

Could enemy release explain invasion success of *Sagittaria platyphylla* in Australia and South Africa?

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ABSTRACT

Sagittaria platyphylla (delta arrowhead) is an emergent aquatic macrophyte native to southeastern United States of America that has been introduced into Australia and South Africa as an ornamental pond and aquarium plant. Compared to plants in the native range, *S. platyphylla* in the introduced range have greater reproductive capacity and form extensive infestations that dominate shallow waterbodies. One explanation for the invasive success of *S. platyphylla* in introduced countries is that plants are devoid of biotic pressures that would regulate population abundance in their native range (the enemy release hypothesis). We previously reported on field surveys that documented the number of pathogens and insect herbivores associated with *S. platyphylla* in native and introduced ranges. Here, we quantify the damage caused by these natural enemies to *S. platyphylla* in the two ranges. As predicted, damage to plants caused by pathogens and insect herbivores was much greater in the native than the introduced range at both the plant and population level. In introduced regions herbivory was low (less than 10%) in every plant part, while in North America insect damage to fruiting heads was 46% (of fruiting heads attacked), damage to leaves was between 33 to 57%, and internal herbivore damage to petioles and the inflorescence scapes was 56% and 43% respectively. Pathogen damage to leaves was between 39 to 57% of leaves per plant affected, compared to 9% in Australia and 8% in South Africa. This lack of biotic resistance from herbivores and disease may have facilitated *S. platyphylla* invasion in Australia and South Africa.

1. Introduction

Since Charles Darwin first proposed the enemy release hypothesis (ERH) over 150 years ago (Darwin, 1859), ecologists have debated the theories of biological invasions and as a result, several hypotheses have been postulated. But the ERH still remains the most widely cited and is based on the assumption that non-native species, when liberated from herbivores, pathogens and endophytes upon introduction into a new region, gain a substantial competitive advantage over natives that are themselves experiencing top-down regulation from their own natural enemies (Evans, 2008; Keane and Crawley, 2002; Liu and Stiling, 2006).

If the ERH was broadly applicable, then most exotic plant species should become invasive when released from herbivore pressure in their

new environment (Maron and Vilà, 2001). Yet in Australia, only 10% of the 2700 known alien plant species introduced into Australia since European settlement have become serious pests of agriculture and the environment (Groves et al., 2005), a proportion that accords with the ‘tens’ rule proposed by Williamson and Fitter (1996). Clearly, the ERH does not hold for all cases and there is growing evidence to suggest that interrelated causes such as disturbance, resource availability and niche opportunities contribute to invasion success (Mack et al., 2000; Shea and Chesson, 2002; Hierro et al., 2005; Catford et al., 2009; van Kleunen et al., 2014).

Classical biological control is predicated on the underlying assumptions of the ERH (Liu and Stiling, 2006), yet few studies have specifically tested the ERH as an *a priori* assessment for determining the likely success of a new biocontrol program. While recent studies have

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shown that the worldwide success rates of weed biocontrol programs has greatly improved since estimates conducted 30 years ago (Julien et al., 1984), nevertheless around 34% of programs have failed to have any impact upon their target weed (Schwarzländer et al., 2018).

We used the North American native aquatic macrophyte, *Sagittaria platyphylla* (Engelm.) J.G.Sm. (Alismataceae) to test several predictions of the ERH. Initially valued as an ornamental pond and aquarium plant, *S. platyphylla* has become a serious aquatic weed in Australia and South Africa. It invades shallow water bodies such as irrigation channels, drains, creeks and wetlands and can rapidly form dense and extensive infestations that impede water flow and displace native species (Adair et al., 2012). With increasing pressure from management authorities to initiate a biological control program against this aquatic weed, we conducted a series of biogeographical studies to address the fundamental question: could enemy release explain the invasion success of *S. platyphylla* in two introduced regions: Australia and South Africa?

In a previous study, we compared measures of population and individual performance (plant density, morphological traits and sexual reproduction) between native and introduced ranges to determine if any differences were apparent after controlling for influential abiotic factors (water depth and habitat type) (Kwong et al., 2017). Contrary to a common prediction of the ERH that exotic plants perform better in their introduced regions (Keane and Crawley, 2002), we found no difference in plant density between native and introduced range populations, however introduced range populations dominated the landscape through an increase in percentage cover. While morphological differences existed in some traits between native and introduced locations, these were not always consistently different between the two invaded ranges. For instance, plants were about 50% taller in South Africa than in either the USA or Australian regions, but there was no difference in height between USA or Australian plants. However, a clear difference was found between introduced countries and the USA for reproductive success, with the number of achenes per fruit being 40% greater and achene weight being 50% heavier for introduced plants. These differences were similar for both introduced countries, with different habitat types, irrespective of water depth and in different sampling years. We hypothesized that this result is evidence that there are biotic factors in the USA that are causing *S. platyphylla* plants to produce fewer and smaller achenes.

In the second component of our biogeographical study, we assessed the hypothesis that introduced plants would be released from pathogens and herbivores that would otherwise have kept them “in check” in their native range (Maron and Vilà, 2001). We found that plants in the native range hosted a diverse but modest guild of natural enemies ranging from specialist endophagous flower and fruit feeders, crown, root and tuber feeders and generalist foliage-feeding herbivores and pathogens, while populations of *S. platyphylla* in the introduced range were host to just a few generalist arthropod herbivores and pathogens (Kwong et al., 2014).

Here, we complete our series of biogeographical studies by examining a third prediction of the ERH, that weed populations in the introduced range will have a lower incidence of herbivory and disease compared to populations in the native range.

2. Methods

2.1. Field surveys

Populations of *S. platyphylla* were sampled at a range of localities in the USA, Australia and South Africa (Fig. 1, Supplementary material Table S1). A wide geographic range was surveyed in both native and invaded ranges and included natural (e.g. creeks, rivers, lakes, swamps) and ruderal (e.g. irrigation, roadside drainage ditches, impoundments) habitat types. Potential sampling locations were determined by accessing species occurrence records from databases including the Global Biodiversity Information Facility (GBIF; www.gbif.org), Australia's

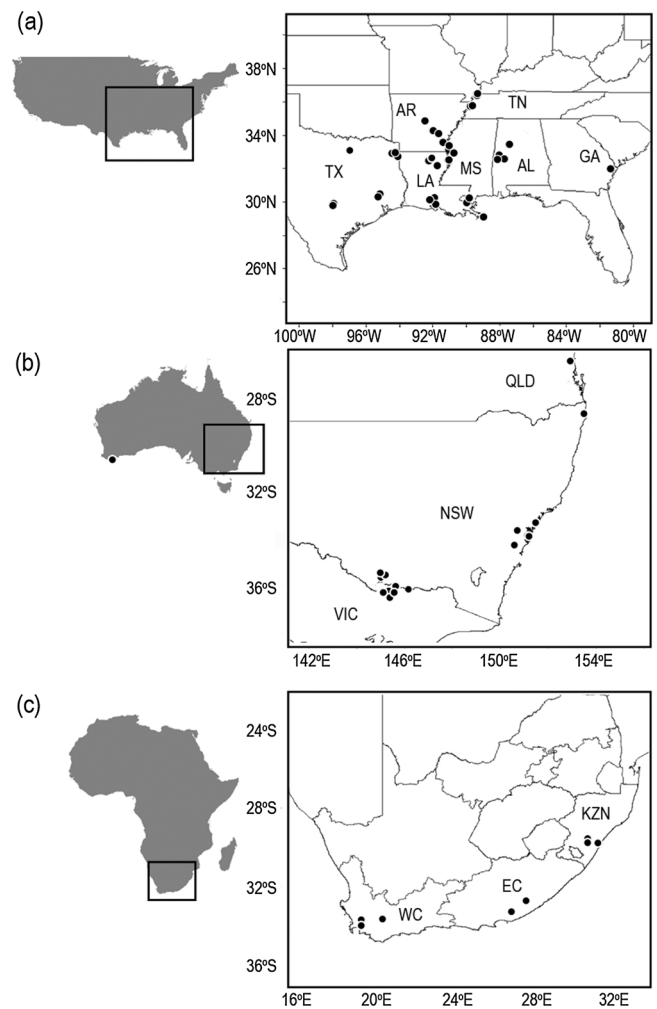


Fig. 1. Populations of *Sagittaria platyphylla* sampled across; (a) native (United States of America) and introduced ranges in (b) Australia and (c) South Africa from 2010 to 2015. Each black dot represents a population sampled: USA (AL-Alabama, AR-Arkansas, GA-Georgia, LA-Louisiana, MS-Mississippi, TN-Tennessee, TX-Texas); Australia (NSW-New South Wales, QLD-Queensland, VIC-Victoria); South Africa (EC-Eastern Cape, KZN-Kwa-Zulu Natal, WC-Western Cape).

Virtual Herbarium (AVH; <http://avh.chah.org.au/>) or the South African Plant Invaders Atlas (SAPIA; www.agis.agric.za). We also relied on prior knowledge of populations by local land management authorities, project participants and colleagues. Populations were defined as discrete stands located at least one km away from adjacent stands.

2.2. Herbivore and pathogen damage

To quantify levels of pathogen and herbivore damage, around 20 plants were harvested from a surveyed site. Plants were selected haphazardly from the middle section of the stand from between 1 to 10 m intervals, based on the overall estimated length of the stand. For each plant, we recorded whether individuals showed evidence of pathogen damage to the leaves (leaf spots), as well as herbivory of leaves, petioles, scapes (inflorescence stems), fruiting heads and the plant crown. Assessments were conducted during early to mid-autumn and were conducted on two occasions in the USA: five sites in 2013 and eight sites in 2015, and during 2014 in Australia (six sites) and South Africa (four sites). Additional data on fruit herbivory collected during natural enemy and plant biogeographical surveys, were also included in these analyses. Hence fruit herbivory was assessed at a total of 41 sites in the USA (2010–2015), 20 sites in Australia (2010–2014) and eight sites in

Table 1

Proportion of plants affected by pathogens and insect herbivores at each site. USA denotes United States of America, RSA denotes South Africa, AUS denotes Australia. Samples not available are indicated by nd.

	Angular transformation of estimated proportion ($\arcsin(\sqrt{p})^a$)							Estimated proportion (back transformation) ^b									
	Native			Introduced				Native			Introduced				P value ^c	Year within USA	AUS v RSA ^f
	USA	2010	2013 ^d	AUS	2010	2014	2014	SED ^e	USA	2010	2013 ^d	2015	2010	2014			
Plant part	2010	2013 ^d	2015	2010	2014	2014	SED ^e	2010	2013 ^d	2015	2010	2014	2014	Native v Introduced			
Damage	2011			2011				2011			2011						
Fruit																	
Herbivory	56.8	nd	54.1	0.0	0.0	4.2	5.44-9.54	0.70	nd	0.66	0.00	0.00	0.01	< 0.001 (F = 175)	0.30	0.56	
Leaf																	
Pathogens	nd	67.6	74.8	nd	38.7	41.5	7.84-9.74	nd	0.85	0.93	nd	0.39	0.44	< 0.001 (F = 28)	0.39	0.76	
Herbivory	nd	73.5	58.7	nd	21.8	41.7	11.14-13.83	nd	0.92	0.73	nd	0.14	0.44	0.001 (F = 16)	0.23	0.15	
Petiole																	
Herbivory	nd	81.1	74.2	nd	0.0	12.4	3.78-4.70	nd	0.98	0.93	nd	0.00	0.05	< 0.001 (F = 595)	0.099	0.016 (F = 8)	
Scape																	
Herbivory	nd	49.7	36.7	nd	0.0	9.1	8.99-10.84	nd	0.58	0.36	nd	0.00	0.03	< 0.001 (F = 31)	0.18	0.39	
Crown																	
Herbivory	nd	11.1	22.5	nd	0.0	0.0	7.35-8.87	nd	0.04	0.15	nd	0.00	0.00	0.007 (F = 10)	0.16	1.00	

^a Angular transformed values are best for statistical comparison of regions/years.

^b Back transformed proportions are best for examining the biological importance of statistical comparisons.

^c P values represent the presence of region/year effects and are calculated using permutation tests on the F statistics. The P value of fruit herbivory for a year effect within Australia is 1.00.

^d There were no fruit measurements taken in the USA in 2013.

^e Standard error of difference is denoted as SED.

^f AUS (years combined) versus RSA (2014).

South Africa (2014). For all other measures (leaf spots, foliage herbivory and crown damage) the total number of sites assessed were 13 in the USA, six in Australia and four sites in South Africa. The assessments conducted at each site are indicated in Table S1 provided in the online supplementary material.

2.3. Statistical analysis

Herbivory and pathogen damage to *S. platyphylla* at each site was examined in two ways. Firstly, the proportion of sampled plants affected by each type of damage was calculated. Secondly, the proportion of plant parts (e.g. fruit, leaves etc.) that were damaged on each plant was calculated, and then averaged over a site.

The unit of analysis was always a single site, observed on one occasion. Prior to statistical analysis, the site proportions were angularly transformed. This is a standard transformation to make the residual variation more homogeneous over a range of proportions from 0 to 1. Except for fruit herbivory, the transformed data were analyzed as an analysis of variance with effects for (i) origin (i.e. 'native' vs 'introduced'), (ii) year of sampling (2013 vs 2015) within the USA and (iii) country (Australia vs RSA) within the 'introduced' level of origin. We note that the effect of origin is marginal to both the other two effects, and thus it is natural to fit this effect first. We also note that, because of the sampling structure of sites in the study, the effect of year of sampling in the USA and the effect of country within introduced origin are orthogonal to each other. A consequence is that the order of examining these two effects does not affect the results.

With fruit herbivory, there were no data collected in the USA in 2013 but there were extra data collected in the USA for 2010, 2011 and 2012 and extra data collected in Australia in 2010 and 2011. Thus, the analyses of variance for fruit herbivory were modified to have effects for (i) origin (i.e. native vs introduced), (ii) year of sampling within the USA (iii) country (Australia vs RSA) within an introduced origin, and

year of sampling within Australia.

All analyses used a residual variation calculated from a saturated model that is calculated after fitting all combinations of country and year. There were many 0, and some 1, values in the data. Thus, to avoid statistical over-sensitivity due to data discreteness, all P values were calculated using non-parametric permutation tests on the F statistics rather than comparing the F statistics to the F distribution. Statistical analysis was carried out using GenStat 16, using the ANOVA directive and APERMTEST procedure.

3. Results

Pathogenic damage and insect herbivory to all above ground parts of the plant was much greater in the native range than in the introduced range at both the plant and population level (Tables 1 and 2, see also Fig. S2-S3 in the online supplementary material). In introduced regions herbivory was low (less than 10%) in every plant part (Table 2). In the USA, there was generally no evidence ($P > 0.05$) of differences in the proportion of plants attacked per population between years. Except for external scape herbivory, no inter-year variation was evident in the proportion of plant parts attacked for leaf pathogen damage, leaf herbivory or internal petiole and scape herbivory (Table 2).

Except for one site in South Africa (Umgeni Rd Canal, Durban), where 8.5% of fruit showed signs of external feeding damage, herbivore damage to fruit was not observed on plants across the introduced ranges (Tables 1 and 2). In contrast, fruit herbivory in the USA was recorded at 95% of sites and was highly variable between sites, ranging from no fruit damaged to 100% of fruit damaged (Fig. 2a). The proportion of fruit per plant damaged by insect herbivores in the USA also differed considerably between years ($P = 0.007$, Table 2, Fig. 2b) with the estimated proportion of damaged fruit varying from 0.3 to 0.6 (back transformed mean, Table 2). The differences between years in the proportion of fruit in the USA with herbivory were not reflected in the

Table 2

Proportion of plant parts affected by pathogens and insect herbivores at each site. USA denotes United States of America, RSA denotes South Africa, AUS denotes Australia. Samples not available are indicated by nd.

Plant part	Angular transformation of estimated proportion ($\arcsin(\sqrt{p})^a$)							Estimated proportion (back transformation) ^b								
	Native			Introduced				Native			Introduced				P value ^d	
	USA ^c	2013 ^e	2015	AUS	2014	RSA	USA ^c	2013 ^e	2015	AUS	2014	RSA				
Damage	2010	2011	2012	2011	2011	2014	2010	2011	2012	2011	2011	2011	2011	Year within USA	AUS v RSA ^g	
Fruit																
Herbivory	42.5	nd	42.9	0.0	0.0	2.1	4.61-8.08	0.46	nd	0.46	0.00	0.00	0.00	< 0.001 (F = 144)	0.007 (F = 4)	0.74
Leaf																
Pathogens	nd	38.7	49.0	nd	17.8	16.4	6.46-8.02	nd	0.39	0.57	nd	0.09	0.08	< 0.001 (F = 31)	0.15	0.86
Herbivory	nd	49.0	34.8	nd	8.7	17.4	7.38-9.17	nd	0.57	0.33	nd	0.02	0.09	< 0.001 (F = 24)	0.091	0.33
Petiole																
External herbivory	nd	25.8	21.0	nd	0.0	4.8	3.04-3.78	nd	0.19	0.13	nd	0.00	0.01	< 0.001 (F = 78)	0.15	0.20
Internal herbivory	nd	48.5	46.0	nd	0.0	0.0	4.51-5.60	nd	0.56	0.52	nd	0.00	0.00	< 0.001 (F = 179)	0.61	1.00
Scape																
External herbivory	nd	26.9	4.9	nd	0.0	0.0	4.11-4.96	nd	0.20	0.01	nd	0.00	0.00	< 0.001 (F = 20)	< 0.001 (F = 26)	1.00
Internal herbivory	nd	40.9	40.6	nd	0.0	0.0	6.45-7.77	nd	0.43	0.42	nd	0.00	0.00	< 0.001 (F = 67)	0.96	1.00

^a Angular transformed values are best for statistical comparison of regions/years.

^b Back transformed proportions are best for examining the biological importance of statistical comparisons.

^c Angular transformed values of fruit herbivory in the USA in each year are (back transformed values in parentheses): 30.1 (0.25) for 2010, 51.8 (0.62) for 2011, 45.6 (0.51) for 2012 and 42.9 (0.46) for 2015, with the standard error of difference ranging from 6.11 to 7.02.

^d P values represent the presence of region/year effects and are calculated using permutation tests on the F statistics. The P value of fruit herbivory for a year effect within Australia is 1.00.

^e There were no fruit measurements taken in the USA in 2013.

^f Standard error of difference is denoted as SED.

^g AUS (years combined) versus RSA (2014).

proportion of plants with herbivory, with about 70% of plants at a site having fruit herbivory in every year. In the USA, nine insect herbivores were found to attack the fruit with the curculionid, *Listronotus appendiculatus* (Boheman) being the most common and damaging of the fruit-feeding insects (Supplementary material Fig. S1a) (Kwong et al., 2014).

Much of the internal petiole and scape damage observed in the USA was also caused by *L. appendiculatus*, the larvae of which had, after consuming the fruit, migrated down the stems to pupate. The larvae of a different species of weevil, *Listronotus sordidus* (Gyllenhal) were more damaging to the petiole and scape tissue than *L. appendiculatus*, but were less common. In the introduced range, there were more plants with petiole herbivory in South Africa than Australia, although the proportion of plants per site in RSA with this damage was still only 5% and the average proportion of damaged petioles per plant was only about 1% (Tables 1 and 2). No other differences between Australia and South Africa were found ($P > 0.1$).

Crown herbivory was the least common form of plant damage observed on *S. platyphylla* in the native range with the greatest damage (15% of plants per population attacked) observed in 2015. Two *Listronotus* weevil species (*L. sordidus* and *L. frontalis* LeConte) and one unidentified tipulid dipteran were associated with root crowns, of which *L. sordidus* was the most common, being found at 17% of sites (Supplementary material Fig. S1b) (Kwong et al., 2014). No crown damage was observed in Australia and South Africa.

4. Discussion

The enemy release hypothesis (ERH) attributes the increased performance of plant invaders to their escape from natural enemies (Keane

and Crawley, 2002; Hierro et al., 2005). The simplest method used to test the ERH has been to compare the number of herbivore and/or pathogenic taxa associated with the target species in its native and invaded areas through lists compiled from literature and database records (Mitchell and Power, 2003; van Kleunen and Fischer, 2009). However, in our preliminary test of the ERH we found no records of insects, nematodes or plant diseases associated with *Sagittaria platyphylla* in either the USA or Australia and South Africa, making predictions about enemy release based on existing records impossible (Kwong, 2016).

Another approach used to test the ERH hypothesis has been to compare guilds of natural enemies between native and invaded ranges, such as the shift from specialists (feeding on one or a few closely related plant species) to generalists (feeding on several non-related plant species) (Cripps et al., 2006; Halbritter et al., 2012; Wolfe, 2002). From field surveys conducted in a concurrent study (Kwong et al., 2014), we found a 9.5-fold increase in the number of arthropod species and a 29-fold increase in the number of pathogens associated with *S. platyphylla* in the native compared to the introduced (Australian) range. In contrast to Australia and South Africa where no specialist herbivores were found, 21% ($n = 4$) of arthropods reared from *S. platyphylla* in the USA were specialists, 32% ($n = 6$) were generalists and 47% ($n = 9$) were unknown because their identities were not determined. The lack of specialist herbivores or pathogens on introduced populations of *S. platyphylla* is consistent with the suggestions of Memmott et al. (2000) and Hill and Kotanen (2009) that introduced plant species tend to host fewer herbivores and diseases when they are taxonomically isolated from native species. *Sagittaria platyphylla* is from the Alismataceae family of which only seven species are indigenous to Australia: *Alisma*

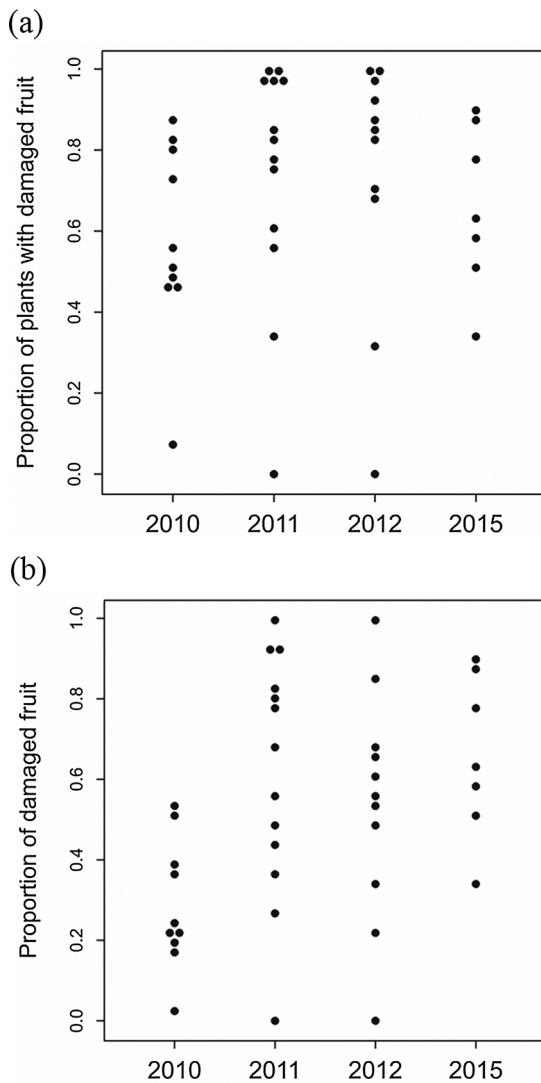


Fig. 2. Dot histograms of fruit herbivory assessments conducted over four years in the USA (native range) for: (a) the proportion of plants per site with herbivore-damaged fruiting heads; and (b) the proportion of fruiting heads per plant attacked by insect herbivores.

plantago-aquatica L., *Damasonium minus* (R.Br.) Buchanan, *Caldesia oligococca* (F.Muell.) Buchenau, *C. parnassifolia* (L.) Parl., *C. acanthocarpa* (F. Muell.) Buchenau, *Astonia australiensis* (Aston) S.W.L. Jacobs, and *Butomopsis latifolia* (D. Don) Kunth (Jacobs and McColl, 2011). A recent comprehensive phylogenetic analysis of the Alismataceae family suggests that *Astonia* and *Caldesia* species are more closely related to *Sagittaria*, than *Alisma* and *Damasonium*, which belong to a separate clade (Chen et al., 2012). However, only *A. plantago-aquatica* and *D. minus* have geographic distributions that overlap with *S. platyphylla*, yet the general lack of herbivores and pathogens on *S. platyphylla* suggests that these native confamilials have not shared these with their invasive exotic relative. The one exception is the cosmopolitan waterlily aphid, *Rhopalosiphum nymphaeae* (Linnaeus), which has been observed on *A. plantago-aquatica*, *D. minus*, *S. platyphylla* and *S. calycina* in south-eastern Australia (Supplementary material Fig. S3a-b) (Kwong personal observation).

The second ERH prediction that native species should sustain higher total herbivore damage than introduced species was supported by this study. While Australian and South African populations were not devoid of herbivores or pathogens, the damage to individual plants in the USA was considerably greater, especially herbivore damage to leaves,

petioles, scapes and fruiting heads. While herbivory of the root crowns was uncommon in the native range, where it did occur plant dieback and death were observed in crown-damaged plants (Supplementary material Fig S1).

The third prediction of the ERH is that reduced herbivore pressure in the introduced range will translate to increased competitive ability and plant performance (Blossey and Nötzold, 1995; Keane and Crawley, 2002; Liu and Stiling, 2006). For *S. platyphylla*, there is some support for this third prediction. In our other study on the biogeographical comparison of plant and population traits, we found evidence for an increase in plant dominance (percentage cover) and reproductive performance (achene production and weight) in introduced versus native range populations (Kwong et al., 2017). As these trait differences could not be explained by differences in environmental conditions between the native and introduced ranges, we hypothesize that these may be related to release from enemy pressure. While this may have led to a subsequent evolutionary change in resource allocation from defense to growth and reproduction (i.e. the Evolution of Increased Competitive Ability hypothesis (Blossey and Nötzold, 1995), it was beyond the scope of our study to test this. While a few studies have shown that seed-feeding herbivores play an important role in plant population dynamics (Louda and Potvin, 1995; Jongejans et al., 2006), in general, natural enemy impacts on plant fitness at an individual scale may not always translate to population-level effects (Maron and Vilà, 2001; Keane and Crawley, 2002). As demographic responses to herbivore damage were not included in our study, we are unable to address the final and most critical prediction of the ERH, that negative effects of herbivores and/or pathogens will limit the abundance of plants in their native range.

An inherent shortcoming of biogeographical studies in tests of the ERH is the inability to link comparisons of natural enemy richness, damage and effects on individual plant performance with invasiveness success at the population and regional level (Colautti et al., 2004). One way to overcome this would be to undertake community-level studies under controlled conditions (Hierro et al., 2005; Hinz and Schwarzaender, 2009) or through exclusion studies using insecticides and fungicides (Nachtrieb et al., 2011). We have made some progress in this regard through an exclusion experiment to compare *S. platyphylla* changes in vegetative growth and sexual reproduction across a growing season with and without insect herbivores (Kwong et al., 2018 in press).

There is increasing evidence to suggest that the ERH hypothesis is an exception rather than the rule for why introduced plants become invasive. Instead, it probably applies to a small subset of plants that possess life-history features that are particularly vulnerable to herbivore damage, such as relatively short-lived plants with short-lived seed banks (Maron and Vilà, 2001). Through our series of biogeographical studies, we have demonstrated that *S. platyphylla* has been released from natural enemies that would otherwise play some part in the regulation of populations in the native range (Kwong et al., 2014). We have also demonstrated that there is a lack of biotic resistance from native plant competitors (Kwong et al., 2017), pathogens and herbivores in introduced ranges which might enable *S. platyphylla* to take advantage of available resources and obtain a strong-hold in the novel environments. But does *S. platyphylla* fall into the limited subset of plants for which biological control may be successful? Clearly, further studies are required to: (1) assess the impact of specialist herbivore and herbivore guilds on population vital rates (growth, survival and reproduction), (e.g. Liu and Stiling, 2006), (2) improve our understanding of the population dynamics of *S. platyphylla* in both its native and invaded range to determine if *S. platyphylla* possesses life-history features that are vulnerable to herbivore damage (e.g. Davis et al. (2006)), and (3) extend our understanding of the population genetics of *S. platyphylla* to determine if local adaptation is the driving force behind *S. platyphylla* invasiveness and if so, the implications this may have for future biological control attempts.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.aquabot.2018.11.011>.

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