

# Do invasive species have bigger seeds? Evidence from intra- and inter-specific comparisons

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## Abstract

Shifts in seed mass associated with the process of plant invasion may potentially enhance the competitiveness of introduced species and contribute to invasiveness. Here we test this premise using two complementary approaches. Firstly we compare the seed mass of 114 species from 31 families in both their native and introduced ranges. Secondly we compare the seed mass of 376 co-occurring native and invasive species from two families (Asteraceae and Poaceae) from California. Our results demonstrate that across the 31 families there is a significant tendency for seed mass to increase from the native to invasive ranges. In addition, the analysis on the two families revealed that such a shift in seed mass may contribute to invasive species having, on average, a higher seed mass than co-occurring native species in the same family. Consequently, these results suggest that invasion-associated upward shifts in seed mass may foster plant invasions by increasing the competitiveness of invasive species relative to natives.

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## 1. Introduction

Invasive species are considered to be among the five most serious threats to natural systems and biodiversity (Wilcove et al., 1998), with the economic cost of invasive species running into \$137 billion per year in the USA alone (Pimental et al., 2000). Consequently an ability to predict the invasive potential of new introductions could reduce the level of threat to natural areas (Reichard and Hamilton, 1997). However, it is unclear what aspects of the population biology of invasive species account for their “invasive” ability. Thus, predictions of the invasive potential of species are difficult.

Invasive species represent a small component of the world’s flowering plants. For example, two recent compilations of invasive species list c. 550 species (Weber, 2003; Haysom and

Murphy, 2003) compared to c. 250 k species of plant world-wide. Williamson and Fitter (1996) have proposed the “Tens Rule” based on analysing the incidence of invasive species in the United Kingdom. They found that on average, one in ten introduced species will escape cultivation, one in ten of these will become naturalised and form self-sustaining populations, and one in ten of these will become invasive. Since so few species that have the opportunity to, actually become invasive, it seems parsimonious to suggest that a limited number of key traits could influence this response.

A number of potential contributing factors for successful plant introductions/invasions have been suggested. These include greater disturbance which increases community susceptibility to invasion (Baker, 1974), high propagule pressure of invasive species (Lockwood et al., 2005) and the enemy release hypothesis (Mitchell and Power, 2003). These factors are likely to facilitate invasiveness by both increasing the opportunity for invasions and by increasing the competitiveness of invasive relative to native species. However, the plant traits that contribute to invasiveness are still unclear (Shea and Chesson, 2002).

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Seed germination and seedling establishment are high risk phases in the life-cycles of most plants (Harper, 1977). Consequently any differences in the way species respond to the environment may be most apparent at these stages. Thus, in the same way that differences in reproductive traits (regeneration niche *sensu* Grubb, 1977) may contribute to species coexistence (Daws et al., 2002), they may also potentially contribute to differential success between invasive and native species, i.e. preferential existence.

Reproductive success appears to be one of the few unifying features of invasiveness in earlier studies on plants. Many aspects of reproductive biology may contribute to invasiveness, including effective seed dispersal (McIntyre et al., 2005), the production of a persistent soil seed bank (Van Clef and Stiles, 2001) and seed mass (Rejmánek and Richardson, 1996; Buckley et al., 2003), although dispersal and persistence are themselves related to seed mass (Leishman et al., 2000). Amongst reproductive traits, seed mass is also likely to be pivotal because it influences two key components of plant life-history. Firstly, the seed mass of a plant is negatively correlated with the number of seeds that it produces (Leishman et al., 2000). Secondly, seed mass is positively associated with seedling survival; larger seeds generally result in larger seedlings which often have a higher probability of survival (Daws et al., 2005). For larger seeded species a higher seedling survival probability results from a greater ability to withstand either low levels of resources or various hazards (Leishman et al., 2000).

Seed mass has already been included in analyses comparing invasive and non-invasive *Pinus* species (Rejmánek and Richardson, 1996) and in determining whether there are functional types, or syndromes associated with invasiveness (Lloret et al., 2005; McIntyre et al., 2005). These studies found that for *Pinus* species, small seeded species were more likely to be invasive (Rejmánek and Richardson, 1996), while both Lloret et al. (2005) and McIntyre et al. (2005) identified functional groups of invasive species of which “large” seeded forbs were a key group. These studies suggest that seed mass is important for ‘invasiveness’. However, to better understand the traits that contribute to invasiveness, two types of studies on plant traits are needed: 1) intra-specific comparisons of individual species in their native and invasive ranges, and 2) inter-specific comparisons of co-occurring invasive and non-invasive species (Hiero et al., 2005).

Taking this general approach, Buckley et al. (2003) found that for *Cytisus scoparius*, but not for *Ulex europaeus*, that seed mass is greater in the invasive than native range. Similarly, Schmitt and Rivière (2002) found that on La Réunion the invasive species *Syzygium jambos* had larger seeds than the native con-gener *Syzygium cymosum* and Baker (1972) found, in a comparison of native and invasive forbs in California, that the invasive species had larger seeds. However, we more rigorously apply these approaches to a broad range of species. Firstly, for 114 invasive species from both Weber (2003) and Haysom and Murphy (2003), we compare seed mass values in both their native and invasive ranges. Secondly, for two key invasive families (Asteraceae

and Poaceae), which together contribute c. 23% of the most serious invasive plants in Weber (2003), we compare seed mass data for co-occurring native and invasive species in California to test whether within the same family invasive species have a larger seed mass than co-occurring species. Unlike the earlier study by Baker (1972), this intra-familial as opposed to cross-species approach has the advantage that both native and invasive species in the analysis are likely to have both similar growth forms and reproductive biology, reducing the potentially confounding influence of phylogenetic un-relatedness on seed mass.

## 2. Materials and methods

### 2.1. Intra-specific comparisons

Weber (2003) and Haysom and Murphy (2003) were used to compile a list of invasive species. Weber (2003) lists native and invasive ranges for the species it contains, while Haysom and Murphy (2003) only provides species’ invasive ranges. Consequently, the Pacific Island Ecosystems at Risk, Risk Assessment (<http://www.hear.org/pier>), the Global Compendium of Weeds Database (<http://www.hear.org/gcw>) and the GRIN taxonomy database (<http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl>) were used to identify species’ native ranges.

For species for which both the native and invasive ranges could be identified, seed mass data was obtained from the Royal Botanic Garden Kew’s Seed Information Database (SID; Flynn et al., 2004, <http://www.rbgekew.org.uk/data/sid>). For the seed mass data, the original source references were checked to determine whether seed collections came from the native or invasive range and to verify the seed mass data. This approach resulted in 114 species for which we had seed mass data for both ranges (see Appendix A for families and genera included in this analysis). For different species, seed mass data in SID is presented on a fresh, air-dried or oven-dried basis with it often being unclear (from the scientific literature) how seed mass has been determined. In addition, the unit for which seed mass is reported can vary between studies (seed, fruit, dispersule, propagule etc.). Consequently, we assumed that such variations in the means of reporting seed mass were random across our dataset, i.e. there was no systematic bias in the method of determination/reporting seed mass in relation to native and invasive ranges.

### 2.2. Inter-specific comparisons

The Baker seed mass dataset (Baker, 1972), contains seed mass data for c. 2500 taxa that occur in California, including a wide range of invasive species. Subsequently, for the two largest families containing invasive species in the dataset (Asteraceae and Poaceae), all seed mass values were extracted from the Baker dataset and, as in the analysis by Baker (1972), species assigned as either ‘native’ or ‘invasive’ based on Munz (1959). Species were classified as invasive when they were referred to as both ‘non-native’ and

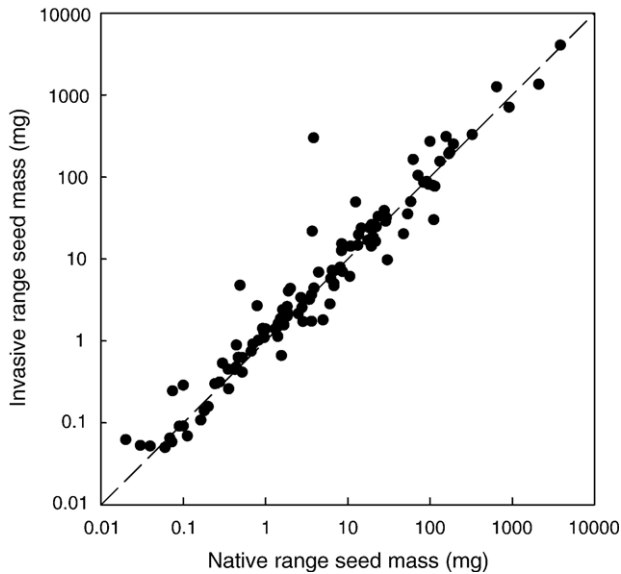


Fig. 1. Comparison of mean seed mass in both their native and invasive ranges for 114 invasive species. The dashed line indicates the expected relationship if seed mass in the invasive range matches that in the native range. For 71 of the species seed mass is higher in the invasive than native range. For the remaining 43 species seed mass is smaller in the invasive range.

also as ‘escape’, ‘weedy’ or ‘common’ (see Appendices 2 and 3 for genera used in these comparisons). Unlike the SID analysis, this study has the advantage that seed mass data in Baker (1972) was determined in a consistent manner across species.

### 2.3. Statistical analyses

For the 114 species for which we had seed mass data for both the invasive range and native ranges, we firstly for each species in turn determined the mean seed mass in each range (where we had more than one seed mass value per range).

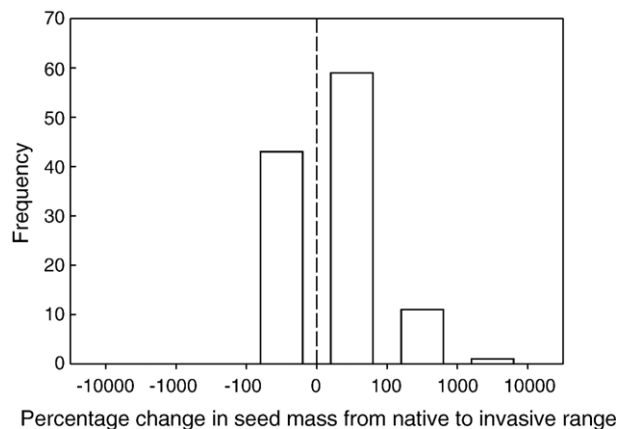


Fig. 2. The percentage change in seed mass from the native to invasive range for 114 invasive species. Bars to the right of the dashed vertical line at  $x=0$  indicate an increase in seed mass from native to invasive range, while those to the left indicate a decrease in mass.

Secondly, a sign test was used to assess whether there was an overall tendency for seed mass test to be larger or smaller in the invasive than native range. The test was applied by calculating the number of species for which seed mass in the invasive range was (1) greater or (2) lower than seed mass in the native range. Subsequently, the significance of the number of species for which seed mass differed between the native and invasive ranges was tested using the binomial distribution (Sokal and Rohlf, 1995).

We used one-way ANOVA to test for differences in the mean seed mass of native and invasive Poaceae in California since the data was both normally distributed with homogeneous variances. However, since for the Asteraceae, the seed mass data had unequal variances, a Mann-Whitney  $U$ -test was used to compare the median seed mass of the native and invasive species. Both tests were carried out on  $\log_{10}$  transformed data.

## 3. Results

### 3.1. Intra-specific seed mass comparisons

Based on comparisons of the species list in Weber (2003) and Haysom and Murphy (2003) with the SID there were 114 species for which we had seed mass data for both their native and invasive ranges. Comparisons of mean seed mass for each range revealed that there was a significant tendency for the

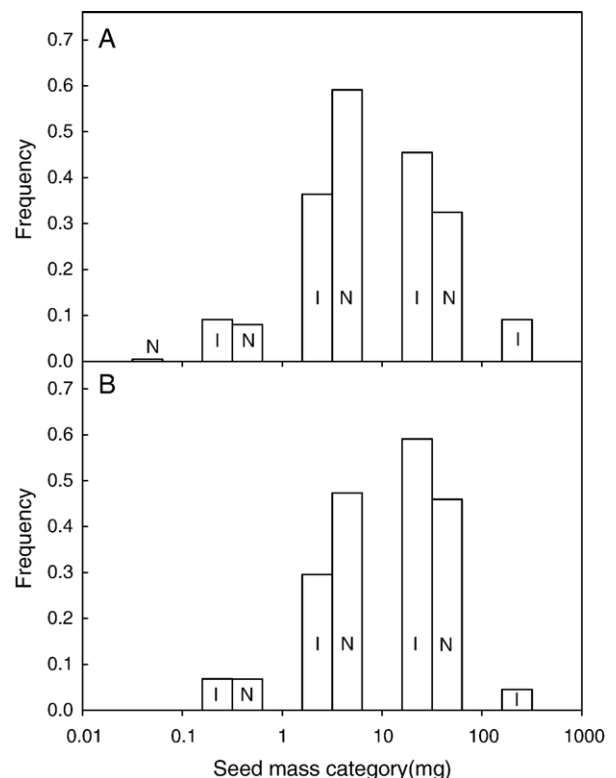


Fig. 3. Frequency distribution of seed mass classes for co-occurring native and invasive (A) Asteraceae and (B) Poaceae in California. I and N correspond to invasive and native species, respectively.

seed mass of a species to be higher in the invasive than native range (71 species for which seed mass was larger and 43 smaller in the invasive compared to the native range, Sign-test  $P=0.01$ ; Figs. 1 and 2).

### 3.2. Intra-familial seed mass comparisons

Based on a comparison of the Baker dataset (1972) and Munz (1959) we had 225 and 33 native and invasive Asteraceae and 74 and 44 native and invasive Poaceae, respectively in California, for which we had seed mass data. For both plant families, the mean seed mass of the invasive species was significantly higher than that of the native species ( $P<0.05$ ; Fig. 3A and B). Thus for the Asteraceae, the geometric mean seed mass was 0.5 versus 1.1 mg for the native and invasive species respectively. Similarly for the Poaceae the geometric mean seed mass values were 0.8 versus 1.3 mg for the native and invasive species respectively. Consequently, the average seed mass of invasive species was 101 and 68% higher than that of natives for the Asteraceae and Poaceae, respectively.

## 4. Discussion

We have shown by meta-analysis that, on average, the seed mass of an invasive species is higher in its invasive than native range. This has previously been demonstrated for only two species (Buckley et al., 2003). However, we have also demonstrated that not only does seed mass tend to increase with the process of invasion, but that the seed mass of invasive species from two invasive families (Asteraceae and Poaceae), in California, is generally higher than for co-occurring native species in the same families.

The greater seed mass of species in their invasive than native ranges could result from several causes. Firstly, the seed mass of species transported to non-native countries may have been higher than in the general population i.e. there was pre-introduction selection for larger seeded genotypes. This could result, for example, if the seed mass of species used for ornamental purposes was higher than for seed from wild (native) populations. However, at least for *C. scoparius* such selection has been shown not to operate: commercial seeds used for ornament were no heavier than seeds from wild populations (Buckley et al., 2003). If this is the case across our species, it suggests a post-introduction increase in seed size.

Secondly, larger seed mass could result from the absence of specialist herbivores which in the native range affect seed mass through reduced vigour/size of parent plants (Callaway et al., 2004) or by direct selection for small seeds (Moegenburg, 1996). It is interesting to note that although species in their invasive range(s) may produce larger seeds, this may not result in fewer seeds per capita: reduced pathogen pressure can result in larger parent plants (Rees and Paynter, 1997) which are able to maintain a high (in terms of both size and number) seed output (Venable, 1992). A third possibility is selection for large seeds. This could result from

the corollary of selection for small seeds in the native range coupled with direct selection for large seed size in the invasive range. Direct selection for large seed size could potentially result from both intra- and inter-specific competition. Intra-specific competition can be higher in a species' invasive than native range as a result of higher seedling densities (e.g. Rees and Paynter, 1997) and large seed size can potentially improve a seedling's competitiveness because seedlings from large seeds typically have a lower probability of mortality (Daws et al., 2005) – seedlings are more tolerant of shade, drought, low nutrient availability and defoliation (Leishman et al., 2000). Thus they are potentially more competitive because larger size means that they are both more “robust” and able to pre-empt resources e.g. water and light, in advance of smaller seedlings.

There are other potential contributing factors related to the initiation and perpetuation of invasive behaviour besides having a greater seed mass. For example, we might expect that if species are to become invasive, there is a significant role for the regular production of large seed quantities and for efficient long distance dispersal. These two factors could partly explain why for 24 *Pinus* species, Rejmánek and Richardson (1996) found it was the smaller seeded species that were more likely to be invasive. Many larger seeded *Pinus* species (e.g. *P. coulteri* and *P. sabiniana*) not only have ineffective primary dispersal (Johnson et al., 2003), but many produce seeds at irregular multi-year intervals (Rejmánek and Richardson, 1996). However, at least in their native ranges, these species have a suite of secondary dispersers which collect and cache seeds for later use (Johnson et al., 2003). This results in greater dispersal distances and regeneration can occur because not all seeds are subsequently recovered (Johnson et al., 2003). However, these specialist dispersers may be absent in the introduced range resulting not only in limited seed dispersal but also potentially high rates of seed predation since such large, oil rich seeds represent an attractive resource for seed predators (Vander Wall, 1998).

In summary, we found that (1) seed mass of a species increases, on average, during the invasion process, and (2) that invasive species tend to have larger seeds than co-occurring con-familials. Thus, even within plant families where there will be a shared growth form and similar reproductive biology, invasives tend to have larger seeds. Thus the success of invasive species may result from upward shifts in seed mass, increasing seedling survival, while the seed mass of native species is constrained by, *inter alia*, specialist predators from which the invasive species have been ‘liberated’. These findings should contribute to a general discussion on the “genetic paradox”, whereby invasive species out-perform presumably locally adapted genotypes.

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## Appendix A

### Families and genera of the 114 species used in the intra-specific seed mass comparison

Family	Genus	Family	Genus	Family	Genus
Aceraceae	<i>Acer</i>	Fabaceae	<i>Robinia</i>	Poaceae	<i>Eragrostis</i>
Apiaceae	<i>Foeniculum</i>		<i>Samanea</i>		<i>Festuca</i>
	<i>Pastinaca</i>		<i>Senna</i>		<i>Holcus</i>
Asteraceae	<i>Centaurea</i>		<i>Trifolium</i>		<i>Hordeum</i>
	<i>Cirsium</i>		<i>Ulex</i>		<i>Imperata</i>
	<i>Hypochaeris</i>	Fagaceae	<i>Castanea</i>		<i>Lolium</i>
	<i>Silybum</i>	Geraniaceae	<i>Erodium</i>		<i>Melinis</i>
Brassicaceae	<i>Alliaria</i>	Lamiaceae	<i>Mentha</i>		<i>Pennisetum</i>
	<i>Brassica</i>	Liliaceae	<i>Asphodelus</i>		<i>Phalaris</i>
	<i>Lepidium</i>	Lythraceae	<i>Lythrum</i>		<i>Phleum</i>
Casuarinaceae	<i>Casuarina</i>	Meliaceae	<i>Azadirachta</i>		<i>Phragmites</i>
Chenopodiaceae	<i>Chenopodium</i>		<i>Cedrela</i>		<i>Poa</i>
Convolvulaceae	<i>Turbina</i>		<i>Melia</i>		<i>Sporobolus</i>
Cupressaceae	<i>Cupressus</i>	Myrtaceae	<i>Eucalyptus</i>		<i>Vulpia</i>
Dipsacaceae	<i>Dipsacus</i>		<i>Psidium</i>	Polygonaceae	<i>Fallopia</i>
Elaeagnaceae	<i>Elaeagnus</i>		<i>Syzygium</i>		<i>Polypogon</i>
	<i>Hippophae</i>	Oleaceae	<i>Ligustrum</i>		<i>Rumex</i>
Euphorbiaceae	<i>Ricinus</i>	Papaveraceae	<i>Argemone</i>	Proteaceae	<i>Grevillea</i>
	<i>Triadica</i>	Pinaceae	<i>Pinus</i>	Rhamnaceae	<i>Frangula</i>
Fabaceae	<i>Acacia</i>		<i>Pseudotsuga</i>		<i>Maesopsis</i>
	<i>Cytisus</i>	Poaceae	<i>Agrostis</i>		<i>Rhamnus</i>
	<i>Dalbergia</i>		<i>Ammophila</i>	Rosaceae	<i>Crataegus</i>
	<i>Genista</i>		<i>Anthoxanthum</i>		<i>Prunus</i>
	<i>Leucaena</i>		<i>Bromus</i>		<i>Rosa</i>
	<i>Lotus</i>		<i>Cenchrus</i>	Rubiaceae	<i>Coffea</i>
	<i>Lupinus</i>		<i>Chloris</i>	Scrophulariaceae	<i>Verbascum</i>
	<i>Melilotus</i>		<i>Cynodon</i>	Simaroubaceae	<i>Ailanthus</i>
	<i>Mimosa</i>		<i>Dactylis</i>	Solanaceae	<i>Nicotiana</i>
	<i>Parkinsonia</i>		<i>Ehrharta</i>	Verbenaceae	<i>Lantana</i>

## Appendix B

### Native and invasive Poaceae genera (in the Californian flora) used in the intra-familial seed mass comparisons

Invasive Poaceae genera	Native Poaceae genera (1)	Native Poaceae genera (2)
<i>Agropyron</i>	<i>Agrostis</i>	<i>Puccinellia</i>
<i>Agrostis</i>	<i>Alopecurus</i>	<i>Scribneria</i>
<i>Agrostis</i>	<i>Aristida</i>	<i>Spartina</i>
<i>Alopecurus</i>	<i>Beckmannia</i>	<i>Stipa</i>
<i>Anthoxanthum</i>	<i>Bouteloua</i>	<i>Torreyochloa</i>
<i>Arrhenatherum</i>	<i>Bromus</i>	<i>Trisetum</i>
<i>Avena</i>	<i>Calamagrostis</i>	<i>Vulpia</i>
<i>Briza</i>	<i>Cynodon</i>	
<i>Bromus</i>	<i>Danthonia</i>	
<i>Chloris</i>	<i>Deschampsia</i>	
<i>Crypsis</i>	<i>Distichlis</i>	
<i>Cynosurus</i>	<i>Elymus</i>	
<i>Dactylis</i>	<i>Festuca</i>	
<i>Digitaria</i>	<i>Glyceria</i>	
<i>Echinochloa</i>	<i>Hackelia</i>	
<i>Festuca</i>	<i>Hesperostipa</i>	
<i>Gastridium</i>	<i>Hierochloa</i>	
<i>Holcus</i>	<i>Hordeum</i>	
<i>Hordeum</i>	<i>Leymus</i>	
<i>Lamarckia</i>	<i>Melica</i>	
<i>Lolium</i>	<i>Muhlenbergia</i>	
<i>Paspalum</i>	<i>Nassella</i>	
<i>Phalaris</i>	<i>Phalaris</i>	
<i>Poa</i>	<i>Phleum</i>	
<i>Setaria</i>	<i>Phragmites</i>	

### Appendix B (continued)

Invasive Poaceae genera	Native Poaceae genera (1)	Native Poaceae genera (2)
<i>Sorghum</i>	<i>Pleuraphis</i>	
<i>Taeniatherum</i>	<i>Pleuropogon</i>	
<i>Vulpia</i>	<i>Poa</i>	

## Appendix C

### Native and invasive Asteraceae genera (in the Californian flora) used in the intra-familial seed mass comparisons

Invasive Asteraceae genera	Native Asteraceae genera (1)	Native Asteraceae genera (2)	Native Asteraceae genera (3)	Native Asteraceae genera (4)
<i>Achillea</i>	<i>Acamptopappus</i>	<i>Conyza</i>	<i>Holocarpa</i>	<i>Pyrrocoma</i>
<i>Ageratina</i>	<i>Achyrrachaena</i>	<i>Coreopsis</i>	<i>Hulsea</i>	<i>Rafinesquia</i>
<i>Bellis</i>	<i>Adenocaulon</i>	<i>Crepis</i>	<i>Hymenoclea</i>	<i>Rigiopappus</i>
<i>Bidens</i>	<i>Ageratina</i>	<i>Crocidium</i>	<i>Isocoma</i>	<i>Rudbeckia</i>
<i>Calendula</i>	<i>Agoseris</i>	<i>Dicoria</i>	<i>Iva</i>	<i>Senecio</i>
<i>Carduus</i>	<i>Amblyopappus</i>	<i>Dugaldia</i>	<i>Jaumea</i>	<i>Solidago</i>
<i>Carthamus</i>	<i>Ambrosia</i>	<i>Encelia</i>	<i>Lagophylla</i>	<i>Soliva</i>
<i>Centaurea</i>	<i>Anaphalis</i>	<i>Enceliopsis</i>	<i>Lasthenia</i>	<i>Stebbinsoseris</i>
<i>Centaurea</i>	<i>Anisocoma</i>	<i>Ericameria</i>	<i>Lepidospartum</i>	<i>Stephanomeria</i>
<i>Chrysanthemum</i>	<i>Antennaria</i>	<i>Erigeron</i>	<i>Lessingia</i>	<i>Stylocline</i>
<i>Cirsium</i>	<i>Arnica</i>	<i>Eriophyllum</i>	<i>Machaeranthera</i>	<i>Syntrichopappus</i>
<i>Coreopsis</i>	<i>Artemisia</i>	<i>Filago</i>	<i>Madia</i>	<i>Tanacetum</i>
<i>Cotula</i>	<i>Aster</i>	<i>Geraea</i>	<i>Malacothrix</i>	<i>Tetradymia</i>

## Appendix C (continued)

Invasive genera	Native genera (1)	Native genera (2)	Native genera (3)	Native genera (4)
<i>Cynara</i>	<i>Baccharis</i>	<i>Gnaphalium</i>	<i>Matricaria</i>	<i>Trixis</i>
<i>Erechtites</i>	<i>Baileya</i>	<i>Grindelia</i>	<i>Micropus</i>	<i>Venegasia</i>
<i>Filago</i>	<i>Balsamorhiza</i>	<i>Gutierrezia</i>	<i>Microseris</i>	<i>Viguiera</i>
<i>Hedypnois</i>	<i>Bebbia</i>	<i>Hazardia</i>	<i>Monolopia</i>	<i>Wyethia</i>
<i>Hypochoeris</i>	<i>Bidens</i>	<i>Helenium</i>	<i>Monoptilon</i>	
<i>Lactuca</i>	<i>Blennosperma</i>	<i>Helianthella</i>	<i>Pectis</i>	
<i>Senecio</i>	<i>Brickellia</i>	<i>Helianthus</i>	<i>Perityle</i>	
<i>Silybum</i>	<i>Calycadenia</i>	<i>Hemizonia</i>	<i>Petasites</i>	
<i>Sonchus</i>	<i>Chaenactis</i>	<i>Hesperervax</i>	<i>Peucephyllum</i>	
<i>Taraxacum</i>	<i>Chrysothamnus</i>	<i>Heterotheca</i>	<i>Psathyrotes</i>	
<i>Tragopogon</i>	<i>Cirsium</i>	<i>Hieracium</i>	<i>Psilocarphus</i>	

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