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It doesn't take two to tango: increased capacity for self-fertilization towards range edges of two coastal invasive plant species in eastern Australia

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Abstract Understanding how selection pressures change during the course of an invasion is a key question in invasion biology. Shifts to greater reproductive success and output are expected to occur towards range edges of expanding invasive species as a means of increasing colonization opportunities and accelerating further spread. In a glasshouse experiment, we investigated shifts in reproductive traits (allocation to reproduction, seed number vs. seed size, capacity for self-fertilization) across multiple populations spanning the entire range of two coastal exotic invasive plant species (*Gladiolus gueinzii* Kunze and *Hydrocotyle bonariensis* Lam.) in eastern Australia. Although there was no significant increase in allocation to reproduction towards range edges or changes in seed provisioning, range edge populations displayed an increased capacity for self-fertilization in the absence of pollinators for both species. For *H. bonariensis* this entailed an increase in the probability of fruit production towards range edges while for *G. gueinzii* it was an increase in the probability of forming developed seeds towards range edges. Greater capacity for self-fertilization may facilitate further range expansion as it alleviates any reliance on external factors for pollination at the range edge. Our results suggest that increased capacity for self-fertilization towards range edges may be a key factor in promoting range expansion in some invasive species.

Keywords Autonomous self-fertilization · Invasive species · Introduced range · Range expansion · Reproductive traits

Introduction

Invasive species have been implicated in a number of adverse environmental outcomes such as loss of biodiversity and ecosystem function (Clavero and García-Berthou 2005; Molnar et al. 2008; Hedja et al. 2009). As such, much research has been dedicated to studying the key life history traits of successful invasive species in order to best understand what makes a species a successful invader. Studies comparing trait differences between invasive species from their native range compared to their introduced range have found that introduced populations of invasive species have a suite of different traits including greater biomass (Siemann and Rogers 2001; Caño et al. 2008), fecundity (Caño et al. 2008; Correia et al. 2016), and

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plasticity (Davidson et al. 2011). However, many of our existing ideas regarding successful invasions can be applied within the invaded range of species as invasive species rarely remain static in their introduced range, with many still undergoing range expansion and continually experiencing novel environments and selection pressures towards range edges. As species expand in their range, the process of range expansion itself may select for advantageous "invasive" traits in range edge populations to facilitate further range expansion (Phillips et al. 2010).

Increased allocation to reproductive structures and increased fecundity have commonly been associated with the success of invasive species when introduced to novel environments (e.g. Brown and Eckert 2005; Caño et al. 2008; Masson et al. 2008; Correia et al. 2016). As populations expand, these traits are likely to be under strong selection towards range edges as a means of significantly increasing colonization opportunities, hence facilitating further range expansion. Increased allocation to reproductive biomass in frontal populations has been found in a variety of range expanding invasive taxa (e.g. Lester et al. 2007; Ling et al. 2008; Gutowsky and Fox 2012; Lopez et al. 2012; Houston et al. 2013; Kambo and Kotanen 2014; Masson et al. 2016). However, within a given reproductive event, organisms can produce a small number of large offspring or a large number of small offspring due to resource allocation trade-offs (Westoby et al. 1992). Although offspring with greater maternal provisioning have been shown to be more competitive (Jakobsson and Eriksson 2000, 2003), lower conspecific density towards range edges of invasive taxa is expected to drive selection for increased reproductive rate at the expense of competitive ability (Burton et al. 2010; Alex Perkins et al. 2013). In terms of reproduction in plants, producing smaller seeds will result in a greater number of offspring for a given reproductive event and as such small seed size has been widely regarded as a key element in ecological strategies that rely on frequent colonization events (Henery and Westoby 2001) such as at invasion fronts. Changes in seed number (Alexander et al. 2007) and seed provisioning (Huang et al. 2015; Tabassum and Leishman 2018; but see Kambo and Kotanen 2014) have been reported towards range edges of many invasive plants, however a shift towards a greater number of smaller seeds towards range edges has not been explored.

Another trait associated with successful invasions in novel environments (particularly with respect to invasive plants) is the ability to produce offspring through self-fertilization (Petanidou et al. 2012; but see Atlan et al. 2015). Plants that are able to self-pollinate and self-fertilize are likely to be successful invaders because reproduction is not constrained by external factors such as mate and/or pollinator limitation (Baker 1974; Pannell et al. 2015). Numerous studies have found significantly higher numbers of self-compatible invasive plants than self-incompatible ones in given regional floras, many of which have also been found to autonomously self-fertilize (self-fertilize without pollination) (Rambuda and Johnson 2004; van Kleunen and Johnson 2007; van Kleunen et al. 2008; Hao et al. 2011; but see Sutherland 2004). Increased capacity for uniparental reproduction is not only beneficial for initial establishment but also at range edges of expanding species where individuals may occur at lower densities (experiencing mate limitation) and also be less apparent to pollinators (Pannell and Barrett 1998; Herlihy and Eckert 2005; Pannell et al. 2015). Many studies have found increased capacity for self-fertilization in peripheral populations of native species where local extinction and continual re-colonisation may be occurring (e.g. Busch 2005; Herlihy and Eckert 2005; Moeller 2006; Darling et al. 2008; Griffin and Willi 2014). However, few studies have examined whether this is a mechanism facilitating range expansion in invasive plants (Colautti et al. 2010).

Despite ongoing research into understanding traits of successful invasive species, we still know relatively little about how selection for traits alters during the course of an invasion (Gaston 2009; Lankau et al. 2009; Kilkenny and Galloway 2012). Reproductive traits such as increased fecundity and increased capacity to self-fertilize are likely to be under strong selection towards range edges, however few studies have examined these relationships. Additionally, most of these studies have sampled from a single range edge and/or only compared populations from the range centre and range edge, potentially obscuring our ability to find consistent patterns (Sagarin and Gaines 2002b; Sexton et al. 2009; Vaupel and Matthies 2012; Nunes et al. 2016).

In this study, we explored shifts in key reproductive traits across the entire distribution of two coastal exotic invasive species growing along the east coast of

Australia. Coastal species represent an ideal system to study such questions as their range is essentially linear with the capacity for spread being on two range edges only (Sagarin and Gaines 2002a, b; Samis and Eckert 2007). We hypothesised that range edge populations would: (1) allocate a greater proportion of biomass to reproduction; (2) display a greater capacity for autonomous self-fertilization (ability to self-fertilize without pollination); and (3) produce a greater number of smaller seeds, compared to populations from where they were first introduced (range core populations).

Methods

Study species

Hydrocotyle bonariensis Lam. (Araliaceae) is a perennial plant native to Africa, North and South America and has become widely naturalized on coastal dunes along eastern Australia. The first record of *H. bonariensis* in Australia was made in 1893 near Botany Bay, New South Wales. Although *H. bonariensis* is primarily found on dune systems, it occasionally occurs along rivers and lagoon outlets (Heyligers 1998). Its distribution in Australia is along the east coast from southern Queensland to Victoria (approximately 1200 km). *H. bonariensis* was accidentally introduced to Australia, possibly through ballast water (Heyligers 2008; Murray and Phillips 2012). It is facultatively sexual, reproducing clonally using rhizomes (modified underground stems) and sexually using flowers. *H. bonariensis* produces compound inflorescences containing hundreds of cream coloured flowers throughout the year, with each flower potentially producing one indehiscent schizocarp containing two seeds (Evans 1992). Roots, leaves and inflorescences arise from nodes along the rhizome which is generally buried in the sand at a depth of 2–5 cm (Knight and Miller 2004). The extensive rhizome systems of *H. bonariensis* can be comprised of over a thousand individual ramets that span many square meters of dune systems (Evans 1991).

Gladiolus gueinzii Kunze (Iridaceae) is a perennial dune plant native to dune systems in South Africa. The first record of *G. gueinzii* in Australia was from the port of Stockton, New South Wales in 1950, suggesting that the species was accidentally introduced through ballast water (Heyligers 1999). This species is solely confined to beach dunes and has become naturalized nearly 800 km along the east coast of Australia, from South West Rocks, New South Wales to Mallacoota, Victoria. *G. gueinzii* is facultatively sexual, reproducing clonally by cormels (round, buoyant, underground growths) and sexually through self-compatible flowers (Heyliger 1999; Manning et al. 2011). Flowering occurs between October to December, with plants producing a single flower stem containing 1–6 pink flowers that open sequentially (Heyligers 1999). Fruits ripen through the austral summer (December–February), with each fruit producing up to 40 winged seeds (samaras) (Heyligers 1999). This species typically occurs in dense populations close to the high-tide mark, with individuals occurring 20–30 cm apart (Manning et al. 2011).

Field collection

The distribution of *H. bonariensis* and *G. gueinzii* along the east coast of Australia was determined based on occurrence records from Australia's Virtual Herbarium (AVH). From November to December 2015 populations of *H. bonariensis* and *G. gueinzii* from their entire range along the east coast of Australia were sampled. We travelled 100 km further than the last recorded occurrence of both species on AVH at each range edge to ensure accurate sampling. For *G. gueinzii* we collected seeds from 23 populations (Fig. 1a). From each population we collected approximately 100 seeds from up to ten individuals that were at least 5 m apart. As *H. bonariensis* was not seeding throughout its range during fieldwork, we collected 3–4 5 cm long rhizomes from 24 populations (Fig. 1b).

Plant growth

Hydrocotyle bonariensis rhizomes were wrapped in moist paper towel and transported back to Macquarie University, North Ryde, New South Wales. Rhizomes were lightly buried in shallow trays (20 cm × 25 cm × 5 cm) using 100% washed beach sand sourced from a commercial supplier (Australian Native Landscapes, Sydney, New South Wales). Due to space constraints in the glasshouse, 2–3 rhizomes from each population were grown together in one tray. For *G. gueinzii*, 20 randomly selected seeds from each

Fig. 1 Maps of the populations of **a** *Gladiolus gueinzii* and **b** *Hydrocotyle bonariensis* from which seeds or rhizomes were collected for this study. Open circles represent sample sites and closed circles represent the assumed introduction point based on herbarium records. Dotted lines represent range boundaries

population were lightly scarified before being set to germinate on moist filter paper in petri dishes. Seeds were kept moist using 1% bleach solution to reduce the chance of mould. Petri dishes were placed in a temperature controlled growth cabinet set at 20 °C with a 12 h photo-period until germination (approximately 1–2 weeks). Ten randomly selected germinated seedlings from each population were then transplanted into separate pots (diameter 17 cm, depth 17 cm) containing 100% washed beach sand sourced from a commercial supplier (Australian Native Landscapes, Sydney, New South Wales). Glasshouse temperatures were set to 25 ± 3 °C during the day and 18 ± 3 °C during the night. Temperature was monitored continuously using a Multigrow Controller System (Autogrow Systems, Auckland, New Zealand). Plants were mist watered twice daily for two minutes with additional watering being provided on hot days. After 2 weeks of growth, plants were provided with a low concentration (0.15 g dissolved in 125 mL of water) of liquid fertiliser (Aquasol, Hortico Nurseries, 23 N:3.95 P:14 K). This was repeated every 2 weeks to prevent nutrient depletion. To help control an outbreak of leaf scale on *H. bonariensis*, plants were sprayed with a non-hazardous insecticide (PestOil^{TM}, Arthur Yates & Company, Homebush, Australia) every week.

Reproductive traits

After approximately 1 year (*H. bonariensis*) and 1.5 years (*G. gueinzii*) of growth, plants began to flower. For each population, up to 20 inflorescences were randomly selected to assess fertilization and seed traits. More inflorescences were sampled for *G. gueinzii* due to the significantly lower number of flowers per inflorescence compared to *H. bonariensis*. The number of flowers were counted on each inflorescence unaided (*G. gueinzii*) or with a 10 × magnifying hand lens (*H. bonariensis*) to determine autonomous self-fertilization ability. Flower counting occurred from November 2016 to January 2017 (*H. bonariensis*) and July 2017 to December 2017 (*G. gueinzii*), with flowers counted randomly across populations. As flowers on inflorescences opened sequentially, for each inflorescence, flowers and developing flower buds were counted when 75% of the flowers on the inflorescence were open. Counted inflorescences were tagged and subsequently bagged with mesh cloth to prevent the loss of developing fruit and seeds.

After approximately 1–3 months the bagged inflorescences developed fruit and began to wither or dehisce. At this stage fruit were harvested and allowed to air dry in their mesh bags in the lab for 2 weeks. We then counted the number of fruit produced per inflorescence for each species. Additionally for *G. gueinzii* we counted the number of filled and aborted seeds within each seed pod on each inflorescence. This could not be performed for *H. bonariensis* as the fruit were indehiscent and therefore did not open to release their seeds, although each fruit typically contains two seeds (Evans 1992). Once the seeds were counted they were then weighed to the nearest 0.0001 g using an analytical electronic balance (Mettler Toledo, Switzerland).

Once flowering and seed set had completely finished, all *G. gueinzii* plants were destructively harvested to examine biomass allocation to sexual and asexual reproduction. For *H. bonariensis*, ongoing problems with leaf scale infestation and the frequent trimming of vegetative growth that was required to try and control this infestation throughout the experiment meant that we were unable to adequately measure biomass allocation for this species. For *G. gueinzii*, biomass was separated into vegetative (leaves and roots), clonal (cormels) and sexual (flower stalks, flowers, seed pods and seeds) components, dried at 70 °C for 48 h and weighed. As we required the seeds for future experiments, we left them to air dry to avoid heat damaging them. Sexual reproductive effort (SRE) and clonal reproductive effort (CRE) were then calculated as:

$$\mathrm{SRE} = \mathrm{S}/(\mathrm{C} + \mathrm{V} + \mathrm{S})\ \mathrm{CRE} = \mathrm{C}/(\mathrm{S} + \mathrm{V} + \mathrm{C})$$

where S is the total dry mass of sexual components, C is the total dry mass of clonal components and V is the total dry mass of vegetative components.

Statistical analysis

To assess the spread distance of each population from the site of introduction, we designated the first herbarium record for each species [Stockton (32 55 00S, 151 46 00E) for *G. gueinzii* and Lady Robinson's Beach (33 58 00S, 151 09 00E) for *H. bonariensis*] as the source population and calculated the straight line distance to each population.

Due to the clonal nature of both of our study species, values for all reproductive traits were averaged for each population. To investigate differences in reproductive effort across the range of *G. gueinzii*, we used linear regressions to examine the relationships between SRE and CRE with distance from source population and total biomass (as reproductive allocation has been shown to correlate strongly with plant size e.g. Samson and Werk 1986). To assess autonomous self-fertilization ability, we examined the probability of flowers developing into fruit for each inflorescence across the range of our study species using logistic regression with a logit link function and binomial distribution. Additionally for *G. gueinzii*, we assessed the probability of forming filled seeds by comparing the number of filled and aborted seeds in each inflorescence using the same analysis. Finally, we conducted linear regressions to assess the relationships between average seed number and seed size per inflorescence with distance from source population for each species. For *H. bonariensis*, populations that produced seed on less than two inflorescences (Callala, Dunbogan, Kingscliffe and Port Macquarie) were excluded from analysis due to inabilities to obtain average values. For *G. gueinzii*, total biomass was included as an additional explanatory variable due to the influence of plant size on seed partitioning (e.g. Jakobsson and Eriksson 2000). Significance of variables in each model was tested using likelihood ratio tests. Variables were log transformed to fulfil assumptions of statistical tests where applicable. All analyses were conducted using R version 3.2.4 (R Development Core Team 2016).

Results

Reproductive effort

For both *G. gueinzii* and *H. bonariensis*, there was no significant relationship between average number of flowers per inflorescence and distance from source population (*G. gueinzii*: $F_{1,21} = 0.26$, $p = 0.61$, $R^2 = 0.012$; *H. bonariensis*: $F_{1,22} = 1.60$, $p = 0.21$, $R^2 = 0.068$). Additionally, for *G. gueinzii* there was no relationship between average number of flowers per plant and distance from source population ($F_{1,21} = 1.52$, $p = 0.22$, $R^2 = 0.067$). For *G. gueinzii*, there was no significant relationship between clonal reproductive effort ($F_{1,21} = 0.0818$, $p = 0.30$, $R^2_{adj} = -0.04$, Fig. 2a) or sexual reproductive effort ($F_{1,21} = 3.13$, $p = 0.11$, $R^2_{adj} = 0.09$, Fig. 2c) with distance from source population. There was, however, a significant positive relationship between clonal reproductive effort ($F_{1,21} = 3.97$, $p = 0.026$, $R^2_{adj} = 0.12$, Fig. 2b) and total biomass but this was not found for sexual reproductive effort ($F_{1,21} = 0.38$, $p = 0.94$, $R^2_{adj} = -0.03$, Fig. 2d).

Autonomous self-fertilization

For *G. gueinzii*, all populations produced fruit through autonomous self-fertilization (fertilization in the absence of pollinators) while for *H. bonariensis* one population (Port Macquarie) did not autonomously self-fertilize. Within populations, the degree of fruit production through autonomous self-fertilization was higher for *G. gueinzii* (60–100%) compared to *H. bonariensis* (13–100%). There was a significant increase in the probability of producing fruit through autonomous self-fertilization with increasing distance from source population for *H. bonariensis* (odds ratio = 1.0005, df = 1,24, $p < 0.0001$, Fig. 3b) but not for *G. gueinzii* (odds ratio = 1.0004, df = 1,22, $p = 0.19$, Fig. 3a). For *G. gueinzii* there was a significant increase in the probability of producing fully formed seeds with increasing distance from source population (odds ratio = 1.001, df = 1,22, $p < 0.0001$, Fig. 3c).

Seed size/seed number

Among populations, seed number varied more than seed size for both *G. gueinzii* (CV seed number = 23%, CV seed mass = 9%) and *H. bonariensis* (CV seed number = 128%, CV seed size = 24%). Seed size and number traits were regressed with distance for both *H. bonariensis* and *G. gueinzii* and also total biomass for *G. gueinzii*. At the inflorescence level, there were no significant relationships between total seed mass, individual seed mass and total seed number with distance for either species (Table 1a, Appendix S1, S2), indicating that there was no increase in biomass investment in seed production towards range edges. For *G. gueinzii*, there were no significant relationships between any of the seed traits measured at the inflorescence level and total biomass (Table 1b). For *G. gueinzii*, seed mass was also

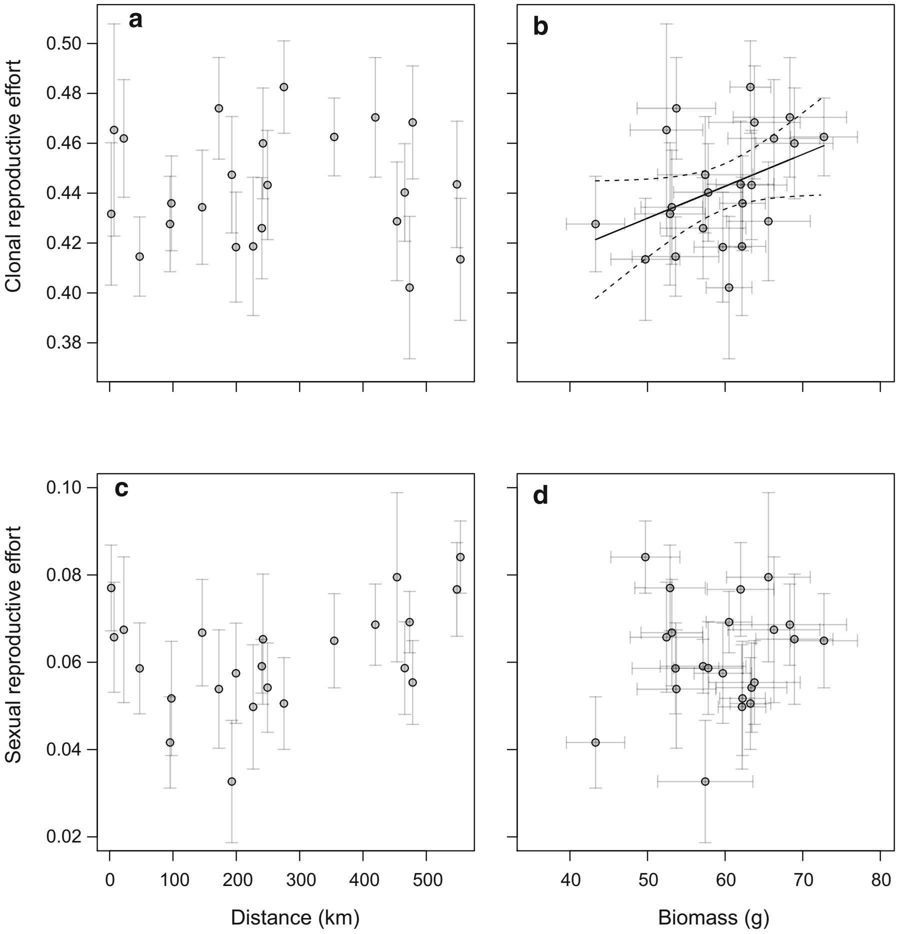

Fig. 2 Linear regressions for the relationships between **a** clonal reproductive effort and distance, **b** clonal reproductive effort and biomass, **c** sexual reproductive effort and distance and **d** sexual reproductive effort and biomass for *Gladiolus gueinzii*. Each point represents the average value for a single population. Error bars represent standard errors. Dotted lines show 95% confidence limits of significant regressions

measured at the whole plant level, with a significant positive relationship between total plant biomass and total seed mass (Table 1b), with larger plants producing a greater volume of seed.

Discussion

This study examined whether there were changes in reproductive strategies across the course of an invasion, namely whether populations at the expanding range edge allocated more resources to reproduction, produced a greater number of small seeds and/or had an increased capacity for autonomous self-fertilization compared to longer established populations. We found evidence for increased capacity to autonomously self-fertilize towards range edges, however range edge populations did not invest more resources into reproduction nor were there any changes in the seed size/seed number relationship across the invaded range. To our knowledge, this is the first study to extensively examine changes in reproductive strategies across the invaded range of species.

Previous studies have found shifts to greater self-fertilization towards range edges of native species to help buffer against the effects of low population size (e.g. Busch 2005; Herlihy and Eckert 2005; Moeller 2006; Darling et al. 2008; Griffin and Willi 2014). In contrast, relatively few studies have examined how reproductive traits vary across the range of invasive

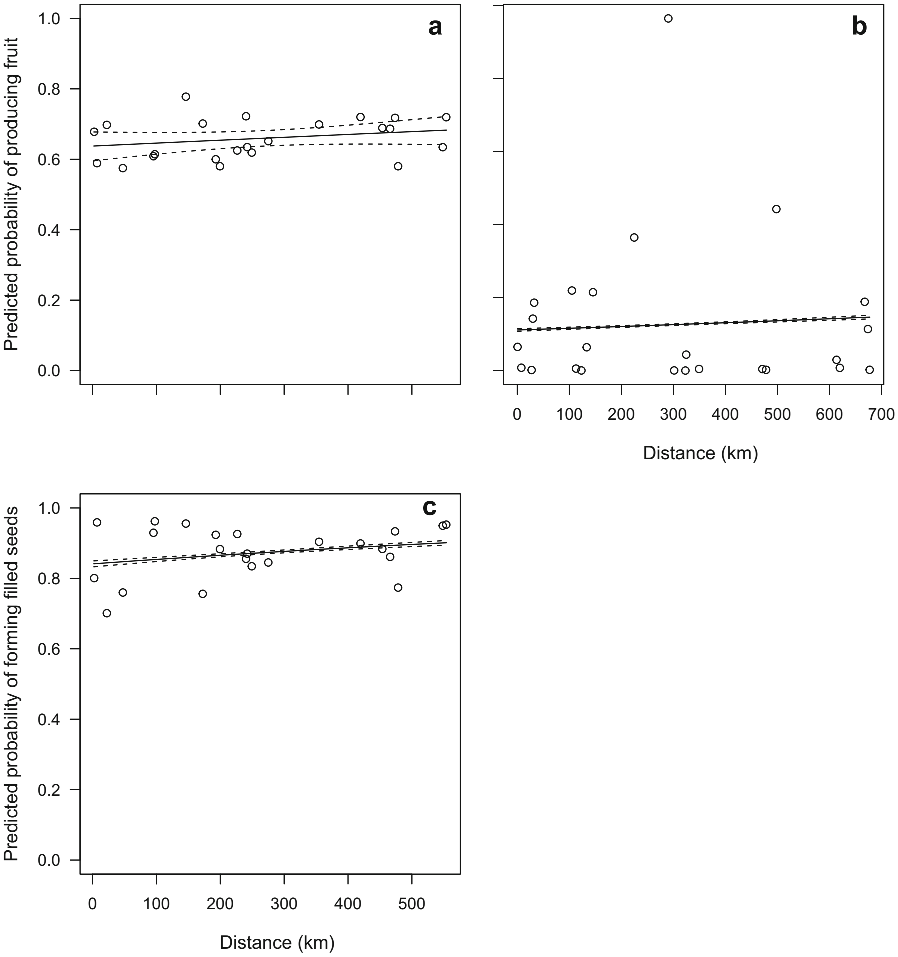

Fig. 3 Logistic regressions showing the predicted probabilities of **a** producing fruit for *Gladiolus gueinzii*, **b** producing fruit for *Hydrocotyle bonariensis* and **c** forming filled seeds for *Gladiolus gueinzii*. Dotted lines show 95% confidence limits for each fitted value. Each point represents the proportion of fruit or filled seeds formed for a single population

species despite similar metapopulation dynamics at range edges. In this study, both *H. bonariensis* and *G. gueinzii* displayed increased capacity for autonomous self-fertilization towards range edges. We found an increase in the probability of fruit production towards range edges for *H. bonariensis* and an increase in the number of developed seeds towards range edges for *G. gueinzii*, indicating that range edge populations are more reproductively assured compared to longer-established populations closer to the core of the range. Increased capacity for autonomous self-fertilization alleviates reliance on pollinators and/or mates for reproduction as low density populations at the range edge may be mate limited and less apparent to pollinators (Moeller 2006; Moeller et al. 2012). This may allow range edge populations to overcome many of the barriers to reproduction associated with small population size, hence facilitating further range expansion. However, in a similar study Colautti et al. (2010) found no significant increase in self-compatibility towards range edges of purple loosestrife spreading across North America. They speculated that the unclear history of introduction of purple loosestrife to North America may have affected their ability to find a latitudinal trend in reproductive traits. Although we cannot be certain that our study species were not introduced multiple times, our results suggest that these relationships can be observed over large geographical scales. Interestingly, these shifts in autonomous self-fertilization were found in as little as 70 years of range expansion (the first record of *G. gueinzii* was in 1950), highlighting the capacity for

Table 1 Linear regressions for the effect of (a) spread distance on total seed mass, individual seed mass and total seed number at the inflorescence level for *H. bonariensis* and *G. gueinzii* (b) total biomass and spread distance on total seed mass, individual seed mass and total seed number at the inflorescence and whole plant level for *G. gueinzii*

	Total seed mass			Individual seed mass			Total seed number		
	df	F	p	df	F	p	df	F	p
(a)									
H. bonariensis									
Distance	1.18	0.0073	0.93	1.18	0.0024	0.96	1.18	0.0007	0.98
G. gueinzii									
Distance	1.21	1.76	0.30	1.21	1.05	0.25	1.21	3.45	0.090
(b)									
Inflorescence level									
Total biomass	1.21	1.47	0.37	1.21	0.11	0.53	1.21	1.10	0.11
Whole plant level									
Distance	1.21	3.84	0.24	–	–	–	–	–	–
Total biomass	1.21	21.1	**< 0.0001**	–	–	–	–	–	–

Significant p values ($p < 0.05$) are highlighted in bold

invasive species to rapidly adapt to new environments within short timescales.

As conspecific density is relatively low in an expanding range front, increased reproductive effort is expected to be selected for in edge populations (Burton et al. 2010). However, for plants this relationship is made more complicated with the trade-off between clonal and sexual reproduction. Many species have been found to reduce investment in sexual reproduction in favour of clonal reproduction towards range edges (Eckert 2002). However, for *G. gueinzii*, we found no increase in reproductive effort (either sexual or clonal) towards range edges. Studies examining allocation to reproduction towards range edges are equivocal, with studies finding increased (e.g. Jump and Woodward 2003; Yakimowski and Eckert 2007; Masson et al. 2016) and decreased (e.g. Brandner et al. 2013; Courant et al. 2017) allocation to reproduction towards range edges. This may in part be due to selection for concurrent traits in range edge populations that may directly trade-off with reproduction (Courant et al. 2017). For example, highly dispersive range edge populations of speckled wood butterflies had reduced allocation to reproduction compared to conspecifics at the range core (Hughes et al. 2003). Hudson et al. 2015 also found a decrease in the probability of female cane toads laying eggs from highly dispersive range edge populations compared to at the range core. However, as plants are sessile, reproduction and dispersal are not mutually exclusive, thus any trade-off with reproduction at the range edge may exist with another unmeasured trait.

We found no relationship between seed number and seed size with distance from source population, with neither species producing a greater number of small seeds towards range edges. A greater number of smaller seeds at the range edge would greatly increase colonization opportunities and facilitate further range expansion. A previous study on *G. gueinzii* found a significant decrease in seed size towards range edges from field collected seeds (Tabassum and Leishman 2018). This reduction in seed size was not associated with a reduction in the probability of germination; in fact smaller seeds germinated faster than larger seeds (Tabassum and Leishman 2018). As *G. gueinzii* is a pioneer species (Heyligers 1999), production of many small seeds may be a viable strategy to increase spread rate. However, range edge populations did not produce smaller seeds in this study when grown in controlled glasshouse conditions, suggesting that smaller seed sizes towards range edges may not have been due to a seed size/number trade-off but rather a reflection of the quality of the maternal environment (Wulff 1986). Furthermore, although strong negative relationships between seed number and seed size have been found between species (e.g. Jakobsson and Eriksson 2000;

Henery and Westoby 2001; Leishman 2001), many studies examining this relationship within species have found no relationship (e.g. Shaal 1980; Wulff 1986; Michaels et al. 1988). This is because seed size is a highly conserved trait within species compared to between species (Westoby et al. 1996; Weiner et al. 1997). Instead, individual plants are more likely to express reproductive differences through variation in seed number rather than individual seed size (Weiner et al. 1997; Leishman et al. 2000). In support of this we did observe greater variation in seed number compared to seed size between population for both *G. gueinzii* and *H. bonariensis* however this was not significantly related to spread distance.

An important caveat of glasshouse studies is that they may not be directly related to advantages in the field. Although we found an increase in the propensity for autonomous self-fertilization towards range edges in our experiment, it is not entirely clear whether this leads to fitness benefits in range edge populations of our study species in the field. Investigating the advantageous of autonomous self-fertilization in natural populations of our study species would therefore be a useful next step. Furthermore, this study only examined the propensity for populations to produce seeds using 'self' pollen and did not investigate how 'self' versus 'non-self' pollen affected fruit/seed set across the range of our study species. Low density range edge populations have been observed to shift towards a greater propensity for self-pollination to increase reproductive assurance (Moeller and Geber 2005; Griffin and Willi 2014). Therefore another interesting future direction would be to compare fruit/seed set of selfed and outcrossed individuals to investigate whether range edge populations have shifted away from an outcrossing system.

Overall, this study revealed some differences between reproductive traits between range edge and range core populations of *G. gueinzii* and *H. bonariensis*. In general, although range edge populations did not invest more resources into reproduction or alter seed number or partitioning, edge populations were more reproductively assured due to greater capacity for autonomous self-fertilization. This is an important finding as increased capacity for autonomous self-fertilization in range edge populations allows establishment of new populations quickly after dispersal without reliance on external factors such as mate and/or pollinator availability, hence facilitating further range expansion. Understanding how selection varies in range edge populations has important implications for not only expansion of invasive species but also range contractions of endangered species and range shifts due to climate change (Hargreaves and Eckert 2014). Because of this, studies such as our own will become increasingly valuable for understanding species' range shifts in the face of future global change.

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