

Can a breakdown in competition–colonization tradeoffs help explain the success of exotic species in the California flora?

Marco A. Molina-Montenegro, Elsa E. Cleland, Sean M. Watts and Bernardo R. Broitman

M. A. Molina-Montenegro (marco.molina@ceaza.cl) and B. R. Broitman, Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Facultad de Ciencias del Mar, Univ. Católica del Norte, Larrondo 1281, Coquimbo, Chile. Present address for MAMM: Colina El Pino s/n, La Serena, Chile. BRB also at: Center for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Univ. Católica de Chile, Santiago, Chile. – E. E. Cleland, Ecology, Behavior and Evolution Section, Univ. of California San Diego, La Jolla, CA 92093, USA. – S. M. Watts, Environmental Studies Inst., Santa Clara Univ., 500 El Camino Real, Santa Clara, CA 95053, USA.

Determining combinations of functional traits that allow a species to colonize new habitats has been central in the development of invasion ecology. Species able to establish in new communities harbor abilities or traits that allow them to use resources or tolerate stress in ways that native species cannot. Tradeoffs among species functional traits along the competition–colonization (CC) continuum, where competitive ability is a decreasing function of dispersal capacity, may allow invasive species to establish themselves in new habitats. The California flora offers a well-characterized model system to examine whether native and exotic species differ in the distribution of functional traits and to examine whether a breakdown of the CC tradeoff is present. We used a random subset of 1000 plants and examined seed traits and life form characteristics along with their seed size and adult height using the Jepson Manual of the plants of California. To test the hypothesis that active dispersal strategies aid in the success of exotic species, we classified species into four seed types according to the presence/absence of mechanisms associated with efficient dispersal. In addition, for each species we compiled data on seed size and adult plant height. We conducted all comparisons between native and exotic species within the four most speciose families to control for potential taxonomic non-independence. Exotic species had smaller seed size but greater plant height than natives of the same families. On the other hand, exotic species also displayed significantly greater proportions of functional traits that enhanced dispersal ability. Additionally, certain sets of functional traits were significantly associated with exotic species, such as annual life histories with small seeds and high dispersal capacity. In the random subset of the California flora examined, exotics of the most speciose plant families show functional trait combinations that appear to violate the tradeoff structures observed in their California counterparts. Our results suggest that taxonomically controlled comparisons of the CC tradeoff structure between natives and exotic species may shed light of the capacity of those exotic species invasive ability to colonize new habitats.

Ecologists have long been fascinated by the question of which traits can predict species potential to colonize new environments. Elton (1958) hypothesized that species able to establish themselves in new communities possess abilities or traits that allowed them to use resources or tolerate stresses in ways that native species cannot. Tradeoffs among species traits reflect different strategies for resource capture and interspecific interactions that may influence community structure and ecosystem processes (Craine et al. 2001, Lavorel and Garnier 2002).

The original competition–colonization (CC) tradeoff models proposed that although superior competitors might consistently displace subdominants, inferior competitors are able to compensate at the population level through superior colonization ability (Levins and Culver 1971, Horn and MacArthur 1972). The ambiguity of the term ‘competition’ (how to measure it, what life history stages or species interactions to include) has resulted in a protracted debate between ostensibly opposing theories on the role of competition in

vegetation dynamics (Grace 1991). Partly for this reason, many investigators have used seed size as a direct measure of the CC tradeoff (Kneitel and Chase 2004). Seed size is the most predictable and consistently measurable plant functional trait (Harper et al. 1970, Turnbull et al. 1999) and is correlated with habitat, phylogeny and rooting depth (Baker 1972, Guerrero-Campo and Fitter 2001). Small seed size is associated with greater dispersal distance, longevity in seed banks, is strongly correlated with high per capita seed output, and may yield greater propagule dispersal in space or time (Guo et al. 1995, Weiher et al. 1998, Kneitel and Chase 2004), while large seed size shows an opposite pattern (Jakobsson and Eriksson 2000, Leishman and Murray 2001). Turnbull et al. (1999) provided convincing experimental support for seed size as a proxy for colonization ability, demonstrating that small-seeded species were superior colonizers at natural sowing densities, while large-seeded species were able to dominate plots if recruitment limitation was overcome by increased sowing density. Although small-seeded

species show higher dispersal ability than large-seeded species, this is not really a measure of effective colonization per se (Cadotte et al. 2006). Yet it has been widely suggested that higher dispersal does increase the chances of establishing new populations (Lockwood et al. 2005).

While seed size may be a good proxy for the CC tradeoff, it only allows for inquiries along one trait axis. Therefore, considering the variation of other traits as proxies of colonization and competition ability such as dispersal mode, adult plant height and life form, could provide more information about the occurrence of the CC tradeoff within native and exotic species in a given region. It is very likely that functional traits such as those related to physiology, biomass allocation, growth rate, height at maturity and dispersal modes can promote invasiveness (van Kleunen and Richardson 2007). For example, several traits linked to dispersal for wind and animals are related to higher colonization ability and invasiveness (Rejmánek and Richardson 1996, Rejmánek et al. 2004). On the other hand, taller individuals and annual life forms are better represented among exotics than native species, as both are characteristics a proxy of competitive ability (Godoy 2009). In fact, it has been suggested that species with larger body size possess higher competitive ability than those with smaller body size (Cadotte et al. 2006).

Examination of multiple traits simultaneously may yield deeper insights into the process of invasion as certain dispersal strategies could allow a species to 'break' the CC tradeoff, thus maximizing colonization ability (Howe and Smallwood 1982, van der Wall 2003). Although there are mixed results linking invasiveness to competitive ability (Turnbull et al. 2010), considering plant height in conjunction with dispersal traits might reveal advantages among exotic species that may not be otherwise apparent by evaluating size alone, for example, the ability to achieve large adult size while maintaining dispersal ability. Studies evaluating how differences in traits that enhance the competitive ability of alien vs. native species are seldom found in the literature (Pysek and Richardson 2007). Recently, a meta-analysis showed that invasive species had significantly higher values than native species for many traits related to invasiveness (van Kleunen et al. 2010).

On the other hand, theoretical studies of tradeoffs between ecological strategies in plants have concentrated on the processes that regulate species diversity and coexistence under scenarios of dominant competitors versus dominant colonizers (Tilman 1994). Attempts to develop a predictive science of invasion ecology have generally sought to identify specific traits characterizing invasive species (D'Antonio 1993, Rejmánek and Richardson 1996, Maron and Vila 2001, Kyle and Leishman 2009, van Kleunen et al. 2010). For the most part, results have been equivocal: Daehler (2003) reviewing 79 comparative field studies found that invasion success is highly context dependent. Depending on site conditions, the competitive abilities of an invasive species to outperform a native correlated with maximal relative growth rate (lower tissue construction costs, higher leaf area) and greater phenotypic plasticity (Richards et al. 2006, Hussner 2009, van Kleunen et al. 2010).

Considering the constraints demonstrated in theoretical and experimental tests of the competition–colonization hypothesis (Yu and Wilson 2001, Levine and Rees 2002),

it would appear that combinations of traits that break the expected tradeoff between dispersal and establishment ability may be characteristic of species that successfully establish in new communities (i.e. 'the ideal weed,' sensu Baker 1974). Therefore, we expect tradeoffs among traits that compromise competitive abilities and colonization capacity to be less strong or less evident in exotic than in native species with similar ecological and/or phylogenetic characteristics.

Functional traits integrate the evolutionary and ecological history of a species, so we might expect that natives and exotics within a given taxonomic group would have similar traits and tradeoff structures (Schwinning and Ehleringer 2001, Westoby et al. 2002). The principle of limiting similarity predicts that differences in functional traits allow exotic species to invade (Stachowicz and Tilman 2005, van Kleunen et al. 2010). In this way, we might expect to find tradeoffs combinations that are advantageous, such that within taxonomic groups, exotic species will be significantly different from their native counterparts on only one or a subset of these trait axes. For example, it has been shown that exotic species have an advantage over natives because they are able to enhance or maintain their performance under high or low levels of resources, respectively (Pysek and Richardson 2007, Godoy 2009). Hence, if exotic colonisation of open patches is aided by enhanced seed dispersal traits, and they simultaneously have less constrained resource requirements to maintain higher growth rates than natives, the CC tradeoff would not hold. Such an unexpected pattern of trait correlation would give rise to a 'Hutchinsonian demon' (sensu Cadotte et al. 2006).

The flora of California hosts an exceptional diversity of native plant species but exotic species are being incorporated at elevated rates (Levine and D'Antonio 2003). Alien species reach ca 1200 species, representing nearly 20% of the Californian flora (Rejmánek et al. 2004). Because the California flora is so well characterized, it offers a model system to test the hypothesis that native and exotic species differ in the frequency of functional traits related to successful establishment in a new environment or location. Specifically, we asked: 1) do trait correlations among invasive plant species constitute a break down of the competition–colonization tradeoff? 2) are the relative frequencies of invasive life forms and seed dispersal traits higher among non-native plants than among native species? And 3) are there consistent differences in seed size and plant height between native and non-native species within the four most speciose families of the California flora?

Methods

We characterized a subset of the California flora with respect to plant traits by randomly selecting 1054 species from the Jepson Manual of the plants of California in order to complete 1000 species trait profiles using a latin square design on the alphabetical list of species publicly available for the flora (Hickman 1993); <http://ucjeps.berkeley.edu/jepson_flora_project.html>. All species were selected from a single pool and then separated into native and alien categories for analysis. To test the hypothesis that particular dispersal strategies aid in the success of exotic species, we classified species

into four seed types according to the presence/absence of mechanisms associated with a dispersal strategies associated to long-range dispersal (Van der Pijl 1972; Table 1A). As a conservative classification, the polychorous-indeterminate category included seeds with secondary structures that could not be clearly ascribed to either secondary (zoochorous) or anemochorous dispersal (Cornelissen et al. 2003). Seeds were considered polychorous-indeterminate if awns, pappus or wings were less than or equal to half of the seed size; the influence of this criterion on the interpretation of results is covered in the Discussion. To test the hypothesis that rapid growth aids the success of exotic species, we classified species into four life forms according to their biomass accumulation strategy (Table 1B). These life forms (annuals, root perennials, stem perennials and leaf perennials) represent composite categories according to the perennating structures deployed by plants during the unfavorable (dormant) season. In addition, for each species we compiled data on seed size (in mm) and maximum adult plant height (in cm). Seed size was considered as an estimate of the mature ovule and immediate surrounding hardened pericarp (dispersal unit minus ‘adornment’

Table 1. Description of traits compiled from the Jepson manual for (A) seed type and (B) life form.

(A)	Description
Simple	Seeds and associated pericarp without flesh or dispersal structures, usually small in size
Polychorous indeterminate	Associated structures not clearly associated with the following categories of dispersal
Secondary dispersal	Structures that clearly suggest animal dispersal (zoochory); e.g. recurved awns, mucilaginous seeds, eliasomes or fleshy fruit
Anemochorous	Clearly wind-dispersed, winged, pappused, or minute (<0.5 mm) seeds
(B)	Description
Annuals	Aboveground and belowground structures die over periods of time of one or very few years. Includes biennials and parasites
Root perennials	Aboveground structures die each year, translocating water and nutrients to perennating belowground structures. The Jepson defines this category more broadly as plants with no woody aboveground structures-i.e. herbaceous perennials
Stem perennials	Aboveground structures die back to lower stems each year. This category includes subshrubs and cushion-forming or clonal species
Leaf perennials	Above ground structures persist but leaves may be annual or persist for 1+ years. This category includes evergreen and deciduous trees, shrubs and succulents

or an individual seed for compound or aggregate fruit). For Poaceae, the ‘seed’ (caryopsis) included palea only if fused or persistent and did not include subtending lemma or glumes that might constitute the diaspore unit (e.g. in *Hordeum* spp.). Wherever possible, we deferred to the Jepson manual for all traits and supplemented it from other sources (Munz and Keck 1968, Mabberley 1997).

In order to control for potential taxonomic non-independence within origins, we conducted our analyses for all species taken together and also separately within the four most speciose families in California: Asteraceae (composites), Brassicaceae (crucifers), Fabaceae (legumes) and Poaceae (grasses). The Brassicaceae present in California range only from annual to subshrub life forms (i.e. annuals, and root and stem perennials). The rest of the families occur across all life form categories, although they are mostly represented by herbaceous forms (annuals and root perennials).

Statistical analysis

We used one-way ANOVA to evaluate differences between all native and exotic species in seed size and plant height at maturity (both measures were log₁₀ transformed to meet parametric assumptions; Zar 1999). Considering that seed size might be affected by plant height, we used standard Pearson correlations to investigate the relationship between seed size and adult plant height for natives and exotics. A two-way ANOVA was performed using plant family and native status as fixed factors to test for differences in seed size or height within the four most speciose families. Due to the unbalanced nature of this analysis (inherently unequal sample sizes of species within family and native status), we followed a mixed-model procedure in SAS ver. 9.1, which uses maximum likelihood estimation and corrects for unbalanced designs (Littell et al. 2002). We examined the frequency distributions of native and exotic plant species within dispersal and life form categories using χ^2 statistics and tested for significance using Fisher’s exact test, which is more appropriate

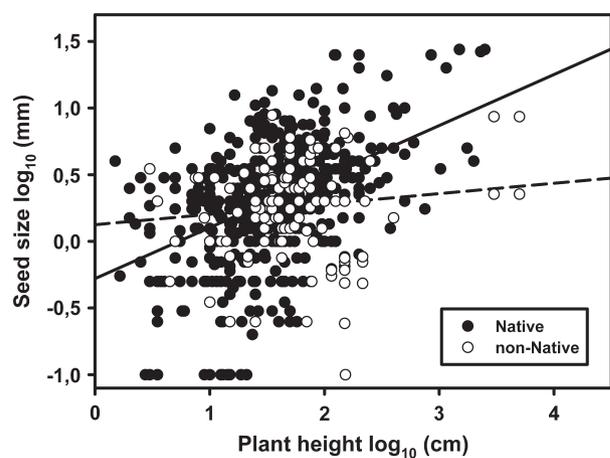


Figure 1. Relationship between plant height (log₁₀ (cm)) and seed size (log₁₀ (mm)) for 1000 randomly selected plant species from the Jepson manual. Filled dots and solid line indicate plants that are native and open dots and dashed line indicate exotic species to California. Traits were significantly correlated among natives but not exotic plant species ($r = 0.47$; $p < 0.001$ and $r = 0.10$; $p = 0.22$, respectively).

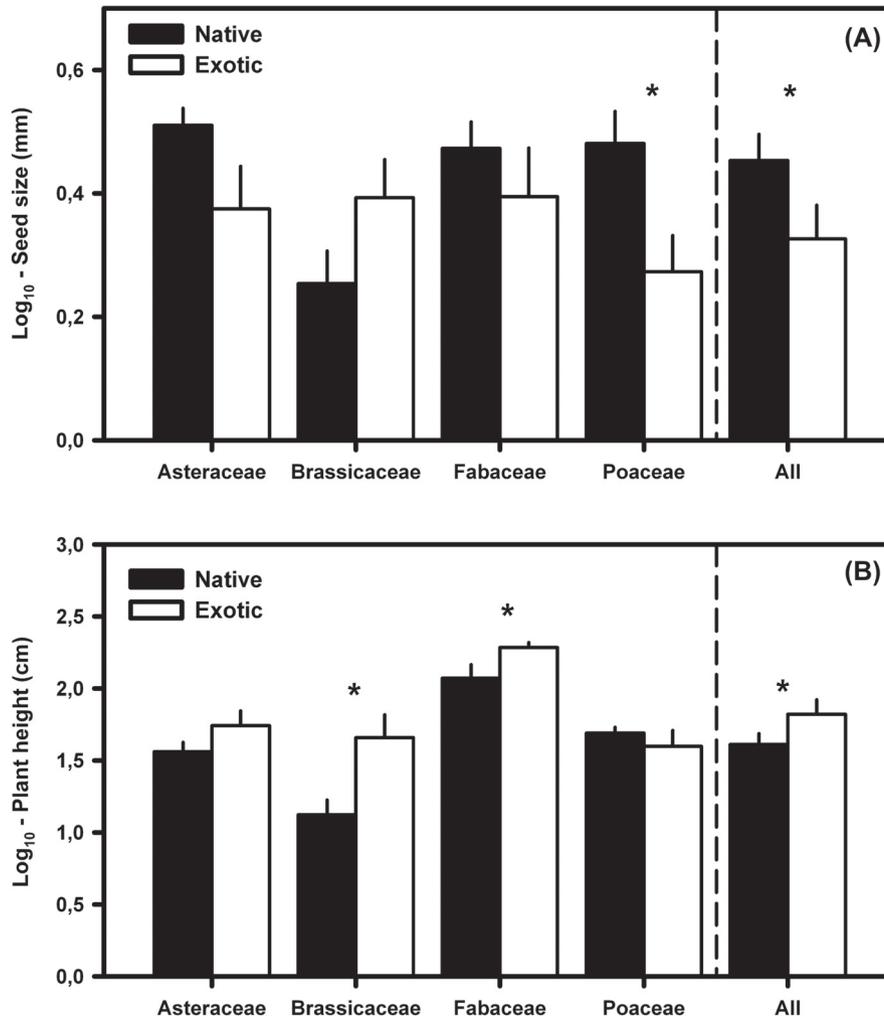


Figure 2. Comparison between seed size (\log_{10} (mm)) and plant height (\log_{10} (cm)) of native and exotic species in the four most speciose families (Asteraceae, Brassicaceae, Fabaceae and Poaceae). Native and exotic species are indicated by filled and open bars, respectively. An asterisk indicates significant differences ($p < 0.05$). Samples sizes used in the analysis were the following: Asteraceae (119 and 28), Brassicaceae (29 and 15), Fabaceae (64 and 17) and Poaceae (55 and 16), for native and exotic species respectively.

if any cell in the contingency table has fewer than five observations (Zar 1996). All analyses were carried out using SAS ver. 9.1 (SAS Inst. 2004) and Matlab ver. 7.1.0.246 (R14) (Mathworks, Natick, MA).

Results

Across the 1000 selected species (831 and 169 species for native and non-native, respectively) there was a positive correlation between seed size and plant height, but this correlation was only statistically significant for native species (Fig. 1). Additionally, the slopes of correlations for native and non-native species were statistically different ($F_{1,997} = 12.42$; $p < 0.001$; Fig. 1). Overall, exotics had significantly smaller seed sizes than natives ($F_{1,998} = 5.97$; $p = 0.039$ Fig. 2A). There were significant differences in seed size among families ($F_{3,339} = 4.62$; $p = 0.045$) and a marginal family \times native status interaction ($F_{3,339} = 3.61$; $p = 0.054$). While smaller seed sizes were found in exotic versus native species within the Poaceae and Asteraceae (post hoc Tukey's test $p = 0.015$ and $p = 0.058$,

respectively; Fig. 2A), in the Brassicaceae family, smaller seed size was found in native than exotic species (Fig. 2A).

Across all species, exotics were significantly taller at maturity than natives ($F_{1,998} = 6.11$; $p < 0.01$, Fig. 2B). There were significant differences among the four most speciose families in their plant heights ($F_{3,339} = 7.58$; $p < 0.001$, Fig. 2B), but most importantly, differences between native and exotic species depended on the family (family \times native status interaction: $F_{3,339} = 5.78$; $p = 0.010$). Exotics were significantly larger than natives in the Brassicaceae, and in the Fabaceae (post hoc Tukey's test, $p = 0.002$ and $p = 0.039$, respectively; Fig. 2B).

Native and exotic species differed in the distribution of their seed dispersal traits and life forms within some families as well as when taken as a whole. Overall, exotic species were more likely to have an annual life history, and were less likely to be perennial, particularly root perennials. These trends held for species within the Poaceae and Fabaceae, but were not apparent in the other families (Table 2). With regard to seed type, across all species, exotics were more likely to display seed types associated with long-range dispersal than natives, which were more likely to have simple seeds. Within

the Asteraceae, native species were most frequently wind-dispersed, with a large fraction (relative to exotics) lacking any clear dispersal mechanisms. Seeds of exotic Asteraceae were most frequently polychorous-indeterminate or clearly wind-dispersed (Table 3).

Discussion

The presence of a positive correlation between seed size and plant height in natives but not in exotic species suggests that the latter may violate the competition–colonization tradeoffs by maintaining high dispersal ability even in large sized plants. Exotic species in the California flora were generally larger, suggesting greater competitive ability than their native counterparts, particularly in the annual life-form category. The greater tendency for exotic species to possess smaller seeds and to present seed types associated with long-range dispersal also suggests that they are superior to natives in colonization ability. From results at this flora-wide scale of resolution we might conclude that large plant height, small seed size, annual life form and seed types associated

Table 2. Contingency table of the relative frequencies of life forms among plants native and exotic to California for the four most speciose families and for all species grouped together. Fisher's exact p-values in boldface indicate that the null hypothesis of no difference is rejected at the 0.05 confidence level. Numbers in parentheses indicate the percentage of native or exotic species.

Family	Native	Exotic
Asteraceae		
Annuals	28 (25)	8 (44)
Root perennials	58 (51)	9 (50)
Stem perennials	14 (12)	1 (6)
Leaf perennials	13 (12)	0
χ^2	4.895	
Fisher's exact p	0.215	
Brassicaceae		
Annuals	9 (31)	6 (46)
Root perennials	18 (62)	9 (54)
Stem perennials	2 (7)	0
Leaf perennials	0	0
χ^2	1.989	
Fisher's exact p	0.414	
Fabaceae		
Annuals	10 (16)	6 (50)
Root perennials	43 (68)	2 (17)
Stem perennials	4 (6)	0
Leaf perennials	6 (10)	4 (33)
χ^2	12.761	
Fisher's exact p	0.004	
Poaceae		
Annuals	7 (12)	11 (65)
Root perennials	40 (70)	2 (12)
Stem perennials	4 (7)	0
Leaf perennials	6 (11)	4 (23)
χ^2	9.087	
Fisher's exact p	0.007	
All families		
Annuals	209 (25)	61 (45)
Root perennials	373 (45)	43 (32)
Stem perennials	131 (16)	16 (12)
Leaf perennials	113 (14)	15 (11)
χ^2	22.288	
Fisher's exact p	0.0002	

Table 3. Contingency table of the relative frequencies of seed dispersal traits among plants native and exotic to California for the four most speciose families and for all species grouped together (PI = polychorous indeterminate). Fisher's exact p-values in boldface indicate that the null hypothesis of no difference is rejected at the 0.05 confidence level. Numbers in parentheses indicate the percentage of native or exotic species.

Family	Native	Exotic
Asteraceae		
Simple	28 (25)	2 (11)
PI	28 (25)	9 (50)
Secondary dispersal	2 (1)	2 (11)
Anemochorus	55 (49)	5 (28)
χ^2	10.681	
Fisher's exact p	0.017	
Brassicaceae		
Simple	14 (57)	8 (62)
PI	10 (39)	3 (23)
Secondary dispersal	0	0
Anemochorus	1 (4)	2 (15)
χ^2	1.899	
Fisher's exact p	0.391	
Fabaceae		
Simple	12 (20)	2 (18)
PI	47 (77)	8 (73)
Secondary dispersal	2 (3)	1 (9)
Anemochorus	0	0
χ^2	0.766	
Fisher's exact p	0.530	
Poaceae		
Simple	12 (29)	6 (38)
PI	18 (43)	9 (50)
Secondary dispersal	12 (29)	2 (13)
Anemochorus	0	0
χ^2	1.668	
Fisher's exact p	0.523	
All families		
Simple	502 (62)	68 (52)
PI	133 (16)	37 (28)
Secondary dispersal	101 (12)	17 (13)
Anemochorus	81 (10)	9 (7)
χ^2	11.234	
Fisher's exact p	0.011	

with long-range dispersal contribute to exotic naturalization. However, we also found that these broad patterns of trait correlation do not necessarily apply to all major families in the flora of California.

Comparing natives and exotics at the family level produced more specific conclusions, showing that exotics do not conform to classic tradeoffs in different ways. For instance, exotic Fabaceae appear to break the CC tradeoff by attaining large plant heights while maintaining seed sizes and dispersal modes similar to those seen in the native species. In addition, exotic Fabaceae show a greater proportion of annual and leaf perennial species than native Fabaceae, which are predominantly root perennials. These differences imply that while native and exotic Fabaceae appear well-matched with regard to dispersal, exotics may break the predicted tradeoff structure of the California flora by also expressing a life strategy of high relative biomass accumulation within both short-lived (annual) and long-lived perennials (leaf perennials). In contrast to the Fabaceae, exotic Poaceae appear to break the CC tradeoff through greater dispersal ability (smaller seed size) and by attaining similar heights, relative to natives,

despite having shorter life spans. Exotic Poaceae are better represented in the annual life form, while native California grasses are disproportionately composed of stem perennials (i.e. bunchgrasses; Pitt and Heady 1978). Lack of differences between exotic and native Poaceae height at maturity suggests that exotics may attain a competitive advantage through other strategies. For instance, exotic Poaceae may be able to produce greater numbers of propagules per unit biomass, display a greater phenotypic plasticity or a better resource-use efficiency – all traits related with invasiveness – than natives (van Kleunen et al. 2010). In fact, some studies have showed that propagule pressure is one of the most important factors in explaining biological invasions (Lockwood et al. 2005). Indeed, Seabloom et al. (2003) found that exotic annuals, which were predominately invasive grasses in their experiment in California grasslands, were not necessarily superior competitors but were more likely to dominate because of severe recruitment limitation in native perennials.

At first glance, the exotic Asteraceae do not appear to break the CC tradeoff; both natives and exotics have similar plant height and a similar distribution of early-successional life forms (annual/root-perennial). However, the Asteraceae were marginally smaller in seed size and were the only family for which natives and exotics differed significantly in dispersal mode. Although most native Asteraceae are clearly anemochorous (i.e. seeds with a large pappus), a large fraction have simple seeds. In contrast, the seeds of exotic species were predominately polychorous-indeterminate or anemochorous; this suggests that increased dispersal in space or time is an advantage for colonization, being showed mainly by exotic Asteraceae in this study. Seed morphology in the Asteraceae is famously variable and mutable (Cody and Overton 1996) and the polychorous-indeterminate category of exotic Asteraceae includes winged or barbed seeds or awned capitula that disperse as a unit (e.g. *Taraxacum* and *Centaurea* species). These structures increase dispersal through wind/water resistance and may also improve burial or seed placement for germination (Harper et al. 1970). It is also possible that these variable seed morphologies serve a number of concurrent adaptive purposes. Some refinement of the polychorous-indeterminate category to tease apart their adaptive significance might be helpful in the future, but would also reduce the statistical power of this analysis. The critical point, however, is that with a greater proportion of simple seeds native Asteraceae are more likely to be dispersal-limited than their exotic counterparts.

According to our analysis, exotic Brassicaceae do not appear to breakdown the CC tradeoff in any way. Nevertheless, they are the only family out of the four most speciose for which exotic species tend to have larger seeds than native species. As pointed out in the Methods section, the Brassicaceae are limited to short-lived perennial life forms, generally early successional species. The predominately annual or herbaceous perennial exotic Brassicaceae (e.g. *Brassica nigra*) and *B. rapa* tend to be restricted to disturbed habitats and larger seeds are correlated with greater success in stressful or disturbed habitats (Sans et al. 2004). Thus the success of exotic Brassicaceae in native California plant communities may rely on the advantages of large seed size in disturbed habitats.

Finally, vegetative growth may be one of few stand-alone characteristics that should be taken as a warning sign for any

exotic species. Kolar and Lodge (2001) point out that vegetative growth may be an important indicator of invasiveness, and one invasive member of the Brassicaceae in our random sample, *Cardaria chalepensis*, is the only clonal member of the Brassicaceae (native or exotic). Another example of a species that is highly invasive through vegetative reproduction is *Oxalis pes-caprae* (Oxalidaceae), for which viable seed has never been reported in California (Sigg 2003). Identifying such rare ‘super-invaders’ was not the goal of our study; instead, we attempted to develop a framework for evaluating trait combinations that may not conform to fundamental ecological tradeoffs, thereby exposing more subtle strategies employed by naturalized exotic species.

In summary, we found that for a random subset of the California flora, exotics of the most speciose families showed functional trait combinations that appear to violate the trade-off structures observed among their California counterparts. Earlier studies comparing exotic and native plants have found both no difference in growth rate, fecundity or competitive ability (Daehler 2003) and/or strong competitive interactions among them (Levine et al. 2003). Seemingly conflicting results can be reconciled by the fact that different sets of strategies involved in the competition–colonization tradeoff evolved in different plant families. Thus, comparative approaches involving multiple families and species traits available from the literature could provide unique insights to the invasion process.

Acknowledgements – Thanks to Lindy Smith and Jessica Reimer for their contributions in developing the database and Anibal Pauchard for his comments on an earlier draft. This research was supported by funding from the A. W. Mellon foundation, the EBM initiative funded by the David and Lucile Packard Foundation and the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (grant no. DEB-0072909), the Univ. of California, and the Santa Barbara campus.

References

- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. – *Ecology* 53: 997–1010.
- Baker, H. 1974. The evolution of weeds. – *Annu. Rev. Ecol. Syst.* 5: 1–24.
- Cadotte, M. W. et al. 2006. On testing the competition–colonization tradeoff in a multispecies assemblage. – *Am. Nat.* 168: 704–709.
- Cody, M. L. and Overton, J. M. 1996. Short-term evolution of reduced dispersal in island plant populations. – *J. Ecol.* 84: 53–61.
- Cornelissen, J. et al. 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. – *Aust. J. Bot.* 51: 335–380.
- Craine, J. M. et al. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. – *Oikos* 93: 274–285.
- D’Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. – *Ecology* 74: 83–95.
- Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. – *Annu. Rev. Ecol. Evol. Syst.* 34: 183–211.
- Elton, C. 1958. The ecology of invasions by animals and plants. – Methuen.

- Godoy, O. 2009. Rasgos funcionales y plasticidad fenotípica de plantas exóticas invasoras. – PhD thesis, Univ. de Alcalá, Madrid.
- Grace, J. B. 1991. A clarification of the debate between Grime and Tilman. – *Funct. Ecol.* 5: 583–587.
- Guerrero-Campo, J. and Fitter, A. H. 2001. Relationships between root characteristics and seed size in two contrasting floras. – *Acta Oecol.* 22: 77–85.
- Guo, Q. F. et al. 1995. The effects of vertebrate granivores and folivores on plant community structure in the Chihuahuan desert. – *Oikos* 73: 251–259.
- Harper, J. L. et al. 1970. The shapes and sizes of seeds. – *Annu. Rev. Ecol. Syst.* 1: 327–356.
- Hickman, J. C. 1993. The Jepson manual. Higher plants of California. – Univ. of California Press.
- Horn, H. S. and MacArthur, R. H. 1972. Competition among fugitive species in a harlequin environment. – *Ecology* 53: 749–752.
- Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – *Annu. Rev. Ecol. Syst.* 13: 201–228.
- Hussner A. 2009. Growth and photosynthesis of four invasive aquatic plant species in Europe. – *Weed Res.* 49: 506–515.
- Jakobsson, A. and Eriksson, O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. – *Oikos* 88: 494–502.
- Kneitel, J. M. and Chase, J. M. 2004. Tradeoffs in community ecology: linking spatial scales and species coexistence. – *Ecol. Lett.* 7: 69–80.
- Kolar, C. S. and Lodge, D. M. 2001. Progress in invasion biology: predicting invaders. – *Trends Ecol. Evol.* 16: 199–204.
- Kyle, G. and Leishman M. R. 2009. Functional traits differences between extant exotic, native and extinct native plants in the hunter river, NSW: a potential tool in riparian rehabilitation. – *River Res. Applic.* 25: 892–903.
- Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – *Funct. Ecol.* 16: 545–556.
- Leishman, M. R. and Murray, B. R. 2001. The relationship between seed size and abundance in plant communities: model predictions and observed patterns. – *Oikos* 94: 151–161.
- Levine, J. M. and D'Antonio, C. 2003. Forecasting biological invasions with increasing international trade. – *Conserv. Biol.* 17: 322–326.
- Levine, J. M. and Rees, M. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. – *Am. Nat.* 160: 452–467.
- Levine, J. et al. 2003. Mechanisms underlying the impacts of exotic plant invasions. – *Proc. R. Soc. Lond. B* 270: 775–781.
- Levins, R. and Culver, D. 1971. Regional coexistence of species and competition between rare species. – *Proc. Natl Acad. Sci. USA* 68: 1246–1248.
- Littell, R. C. et al. 2002. SAS for linear models, 4th ed. – SAS Inst., Cary, NC.
- Lockwood, J. L. et al. 2005. The role of propagule pressure in explaining species invasions. – *Trends Ecol. Evol.* 20: 223–228.
- Mabberley, D. J. 1997. The plant-book, 2nd ed. – Cambridge Univ. Press.
- Maron, J. L. and Vila, M. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. – *Oikos* 95: 361–373.
- Munz, P. A. and Keck, D. D. 1968. A California flora and supplement. – Univ. of California Press.
- Pitt, M. D. and Heady, H. F. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. – *Ecology* 59: 336–350.
- Pysek, P. and Richardson, D. M. 2007. Traits associated with invasiveness in alien plants: where do we stand? – In: Nentwig, W. (ed.), *Biological invasions*. Springer, pp. 97–125.
- Rejmánek, M. and Richardson, D. M. 1996. What attributes make some plant species more invasive? – *Ecology* 77: 1655–1661.
- Rejmánek, M. et al. 2004. Plant invasions and invisibility of plant communities. – In: van der Maarel, E. (ed.), *Vegetation ecology*. Blackwell, pp. 332–355.
- Richards, C. L. et al. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. – *Ecol. Lett.* 9: 981–993.
- Sans, F. X. et al. 2004. Life-history traits of alien and native *Senecio* species in the Mediterranean region. – *Acta Oecol.* 26: 167–178.
- Schwinning, S. and Ehleringer, J. R. 2001. Water use tradeoffs and optimal adaptations to pulse-driven arid ecosystems. – *J. Ecol.* 89: 464–480.
- Seabloom, E. et al. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. – *Proc. Natl Acad. Sci. USA* 100: 13384–13389.
- Sigg, J. 2003. Species focus: *Oxalis pes-caprae*. – *Q. Newslett. California Exotic Pest Plant Council* 11: 7–9.
- Stachowicz, J. J. and Tilman, D. 2005. Species invasions and the relationships between species diversity, community saturation and ecosystem functioning. – In: Sax, D. F. et al. (eds), *Species invasions: insights into ecology, evolution and biogeography*. Sinauer, pp. 41–64.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Turnbull, L. A. et al. 1999. Seed mass and the competition/colonization tradeoff: a sowing experiment. – *J. Ecol.* 87: 899–912.
- Turnbull, L. A. et al. 2010. Species diversity reduces invasion success in pathogen-regulated communities. – *Oikos* 119: 1040–1046.
- Van der Pijl, L. 1972. Principles of dispersal in higher plants, 2nd ed. – Springer.
- Van der Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. – *Oikos* 100: 25–34.
- Van Kleunen, M. and Richardson, D. M. 2007. Invasion biology and conservation biology – time to join forces to explore the links between species traits and extinction risk and invasiveness. – *Progr. Phys. Geogr.* 31: 447–450.
- van Kleunen, M. et al. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. – *Ecol. Lett.* 13: 235–245.
- Weier, E. et al. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. – *Oikos* 81: 309–322.
- Westoby, M. et al. 2002. Plant ecological strategies: some leading dimensions of variation between species. – *Annu. Rev. Ecol. Syst.* 33: 125–159.
- Yu, D. W. and Wilson, H. B. 2001. The competition–colonization tradeoff is dead; long live the competition–colonization tradeoff. – *Am. Nat.* 158: 49–63.
- Zar, J. H. 1996. Biostatistical analysis. – Prentice-Hall.