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Reduced seed predation after invasion supports enemy release in a broad biogeographical survey

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Abstract The Enemy Release (ER) hypothesis predicts an increase in the plant invasive capacity after being released from their associated herbivores or pathogens in their area of origin. Despite the large number of studies on biological invasions addressing this hypothesis, tests evaluating changes in herbivory on native and introduced populations and their effects on plant reproductive potential at a biogeographical level are relatively rare. Here, we tested the ER hypothesis on the South African species *Senecio pterophorus* (Asteraceae), which is native to the Eastern Cape, has expanded into the Western Cape, and was introduced into Australia (> 70-100 years ago) and Europe (> 30 years ago). Insect seed predation was evaluated to determine whether plants in the introduced areas were released from herbivores compared to plants from the native range. In South Africa, 25% of the seed heads of sampled plants were damaged. Plants from the introduced populations suffered lower seed predation compared to those from the native populations, as expected under the ER hypothesis, and this release was more pronounced in the region with the most recent introduction (Europe 0.2% *vs.* Australia 15%). The insect communities feeding on *S. pterophorus* in Australia and Europe differed from those found in South Africa, suggesting that the plants were released from their associated fauna after invasion and later established new associations with local herbivore communities in the novel habitats. Our study is the first to provide strong evidence of enemy release in a biogeographical survey across the entire known distribution of a species.

Key words Enemy Release hypothesis, herbivory, insects, *Senecio*, reproductive potential

Introduction

Biological invasions are one of the major causes affecting biodiversity worldwide (Pimentel et al. 2000). The introduction of an exotic plant into a new habitat can strongly affect the composition, structure and functioning of the invaded ecosystem (Vitousek et al. 1996; Pimentel et al. 2000) and may drive evolutionary changes in the native species (Maron and Vilà 2001; Siemann et al. 2006). Not all species introduced into new habitats become invasive, however (Richards et al. 2006). Of the many hypotheses that attempt to unravel the factors affecting potentially invasive alien species, those involving the role of herbivores in controlling plant populations predominate (Colautti et al. 2004; Hierro et al. 2005; Gurevitch et al. 2011).

The most frequently invoked hypothesis for the success of invasive species is the Enemy Release (ER) hypothesis (Elton 1958). This hypothesis predicts that alien plants will be more successful when colonizing a new environment due to being released from herbivores and pathogens in their area of origin. The ER hypothesis is based on three components (Keane and Crawley 2002): 1) plant populations are regulated by their associated enemies in the indigenous area; 2) herbivore pressure decreases after introduction into a novel range; and 3) the individual-level benefits of enemy release to exotic plants translate into increased population size, geographic distribution, and overall invasive ability. Plants that are strongly regulated by herbivores in their areas of origin can experience immediate benefits after enemy release, with increased growth, reproductive capacity and survival (Colautti et al. 2004).

A decrease in herbivore pressure on exotic plants, as predicted by the ER hypothesis, is not determined exclusively by the plants’ escape from the natural enemies left behind during an invasion. Once in the introduced range, alien plants may be colonized by native herbivores from the novel habitat, a process known as Native Enemy Host Switching (Keane and Crawley 2002; Agosta 2006). The diversity of consumers in each novel location limits the types and strengths of the interactions that are ultimately established. For example, *Lepidum draba*, a herbaceous perennial mustard, is associated with 16 phytophagous species in its native range, 18 in its extended range and 11 in its introduced range; only 4 of these species are common to all three regions (Cripps et al. 2006). When novel interactions as a result of host switching are quantitatively significant, exotic plants may never be released from herbivore pressure but may merely exchange the species involved. The process of enemy release can be understood as the net effect of the loss of associated enemies from the native range and the acquisition of fewer new enemies in the introduced range (Colautti et al. 2004; Verhoeven et al. 2009).

The fact that an important element of the ER hypothesis (i.e., host switching) strongly depends upon the biotic community and the characteristics of the receiver ecosystem (Graves and Shapiro 2003; Tallamy et al. 2010) highlights the importance of studies that account for this geographic mosaic of species assemblages. Commonly performed experiments addressing the ER hypothesis include laboratory bioassays, which determine the preference and performance of selected phytophagous species feeding on plants from the native and introduced ranges (Caño et al. 2008; Schaffner et al. 2011), and common-garden experiments performed in a single area, usually in the invasive range (Agrawal and Kotanen 2003, but see Maron et al. 2004). Although these experiments can help to determine levels of plant resistance against certain herbivores, they do not inform on the actual plant-herbivore interactions established under field conditions. Biogeographical surveys comparing *in situ* herbivory on native and alien plant populations in areas where the plants naturally occur, are more appropriate to determine realized (not merely potential) herbivore-induced selective pressures. Due to the high spatial variation in the interactions between plants and herbivores

(Kolb et al. 2007) comprehensive tests of the enemy release hypothesis should cover large distribution areas of the plant species both in the native and the invasive range.

Several authors have stressed the importance of biogeographical comparisons when testing major hypotheses related to biological invasions (Maron and Vilà 2001; Hierro et al. 2005), but this area of research has advanced little in recent years. We found 13 studies published to date that quantified *in situ* herbivory between native and introduced populations in a replicated biogeographical survey (Sheppard et al. 1996; Memmott et al. 2000; Fenner and Lee 2001; Wolfe 2002; De Walt et al. 2004; Prati and Bossdorf 2004; Vilà et al. 2005; Cripps et al. 2006; Ebeling et al. 2008; Adams et al. 2009; Cripps et al. 2010; Williams et al. 2010; Hinz et al. 2012). Of those, only four (Fenner and Lee 2001; Wolfe 2002; Prati and Bossdorf 2004; Cripps et al. 2010) evaluated seed predation, which is more closely related to plant fitness and population success (Kolb et al. 2007), and none covered a large distributional area across the native and invasive ranges. These numbers contrast markedly with the nearly 500 papers published in the last 10 years that explicitly address the ER and its evolutionary extension the Evolution of increased Competitive Ability (EICA) hypotheses (ISI Web of Science). Clearly, more biogeographical studies of enemy release are needed.

Here, we conducted a biogeographical test of the second component of the ER hypothesis using *Senecio pterophorus* DC (Asteraceae) as a model species. This species is a perennial shrub native to the Eastern Cape and southern KwaZulu-Natal provinces in South Africa (Hilliard 1977). Its range expanded to the Western Cape during the early 20th century (Levyns 1950). Introduced into Australia in 1908, *S. pterophorus* currently forms persistent populations along the southeastern coast from Port Lincoln to Melbourne and around Sydney and Newcastle in New South Wales (The Council of Heads of Australasian Herbaria 2012). In continental Europe, *S. pterophorus* was first found in 1982 near Barcelona in the northeastern Iberian Peninsula (Casasayas 1989), and additional populations in the Mediterranean basin were found in 1990 on the Ligurian coast in northwestern Italy (Barberis et al. 1998). Preliminary studies using neutral markers have shown that populations from Australia and Europe are not genetically related; thus the colonization of the two continents occurred independently (Vilatersana et al. unpublished).

We performed a biogeographical survey designed to cover a substantial portion of the distribution of *S. pterophorus* and to adequately compare seed predation between native and introduced populations. The relatively restricted worldwide distribution of *S. pterophorus* enabled us to conduct a complete biogeographical survey, determining *in situ* herbivory on *S. pterophorus* in its native, expanded and invaded ranges. The different colonization histories in Australia (> 70-100 years) and Europe (> 30 years) and the native *vs*. expanded ranges in South Africa allowed us to explore the effects of time since introduction and of distance from the source on herbivore release. We aimed to answer the following question: are *S. pterophorus* plants from the extended and introduced ranges released from herbivore predation compared to plants from the native range, resulting in greater reproductive potential?

Materials and methods

Studied species

Senecio pterophorus is a perennial shrub between 0.4 and 2 m in height. The capitula, which are up to 1.5 cm in diameter with c. 13 female ligulate florets measuring from 2 to 4 mm around the periphery, are grouped into terminal corymbose synflorescences (Hilliard 1977). The seeds (technically achenes or cypselae) are approximately 1.5 mm long, cylindrical, somewhat angular and minutely hairy over the surface. The flowering period may extend from late spring to mid autumn (Levyns 1950) but peaks during two to three weeks in early summer, when all plants in a population bloom synchronously (Morante et al. unpublished). This species produces a large number of seeds (up to 1200 heads/individual; Morante et al. unpublished), but its population viability is strongly limited by low seedling emergence and establishment (Sans et al. 2004).

Distributional area and invasion history

Senecio pterophorus is indigenous to an area extending from the eastern parts of the Eastern Cape Province to the southernmost part of the KwaZulu-Natal Province (Hilliard 1977) (Fig. 1). In its native range, *S. pterophorus* forms scattered populations in forest margins, grasslands and fynbos, but it also grows in ruderal habitats, such as road sides. This species was introduced into the Western Cape Province around 1918 (Levyns 1950). The earliest records of *S. pterophorus* in Australia date to 1908 and 1909 in Melbourne, Victoria, but the absence of herbarium records during the following three decades suggests that the species may have failed to establish successful populations in that area. In 1935, *S. pterophorus* was found in Port Lincoln, South Australia. From there, it spread to Adelaide Hills and southeast to Melbourne, Victoria, where it reached high levels of infestation during the 1970s (Parsons and Cuthbertson 1992; The Council of Heads of Australasian Herbaria 2012). Scattered populations have been recorded in Sydney and Newcastle, New South Wales, since 1987 (The Council of Heads of Australasian Herbaria 2012) (Fig. 1). In South Australia, *S. pterophorus* causes heavy productivity losses in agricultural areas, and it is a strong competitor that excludes native species in natural communities and interbreeds with several related native species, thus reducing the diversity of the invaded areas (Parsons and Cuthbertson 1992). In

1994, *S. pterophorus* was classified as a Declared Noxious Weed subject to eradication by the Department of Primary Industries, Victoria (Australia).

The first European populations of *S. pterophorus* were found around wool mills in the United Kingdom in 1913 (Preston et al. 2002), but its presence was erratic and infrequent, with only 8 records from 1913 to 1986. After being absent from the UK for 30 years, *S. pterophorus* is now considered extinct in that country. The introduction of *S. pterophorus* into continental Europe is comparatively recent. First recorded in 1982 near Barcelona, northeastern Iberian Peninsula (Casasayas 1989), *S. pterophorus* is mainly found in disturbed riverbeds and eutrophic waste areas, where it can form very dense populations of approximately 3 individuals/m^2 (Sans et al. 2004). The largest populations occur at the Ripoll River in Sabadell, the most significant textile-manufacturing area in Spain during the 19th and 20th centuries. From 1951 to 1986, Spanish companies processed 208 metric tons of unwashed wool imported from South Africa and Australia (Dirección General de Aduanas de España 1922), suggesting that *S. pterophorus* may have been accidentally introduced to Spain via sheep wool used in the textile industry. Since 1995, this species has been widely reported at numerous localities in the northeastern Iberian Peninsula (Chamorro et al. 2006) (Fig. 1). At present, *S. pterophorus* grows in natural and semi-natural areas, including open forests, road margins and abandoned fields in Sant Llorenç de Munt i l'Obac Natural Park (EC personal observation) and Montseny Natural Park (Morante et al. unpublished). This species has also been found in western Liguria, northwestern Italy, since 1990 (Barberis et al. 1998). The known distribution of *S. pterophorus* in Italy extends from Savone, 45 km south of Genova, to Ventimiglia, near the French border (Barberis et al. 1998) (Fig. 1). Although its geographical range in Europe remains limited, *S. pterophorus* is most likely expanding there, slowly spreading into less-disturbed communities, such as grasslands, shrublands and forests (Chamorro et al. 2006).

Biogeographical survey

The survey was planned with two purposes: 1) to cover the entire known distribution of *S. pterophorus*, including its native, expanded and introduced ranges; and 2) to target the plants' blooming period to evaluate herbivore damage to reproductive plant parts. Distributional data for *S. pterophorus* were first obtained from the herbarium records of the South African National Biodiversity Institute, the Australian National Herbarium (Council of Heads of Australasian Herbaria 2012), the Biodiversity Data Bank of Catalonia (Font 2012) and the literature (Hilliard 1977; Barberis et al. 1998; Chamorro et al. 2006; Caño et al. 2008; Morante et al. unpublished). The consulted sources provided contradictory information on the native area of *S. pterophorus* in South Africa. While Hilliard (1977) stated that the plant "*is found in the eastern parts of the Transkei and just enters Natal across its Southern border*", the distribution of *S. pterophorus* obtained from herbarium records exceeded these limits. Moreover, some records identified as *S. pterophorus* in the South African National Biodiversity Institute herbarium may correspond to other *Senecio* species with coincident flowering times and similar morphologies (e.g., *S. polyanthemoides* Sch. Bip. and *S. juniperinus* L.f.) (M. Welman, South African National Herbarium in Pretoria, personal communication). To ensure that we covered the entire native range of *S. pterophorus* we searched outside the limits cited by Hilliard (1977), including the area from Cape Town (Western Cape Province) to Port Elizabeth (Eastern Cape Province) and up to 225 km north of Durban (KwaZulu-Natal Province). Sampling was conducted during the flowering period of *S. pterophorus,* in December 2009 and January 2010 in the southern hemisphere (South Africa and Australia) and in July 2010 and July 2011 in the northern hemisphere (Catalonia and Liguria).

Senecio pterophorus populations were sought near locations where the species had been previously reported. We attempted to choose populations that were spread across the territory, including populations from the distributional limits. We located the species in most of the searched areas (Fig. 1). In South Africa, *S. pterophorus* was absent from Cape Town to Port Elizabeth (Eastern Cape) and north of Port Shepstone (KwaZulu-Natal), confirming the distribution proposed by Hilliard (1977). The plant was not found in some dry areas in South Australia, including York Peninsula and Murray Bridge. In the State of Victoria, where *S. pterophorus* is declared a noxious weed, the plant was extremely difficult to find, possibly due to the control efforts by local authorities.

A population was defined as a cluster of 15 or more adult individuals. In South Africa and Australia, we chose populations at least 30 km apart; in Catalonia and Liguria, where the plant is more localized, we choose populations at least 5 km apart. A total of 50 populations were surveyed, including 14 native (Eastern Cape and KwaZulu-Natal, South Africa), 5 expanded (Western Cape, South Africa) and 31 introduced (13 in Australia and 18 in Europe) (Fig. 1). Of these populations, a total of 48 contained reproductive individuals for which seed predation could be assessed. In each population, we evaluated the habitat type, the sampled patch size, the level of disturbance (low, medium, high), the number of *S. pterophorus* individuals (< 25, 25-100, 100-500 and > 500 individuals), the percent cover of *S. pterophorus* (< 5%, 5-25%, 25-50%, 50-75% and 75-100%) and the percentage of individuals at the seedling stage as an estimate of population recruitment (<1%, 1-5%, 5-25%, 25-50%, 50-75% and 75-100%) (Table 1). Climate data (mean annual temperature and precipitation) for each location were obtained from the WorldClim database (Hijmans et al. 2005) (Table 1).

Ten individual plants at reproductive stage were sampled at each population to evaluate herbivore damage. The selected individuals were scattered across the plant patch in order to cover the maximum area of distribution and maximize the distance between individuals. A total of 465 plants were surveyed. We collected 20 seed heads from each plant to quantify the proportion damaged by insect herbivores. To ensure homogeneous sampling across populations and regions, ripe seed heads were chosen when possible. Seed heads were dissected on the day of collection by opening them longitudinally through the receptacle, spreading the seeds on a surface, and recording the presence of seed-eating insects therein. A seed head was recorded as “damaged” when predated by phytophagous insects, regardless of their number and developmental stage. We calculated the percentage of damaged heads per individual plant. Insects were raised to adults for identification when possible. Taxonomic identification was performed by Jordi Dantart (Societat Catalana de Lepidopterologia, Spain) (Lepidoptera) and Bernhard Merz (Muséum d’Histoire Naturelle, Switzerland) (Diptera). Other species collected at immature stages (larvae) that were not successfully raised to adults during the collecting trip were classified at the lowest possible taxonomic level.

To determine the frequency of predated seeds within capitula, 5 heads from each of 5 individuals per population (8 populations from South Africa, 5 from the Western Cape, 12 from Australia and 12 from Europe) were collected and stored in separate envelopes. Only healthy, ripe heads with no external damage were collected. These samples could not be processed during the collecting trip; therefore, the heads were frozen for 24 h to prevent further herbivore damage. In the laboratory, the heads were dissected, and the total number of seeds (achenes) was recorded. Each seed was assigned to one of the following categories: damaged, showing signs of predation; aborted, having an undeveloped embryo; and filled, having an undamaged, well-developed embryo. A total of 68,621 achenes (23,610 from South Africa, 21,035 from Australia and 23,976 from Europe) were analyzed. The seeds were categorized by inspection under a stereomicroscope at 10/60 × magnification (Nikon, SMZ800). The proportion of damaged seeds within a head was expressed relative to the total number of achenes after excluding the aborted ones.

Data analyses

Differences among regions were tested using an ANOVA for continuous variables (altitude, temperature and precipitation) and a likelihood-ratio test for categorical variables (population size, percent cover of *S. pterophorus*, percentage of seedlings and disturbance level). To evaluate differences among regions in seed-head predation a zero-inflated negative binomial (ZINB) mixed model was calculated considering damage as the response variable, region as a fixed explanatory variable and population as a random factor. We used this type of model due to the large number of zero values in the data (Hall 2000). A ZINB is a mixture model for count data that incorporates two sources of zero values: a negative-binomial distribution for the process generating the counts (NB, seed head damage greater than or equal to 0) and a zero-inflation process that separately models the occurrence of extra zero values not accounted for by the process generating the counts (ZI, extra undamaged seed heads). Accordingly, each comparison between regions resulted in two *P* values, one for the average seed-head damage and one for the zero inflation. Next, a generalized linear model (GLM) was calculated separately for each region to compare the populations therein. A Levene test was conducted to identify differences in the variance across regions.

Differences among regions in the frequency of herbivore-damaged seeds within heads were assessed by a GLMM (generalized linear mixed model). Region and population nested within region were considered fixed factors, and the individual plant was considered a random factor. A negative binomial distribution was used to model the total number of seeds, and a binomial distribution was used to model the percentage of aborted seeds and the percentage of filled seeds. The percentage of damaged seeds was modeled using the variance-transformation proposal of McCullagh and Nelder (1989), which enabled us to control the variability in these data. The statistical analyses were performed using SAS System ® v9.2 (SAS Institute Inc., Cary, NC, USA). For all statistical tests, a nominal significance level of 5% ($p < 0.05$) was applied. A Tukey adjustment was performed for multiple tests.

Results

Populations of *S. pterophorus* in the native region (South Africa) were located at a higher altitude (750 m a.s.l.) compared to populations in the extended (133 m) and introduced regions (Australia, 140.7 m; Europe, 192.5 m) (South Africa-Western Cape $t = 4.19$; South Africa-Australia $t = 5.60$; South Africa-Europe $t = 5.54$; $P < 0.001$ for all paired-comparisons, ANOVA) (Table 1). Mean annual temperature was significantly higher in the native range in South Africa (16.6°C) than the introduced ranges in Australia (15.1°C) and Europe (15.1°C) (South Africa-Australia $t = 3.25$, $P = 0.011$; South Africa-Europe $t = 3.52$, $P = 0.005$, ANOVA) but did not differ between the native and extended ranges (16.1°C) (South Africa-Western Cape $t = 0.80$, $P = 0.85$, ANOVA). Mean annual rainfall, *S. pterophorus* population size, percent cover and seedling relative abundance were similar across all four regions (data not shown). Disturbance level differed significantly among regions ($\chi^2 = 18.36$, $P = 0.005$, likelihood ratio test), with the highest levels found in European populations (Table 1).

Plants in the native range had an average of 25.2% of their seed heads damaged by herbivores (Fig. 2). In the expanded range, herbivores attacked 33.4% of the heads per plant, but this value did not differ significantly compared to the native area (NB: $F = 1.54$, $P = 0.221$; ZI: $F = 2.98$, $P = 0.091$). In Australia, where *S. pterophorus* has coexisted 70-100 years with the native fauna, herbivory levels were lower than in the native area (NB: $F = 5.81$, $P = 0.020$; ZI: $F = 4.69$, $P = 0.035$), with an average of 15.4% of the seed heads damaged

(Fig. 2). In Europe, where *S. pterophorus* was introduced more recently compared to Australia (> 30 years ago), only 0.2% of the seed heads per plant were damaged by herbivores, significantly lower than in South Africa (NB: $F = 13.43$, $P = 0.001$; ZI: $F = 110.62$, $P < 0.001$) or Australia (NB: $F = 6.72$, $P = 0.013$; ZI: $F = 85.13$, $P < 0.001$) (Fig. 2). Cross-regional comparison of the extra occurrence of zero values (ZI), which indicates the absence of plant-herbivore associations, showed that the South African populations had significantly fewer predation-free seed heads compared to the Australian and European populations. The variances of the frequency of damaged seed heads differed significantly among regions ($F = 27.02$, $P < 0.0001$, Levene test). The highest variability, as estimated by the standard deviation (SD), was found in the native and extended ranges ($SD_{\text{South Africa}} = 19.73$; $SD_{\text{Western Cape}} = 20.03$), followed by the introduced ranges ($SD_{\text{Australia}} = 14.96$; $SD_{\text{Europe}} = 1.29$).

The number of achenes per head varied across regions, but these differences were not related to the native or invasive status of the populations (Fig. 3a). The seed-predation pattern was similar to the head-predation pattern (Fig. 3b). Plants from the native populations (South Africa) showed significantly higher seed predation compared to plants from the introduced populations (South Africa-Australia $t = 14.90$, $P < 0.001$; South Africa-Europe $t = 99.94$, $P < 0.001$, GLMM) (Fig. 3b). However, in contrast to the results found at the head level, achene predation was higher in the extended range than in the native range (South Africa-Western Cape $t = -3.52$, $P = 0.002$, GLMM). The percentages of aborted and filled seeds varied across regions but showed no pattern related to the native or invasive plant origin (Fig. 3c, d).

The morphology of the collected insects and the analyses of the damage to the heads and seeds showed that the herbivores were similar for plants in the native and expanded ranges but highly distinct in the invaded ranges. In the native and expanded populations in South Africa, the phytophagous insects included monkey beetles (Coleoptera: Scarabeidae, Hopliini) and other unidentified Lepidoptera, Diptera and Coleoptera. In Australia, 30.3% of the predated heads were damaged by *Sphenella ruficeps* (Macquart 1851) (Diptera: Tephritidae), a species endemic to Australia that is monophagous on *Senecio* (Hardy and Drew 1996), while an additional 69.6% of the damaged heads were attacked by various species of microlepidoptera, including members of the family Pyralidae. In Europe, herbivore damage to seed heads was caused exclusively by microlepidoptera belonging to Pyralidae, such as the oligophagous species *Phycitodes albatella* (Ragonot 1887), which is native to Eurasia and is known to consume three genera within Asteraceae (*Senecio*, *Crepis* and *Solidago*) (Roesler 1973).

Discussion

Insect seed predation was significantly lower in *S. pterophorus* growing in its introduced ranges (Australia and Europe) than in plants in the native range (South Africa), as predicted by the ER hypothesis. This pattern was confirmed by two complementary measures of herbivore predation: the frequency of damaged seed heads per plant, and the frequency of damaged achenes within a seed head. Similarly, previous biogeographical studies evaluating differences across native and invaded ranges have mostly supported the ER hypothesis (Memmott et al. 2000; Fenner and Lee 2001; Wolfe 2002; Prati and Bossdorf 2004; De Walt et al. 2004; Vilà et al. 2005; Ebeling et al. 2008; Adams et al. 2009; Cripps et al. 2010) although in some cases this trend was not significant (Sheppard et al. 1996; Cripps et al. 2006; Williams et al. 2010; Hinz et al. 2012). However, the near complete absence of herbivory in some parts of the invaded range, as we found in Europe, has been rarely reported.

We also evaluated herbivory levels on *S. pterophorus* in an extended distributional area, the Western Cape (South Africa). We considered these populations in a separate category because *S. pterophorus* has been introduced recently to that area and thus may exhibit some traits common to cross-continental introductions, even though these populations are relatively close to the area of origin. However, the genetic origin of these populations is unknown, and we cannot ignore the possibility that these plants behave differently from their native counterparts. A recent study analyzing six plant species (Engelkes et al. 2008) has suggested that species whose range is expanding (for example, in response to climate change or habitat availability) will experience reduced herbivory, as expected for enemy release in intercontinental introductions. Contrary to these predictions, predation levels on *S. pterophorus* in the Western Cape were higher than those in the indigenous range, although the difference was significant only for the percentage of damaged achenes and not for the percentage of damaged heads. The relatively small distance between the native range and the extended range may have facilitated the co-introduction of insect species from the native range. Alternatively, if the native insect species have a wider spatial distribution overlapping with the extended range of *S. pterophorus*, plants in the Western Cape may have had uninterrupted interactions with herbivores, or experience a release from their natural enemies followed by a reassociation in the new environment. Some examples of plants that escaped from herbivory after invasion but later reassociated with their coevolved specialist herbivores in a novel range include *Pastinaca sativa* in Unites States and New Zealand and *Conium maculatum* in United States. These species showed high herbivory in the introduced ranges where they had reassociated with their natural enemies (Castells et al. 2005; Zangerl et al. 2008).

Predation levels following an invasion depend upon the balance between the loss of interactions with herbivores native to the area of origin (escape from natural enemies) and the establishment of new interactions with herbivores native to the novel habitat (native-enemy host switching) (Colautti et al. 2004; Verhoeven et al. 2009). Novel associations between noncoevolved plants and herbivores are frequent in invaded communities (Keane and Crawley 2002; Graves and Shapiro 2003; Parker and Hay 2005; Tallamy et al. 2010) and therefore may be an important component of plant-herbivore networks in the invaded habitat (Colautti et al. 2004). However, very few studies have compared insect identities and abundance between native and invasive locations in a biogeographical survey (Cripps et al. 2006), and thus the information available to date is not sufficient to determine whether herbivory levels in a novel range are mostly explained by partial escape from associated insects in the indigenous range, by the establishment of new interactions via host switching in the novel habitat, or by a combination of both mechanisms. These different scenarios have no small consequences on the plant evolutionary outcomes as new plant-herbivore associations may alter the herbivore selection regimes, causing plant traits to evolve toward different traits in native and invasive communities (Thompson 1994).

Here, based on taxonomic identifications and the morphology of non-identified insect species in the native and introduced populations, we found that insects present in *S. pterophorus* from Europe and Australia differed from those in South Africa, indicating that plant populations in the two introduced areas escaped from coevolved phytophagous species and established novel interactions with herbivores from the introduced range. Host switching was particularly intense in Australia, the region with a longest invasion history, compared to Europe.

Contrary to the assumption that generalist insects are the main component of host shifting in invaded communities (Keane and Crawley 2002; Hinz et al. 2012), we found that monophagous species participated in a novel interaction. One of the most abundant insect species feeding on *S. pterophorus* in Australia was the endemic specialist *Sphenella rucifeps* (Macquart 1851) (Diptera: Tephritidae). This fly, which develops and pupates within seed heads, is monophagous on the genus *Senecio* and has been reported to consume native

(*Senecio lautus* and *S. amygdalifolius*) and exotic species (*S. madagascariensis*) in Australia (Hardy and Drew 1996). Specialist herbivores that are adapted to feed on native plants may readily establish interactions with exotic congeners because they share a similar chemical composition that facilitates recognition, selection and resistance (Verhoeven et al. 2009). The presence of other native and introduced *Senecio* species in Australia may have facilitated host switching by the specialist *S. rucifeps*.

In addition to evaluating changes in herbivory after invasion, our study system also enabled us to test differences in seed predation between two cross-continental introductions with independent invasion histories. Plants in both non-native ranges experienced less herbivory than those in native areas, but this release was more pronounced in European individuals than in Australian individuals. Higher levels of host switching in Australia compared to Europe may be explained by differences in the time since the introduction of *S. pterophorus*. In Australia, this species has coexisted with local fauna for at least 70-100 years, approximately 50 years longer than in Europe. A longer time since introduction may lead to more host shifts because time increases the probability of plant-herbivore encounters and, potentially, the adaptation of local insects to new hosts (Hawkes 2007; Mitchell et al. 2010). For example, invasive populations of Chinese tallow tree (*Sapium sebiferum*) in the United States were released from herbivores only during the early stages of introduction (Siemann et al. 2006). Similarly, herbivore richness and abundance have been reported to increase with the time since the host-plant introduction, reaching levels similar to those found on native plant species 30 to 200 years following an invasion (Hawkes 2007; Brändle et al. 2008). Our results are consistent with this hypothesis, but we cannot reject the possibility that the higher levels of host switching in Australia compared to Europe were due to other causes, such as the local composition of the biotic community.

This biogeographical survey was designed to capture the spatial variability of the biotic community naturally encountered by *S. pterophorus* and its effects on the native and introduced populations. Our study is the first to show strong evidence of enemy release in a survey covering most of a species' distributional area, including two independent areas of introduction. The different patterns of herbivore predation in the two introduced areas are consistent with the longer period of coexistence between *S. pterophorus* and the local fauna in Australia compared to Europe. Whether the reduction of herbivory on the exotic *S. pterophorus* populations determines a higher invasion success remains undetermined. Increased seed production due to lower herbivore damage is a good estimate of plant fitness, but benefits at the individual level do not necessarily translate into enhanced population recruitment, growth, density and spatial distribution (Kolb et al. 2007). An analysis of the plant population dynamics in the native, expanded and invaded areas accounting for the time since plant introduction is necessary to elucidate the role of enemy release in invasion success.

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Figure legends

Fig. 1 Maps showing locations of populations of *S. pterophorus* surveyed at the native range (South Africa, populations 6 to 19), the expanded range (South Africa, populations 1 to 5), and the two invasive ranges (Australia and Europe). All populations had reproductive individuals to which damage of herbivores on seed heads and seeds could be evaluated, except for populations 1 and 13 in Australia. Abbreviations for regions or States: in South Africa ECP = Eastern Cape, WCP = Western Cape, KZN = KwaZulu-Natal; in Australia NSW = New South Whales, SA = South Australia, VIC = Victoria; in Europe CAT = Catalonia (Spain), LIG = Liguria (Italy). The shaded area indicates *S. pterophorus* distribution based on herbaria databases and literature. Population numbers correspond to the codes in Table 1

Fig. 2 Herbivory damage, estimated as the percentage of damaged seed heads among populations from the native (South Africa), expanded (Western Cape, South Africa) and introduced regions (Australia and Europe). Bars represent mean (+ SE, n = 10 individuals per population). Population codes correspond to numbers given in Figure 1. Inserted graph shows herbivory damage by regions (mean + SE). Different letters indicate significant differences between regions ($P < 0.05$) based on the Zero-Inflation process for ZINB model for count data

Fig. 3 Comparison of seed production and viability in native, expanded and introduced range across regions: a) total number of seeds per head, b) percentage of damaged seeds within a head, c) percentage of aborted seeds, and d) percentage of well-developed, undamaged, filled seeds within a head. Bars represent mean (+SE) for heads within each region (n = 200 for native South Africa, n = 125 for Western Cape, n = 300 for Australia and Europe). Different letters indicate significant differences between regions (*P* < 0.05)

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Table 1. Locations and habitat characterization of *Senecio pterophorus* populations surveyed in the native range (South Africa), the expanded range (Western Cape, South Africa) and introduced ranges (Australia and Europe)

Location[1]	**Population**	**Code**[2]	**Origin**[3]	**Coordinates**	**Alt. (m)**[4]	**Temp. (ºC)**[4]	**Rainfall (mm)**[4]	**Habitat type**	**Patch size (m)**	**Pop. Size (No. ind.)**	**SP Cover (%)**[5]	**Seedlings (%)**[6]	**Disturb. Level**[7]	**No. sampled ind.** [8]
SOUTH AFRICA														
ECP	Colchester	S06	N	33º41'S 25º49'E	6	16.4	440	Perennial grassland	50	25-100	5-25	1-5	M	10
ECP	Grahamstown	S07	N	33º19'S 26º32'E	668	18.5	741	Meadow	400	>500	5-25	n/a	M	10
ECP	Alexandria	S08	N	33º36'S 26º24'E	124	16.1	548	Grassland	10	25-100	5-25	<1	M	10
ECP	Port Alfred	S09	N	33º36'S 26º52'E	61	18.2	595	Grassland	100	100-500	25-50	<1	M	10
ECP	Fort Hare	S10	N	32º47'S 26º52'E	535	18.2	593	Perennial grassland	100	25-100	25-50	1-5	M	10
ECP	Courtlands	S11	N	32º40'S 28º00'E	471	17.9	802	Grassland	50	25-100	5-25	1-5	H	10
ECP	Umtentu	S12	N	31º51'S 28º30'E	716	17.4	713	Meadow	75	25-100	5-25	<1	M	10
ECP	Flargstaff	S13	N	31º11'S 29º26'E	884	16.0	912	Meadow	125	>500	50-75	5-25	M	10
ECP	Mt. Ayliff	S14	N	30º50'S 29º15'E	1116	15.9	827	Meadow	25	>500	50-75	n/a	M	10
ECP	Bizana	S15	N	30º50'S 29º35'E	1076	15.6	907	Meadow	150	>500	75-100	n/a	M	10
ECP	Mount Frere	S18	N	30º57'S 28º57'E	1242	15.6	856	Grassland	35	25-100	75-100	<1	H	10
ECP	Antioch	S19	N	30º42'S 28º51'E	1261	16.0	787	Meadow	200	25-100	5-25	<1	M	10
KZN	Stafford's Post	S16	N	30º31'S 29º46'E	1141	15.6	927	Perennial grassland	10	25-100	5-25	n/a	M	10
KZN	Franklin	S17	N	30º23'S 29º38'E	1200	15.5	834	Perennial grassland	50	25-100	5-25	1-5	M	10
WCP	Groenfonteinkop	S01	E	33º47'S 18º52'E	176	16.9	786	Shrubland	125	<25	5-25	1-5	M	10
WCP	Cape Town	S02	E	34º07'S 18º23'E	26	16.4	825	Perennial grassland	100	25-100	5-25	1-5	M	10
WCP	Elgin	S03	E	34º09'S 19º01'E	326	14.7	996	Annual grassland	200	100-500	5-25	<1	H	10
WCP	Hermanus	S04	E	34º24'S 19º11'E	23	16.2	589	Annual grassland	25	100-500	25-50	1-5	M	10
WCP	Cape Town	S05	E	33º56'S 18º26'E	114	16.5	1086	Annual grassland	125	100-500	5-25	25-50	H	10
AUSTRALIA														
NSW	Doonside	A01	I	33º45'S 150º52'E	48	17.2	873	Perennial grassland	600	25-100	5-25	<1	M	0
NSW	Newcastle	A02	I	32º52'S 151º41'E	13	17.9	1092	Perennial grassland	50	25-100	5-25	1-5	L,M	10
SA	Port Lincoln	A03	I	34º33'S 135º49'E	13	16.0	509	Perennial grassland	75	>500	50-75	<1	M	10
SA	Wangary	A04	I	34º30'S 135º25'E	15	16.2	531	Annual grassland	30	>500	25-50	<1	L	10
SA	Lincoln NP	A05	I	34º48'S 135º46'E	6	16.2	516	Shrubland	30	>500	5-25	50-75	H, M	10
SA	Hincks NP	A06	I	33º55'S 136º14'E	84	16.4	399	Annual grassland	4700	<25	<5	<1	L	7
SA	Mt. Compass	A07	I	35º20'S 138º36'E	262	14.6	801	Schubland	30	100-500	50-75	50-75	M	10
SA	Cleland NP	A08	I	34º57'S 138º42'E	602	13.0	1101	Forest	20	25-100	<5	5-25	M	10
SA	Warren CP	A09	I	34º40'S 138º51'E	257	14.9	616	Forest	25	25-100	<5	<1	L	10
SA	Mt. Burr	A10	I	37º35'S 140º28'E	171	13.3	867	Plantation	30	100-500	<5	5-25	L	10

VIC	Mt. Napier NP	A11	I	37º55'S 142º02'E	223	12.9	757	Forest	15	100-500	5-25	75-100	H	10
VIC	Hastings	A12	I	38º17'S 145º11'E	15	14.5	785	Shrubland	15	25-100	25-50	<1	H	2
VIC	Gumbaya Park	A13	I	38º04'S 145º39'E	121	13.7	960	Perennial grassland	10	<25	<5	<1	M	0
EUROPE														
CAT	Cambrils	C01	I	41º04'N 1º04'E	20	16.3	549	River bed	100	25-100	5-25	n/a	H	10
CAT	Palafolls	C02	I	41º39'N 2º42'E	66	15.6	722	Forest	75	>500	25-50	50-75	H	10
CAT	Calella	C03	I	41º37'N 2º39'E	144	15.6	717	Shrubland	40	>500	75-100	5-25	M	10
CAT	Castellbisbal	C04	I	41º27'N 1º59'E	51	16.3	589	River bed	100	25-100	<5	<1	H	10
CAT	Castellar V.	C05	I	41º36'N 2º04'E	288	15.3	631	Annual grassland	50	25-100	5-25	n/a	M	10
CAT	Bigues i Riells	C06	I	41º41'N 2º12'E	295	15.1	667	Wasteland	50	25-100	50-75	n/a	H	10
CAT	Sabadell	C07	I	41º31'N 2º07'E	124	16.1	594	Annual grassland	30	25-100	5-25	5-25	H	10
CAT	Ripollet	C08	I	41º29'N 2º10'E	61	16.3	599	Wasteland	50	25-100	<5	<1	H	10
CAT	Matadepera	C09	I	41º35'N 2º01'E	413	14.5	662	River bed	50	100-500	25-50	<1	M	10
CAT	Sant Llorenç NP	C10	I	41º36'N 2º05'E	332	14.9	654	Grassland, Forest	30	<25	5-25	<1	M	10
CAT	Campins	C11	I	41º43'N 2º28'E	519	14.2	798	Forest	25	<25	25-50	n/a	L	10
CAT	Montseny NP	C12	I	41º43'N 2º24'E	622	13.0	822	Forest	25	25-100	25-50	n/a	L	10
LIG	Pietra Ligure	L01	I	44º08'N 8º16'E	10	14.7	846	Grassland	100	100-500	5-25	1-5	H	10
LIG	Zucarello	L02	I	44º06'N 8º07'E	172	14.2	807	Annual grassland	100	25-100	5-25	25-50	H	10
LIG	Pontedassio	L03	I	43º56'N 8º00'E	283	14.4	794	Annual grassland	75	100-500	50-75	25-50	H	10
LIG	Arma di Taggia	L04	I	43º50'N 7º51'E	14	15.7	812	River bed	500	100-500	50-75	<1	H	10
LIG	Ventimiglia	L05	I	43º49'N 7º35'E	21	15.7	804	Annual grassland	80	<25	5-25	<1	M	5
LIG	Vado Ligure	L06	I	44º16'N 8º25'E	30	14.5	884	Annual grassland	50	<25	<5	<1	M	10

[1] Abbreviation for regions and States. In South Africa: ECP = Eastern Cape, WCP = Western Cape, KZN = KwaZulu-Natal; in Australia: NSW = New South Whales, SA = South Australia, VIC = Victoria; in Europe: CAT = Catalonia (Spain), LIG = Liguria (Italy)

[2] Code assigned to each population. Population number corresponds to Fig. 1

[3] Origin: N = native, E = expanded, I = introduced

[4] Altitude, mean annual temperature and mean annual rainfall

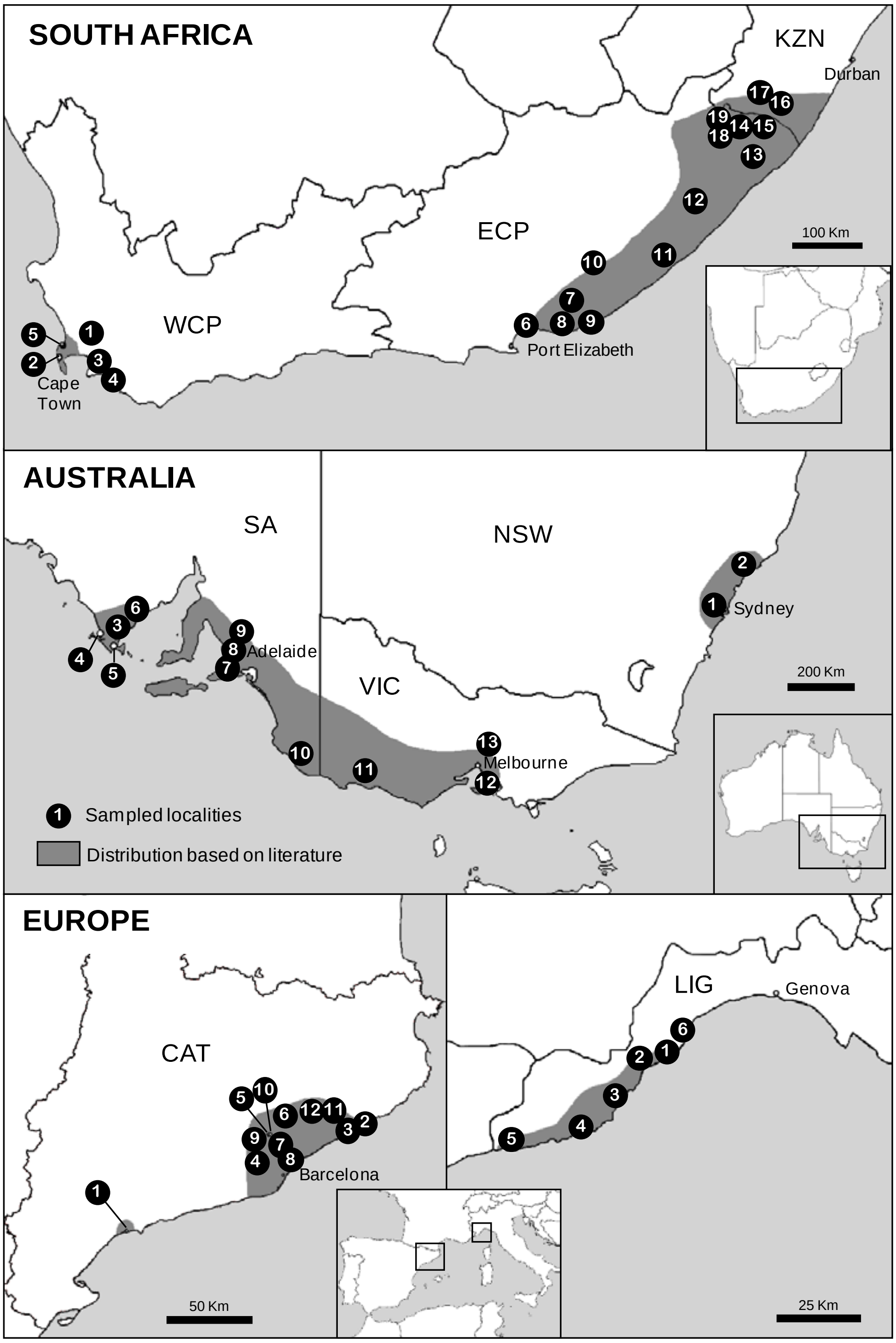
[5] Relative cover of *S. pterophorus* in the sampling area

[6] Relative abundance of *S. pterophorus* seedlings in the population, n/a: data not available

[7] Disturbance level: L = low, M = medium, H = high

[8] Number of reproductive individuals that were sampled to assess herbivory on capitula and seeds

Figure 1


SOUTH AFRICA
KZN
Durban
17
16
19
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ECP
100 Km
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WCP
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Port Elizabeth
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Town
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AUSTRALIA
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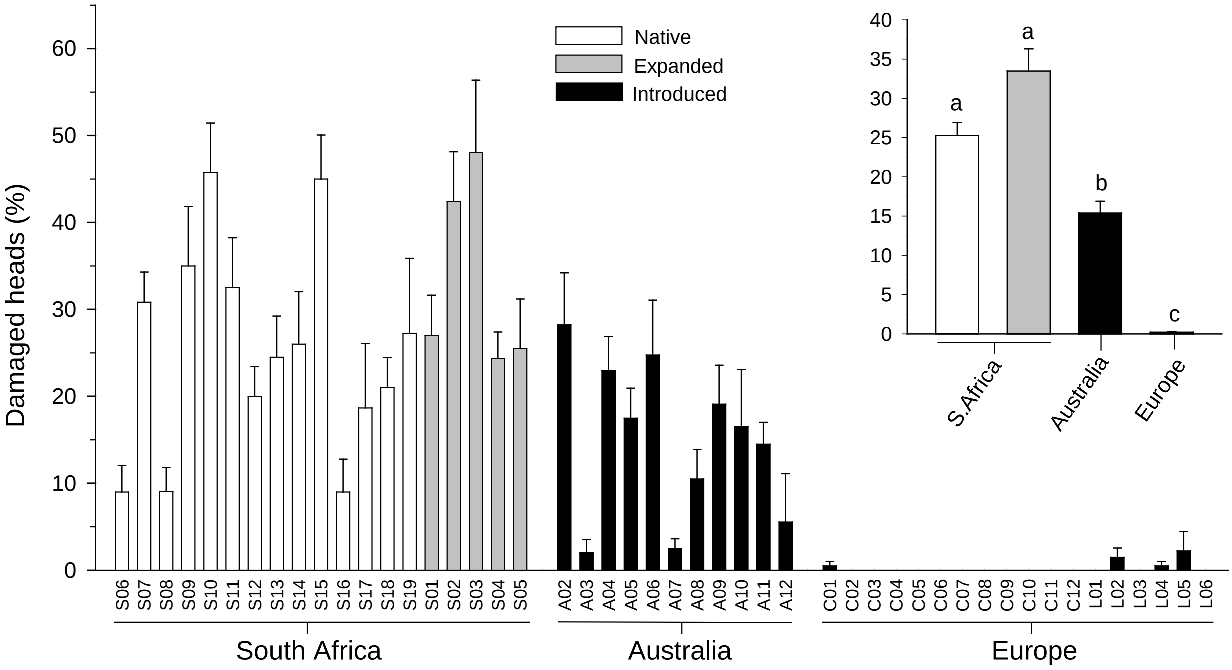
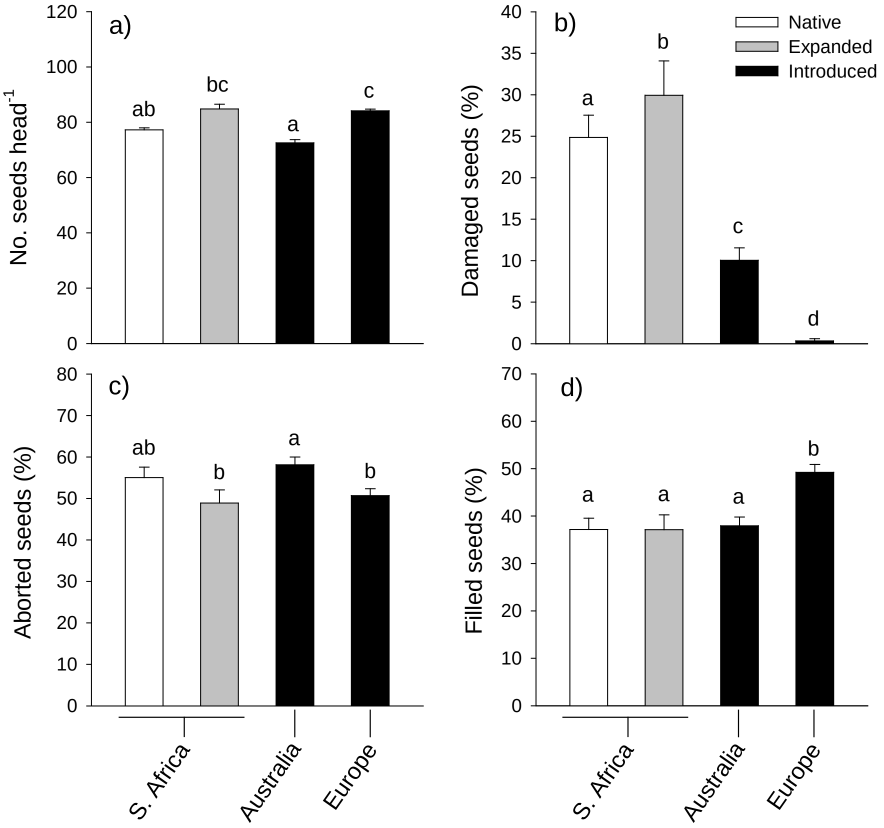
8
Adelaide
4
7
5
VIC
200 Km
13
Melbourne
10
11
12
1
Sampled localities
Distribution based on literature
EUROPE
LIG
Genova
6
2
1
CAT
3
5
10
6
12
11
2
3
9
7
4
8
4
5
Barcelona
1
50 Km
25 Km

Figure 2



Castells et al. (2013) Oecologia 173: 1397-1409
DOI 10.1007/s00442-013-2718-4

Figure 3



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