Philadelphia). References cited in articles found through the database were also searched. Criteria for inclusion were set in advance to avoid bias in selection. Studies were included only if they compared size or herbivory for plant species in home versus away ranges or for congeneric pairs in the invaded range. In addition, the following conditions were required for inclusion: (1) response variables were a measure of plant size (biomass, height, leaf area, or relative growth rate), allocation to reproduction (number or biomass of flowers, fruits, or seeds), herbivory (measures of damage or area lost, attack rate, herbivore abundance), or pathogen severity (number or percent pathogen infection, damage, or resulting plant mortality); (2) data reported were averages, sample sizes, and either standard deviations or standard errors; and (3) data were nonzero. When more than one record from a given study was appropriate, ad-

ditional records were only included when measurements were made of different groups of plants or in different years (which often showed opposing trends). If multiple measurements were made on the same plants, the record that most closely matched the above criteria was selected or a record was chosen randomly if all were equally suitable. Graphical data were captured using DataThief II (Tummers 1999). If some of the required data were not reported, I attempted to contact the corresponding author.

### Attribute Coding

For each record, the invasive ranking (see app. A in the online edition of the *American Naturalist*), date of introduction, and geographic range were established. Invasive status was based on government and plant society rankings at national and state levels for the location of the study, which resulted in four classes: noxious weeds, invasive plants, abundant aliens, and unranked species. Species are indicated by these categories in figures throughout.

Date of introduction was established either from published literature or herbarium records. Both of these are probably conservative estimates of the actual introduction date. Three online herbaria were used for North America: the CalFlora Database (<http://www.calflora.org/>), the New York Botanical Garden Virtual Herbarium (<http://sciweb.nybg.org/science2/hcol/allvasc/index.asp>), and the University of Montana Invaders Database (<http://invader.dbs.umt.edu/>). For European invaders, only a small number of records from France did not have published dates of introduction, and for these, dates were obtained from Herbarium Musei Parisiensis (<http://coldb.mnhn.fr/colweb/>). Time since introduction (or residence time) was calculated by subtracting the year of introduction from the year of the study.

Geographic distribution for each record was estimated as the number of biogeographic realms currently occupied (Nearctic, Neotropic, Palearctic, Afrotropic, Indo-Malay, Australasia, Oceania, and Antarctic). When this information was not available in the published literature, it was obtained from the Global Compendium of Weeds (<http://www.hear.org/gcw/>) and the Nature Conservancy's Global Invasive Species Initiative (<http://tncweeds.ucdavis.edu/control.html>). Current plant distributions or occupancies have been significantly correlated with herbivorous insect and parasitic fungal species richness on host plants (e.g., Kennedy and Southwood 1984; Brändle and Brandl 2001, 2003). The scale of biogeographic realms provides only a coarse estimate of current geographic distribution, but finer resolution of either distribution or area was not possible for most species. Thus, the analysis of distribution can only provide a conservative measure of how current global geographic distribution is broadly re-

lated to the size, reproductive allocation, and enemy release of introduced plants.

### Numerical Methods

The log response ratio ( $L$ ) was used as an index of effect size because it quantifies the proportionate difference in the invasive relative to the native congener or in the invaded relative to the native range and therefore eliminates differences due to plant size or metric. All calculations follow Hedges et al. (1999). Briefly, effect sizes were calculated as

$$L = \ln(\bar{X}_i) - \ln(\bar{X}_n),$$

where  $\bar{X}$  is the sample mean and the subscripts  $i$  and  $n$  represent either the invaded (away) and native (home) ranges or invasive and native congeners. The variance estimate for each record was calculated as

$$v = \frac{s_i^2}{n_i \times \bar{X}_i^2} + \frac{s_n^2}{n_n \times \bar{X}_n^2},$$

where  $s$  is the standard deviation and  $n$  is the sample size. The weighted mean effect size and standard error across studies were calculated as recommended by Hedges et al. (1999). Effect sizes were considered significant when 95% confidence intervals (CIs) did not overlap 0.

To examine heterogeneity among the four classes of invasion ranking in each data set, the  $Q_b$  statistic (Gurevitch et al. 1992) was used to test the null hypothesis of common effect size against the alternative of at least one effect size that differs from the rest. The  $Q_b$  statistic has a  $\chi^2$  distribution with degrees of freedom equal to one less than the number of classes. When  $Q_b$  was significant ( $P < .05$ ), we examined the mean log response ratios for the classes.

The sign of the log response ratio indicates the qualitative pattern of plant size, allocation to reproduction, herbivory, or pathogen attack. In all cases, an  $L$  of 0 means there is no difference between the groups. If plants in the away range are larger, allocate more to reproduction, experience more herbivory, or are subject to more pathogens,  $L$  will be positive (or vice versa). Similarly, for congeneric pairs, if the invading congener is larger or is subject to greater damage from herbivores or pathogens,  $L$  will be positive. In this meta-analysis, the log response ratio for individual comparisons ranged from 0, no difference, to approximately  $\pm 4$ , representing a 50-fold difference between congeners in the invaded range or between conspecifics in the home and away ranges.

**Table 1:** Classes of invasive species included in this meta-analysis

Class and subclass	No. species
Noxious weeds:	
Federally listed (United States)	10
State listed (United States)	5
Invasive aliens:	
Highly invasive (United States)	6
Moderately invasive (United States)	2
Invasive (international)	5
Invasive (state plant society)	2
Abundant aliens:	
Widespread (United States)	17
Local (United States)	2
Not ranked	18

Note: See appendix A for references used to define status.

### Statistical Analyses

Stepwise linear multiple regression, nonlinear regression, and curve-fit analyses were used to examine linear and nonlinear relationships between time since introduction, geographic range, and the log response ratio for the eight data sets: plant size, reproductive allocation, herbivory, and pathogen damage for conspecifics and congeners. All statistics were performed with SPSS version 14.0.1 (SPSS 2005).

## Results

### Species Included in the Meta-analysis

Data for the meta-analyses were extracted from a total of 62 studies (see tables B1, B2, in the online edition of the *American Naturalist*). The species included represent a nonrandom subset of invasive species. There were 67 species from 55 genera in 29 families, representing 46 herbaceous dicots, 13 woody dicots, and eight herbaceous monocots. Phylogenetically, most of the species were members of four families: Asteraceae (26%), Poaceae (10%), Brassicaceae (9%), and Rosaceae (6%). The species are largely of Eurasian origin (73%), and most were introduced to North America (64%). Time since introduction of the species ranged from 5 to 377 years; geographic distribution ranged from one to seven biogeographic realms.

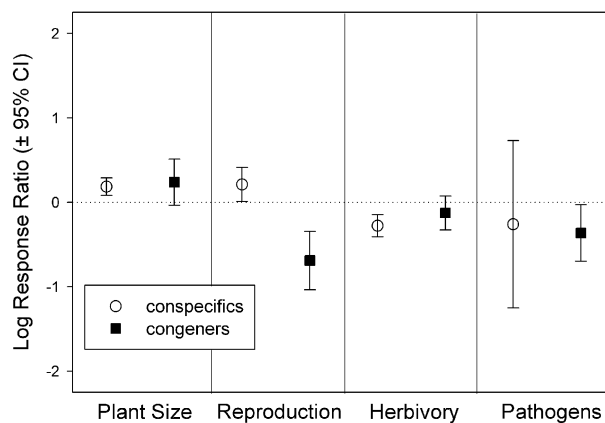
Studies of introduced plants tend to focus on extreme examples of highly invasive species, which can introduce bias into meta-analyses and prevent making any inference to a broader range of nonnative plants. All of the species in this analysis fit the definition of “invasive” put forth by Richardson et al. (2000) as naturalized plants that produce reproductive offspring at considerable distances from parent plants and that have the potential to spread over con-

siderable areas. Many of the species included in this analysis were also ranked by governments and other agencies, suggesting biological or economic impacts (table 1). Species were distributed among four classes: noxious weeds, invasive aliens, abundant aliens, and unranked species (table 1).

### Meta-analysis Outcomes

Conspecifics in native and introduced ranges differed significantly in plant size, allocation to reproduction, and herbivory (fig. 2). Significantly positive weighted average log response ratios indicated that plants invading a new range were larger (62% of cases), allocated more to reproduction (56% of cases), and were subject to less damage from herbivores (62% of cases) compared with those in the native range. However, the log response ratio for pathogen attack was highly variable and did not differ from 0. Sample size was smaller and the variance around the log response ratio was larger for pathogens in home versus away ranges than for any of the other data sets.

In studies of congeners, invasive plants also tended to be larger than natives (59%), but the 95% CI around the log response ratio overlapped 0 (fig. 2). The log response ratio for reproductive allocation in congeneric comparisons was significantly negative, with invasive plants allocating less to reproduction than their native congeners in 11 of 15 comparisons. Herbivory did not differ between invasive and native congeners, with a small negative log response ratio and 95% CI overlapping 0. The log response



**Figure 2:** Weighted mean log response ratios for plant size, reproductive allocation, herbivory damage, and pathogen severity in comparisons of invasive conspecifics in the home range versus the away range and invasive and native congeners in the introduced range. The effect size is considered significant if the 95% confidence interval does not overlap 0. From left to right, the numbers of records in each category were 62, 42, 39, 13, 26, 40, 10, and 24.

ratio for pathogen attack was negative, with the majority (67%) of cases showing lower pathogen severity on exotic congeners compared with natives.

The four classes of invasive ranking were significantly heterogeneous only in the case of comparisons of herbivory on conspecifics in introduced and native ranges ( $Q_B = 30.34$ ,  $df = 3$ ,  $P < .001$ ). Species classified as noxious weeds and invasive aliens escaped herbivory in the away range compared with the home range, while species considered abundant aliens and species that were not ranked did not (fig. 3).

#### Time since Introduction

In comparisons of conspecifics in invaded and native ranges, time since introduction was a significant nonlinear predictor of herbivory and showed a similar trend with pathogen damage (fig. 4), but it was unrelated to plant size or reproductive allocation (data not shown; see table B1). The log response ratio for herbivory in conspecifics was a logarithmic function of residence time (fig. 4A) and explained 9% more of the variation than a linear model (see table C1 in the online edition of the *American Naturalist*). Pathogen attack was an inverse function of residence time, with decreasing escape from pathogen attack in the introduced versus home range over time (fig. 4B). Residence time was also a nonlinear predictor of herbivory and pathogen attack in congener comparisons (fig. 4C, 4D), largely due to a few recent introductions. Reproductive allocation and plant size for congeners did not vary with time (data not shown; see table B2).

#### Geographic Distribution

In comparisons of conspecifics in their native and introduced ranges, global geographic distribution was a significant nonlinear predictor of herbivory and pathogen damage (fig. 5) but not plant size or plant allocation to reproduction (data not shown; see table B1). The log response ratio for herbivory had an inverse relationship with geographic distribution, approaching 0 as the number of biogeographic realms occupied increased (fig. 5A). The log response ratio for pathogens also had an inverse relationship with distribution, but narrower global distributions were associated with greater pathogen damage and wider global distributions with less pathogen damage in the introduced compared with the native range (fig. 5B). Geographic distribution did not explain any of the patterns found in congener comparisons (fig. 5C, 5D; table B2). Time since introduction and geographic distribution were not correlated in either the overall conspecific ( $P = .83$ ) or congener ( $P = .19$ ) data sets (including only one record per species).

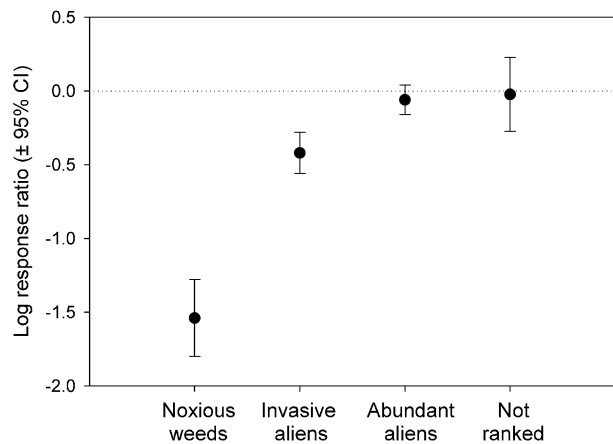


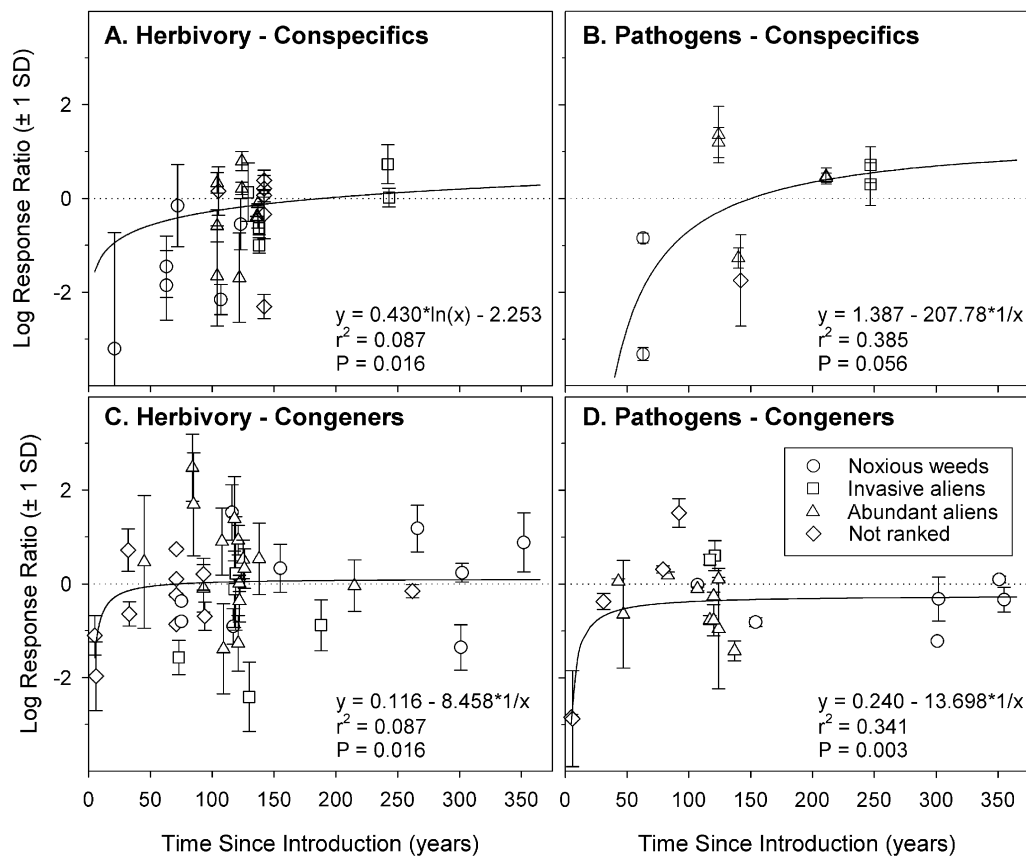
Figure 3: Invasive species ranking classes were heterogeneous in comparisons of herbivore damage on conspecifics in native and introduced ranges. From left to right, the numbers of records in each category were 6, 5, 9, and 6.

## Discussion

### Meta-analysis Outcomes: Enemy Release

Comparisons of conspecifics in native and invaded ranges and comparisons of native and invasive congeners in the same range ask fundamentally different questions about enemy release: have invasive plants escaped enemies from their native range, and do invaders fare better than natives in the invaded range? Colautti et al. (2004) summarized the current enemy-release paradigm: biogeographic studies demonstrate enemy release, and community studies show no differences in terms of the diversity of enemies. Here, I show that enemy release in the form of damage rather than diversity did not always follow this model but varied with the comparison, the type of enemy, and the residence time of the invader. Invasive conspecifics in the introduced range consistently escaped herbivory compared with the native range but experienced wide variation in pathogen attack. Within the introduced range, however, the degree of damage from herbivory was generally equal, and pathogen incidence levels were lower for invasive congeners compared with native congeners. Both comparisons speak to potential mechanisms and barriers for invasion success.

Release from enemies in the invaded range compared with the home range can facilitate invasions. The broad range of pathogen severity on invasive plants in the invaded range compared with the native range observed here was unexpected. Though all studies in this analysis reported data for fungal pathogens, far greater variability was found for pathogen escape than suggested by Mitchell and Power (2003), who found 84% fewer fungal pathogen species on plants from Europe naturalized in the United



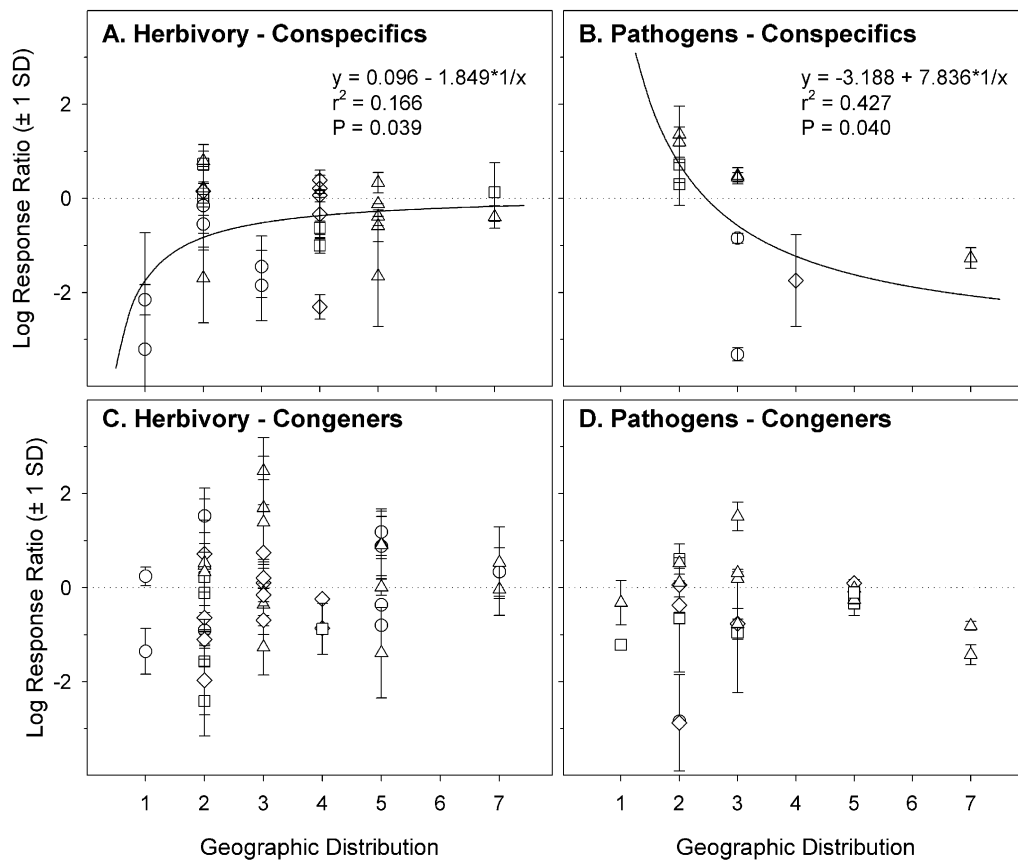
**Figure 4:** Log response ratios as a function of residence time for herbivory and pathogen severity in comparisons of conspecifics from native and introduced ranges (A, B) and congeners in the introduced range (C, D). A negative log response ratio indicates less enemy damage for invasive conspecifics in introduced ranges versus home ranges or for invasive congeners versus native congeners. Symbols represent invasive rank.

States. This difference may be due to the small sample size for pathogens in this meta-analysis, or perhaps it is because a third of the records in this analysis focused on invaders in Europe from North America. Historically, the flow of invaders of all types was predominantly from Europe along trade routes; this long-standing “ecological imperialism” may have delayed invasions into Europe (Crosby 1986; di Castri 1989; Heywood 1989). In addition, Mitchell and Power (2003) based their study on the number of species reported to occur on introduced plants rather than actual attack rates.

The presence of native congeners, given their shared phylogenetic history, in the invaded habitat may be indicative of how easily biotic relationships develop and could reduce the incidence of enemy release. For example, for 15 pairs of congeners, Agrawal et al. (2005) found little evidence for release from herbivory, fungal plant pathogens, viruses, or seed pathogens. In the majority of studies included in this meta-analysis, invasive congeners had a lower incidence of pathogens, and herbivore damage was

no different from what native plants experienced. It is possible that the transition to a new species is more difficult for pathogens than for herbivores, though this should be easier for related species (for review of the development of novel plant-pathogen interactions, see Parker and Gilbert 2004). These results are quite likely, however, to be complicated by the introduction of nonnative herbivores and pathogens either accidentally or through biocontrol efforts (e.g., Willis and Blossey 1999; Daehler 2003; Hinz and Schwarzlaender 2004).

Species ranked into different classes of invasiveness experienced different degrees of release from herbivory for conspecifics in the invaded range compared with the native range. Those species classified as noxious weeds were at the greatest advantage in the away range, followed by invasive aliens. Species considered abundant aliens and those that were not ranked experienced no differences in herbivore damage between the home and away ranges. This may reflect the importance of herbivory in top-down control of the invasion process and how release of that control



**Figure 5:** Log response ratios as a function of geographic distribution for herbivory and pathogen severity in comparisons of conspecifics in native and introduced ranges (A, B) and congener comparisons in the introduced range (C, D). Geographic distribution was estimated as the number of biogeographic zones occupied. Symbols represent the four classes of invasive rank as in figure 4.

is particularly relevant to the worst invaders. There were no differences among invasive ranking classes for any of the other analyses. However, more biogeographic data for pathogen attack on conspecifics will be needed to determine whether invasive ranking also reflects enemy release from pathogens—the small sample size meant that three of the four classes contained only one or two records.

Enemy release does not necessarily translate directly into improved plant fitness or invasion success. For example, in some cases, fitness consequences of rust pathogens can be very low despite incidence levels of 50%–100% (Roy and Kirchner 2000), while in others they can significantly reduce both reproduction and survival (e.g., Paul and Ayres 1986, 1987; Maron et al. 2004a). One model of pathogen accumulation suggests that invading plants can spread even if their fitness is reduced by local generalist pathogens as long as local natives are more affected (Eppinga et al. 2006). The magnitude of release from herbivore damage in this meta-analysis appears to be lower than reported based on enemy species richness (for review, see

Liu and Stiling 2006), but neither damage nor enemy diversity are direct measures of fitness. Only a few studies have used enemy reduction or exclusion (e.g., with fungicide) to demonstrate a link between herbivory or pathogen attack and plant growth, survival, or reproduction (DeWalt et al. 2004b; Maron et al. 2004a). For example, DeWalt et al. (2004b) found that reduction of both insect and fungal enemies in the native range significantly increased survival in understory but not open habitats; in the introduced range, survival was near 100% regardless of habitat or enemy reduction. Linking biotic interactions and their proximate impacts (e.g., leaf damage) to their ultimate effects on plant fitness will be necessary to quantify their role in the demographic success of invasive species.

#### *Meta-analysis Outcomes: Size and Reproduction*

Two measures often correlated with plant fitness are size and reproduction. In this meta-analysis, invasive conspe-



cifics were generally larger and allocated more to reproduction in the introduced range compared with the native range. Invasive congeners also tended to be larger than natives but had lower reproductive allocation. Individuals that are larger or reproduce more might have a greater probability of arrival or successful colonization in the new range compared with less fecund conspecifics, but within the new range, invasive plants apparently do not allocate as much to reproduction as their native congeneric counterparts. It is also likely that larger size and greater reproductive allocation were selected for horticultural purposes in some currently invasive species (e.g., Crawley et al. 1996). Nevertheless, neither larger size nor reproductive allocation was necessary for invasion success. Thebaud and Simberloff (2001) found only 36% of 472 plants introduced to California were taller than in their native European range based on upper limits of height recorded in floras; 35% were smaller and the remainder showed no difference in height between the two ranges. In the current meta-analysis, the majority of studies reported a measure of biomass, but the breakdown was similar to Thebaud and Simberloff (2001), with smaller biomass in 33% of conspecifics in the invaded range compared with the native range and 38% of invasive congeners compared with native congeners in the invaded range. Daehler (2003) suggests that some of the variability in invasive plant performance may be due to growing conditions, which were not examined here.

#### *Time since Introduction*

Plant damage from herbivores and pathogens followed nonlinear patterns with time since introduction. Both the logarithmic and inverse models are consistent with invasive species that undergo rapid change within a few decades of arrival in the introduced habitat relative to their native habitat or new neighbors, followed by a diminishing rate of change thereafter. Eventually, however, the invasive species collectively become quite similar to local congeneric natives or to conspecifics in their home range in terms of both herbivory and pathogen damage. For conspecifics, the log response ratio approached 0 within roughly 150 years for herbivory and 200 years for pathogen attack; for congeners, the log response ratio stabilized within 50 years for both herbivory and pathogen attack. This is based on snapshots of multiple species with different residence times rather than the ideal of species followed from their initial introduction. The fact that we see change over time across species suggests that individual species are likely to change as well, although the exact trajectories will be species specific.

There were replicates of individual species within this meta-analysis measured at different times that could help

to shed light on the variation within species. For enemy release, replicates in time were consistent in the direction of the log response ratio in 63% of cases. The magnitude of the log response ratio for multiple records of the same species across time was also variable, with a standard deviation, on average, of 0.66. Although most of the temporal replication was only across two consecutive growing seasons, the variation was comparable to that observed for spatial replicates that were usually local or regional. For measurements of different populations or subpopulations, 62% of the replicates were consistent in direction and the standard deviation around the magnitude was 0.63. If these nonlinear models hold up for individual species across longer periods of time and broader geographic areas, we can begin to consider time-specific targets and management strategies for invasive plants. For example, the introduction of herbivorous natural enemies from the native range may be most successfully employed before the time when herbivory on the invasive species equalizes between the introduced and native ranges. More studies of individual species through time will be required to determine whether these thresholds are predictable.

In both the conspecific and congeneric comparisons of herbivory and pathogen attack, the nonlinear regressions against residence time were strongly influenced by a small number of recently introduced species. In some cases, these values are confirmed by earlier introductions of the same species. For example, the conspecific herbivory analysis included records from different populations of *Spartina alterniflora* introduced to California in 1980 (Callaway and Josselyn 1992) and 1894 (Sayce 1988, cited in Daehler and Strong 1997). Both of these populations had negative values of  $L$  ( $-3.21$  and  $-2.16$ ), but the variance was nearly 60 times lower in the earlier introduction. In other cases, such as pathogen attack on conspecifics, the most recently introduced species, *Clidemia hirta* (introduced to Hawaii in 1941; DeWalt et al. 2004b), was replicated spatially across different experimental populations, and both had significantly negative log response ratios ( $-3.32 \pm 0.14$ ;  $-0.85 \pm 0.11$ ). Nevertheless, the small number of recent introductions included in this meta-analysis reveals a gap in our understanding of the invasion timeline, which may be particularly important for invasion success or failure. Species are often overlooked during initial colonization phases when they are not considered problematic, and many of the estimates of introduction date probably underestimate the true residence time because of this. Identifying species within the first 10–50 years of arrival will be necessary to determine whether enemy release is a consistent factor in the initial phase of invasion.

While some species may be preadapted for invasiveness, later phases of invasion, such as between colonization and expansion, may be important control points from both

ecological and evolutionary perspectives because the mechanisms driving invasion success can change with time. Dietz and Edwards (2006) reviewed studies examining the evolution of increased competitive ability, which appears to apply for species introduced 200–250 years before but not for those that arrived only 50–150 years earlier. The current meta-analysis cannot be used to distinguish between preexisting differences and changes in response to the new habitat for individual species, nor can it directly evaluate whether or not evolution has occurred. However, the nonlinear loss of release from enemy damage with time since introduction observed here has not been reported in other studies of plant invasions (e.g., Carpenter and Cappuccino 2005) and deserves further scrutiny to distinguish evolutionary from ecological mechanisms.

### *Geographic Distribution*

Geographic distribution has been positively correlated with insect enemy richness (e.g., Kennedy and Southwood 1984; Brändle and Brandl 2001, 2003), and in this meta-analysis, more widespread invasive species were also subject to more herbivore damage and a decreasing degree of escape in the invaded range compared with the native range. However, the opposite pattern was observed for pathogen attack, with increasing escape for more widespread invasive conspecifics in invaded versus native ranges. This contrasts with patterns of pathogen species richness found by Mitchell and Power (2003), who found that more pathogen species accumulated for every increase in geographic distribution in the native range compared with the introduced range. Other regional studies have found that host plant distribution is positively correlated with fungal pathogen richness, though not as well as for herbivore species richness (Strong and Levin 1975; Brändle and Brandl 2003). Improved geographic resolution for invasive species and more studies of pathogen damage on invasive and native conspecifics might help to resolve these differences. Nevertheless, even at this coarse scale, geographic distribution was as important as residence time for comparisons of conspecifics in invaded and native ranges.

### *Conclusions*

Based on the results of this meta-analysis, patterns of enemy release and the relative advantages of size or reproduction differ between biogeographic and community comparisons. Successful invasive plants fare relatively better than conspecifics in the home range, but not necessarily better than native congeners in their new habitat, in terms of size, reproductive allocation, and enemy release. The importance of individual enemy release in these analyses also highlights the lack of studies simultaneously address-

ing multiple biotic interactions. Differential escape from enemies has been demonstrated in several cases where more than one enemy was studied (e.g., Agrawal and Kotanen 2003; Agrawal et al. 2005), and thus individual enemy release is unlikely to be a sufficient mechanism for invasion on its own. Ultimately, the long-term balance of positive and negative interactions, as well as the independence of those interactions (Morris et al. 2007), should be more relevant to determining the success of invasive species.

Enemy release was affected by both residence time and geographic distribution. The overall patterns that emerged are remarkable given that the substitution of multiple species with different histories for individual species followed through time will surely add variability due to species-specific rates of change. Studies of individual species through time will be necessary to confirm these patterns and determine whether the mechanisms are ecological or evolutionary. Identifying the dynamic nature of invasions both in time and space will increase our understanding of invasion processes.

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