



Biogeographical comparison of the emergent macrophyte, *Sagittaria platyphylla* in its native and introduced ranges



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ABSTRACT

Understanding why some plant species become invasive is important to predict and prevent future weed threats and identify appropriate management strategies. Many hypotheses have been proposed to explain why plants become invasive, yet few studies have quantitatively compared plant and population parameters between native and introduced range populations to gain an objective perspective on the causes of plant invasion. The present study uses a biogeographical field survey to compare morphological and reproductive traits and abundance between the native range (USA) and two introduced ranges (Australia and South Africa) of *Sagittaria platyphylla* (Engelm.) J.G. Sm (Alismataceae), a highly invasive freshwater macrophyte. Introduced and native populations differed in sexual reproductive output with the number of achenes per fruiting head and individual achene weight found to be 40% and 50% greater in introduced populations respectively. However, no other morphological traits were found to be consistently different between the native and both introduced ranges, especially after taking into account differences in environmental conditions between the three ranges. Although populations in introduced regions were larger and occupied greater percentage cover, no differences in plant density were evident. Our results suggest that, apart from sexual reproduction, many of the trait patterns observed in *S. platyphylla* are influenced by environmental and habitat conditions within the native and invaded ranges. We conclude that the enemy release hypothesis best explains the results observed for sexual reproduction. In particular, we hypothesise that a release from natural enemies, specifically a pre-dispersal seed predator, may induce reproductive plasticity in *S. platyphylla*.

1. Introduction

For many decades, invasion ecologists have sought to determine the key attributes that make some plant species successful invaders (Elton, 1958; Baker et al., 1965; van Kleunen et al., 2014) and why some communities are more susceptible to invasion than others (Crawley, 1987; Kolar and Lodge, 2001). Understanding why certain plants become invasive is important for predicting and preventing future weed threats (Groves et al., 2001) and for identifying appropriate management strategies (Blumenthal, 2006; Herrera et al., 2011).

The contribution of traits to the success of invasive species must be context dependent (Pyšek and Richardson, 2007; van Kleunen et al., 2014). Nevertheless, certain traits appear to be common amongst many invasive plant species. These traits include high phenotypic plasticity,

rapid growth to sexual maturity, sexual and asexual reproductive strategies, high tolerance to environmental heterogeneity, dispersal capabilities and an ability to outcompete other species (Baker et al., 1965; Sakai et al., 2001). Such traits may be inherent within the species making the species pre-adapted to being invasive (Baker et al., 1965). Alternatively, rapid evolutionary change within the species may pre-dispose the species to being a successful invader following introduction into a new range (Müller-Schärer et al., 2004).

Along with intrinsic factors, extrinsic factors such as climate, disturbance regimes, resource availability and competitive abilities of the resident species, may also facilitate invasion in the new range (Crawley, 1987; Shea and Chesson, 2002).

Many hypotheses have been proposed to explain why some plant species become invasive (Keane and Crawley, 2002; Shea and Chesson,

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2002; Blumenthal, 2005; Catford et al., 2009). A myriad of approaches have been used to test their validity, such as observational and experimental, biogeographical and community comparative studies (see review by van Kleunen et al., 2010).

Prior to testing any hypotheses, empirical comparisons of plant performance between the introduced and native range should be conducted to determine whether there are explicit differences that can be attributed to any of the invasion hypotheses, such as enemy release, evolution of invasiveness, empty niche or novel weapons (Hierro et al., 2005). Surprisingly, few studies have quantitatively compared plant and population parameters between native and introduced ranges to gain an objective perspective on the causes of plant invasion (but see Erfmeier and Bruelheide, 2004; Herrera et al., 2011; Hinz et al., 2012; Williams et al., 2010), and even fewer have considered more than one invasive range.

Sagittaria platyphylla (Engelm.) J.G.Sm (delta arrowhead, or colloquially referred to as “sagittaria” in Australia) (Alismataceae), is an emergent freshwater perennial macrophyte with phyllodial submersed or emersed lanceolate petiolate leaves up to 150 cm tall (Supplementary material Fig. S1) (Haynes and Hellquist, 2000). It is indigenous to south eastern United States of America (USA) but has become highly invasive in some introduced areas, such as Australia and the Republic of South Africa (South Africa) (Supplementary material Fig. S2), where it rapidly dominates shallow fresh water environments such as wetlands, streams, riverbanks, ditches and irrigation channels (Adair et al., 2012). Plants have a prolonged 5–6 month flowering season (summer-fall) and produce multiple fruiting heads arranged in whorls of three on erect, racemose inflorescences (Haynes and Hellquist, 2000). An average of 850 achenes per fruiting head and 6900 achenes per inflorescence has been recorded on *S. platyphylla* in Australia (Flower, 2004). The light, buoyant achenes are dispersed along waterways collecting in still pools and river berms (Broadhurst and Chong, 2011). When water levels recede, exposed achenes germinate readily on the saturated mud (Kwong unpublished data). Vegetative reproduction via stolons is prolific throughout spring and summer. Tubers are produced at the base of roots in autumn and allow populations to rapidly regenerate in spring (Adair et al., 2012).

For the present study, we undertook a four-year biogeographical field survey to compare morphological and reproductive traits and abundance of *S. platyphylla* between the native range (USA) and two introduced ranges (Australia and South Africa). Research questions examined include: (1) Are *S. platyphylla* populations in Australia and South Africa more abundant in terms of population size and plant density?; (2) Are individual plants larger in the introduced ranges?; (3) Is sexual reproductive performance greater in introduced ranges compared to the native range?; and (4) Are observed effects maintained after accounting for differences in native and introduced environments? The findings are used to hypothesise possible mechanisms of invasion success for *S. platyphylla* in its introduced ranges.

2. Methods

2.1. Field surveys

A total of 84 *S. platyphylla* populations were sampled, at least for population size, water depth and habitat type. Of these, 41 were from the native USA range and 35 and eight were from the introduced ranges of Australia and South Africa, respectively (Fig. 1). Of these 84 populations, 25 were assessed for plant density, 47 were used for plant morphology measurements, fruit production was measured on 62 and achene production was measured on 64.

Populations were defined as discrete stands located at least 1 km away from adjacent stands. Based on Köppen-Geiger climate classifications (Kottek et al., 2006), all native range populations occurred within the (Cfa) climate zone, characterised by hot and humid summers with mild winters. South African and Australian populations occurred across

three zones within the moist subtropical mid-latitude climates (Cfa, Cfb, Csb), although eight Australian populations occurred within the cold semi-arid (steppe) climate (BSk) of south-western New South Wales (see Table S1 in Supporting Information). Sampling was conducted during summer-autumn (Aug-Sep in USA; Dec-April in Australia and South Africa), the peak growing and flowering period, and included natural creeks, rivers, lakes, swamps, semi-natural (impoundments) and ruderal (irrigation channels, roadside drainage ditches) habitat types, and a range of water depths. Potential sampling locations were determined by accessing species occurrence records from data bases including the Global Biodiversity Information Facility (GBIF; www.gbif.org), Australia's Virtual Herbarium (AVH; <http://avh.chah.org.au/>) or the South African Plant Invaders Atlas (SAPIA; www.agis.agric.za). Prior knowledge of populations by local land management authorities, project participants and colleagues was also used.

2.2. Population size and plant density

To delineate the size of populations, surveyed populations were assigned one of the following categories: LC (large, continuous population > 500 m in length for linear or occupying the entire water body), LDC (large but discontinuous populations > 500 m in length with scattered populations frequent along the water course), MI (moderate-sized, 20–500 m long), and SI (small, isolated population < 20 m long).

The density of emergent *S. platyphylla* plants (ramets/genets) was assessed in 13 of the 41 populations in the USA, eight of the 35 populations in Australia and four of the eight populations in South Africa. Ten quadrats (0.5 m x 0.5 m) were systematically sampled along the length of each population at intervals of between 2 m and 10 m, depending on the size of the population. As seedlings and rosettes were not visible beneath the water, these stages were not counted. The numbers of visible plant species, other than *S. platyphylla*, in each quadrat also were counted. Depending on water depth at the site, the percentage cover of *S. platyphylla* and other plant species was visually estimated at the surface of the water, or at ground level.

2.3. Plant morphology and fruit production

A number of growth and reproductive parameters from 29 populations in the USA, 14 populations in Australia and four populations in South Africa were compared (see Table S1). The USA and Australian populations were sampled over three years, while the South African sites were sampled over one year. In each population, between 14 and 20 plants were haphazardly collected at about 10 m intervals. Plant height, basal stem diameter (at the widest point), number of leaves and number of inflorescences bearing mature fruiting heads were measured on each of the collected plants.

The production of fruiting heads was measured at 38 of the 41 populations in the USA, 16 of the 35 populations in Australia and at all eight populations in South Africa over a similar time period to the populations used for growth and reproductive parameters. Between four and 20 plants were sampled at each site, depending on the number of plants that were fruiting. The average number of fruiting heads per inflorescence was recorded for each plant.

2.4. Achene production

Achene production was assessed on 39 populations in the USA, 17 populations in Australia and eight populations in South Africa. To assess achene production per fruiting head, a subsample of up to three heads was taken from each sampled plant and air dried in open standard petri dishes for several weeks. Achenes from each head were separated from the receptacle, pooled together and visually inspected to remove insect larvae, dried latex and plant debris. At this time, the level of insect herbivory of each head was visually estimated and scored as:

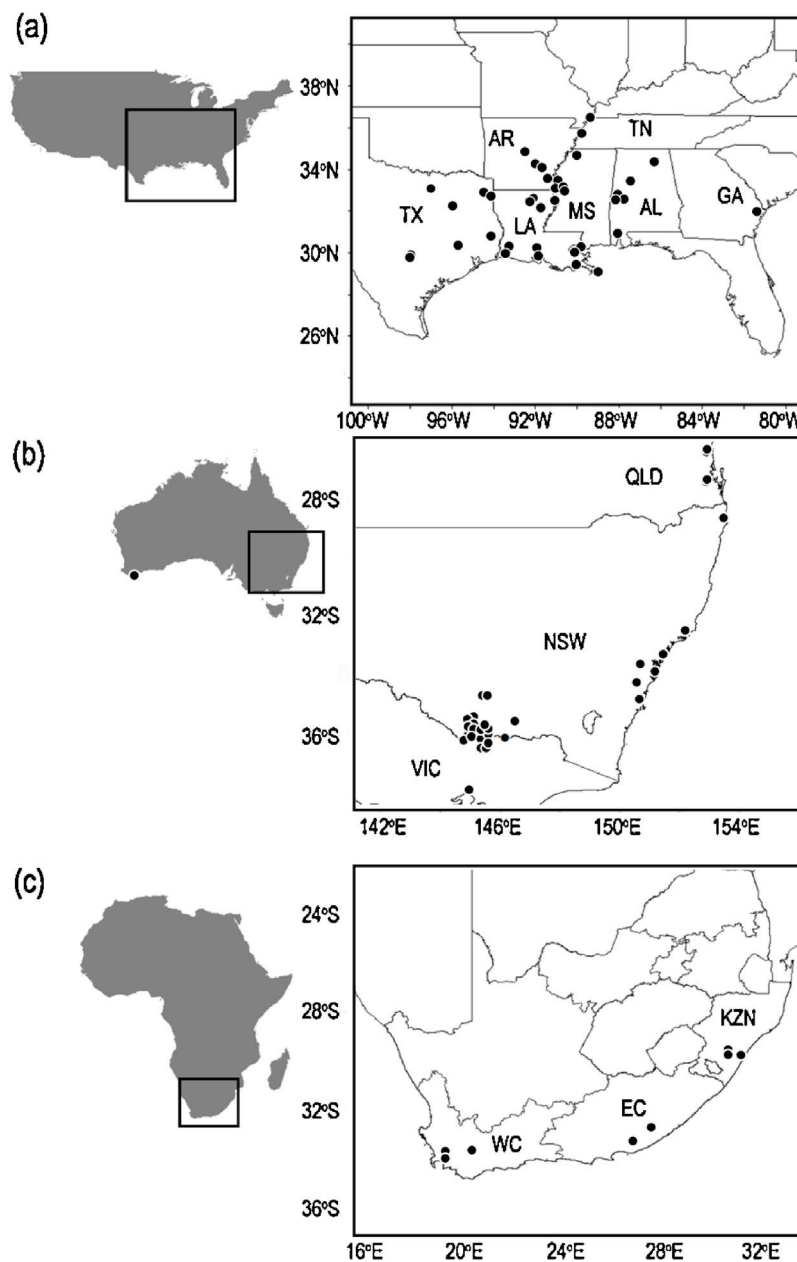


Fig. 1. Populations of *Sagittaria platyphylla* sampled across; (a) native (United States of America) and introduced ranges in (b) Australia and (c) South Africa from 2010 to 2014. Each black dot represents a population sampled: USA (AL-Alabama, AR-Arkansas, GA-Georgia, LA-Louisiana, MS-Mississippi, 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).

0 = 0% achenes damaged, 1 = 1–20% damaged, 2 = 21–50%, 3 = 51–80% damaged, 4 = > 80% damaged, and then averaged over the sampled fruiting heads on each plant. The pooled achenes were weighed and averaged across the sampled heads on each plant to provide a measure of the average weight of achenes per fruiting head for each plant. Individual achene weight was determined by counting the number of achenes present (irrespective of damage or not) in a subsample (ca. 0.01 g) of pooled achenes from each plant. The number of achenes per fruiting head was then calculated as the ratio of the achene weight per head and the individual achene weight. As it proved difficult to accurately count achenes from immature fruiting heads, these were excluded from sampling.

2.5. Statistical analysis

For each plant and site characteristic, the general statistical approach was to fit an appropriate generalized linear model

(McCullagh and Nelder, 1989) that categorised each population as either in an introduced or in the native range (i.e. 2-level ‘origin’ factor). The specific type of generalized linear model (ordinal logistic model, standard general linear model, general linear model with covariate based on damage score of fruit) differed with each characteristic being examined (Appendix S1).

Using these models, the first step was to compare these characteristics according to origin (an introduced or the native range). To allow comparison between the two introduced ranges (Australia and South Africa), an extra term for individual range was then added to the models. Finally, with the exception of population characteristics, an extra term was added for year of sampling within a range, so that consistency of results between years could be examined. If not explicitly reported in the results, with the exception of population characteristics, the reader can conclude that a year within range effect was examined and not found ($P > 0.05$).

Also, the effect of habitat type (natural, semi-natural or ruderal) and

water depth (linear response) on each characteristic was evaluated using appropriate generalized linear models. When such effects were found on a characteristic, the effects of origin and individual range on the characteristic were re-examined after adjusting for the effects of habitat type and/or water depth (i.e. by comparing a model that included both the examined and adjusting effects to a model including just the adjusting effects). All statistical analyses used population as the unit of analysis and were performed using the statistical software package GenStat 16 (Payne, 2013). With a few exceptions, explicitly stated in the results, models were compared using standard F tests for comparing nested generalized linear models that contain a dispersion parameter. See Appendix S1 in the Supporting Information in the online version for further details on the statistical methods used.

3. Results

3.1. Population characteristics

There were differences in the habitat type occupied by *S. platyphylla* between the native and introduced ranges ($P = 0.031$ using permutation test based on likelihood chi-square statistic; $\chi^2 = 7.16$), but there was no difference between the two introduced ranges, Australia and South Africa ($P = 0.12$ using permutation test based on likelihood chi-square statistic; $\chi^2 = 5.20$). In the native range, 59% of populations occurred in natural or semi-natural habitats such as wetlands, river-banks and along the margins of lakes (Table 1). Where *S. platyphylla* occurred in ruderal habitats, these were mostly roadside drainage ditches. In contrast, about 65% of populations in Australia and South Africa were found in ruderal habitats such as irrigation supply channels, drainage ditches and artificial impoundments (small ornamental lakes, sewerage and fisheries ponds).

Water depths also varied greatly between populations within ranges, with populations in introduced ranges generally occurring at greater water depths compared to the native range (Fig. 2; $F = 17.10$; $df = 1, 82$; $P < 0.001$), whereas there was no difference between the Australian and South African populations ($F = 0.01$; $df = 1, 81$; $P = 0.93$).

3.2. Population size and plant density

Population size and percentage cover of *S. platyphylla* differed between habitat types (ruderal habitats were larger, and had greater percentage cover, than natural habitats) but plant density of *S. platyphylla*, plant species diversity and percentage cover of other species did not differ (Table 2). Water depth was positively related to percentage cover of *S. platyphylla*, negatively related to species diversity and percentage cover of other species, but not related to population size or plant density of *S. platyphylla*.

The populations of *S. platyphylla* varied considerably in size in both native and introduced ranges, from small isolated patches less than 20 m long to large extensive monocultures. Overall, introduced range populations were more extensive than native, with around half of introduced range populations predicted to be greater than 500 m in length compared to only about one fifth in the USA (Table 3).

No statistical difference ($P > 0.1$) was found when the effect of origin (native vs. introduced) on population size was adjusted for

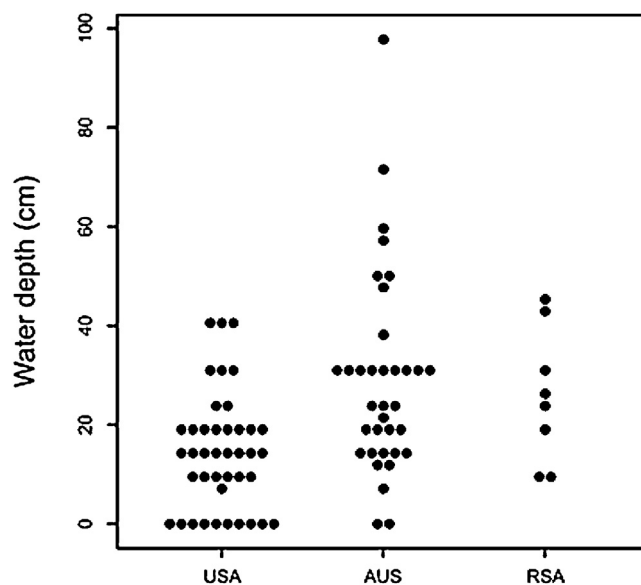


Fig. 2. Dot histogram of water depth at each *Sagittaria platyphylla* population in the native United States of America (USA) and introduced ranges; Australia (AUS) and South Africa (RSA). Each dot represents one population.

habitat type (Table 3). However, although there was no longer statistical significance, the estimated probabilities still indicated that Australia had substantially larger populations than the USA (noting number of sites is less in South Africa). Thus, due to limited statistical precision, it is uncertain whether the difference in size between introduced and native ranges can be explained by the difference in habitat types between introduced and native ranges.

Plant population density was similar between all three ranges, at around 75 plants/m² (Table 3). However, percentage cover of *S. platyphylla* was greater in introduced ranges at about 40% than in USA at about 10%. This difference was maintained when adjusted for water depth or habitat type. There was no difference in percentage cover between Australia and South Africa.

The percentage cover and diversity of other plant species was greater within populations occurring in the native range compared to populations in introduced ranges. However, both measurements were also influenced by water depth. When the effect of origin (introduced vs. native) on other species diversity and cover was adjusted for water depth, the difference between native and invaded ranges was no longer apparent. Despite this lack of statistical significance after adjustment for water depth, the USA still had much greater estimates for diversity and cover of other species.

3.3. Plant morphology and fruit production

Habitat type classification (natural, semi-natural or ruderal) did not affect plant morphology (Table 4). Water depth was only related to plant height and number of fruiting heads per inflorescence, with both relationships being positive. Thus, for these two measurements, the effects of range are reported after adjusting for water depth, as well as unadjusted.

Mean plant height was greater in South Africa (about 100 cm) than in Australia or the USA (about 70 cm), whether or not the comparison was adjusted for water depth (Table 5). There was no difference in basal diameter between the three ranges. South African *S. platyphylla* had more leaves than USA plants. However, the observed differences between Australia and the USA and between South Africa and Australia for the square root of the number of leaves are both around one and a half times the corresponding standard error of difference, and thus it is not clear where Australian *S. platyphylla* is placed in relation to the other two ranges. Australian plants had about half as many inflores-

Table 1
Percentage of *Sagittaria platyphylla* populations with different habitat types in each range.

Range	Total number of populations	Percentage of populations		
		Natural	Semi-natural	Ruderal
USA	41	51	7	41
Australia	35	29	9	63
South Africa	8	0	25	75

Table 2

P values for effects of habitat type and linear effect of water depth on measurements related to intensity of *Sagittaria platyphylla* infestation. Bold font indicates $P < 0.05$.

	Habitat type			Water depth		
	F value	Degrees of freedom	P value	F value	Degrees of freedom	P value
Population size	5.34	2, 79	0.0067	0.87	1, 80	0.36
Logit of % cover of <i>S. platyphylla</i>	3.59	2, 22	0.045	6.87	1, 23	0.015
Square root of density of <i>S. platyphylla</i> (plants per m ²)	1.04	2, 22	0.37	0.01	1, 23	0.91
Negative of diversity of other species + 0.1 to power of -0.5 (species/quadrat)	2.16	2, 22	0.14	5.77	1, 23	0.025
Negative reciprocal (% cover of other species + 1)	2.32	2, 22	0.12	4.90	1, 23	0.037

cences as both USA and South Africa, but the USA and South Africa had a similar number of inflorescences per plant. Whether or not an adjustment is made for water depth, Australian plants had 21% and 38% more fruiting heads per inflorescence than South African and USA plants respectively.

The only effect of sampling year within range was for leaves per plant ($F_{2,42} = 3.96$; $P = 0.027$). The back transformed means for the USA decreased from 6.9 in 2010 to 5.8 in 2011 to 5.2 in 2012, suggesting some year to year variability.

3.4. Achene production

There was no evidence that habitat type or water depth affected the number of achenes per fruiting head or achene size ($P > 0.05$). In the USA, achene production was maintained at approximately 500 achenes per head up to damage score 2, after which achene production declined dramatically (Fig. 3a). Plants from introduced ranges produced about 40% more achenes per fruiting head (700 vs. 500) than native USA plants when herbivory damage score was 0 (Table 6, Fig. 3a). Also, in the invaded range individual achenes were approximately 50% heavier than in the native range (0.14 vs. 0.09 mg; Fig. 3b).

Table 3

Effect of range on measurements related to *Sagittaria platyphylla* population abundance. USA denotes United States of America, RSA denotes South Africa, AUS denotes Australia, LC denotes large and continuous, and LCD denotes large and discontinuous. Bold font indicates $P < 0.05$. Standard error of difference is denoted as SED. In calculating each P value, F denotes the F statistic and df denotes the numerator and denominator (separated by comma) degrees of freedom.

	Range			SED			P-value	
	USA	Australia	South Africa	USA vs. Aus	USA vs. RSA	AUS vs. RSA	Native vs. Introduced	AUS vs. RSA
<i>Logit of probability either LC or LDC</i>								
Unadjusted	-1.44	0.28	-0.73	0.740	1.153	1.169	0.033	0.37
Back transformed probability	0.19	0.57	0.32				(F = 6.8, df = 1,80)	(F = 0.8, df = 1,79)
Adjusted for habitat type	-1.54 [#]	-0.08 [#]	-1.86 [#]	0.726	1.175	1.187	0.12	0.12
Back transformed probability	0.18	0.48	0.13				(F = 2.5, df = 1,78)	(F = 2.5, df = 1,77)
<i>Logit of % cover of S. platyphylla</i>								
Unadjusted	-2.03	-0.63	-0.21	0.375	0.478	0.512	0.00011	0.42
Back transformed	12	35	45				(F = 21.6, df = 1,23)	(F = 0.7, df = 1,22)
Adjusted for water depth	-2.02	-0.63	-0.22	0.501	0.581	0.524	0.0033	0.43
Back transformed	12	35	45				(F = 10.9, df = 1,22)	(F = 0.6, df = 1,21)
Adjusted for habitat type	-2.01 [#]	-0.62 [#]	-0.27 [#]	0.499	0.639	0.592	0.0043	0.56
Back transformed	12	35	43				(F = 10.2, df = 1,21)	(F = 0.4, df = 1,20)
<i>Square root of density of S. platyphylla plants (plants/m²)</i>								
Unadjusted	8.2	9.3	8.4	1.00	1.27	1.36	0.36	0.50
Back transformed	67	87	70				(F = 0.88, df = 1,23)	(F = 0.46, df = 1,22)
<i>Negative of diversity of other species + 0.1 to power of -0.5 (species/quadrat)</i>								
Unadjusted	-1.93	-2.65	-2.94	0.357	0.454	0.486	0.016	0.55
Back transformed	0.17	0.04	0.02				(F = 6.8, df = 1,23)	(F = 0.4, df = 1,22)
Adjusted for water depth	-2.06	-2.51	-2.81	0.468	0.542	0.489	0.21	0.54
Back transformed	0.14	0.06	0.03				(F = 1.6, df = 1,22)	(F = 0.4, df = 1,21)
<i>Negative reciprocal (% cover of other species + 1)</i>								
Unadjusted	-0.54	-0.84	-0.88	0.143	0.182	0.195	0.021	0.82
Back transformed	0.8	0.2	0.1				(F = 6.2, df = 1,23)	(F = 0.1, df = 1,24)
Adjusted for water depth	-0.58	-0.78	-0.84	0.189	0.219	0.197	0.22	0.81
Back transformed	0.7	0.3	0.2				(F = 1.6, df = 1,22)	(F = 0.1, df = 1,21)

[#] Predicted values have proportional weighting for the three habitat types.

4. Discussion

4.1. Population size and plant density

Several of the most widely cited invasion hypotheses, notably the enemy release (ERH) (Keane and Crawley, 2002) and evolution of increased competitive ability (EICA) (Blossey and Nötzold, 1995), predict that a number of plant growth metrics increase in invaded ranges over native areas. In contrast to our first prediction we found no difference in plant density between the native range (USA) and two introduced ranges (Australia and South Africa). However, other biogeographical studies have also shown that invasive clonal species are not always more abundant in their introduced range, suggesting that clonality is not a pre-requisite trait for successful plant invasion (Beckmann et al., 2014).

Although plant density was comparable between ranges, introduced *S. platyphylla* populations occupied more space in other ways; through greater vegetative cover and through more extensive vegetative spread. Percentage cover of populations in introduced ranges was about 40% compared to native range cover of about 10%. The greater cover occurred equally in both introduced ranges, and was maintained after allowing for different habitat and water depth profiles. This is very

Table 4

P values for effects of habitat type (natural, semi-natural or ruderal) and linear effect of water depth on measurements related to *Sagittaria platyphylla* plant morphology. Bold font indicates $P < 0.05$.

	Habitat type			Water depth		
	F value	Degrees of freedom	P value	F value	Degrees of freedom	P value
Plant height (cm)	0.01	2, 44	0.99	50.17	1, 45	7.7×10^{-9}
Square root of basal diameter	2.07	2, 44	0.14	0.27	1, 45	0.61
Square root of number of leaves	1.04	2, 44	0.36	3, 23	1, 45	0.079
Square root of number of inflorescences	0.46	2, 44	0.63	0.05	1, 45	0.82
Square root of number of fruiting heads per inflorescence at fruiting stage	0.23	2, 53	0.80	4.68	1, 54	0.035

strong evidence that *S. platyphylla* is dominating the landscape of introduced ranges in a manner other than via increasing plant density.

In Australia the most severe infestations occurred throughout the Murray-Darling Basin, where extensive monocultures extended for hundreds of metres along watercourses. In the Goulburn-Murray Irrigation district alone, it has been estimated that 85% of 14,000 km of creeks, drains and channels have infestations of *S. platyphylla* (Flower, 2004; Chapman and Dore, 2009). These shallow, high nutrient and frequently disturbed environments appear to favour the establishment, spread and dominance of the plant. Indeed, our analyses showed that introduced populations are generally both larger and more likely to be ruderal (Tables 2 and 4), supporting the suggestion that abiotic factors contribute to the invasiveness of introduced *S. platyphylla*.

In the native range, the diversity and cover of other co-occurring plant species was low, with the back transformed mean diversity being 0.17 species per quadrat and back transformed mean cover being 0.8%. The back transformed mean is a statistical estimate of the median population, which does not preclude the possibility of a very few native populations having much greater values. In fact for two populations, the percentage cover of other species was greater than 80% (despite an estimated median of 0.8%) and three populations had diversity of at least 1 species per square meter (despite an estimated median of 0.17 species per square meter). Despite generally low diversity and cover of other species in the native range, there was a substantial reduction in these measurements in the introduced ranges. This is not necessarily evidence that *S. platyphylla* outcompetes other species because it is possible that there is naturally more species diversity in the native

range than in both introduced ranges. However, the result is in accord with findings reported by Bastlová-Hanzélyová (2001) for *Lythrum salicaria* L., by Alba and Hufbauer (2012) for *Verbascum thapsus* L. and by Hinz et al. (2012) for *Lepidium draba* L., who found that the percentage cover of other plant species was lower in the introduced range (see also the review of biogeographic comparisons by Hinz and Schwarzaender, 2004).

4.2. Plant morphology and fruit production

Another common assumption of the ERH and EICA hypotheses is that plants will be taller in introduced versus native ranges (Blossey and Nötzold, 1995; Keane and Crawley, 2002). However, this was only true for *S. platyphylla* in South Africa, where plants were about 50% taller than in either the USA or Australia. No difference in height was found between USA or Australian plants. We suggest that the greater height in South Africa may have been associated with resource availability as populations occurred in nutrient rich waterways (e.g. water treatment works).

Other differences in plant morphology were found between regions. Plants in South African populations had more leaves than plants in USA populations. Australian populations had plants with fewer inflorescences than plants in the USA and South African populations, and the Australian populations had more fruiting heads per inflorescence than the USA and South African populations. However, no aspect of plant morphology was found to be consistently different between the native range and the two introduced ranges. This indicates that these

Table 5

Effect of range on *Sagittaria platyphylla* plant morphology. USA denotes United States of America, RSA denotes South Africa, AUS denotes Australia. Bold font indicates $P < 0.05$. Standard error of difference is denoted as SED. In calculating each P value, F denotes the F statistic and df denotes the numerator and denominator (separated by comma) degrees of freedom.

	Range			SED			P-value	
	USA	Australia	South Africa	USA vs. AUS	USA vs. RSA	AUS vs. RSA	Native vs. Introduced	AUS vs. RSA
<i>Plant height (cm)</i>								
Unadjusted	63	76	108	6.9	11.3	12.0	0.0045 (F = 9.0, df = 1,45)	0.010 (F = 7.3, df = 1,44)
Adjusted for water depth	69	67	95	5.6	8.8	8.8	0.53 (F = 0.4, df = 1,44)	0.0021 (F = 10.8, df = 1,43)
<i>Square root of basal diameter (cm)</i>								
Unadjusted	1.59	1.46	1.70	0.074	0.121	0.129	0.29 (F = 1.2, df = 1,45)	0.069 (F = 3.5, df = 1,44)
Back transformed	2.5	2.1	2.9					
<i>Square root of number of leaves</i>								
Unadjusted	2.44	2.59	2.86	0.097	0.159	0.169	0.030 (F = 5.1, df = 1,45)	0.11 (F = 2.7, df = 1,44)
Back transformed	6.0	6.7	8.2					
<i>Square root of number of inflorescences</i>								
Unadjusted	1.02	0.70	1.05	0.078	0.128	0.136	0.0028 (F = 10.0, df = 1,45)	0.012 (F = 6.8, df = 1,44)
Back transformed	1.0	0.5	1.1					
<i>Square root of average number of fruiting heads per inflorescence</i>								
Unadjusted	2.47	2.90	2.64	0.073	0.091	0.102	4.9×10^{-6} (F = 25.8, df = 1,54)	0.014 (F = 6.4, df = 1,53)
Back transformed	6.1	8.4	7.0					
Adjusted for water depth	2.47	2.90	2.64	0.081	0.094	0.104	0.000053 (F = 19.3, df = 1,53)	0.017 (F = 6.1, df = 1,52)
Back transformed	6.1	8.4	7.0					

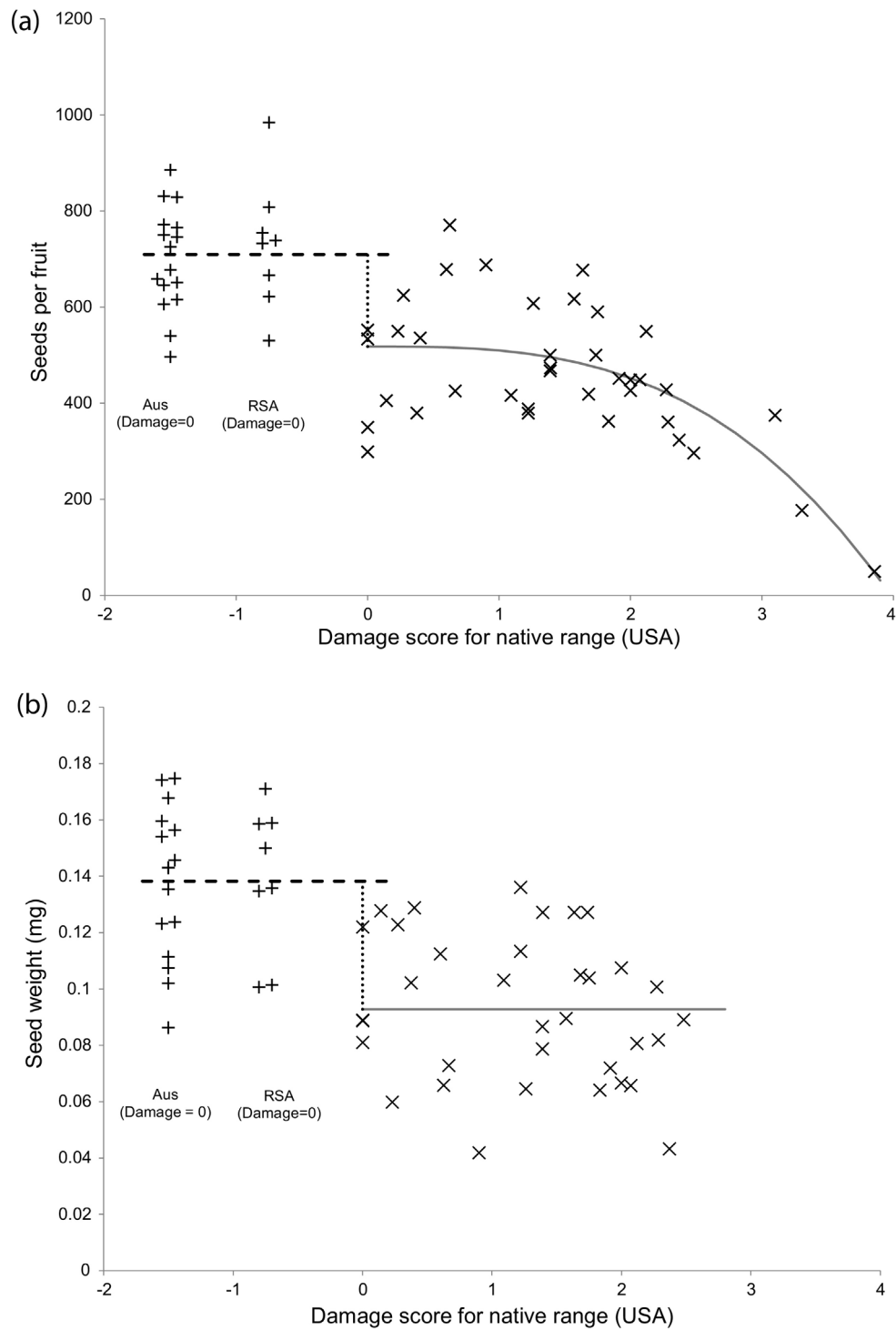


Fig. 3. The relationship between (a) achene per fruiting head (irrespective of damage to individual achene) and (b) individual achene weight and damage score for fruiting head from native (×) and introduced (+) range populations. Solid line is the fitted curves for the native range. Dashed line indicates average value for introduced ranges, that all have a damage score equal to 0. The dotted vertical line represents the predicted difference between introduced and native ranges, when damage score equals 0. The individual achene weight graph excludes sites with damage score greater than 3.

morphological differences are unlikely to be associated with the main invasive hypotheses (i.e. ERH and EICA) operating in a uniform manner over all introduced environments. These results show the importance of considering more than one introduced region in comparative studies between native and introduced populations. Furthermore, they highlight that invasive species management should not solely be based on the findings from a region outside the area of concern.

4.3. Achene production

Despite the lack of consistent differences between native and introduced ranges in plant morphology, there were consistent differences in sexual reproductive traits. Attack of fruiting heads by specialist herbivores had a direct impact on achene production and weight in the native range (Fig. 3, Table 6). Even when we compared fruiting heads with no herbivore damage, the number of achenes per head was 40%

Table 6

Effect of range on *Sagittaria platyphylla* achene production. USA denotes United States of America, RSA denotes South Africa, AUS denotes Australia. Bold font indicates $P < 0.05$. Standard error of difference is denoted as SED. In calculating each P value, F denotes the F statistic and df denotes the numerator and denominator (separated by comma) degrees of freedom.

	Range			SED			P-value	
	USA	Australia	South Africa	USA v AUS	USA v RSA	AUS v RSA	Native v Introduced	AUS v RSA
<i>Achenes per fruiting head</i>								
Unadjusted (excluding damage score from model)	460	700	730	40	52	58	1.4×10^{-9} (F = 51.2, df = 1,60)	0.61 (F = 0.27, df = 1,59)
When damage score is 0	520	700	730	35	45	49	7.3×10^{-8} (F = 37.8, df = 1,59)	0.54 (F = 0.38, df = 1,58)
<i>Individual achene weight (mg)</i>								
Unadjusted	0.093	0.138	0.139	0.0079	0.0102	0.0113	1.4×10^{-8} (F = 43.7, df = 1,57)	0.94 (F = 0.01, df = 1,56)

greater and achene weight was 50% greater in introduced ranges. These differences were similar for both introduced ranges, with different habitat types, irrespective of water depth and in different sampling years. This result suggests biotic factors in the USA are causing *S. platyphylla* plants to produce fewer and smaller achenes than in introduced ranges. Increased seed production and heavier seeds were also shown for other invasive plants including *Buddleja davidii* Franch. (Ebeling et al., 2008) and *Cytisus scoparius* (L.) Link (Buckley et al., 2003). Specialist herbivores in the native range may affect seed size either through reduced vigour of the parent plants and consequent maternal effects (Agrawal, 2001) or through selection against large seeds (Moegenburg, 1996).

In another study, we catalogued the natural enemy flora (pathogens) and fauna (invertebrate herbivores) associated with *S. platyphylla* in the USA and Australia over a three-year period (Kwong et al., 2014). We found a diverse guild of generalist and specialist enemies on *S. platyphylla* in the native range consisting of 32 arthropod and 29 fungal taxa, whereas in Australia, only one pathogen and two insect species were collected. Herbivory of fruiting heads and achenes in the USA was mostly caused by the larvae of the weevil, *Listronotus appendiculatus* (Boheman) (Coleoptera: Curculionidae), (Supplementary material Fig. S2) and, when abundant, had a substantial impact on reproductive output (Fig. 3).

The ability to reproduce both sexually and asexually is a common trait amongst invasive plants (Forman and Kesseli, 2003), with each mode of reproduction being important at different stages during the establishment of a population (Jakobs et al., 2004). For invasive *S. platyphylla*, the prolific production of achenes enables the species to disperse long distances and occupy new habitats. Once established, extensive clonal growth via stolons allows populations to rapidly expand and exploit gaps in native vegetation (Adair et al., 2012). In addition, the formation of underground carbohydrate storage organs (tubers) would enable populations to persist through adverse conditions such as frost, water level drawdown events and weed management applications (Adair et al., 2012). This strategy appears to have favoured the invasiveness of *S. platyphylla* into ruderal habitats, where disturbance events provide gaps in space and time, providing ideal conditions for the mass germination of achenes (Flower, 2004).

5. Conclusions

Our comparison of key trait patterns associated with invasiveness between introduced and native populations of an aquatic weed, *Sagittaria platyphylla* revealed that plants differed in achene production per fruiting head and achene weight. However, no other morphological traits were found to be consistently different between the native and two introduced ranges. Although populations in introduced regions were larger and had greater percentage cover, overall, no differences in plant density were evident between native and introduced populations.

Our results suggest that many of the trait patterns observed in *S. platyphylla* are influenced by environmental differences between native and invaded ranges. We hypothesise that release from natural enemies induces reproductive plasticity in *S. platyphylla*, with pre-dispersal seed predators playing a pivotal role.

Author contributions

R.M.K., J-L.S. and P.T.G. jointly conceived the ideas of the study. Data was collected in each country by various authors: USA (R.M.K, J-L.S. and N.E.H), Australia (R.M.K and J-L.S) and South Africa (R.M.K and G.D.M). K.L.B. performed the statistical analyses. R.M.K led the writing of the manuscript, and all authors contributed substantially to revisions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aquabot.2017.05.001>.

References

- Adair, R., Keener, B., Kwong, R., Sagliocco, J., Flower, G., 2012. The biology of Australian weeds 60. *Sagittaria platyphylla* (Engelmann) JG Smith and *Sagittaria calycina* Engelmann. *Plant Protect. Quart.* 27, 47–58.
- Agrawal, A.A., 2001. Transgenerational consequences of plant responses to herbivory: an adaptive maternal effect? *Am. Nat.* 157, 555–569. <http://dx.doi.org/10.1086/319932>.
- Alba, C., Hufbauer, R., 2012. Exploring the potential for climatic factors, herbivory, and co-occurring vegetation to shape performance in native and introduced populations of *Verbascum thapsus*. *Biol. Invasions* 14, 2505–2518. <http://dx.doi.org/10.1007/s10530-012-0247-4>.
- Baker, H.G., Baker, H., Stebbins, G., 1965. Characteristics and modes of origin of weeds. In: Baker, H., Stebbins, G. (Eds.), *The Genetics of Colonizing Species*. Academic Press, N.Y., pp. 147–168.

- Bastlová-Hanzélyová, D., 2001. Comparative study of native and invasive populations of *Lythrum salicaria*: population characteristics, site and community relationships. In: Brundu, G., Brock, J., Camarda, I., Child, L., Wade, M. (Eds.), *Plant Invasions: Species Ecology and Ecosystem Management*. Backhuys Publishers, Leiden, pp. 33–41.
- Beckmann, M., Bruehlheide, H., Erfmeier, A., 2014. Local performance of six clonal alien species differs between native and invasive regions in Germany and New Zealand. *Aust. Ecol.* 39, 378–387. <http://dx.doi.org/10.1111/aec.12087>.
- Blossey, B., Nötzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J. Ecol.* 887–889. <http://dx.doi.org/10.2307/2261425>.
- Blumenthal, D., 2005. Interrelated causes of plant invasion. *Science* 310, 243–244. <http://dx.doi.org/10.1126/science.1114851>.
- Broadhurst, L., Chong, C., 2011. Examining clonal propagation of the aquatic weed *Sagittaria platyphylla*. RIRDC Publication No. 11/020, Project No. AWRMC 08-65.
- Buckley, Y.M., Downey, P., Fowler, S.V., Hill, R., Memmot, J., Norambuena, H., Pitcairn, M., Shaw, R., Sheppard, A.W., Winks, C., 2003. Are invasives bigger? A global study of seed size variation in two invasive shrubs. *Ecology* 84, 1434–1440. [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[1434:AIBAGS\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[1434:AIBAGS]2.0.CO;2).
- Catford, J.A., Jansson, R., Nilsson, C., 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* 15, 22–40. <http://dx.doi.org/10.1111/j.1472-4642.2008.00521.x>.
- Chapman, M., Dore, D., 2009. *Sagittaria* strategic plan 2009. Unpublished Report to Goulburn Murray Water. Goulburn Broken Catchment Management Authority and the Tri-state *Sagittaria* Taskforce, Goomalibee, Victoria.
- Crawley, M., 1987. What makes a community invisable? In: Gray, A.J., Crawley, M.J., Edwards, P.J. (Eds.), *Blackwell Scientific*. Oxford, UK, pp. 429–453.
- Ebeling, S.K., Hensen, I., Auge, H., 2008. The invasive shrub *Buddleja davidii* performs better in its introduced range. *Divers. Distrib.* 14, 225–233. <http://dx.doi.org/10.1111/j.1472-4642.2007.00422.x>.
- Elton, C.S., 1958. *The Ecology of Invasions by Animals and Plants*. Methuen and Co., Ltd., London.
- Flower, G.E., 2004. *The Biology and Control of Arrowhead*. Unpublished Report. Goulburn-Murray Water, Tatura.
- Forman, J., Kesseli, R.V., 2003. Sexual reproduction in the invasive species *Fallopia japonica* (Polygonaceae). *Am. J. Bot.* 90, 586–592. <http://dx.doi.org/10.3732/ajb.90.4.586>.
- Haynes, R.R., Hellquist, C.B., 2000. *Alismataceae*. Oxford University Press, New York.
- Hierro, J., Maron, J., Callaway, R., 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *J. Ecol.* 93, 5–15. <http://dx.doi.org/10.1111/j.0022-0477.2004.00953.x>.
- Hinz, H.L., Schwarzländer, M., 2004. Comparing invasive plants from their native and exotic range: what can we learn for biological control? *Weed Technol.* 18, 1533–1541. [http://dx.doi.org/10.1614/0890-037X\(2004\)018\[1533:CIPFTN\]2.0.CO;2](http://dx.doi.org/10.1614/0890-037X(2004)018[1533:CIPFTN]2.0.CO;2).
- Hinz, H., Schwarzländer, M., McKenney, J., Cripps, M., Harmon, B., Price, W., 2012. Biogeographical comparison of the invasive *Lepidium draba* in its native, expanded and introduced ranges. *Biol. Invasions* 14, 1999–2016. <http://dx.doi.org/10.1007/s10530-012-0207-z>.
- Jakobs, G., Weber, E., Edwards, P.J., 2004. Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Divers. Distrib.* 10, 11–19. <http://dx.doi.org/10.1111/j.1472-4642.2004.00052.x>.
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170. [http://dx.doi.org/10.1016/S0169-5347\(02\)02499-0](http://dx.doi.org/10.1016/S0169-5347(02)02499-0).
- Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16, 199–204. [http://dx.doi.org/10.1016/S0169-5347\(01\)02101-2](http://dx.doi.org/10.1016/S0169-5347(01)02101-2).
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* 15, 259–263. <http://dx.doi.org/10.1127/0941-2948/2006/0130>.
- Kwong, R., Saggiocco, J.-L., Harms, N., Shearer, J.F., Keener, B., Green, P., 2014. Prospects for the biological control of delta arrowhead (*Sagittaria platyphylla*), an invasive aquatic species in Australia. In: Impson, F.A.C., Kleinjan, C.A., Hoffmann, J.H. (Eds.), *XIV International Symposium on Biological Control of Weeds*. Kruger National Park, South Africa, pp. 53–67.
- Müller-Schärer, H., Schaffner, U., Steinger, T., 2004. Evolution in invasive plants: implications for biological control. *Trends Ecol. Evol.* 19, 417–422. <http://dx.doi.org/10.1016/j.tree.2004.05.010>.
- McCullagh, P., Nelder, J., 1989. *Generalized Linear Models*, second edition. Chapman and Hall, London, UK.
- Moegenburg, S., 1996. *Sabal palmetto* seed size: causes of variation, choices of predators, and consequences for seedlings. *Oecologia* 106, 539–543. <http://dx.doi.org/10.1007/bf00329713>.
- Payne, R.W., 2013. *The Guide to the GenStat® Command Language (Release 16), Part 2: Statistics*. VSN International, Hemel Hempstead, Hertfordshire, UK.
- Pyšek, P., Richardson, D., 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.), *Biol. Invasions*. Springer, Berlin Heidelberg, pp. 97–125. http://dx.doi.org/10.1007/978-3-540-36920-2_7.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 305–332. <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114037>.
- Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176. [http://dx.doi.org/10.1016/S0169-5347\(02\)02495-3](http://dx.doi.org/10.1016/S0169-5347(02)02495-3).
- Williams, J.L., Auge, H., Maron, J.L., 2010. Testing hypotheses for exotic plant success: parallel experiments in the native and introduced ranges. *Ecology* 91, 1355–1366. <http://dx.doi.org/10.1890/08-2142.1>.
- van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M., Fischer, M., 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecol. Lett.* 13, 947–958. <http://dx.doi.org/10.1111/j.1461-0248.2010.01503.x>.
- van Kleunen, M., Dawson, W., Maurel, N., 2014. Characteristics of successful alien plants. *Mol. Ecol.* 1–15. <http://dx.doi.org/10.1111/mec.13013>.