Population ecology of the endangered aquatic carnivorous macrophyte *Aldrovanda vesiculosa* at a naturalised site in North America

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SUMMARY

1. *Aldrovanda vesiculosa* is an aquatic carnivorous plant native to nutrient impoverished wetland systems in Australia, Africa, Asia, and continental Europe that has declined dramatically throughout its native range in the last century. A strong reliance upon carnivory generally limits its occurrence to specific, nutrient-poor, island-like microhabitats. Remaining native populations are generally small and fragmented, and empirical population ecology data for the species arelacking. Developing an understanding of the constraints to growth, establishment and reproduction in *A. vesiculosa* is crucial to conservation of the species.

2. In contrast with the decline of the species throughout its native range, a number of large *A. vesiculosa* populations have become naturalised in North America. This study examines the population ecology of *A. vesiculosa* at one of these naturalised sites and assesses the species' potential invasiveness in terms of its ecological characteristics. Transect and quadrat surveys were used to determine the response of morphology, fecundity and spatial distribution to putative biotic and environmental variables, with glasshouse trials and a bird feeding experiment employed to test the persistence of seeds in the seed bank and after transport in bird guts.

3. Although *A. vesiculosa* is capable of becoming locally abundant (up to 1260 individuals m^{-2}) in wetland areas where biotic and abiotic conditions are optimal, it appears to compete poorly with floating and emergent macrophytes and is limited predominantly to specific microhabitats. The ecological characteristics of *A. vesiculosa* suggest that it poses a low invasion risk. The species' growth and reproductive potential are highest in shallow areas harbouring loose vegetation assemblages, with over two thirds of all individuals recorded from water 10–50 cm in depth and in areas with <50% native macrophyte cover. Seeds are unlikely to play a significant role in seasonal persistence or dispersal, with poor floral success (*c.* 10%), few seeds produced, low seed viability(<50%) throughout the study area and no seeds recovered from the sediment seed bank or recovered from bird faeces following gut transport.

4. The stenotopic ecology of *A. vesiculosa*, and the continuing decline of dystrophic freshwater wetlands globally, indicate that remaining natural populations are highly sensitive and are likely to decline rapidly without adequate management. In addition to wetland management at the catchment scale to mitigate processes such as eutrophication, future conservation and reintroduction initiatives for *A. vesiculosa* must focus particularly on the identification, maintenance and restoration of optimal

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shallow humic microsites harbouring loose, open assemblages of emergent and floating macrophytes.

Introduction

The invasion and naturalisation of exotic species is regarded as a major threat to natural ecosystems. The arrival of non-native species, whether through natural dispersal or anthropogenic introduction, often results in a shift towards new community assemblages and species combinations through altered levels of synergism and trophic interaction (Seastadt, Hobbs & Suding, 2008), and may significantly impact both biodiversity and ecosystem function (Díaz et al., 2004). Among weedy plant taxa, aquatic macrophytes appear to represent some of the most pervasive and noxious invaders of natural ecosystems (Murphy, 1988; Finlayson et al., 1999; Rejmánek, 2000; Pyšek & Richardson, 2007). The effect of these species on ecological function in wetland habitats, as well as the economic costs associated with their control, management and eradication have been well-studied (Murphy, 1988; Rejmánek, 2000; Anderson, 2003; Lovell & Stone, 2005). The majority of invasive aquatic plants share a number of common ecological traits, including a propensity for clonal reproduction, high growth rate, tolerance of a wide range of environmental and climatic conditions, as well as a high vagility and strong propagule pressure, often combined with significant dispersive capability (Barrett, Eckert & Husband, 1993; Philbrick & Les, 1996; Santamaría, 2002; Ricciardi & Kipp, 2008; Wittmann et al., 2014). One of the major threats to aquatic ecosystems globally is anthropogenic eutrophication, particularly nitrogen and phosphorus enrichment from agricultural and urban runoff, and a strong correlation is often apparent between increased nutrient loading and the abundance of aquatic weeds in wetland ecosystems (Carr, Duthie & Taylor,1997; Santamaría, 2002; Lacoul & Freedman, 2006; Jennings & Rohr, 2011; Junk et al., 2013).

With a trend towards eutrophication in wetland habitats and the environmental impact of aquatic weeds becoming increasingly evident (Finlayson et al., 1999; Amezaga, Santamaria & Green, 2002), predicting invasiveness has become one of the major challenges in weed ecology (Rejmánek, 2000; Richardson & Pyšek, 2006). Biodiversity concerns have prompted the development of mechanistic techniques to assess the invasiveness of aquatic plants. Among the most widely utilised methods are predictive trait-based approaches to determining the invasion risk of particular species (Pheloung, Williams & Halloy, 1999; Champion & Clayton, 2000; Clayton & Champion, 2006; Pyšek & Richardson, 2007; Keller & Drake, 2009; Gordon et al., 2012). In addition to providing a crucial tool for the identification, prioritisation and management of invasive exotic macrophytes, these studies suggest that a number of introduced species may pose a comparatively low level of threat to natural ecosystems (Ricciardi & Kipp, 2008; Gordon et al., 2012). These introduced but non-invasive aquatic plants possess traits suggesting they are unlikely to significantly alter community composition (e.g. poor fecundity, low dispersive capacity, slow growth rates), or to reduce ecosystem function through competitive processes (Lovell & Stone, 2005). In some instances, it is possible that their presence may result in habitation of a previously unoccupied ecological niche, rather than influence ecosystem trajectory towards the development of a hybrid association.

Aldrovanda vesiculosa L. (Droseraceae) is a notable example of an aquatic species given an *a priori* classification of 'non-invasive' based on an analysis of plant functional traits and ecology (Gordon et al., 2012). A submerged, free-floating carnivorous macrophyte native to the Old World, *A. vesiculosa* occurs in nutrient impoverished, oligo-mesotrophic and dystrophic (humic) wetland systems in Australia, Africa, Asia and continental Europe (Adamec, 1995; Cross, 2012a). The species possesses a wide thermal tolerance and an expansive bioclimatic envelope, and was historically distributed across a significant latitudinal range spanning a number of different climatic zones. However, it possesses a narrow ecological niche in comparison to other species of similar aquatic affinity and distribution and appears sensitive to eutrophication (Kamiński, 1987a; Adamec, 1995; Cross, 2012a). A stenotopic ecology, combined with a strong reliance upon carnivory, generally limits the species' occurrence within suitable wetlands to specific, nutrient-poor, island-like microhabitats (Adamec, 1995, 1999, 2005). Despite exhibiting a degree of tolerance to thermal variation, irradiance and pH (Kamiński, 1987a,b; Adamec, 1999), changes in the physico-chemical or biotic conditions within an inhabited wetland can lead to rapid local decline (Kamiński, 1987a; Adamec & Lev, 1999;

Adamec, 2005; Cross, 2012a). The majority of terrestrial carnivorous plants display specific adaptations to nutrient-poor conditions (Givnish *et al.*, 1984), and the eutrophication and drying of dystrophic wetland habitats has been implicated as the most significant threat to the viability of many aquatic carnivorous plants (Jennings & Rohr, 2011). Wetland degradation, primarily through eutrophication, has resulted in a global collapse of *A. vesiculosa* populations within the last century (Adamec, 1995; Cross, 2012a), with the species becoming extinct in at least 11 of the 43 countries in which it is known to have occurred naturally (a total decline in abundance of around 87%), and unverified status in a further 21 countries, prompting listing as Endangered B2ab (iii, v) by the International Union for the Conservation of Nature (Cross, 2012b).

Despite the species' increasingly bleak outlook throughout its natural range, populations introduced to several locations in the north-eastern United States during the 1990s appear to have flourished locally (Cross, 2012; Lamont *et al.*, 2013). This presents a novel situation: the successful naturalisation and local proliferation of an aquatic carnivorous plant on a continent in which it has never naturally occurred, completely at odds with the species' natural Old World populations which display an apparent and increasing trajectory toward extinction. Previous research has suggested that *A. vesiculosa* is stenotopic, competes poorly with other aquatic plants, and possesses a narrow ecological niche throughout its natural range (Kamiński, 1987a,b; Adamec, 1995, 1999; Adamec & Lev, 1999; Adamec & Kovářová, 2006). However, these studies have generally focused on quantifying abiotic site suitability and microhabitat specificity for *A. vesiculosa* through analysis of the species' growth rate and morphometrics in response to environmental variation. Empirical data on the population ecology and microhabitat affinity of *A. vesiculosa* at both local and regional scales is lacking, and the collection of such data is becoming increasingly difficult as the number of large natural populations continues to dwindle. We examined the population ecology of *A. vesiculosa* at a large naturalised site in Virginia, United States, through analysis of its spatial distribution and morphological characteristics in response to putative biotic and environmental drivers. Results are presented in the context of the species' unprecedented global decline, as a comprehensive understanding of population biology and habitat specificity in the species is critical for the successful implementation of future conservation and restoration initiatives. Additionally, data are applied to the weed risk assessment classifications of Gordon *et al.* (2012) to further elucidate the species' potential invasiveness in areas outside its native range.

Methods

Site description and population ecology

Meadow Creek is situated in Caroline County, northeast Virginia, on the east coast of the United States (38°08′N, 77°24′W), and consists of a series of highly humic beaver-maintained ponds connected by a braided creek system. Six *A. vesiculosa* individuals of Japanese origin were introduced to this site in the late 1990s, and a large population has since become naturalised (Cross, 2012a). Field surveys were conducted using a canoe in July 2013 to assess the distribution, abundance, vegetation associations and habitat preferences of *A. vesiculosa* in the Meadow Creek catchment. Transects were established across the main channel and in surrounding channels, at intervals of 60–100 m. The number of *A. vesiculosa* individuals, percent cover of *A. vesiculosa*, water depth and the percent cover of native aquatic macrophytes were assessed at seven locations using 0.5×0.5 m quadrats at 0.5 m intervals along shore-shore (north-south) transects. Water depth was measured in the southwest corner of each quadrat. Additionally, in two areas where access by canoe was not possible, 25 quadrats were randomly placed in areas of *A. vesiculosa* occurrence to sample as previously described. A total of 723 quadrats was obtained from nine locations.

Population fecundity

Population fecundity was assessed through counts of the total number of flowering individuals and the number of fertile fruit and secondary vegetative branches per individual within all sampled quadrats. All fertile fruit (capsules) were opened to determine the presence and number of seeds produced. To determine whether *A. vesiculosa* was represented in the sediment seed bank, 50 samples of the top 2 cm of sediment (5×5 cm) were collected from Meadowview Pond in areas where the species was most abundant. Sediment was washed and sieved (250 μm; *sensu* Ter Heerdt *et al.*, 1996), and examined carefully under a dissecting microscope to assay for seeds. The seed testa of *A. vesiculosa* possesses distinctive morphological and sculptural characteristics, and on this basis seeds can be easily distinguished from the seeds of other macrophytes (Cross, 2012a).

To examine the capacity of *A. vesiculosa* seeds to persist in the seed bank, five replicates of 20 freshly

collected seeds (collected from cultivated plants) were placed into fine nylon mesh bags (250 µm gauge), and buried in the sediment of *ex situ A. vesiculosa* cultivation tanks in Perth, Western Australia, for weekly retrieval over 12 weeks (*n* = 1200 seeds). Only filled seeds possessing an undamaged endosperm and embryo were used in the experiment, with seed fill determined non-destructively by high-resolution X-ray imaging (MX-20 Digital X-ray, Faxitron, Tucson, Arizona, USA). Bags were buried at 1 cm depth at the onset of winter (early June), with each attached to a thin plastic stake to facilitate retrieval. Seed fill in retrieved bags was determined using X-ray imaging, and all filled seeds remaining at the conclusion of the experiment were cut tested to confirm viability (Turner *et al.*, 2006). Seeds possessing a firm, white endosperm were deemed to be viable.

To provide a preliminary assessment of endozoochorous dispersive potential in *A. vesiculosa*, a bird feeding trial was employed to assess the internal gut transport of seeds. Two pellets each containing 50 *A. vesiculosa* seeds were force-fed to a captive male Chestnut Teal (*Anas castanea*; body weight 800 g), using a 15 cm crop syringe. Five indigestible plastic beads (2 mm diameter) in each pellet acted as markers for seed recovery. The bird had been maintained on a high-fibre manufactured grain-based diet (Layer Crumble, Milne Feeds, Australia), and pellets were prepared to a similar diameter to ensure they fell within an appropriate food range. The bird had last been fed *c.* 20 h previous to force-feeding. After force-feeding, the bird was kept in a small covered outdoor enclosure with ample food and water. Time to resume feeding was recorded as an approximate indicator of stress. All faeces were collected over the 24 h following force-feeding, with the time of defecation recorded and each faeces examined for the presence of *A. vesiculosa* seeds and plastic marker beads. All recovered material was examined under high magnification to assess its integrity (JCM-5000 Neoscope Scanning Electron Microscope, Jeol, Netherlands).

Morphological characteristics

To assess microsite vigour and the degree to which growth and development in *A. vesiculosa* is influenced by local biotic and abiotic conditions, an assessment of the morphological characteristics of 100 individuals from each of four distinct microhabitats was undertaken. Selected microhabitats are representative of the area's most frequently inhabited by *A. vesiculosa* throughout the study area, and include: (A) the shallow waters of a braided creek, heavily shaded by dense stands of

Peltandra virginica (Location 8); (B) deeper water at the fringe of a large, open lake, with *Utricularia inflata* among *Carex festucacea* and *Peltandra virginica* (Location 9); (C) a shallow swampy area adjacent to the main creek channel, among *Carex alata, Carex lurida, Nuphar advena, Sagittaria latifolia,* and *Typha latifolia* (Transect 4); and (D) shallow, predominantly open water with *Utricularia purpurea* and *Utricularia inflata* among scattered *Peltandra virginica, Nuphar advena,* and *Nymphaea odorata* ssp. *odorata* (Transect 1). Four representative quadrats were selected from transect surveys for each microhabitat, with 25 individuals randomly selected from each quadrat. Digital callipers were used to measure the length, width, trap size and the internode length of each individual (to the nearest 0.1 mm). The total number of living mature whorls, number of leaves per whorl and total number of traps for each individual were also recorded, as well as the percentage of traps containing captured invertebrate prey.

Water chemistry

An analysis of water chemistry was undertaken to facilitate a basic comparison of the abiotic conditions between *A. vesiculosa* microhabitats. The concentrations of NH_4-N, NO_3-N, total phosphorus, total dissolved organic carbon and dissolved oxygen as well as values of pH were determined for 400 mL samples from each of the four selected microhabitats (Mid-Atlantic Laboratories Inc., Virginia, USA). These factors are recognised as being among the most significant in determining habitat suitability for *A. vesiculosa* (Kamiński, 1987a,b; Adamec, 1995, 1999, 2005; Cross, 2012a).

Weed risk assessment

Gordon *et al.* (2012) included *A. vesiculosa* in a weed risk assessment of 130 aquatic plant taxa in the United States (USAqWRA), in which the risk of invasion for each taxa is determined by the total score from 38 questions. However, several of these questions relate to aspects of biology and population ecology that we empirically address for the first time in *A. vesiculosa*, and thus our results are applied to confirm or revise the USAqWRA predicted invasiveness risk level for the species. The USAqWRA questions, score guidance, and score for *A. vesiculosa* are presented in Appendix S1.

Data analysis

Generalised linear models (SPSS Statistics 21, IBM) were fitted to determine the main effects of water depth and

percent cover of native macrophytes on the abundance and morphological characteristics of *A. vesiculosa* (number of total and flowering individuals, percent cover, plant length and width, mean internode length, trap midrib length and the number of apical branches, whorls and traps per individual; cf. Kamiński, 1987a,b; Adamec, 1999; Adamec & Kovářová, 2006). One-way ANOVA with Tukey post hoc tests was used to assess the variation in morphological characteristics within and between each of the seven surveyed areas. Binomial regression models were fitted to *A. vesiculosa* presence/absence data within R (R Development Core Team, 2011) to assess the main effect of water depth and percentage cover of native macrophytes on the species' occurrence, with a squared term to determine whether the species exhibited an optimum response or a monotonic trend. Preliminary analyses of all data were

conducted to test the assumptions of normality (Kolmogorov-Smirnov test), linearity, and homoscedasticity (Levene's test). Where necessary, data were log_{10} transformed to help meet the assumption of normality and equal variance. All statistical tests were conducted using 95% CI, with significance determined by $P < 0.05$. Data are presented as mean $\pm$ 1 standard error of the raw data unless stated otherwise.

Results

Population ecology

Aldrovanda vesiculosa was present in all transects (Fig. 1), with 24,895 individuals recorded from 639 quadrats at an average density of *c*. 150 individuals m^{-2}. The species occurred at higher abundance in shallower waters
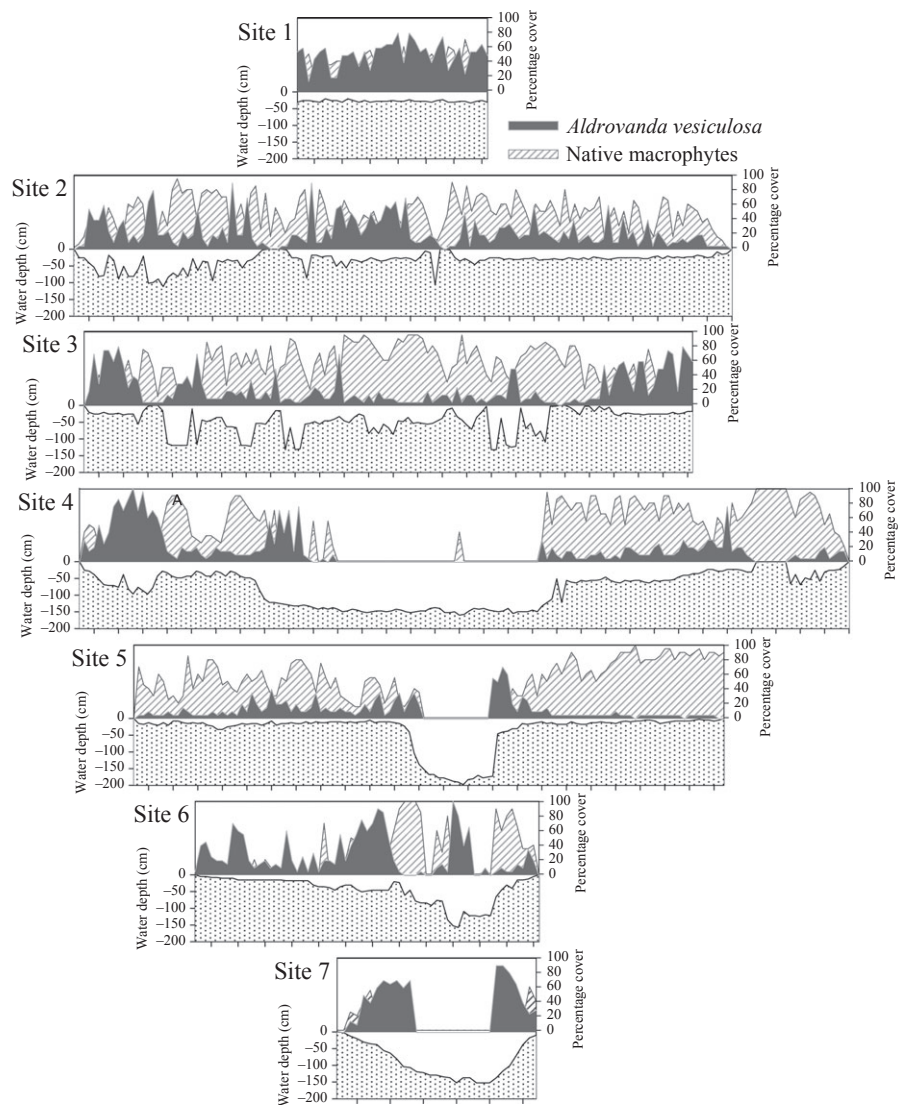

Fig. 1 Transects across Meadow Creek, Virginia, United States, indicating the percentage cover of *Aldrovanda vesiculosa* and native macrophytes in relation to water depth. Graph alignment corresponds with relative transect position. Ticks along the *X* axes indicate 5 metre increments along each transect.

Table 1 Wetland plant taxa recorded from transects (locations 1–7) and randomised quadrats (locations 8 and 9) in the Meadow Creek catchment, Virginia, United States

Family	Species	1	2	3	4	5	6	7	8	9
Alismataceae	*Sagittaria latifolia* Willd.					x				
Araceae	*Peltandra virginica* (L.) Schott	x	x	x		x			x	x
Commelinaceae	*Commelina virginica* L.				x					
Cyperaceae	*Carex alata* Torrey		x		x			x		
	Carex festucacea Schk. ex Willd.		x		x			x		x
	Carex lurida Wahlenb.		x	x	x	x		x		
	Dulichium arundinaceum (L.) Britton				x					
Droseraceae	*Aldrovanda vesiculosa* L.	x	x	x	x	x	x	x	x	x
Eriocaulaceae	*Eriocaulon decangulare* L.				x					
Iridaceae	*Iris virginica* L.				x			x		x
Juncaceae	*Juncus tenuis* Willd.	x	x	x	x			x		
Lemnaceae	*Lemna minor* L.					x				
Lentibulariaceae	*Utricularia purpurea* Walt.	x								
	Utricularia inflata Walt.		x	x			x			x
	Utricularia geminiscapa Benj.					x		x		
	Utricularia macrorhiza Le Conte			x	x			x		
Nymphaceae	*Nuphar advena* (Ait.) Ait.f.	x	x	x	x	x	x			x
	Nymphaea odorata Aiton ssp. *odorata*	x	x	x	x			x		x
Saururaceae	*Saururus cernuus* L.				x					
Typhaceae	*Sparganium americanum* Nutt.				x					
	Typha latifolia L.				x					

harbouring loose, open vegetation assemblages (up to 1260 individuals per m^{-2}), and generally grew among floating or emergent wetland plants including *Carex lurida*, *Peltandra virginica*, *Nuphar advena*, *Nymphaea odorata* ssp. *odorata* and *Sagittaria latifolia* (Table 1). *Aldrovanda vesiculosa* co-occurred with native submerged aquatic carnivorous plants (*Utricularia geminiscapa*, *U. inflata*, *U. purpurea*, and *U. macrorhiza*) in 36 quadrats, predominantly in shallow areas with limited cover (<25%) of emergent or floating macrophytes.

The main effect of increasing water depth was significant on both the number of individuals and the percentage cover of *A. vesiculosa* ($P < 0.001$ in both cases). A strong optimum relationship was evident between the presence of *A. vesiculosa* and water depth ($P < 0.001$), with over two thirds of all individuals (16,787) recorded from water 10–50 cm in depth ($n = 371$ quadrats). The majority of remaining plants (4,635) were recorded from depths of between 50 and 100 cm ($n = 98$), with only around 10% occurring in all remaining quadrats between 0–10 cm or >100 cm ($n = 96$). In contrast, a negative monotonic relationship was evident between increasing water depth and the percentage cover of native macrophytes ($P = 0.001$).

The abundance and cover of *A. vesiculosa* were markedly reduced in areas of dense emergent or floating vegetation (Fig. 1), and a significant negative relationship was present between the cover of native macrophytes and both the number of individuals and percentage cover of *A. vesiculosa* ($P < 0.001$ in both cases). The majority of *A. vesiculosa* individuals (c. 75%) were recorded from quadrats harbouring <50% native macrophyte cover ($n = 402$), and fewer than 3% were recorded in quadrats possessing >80% native macrophyte cover. No interaction effect was evident between water depth and the cover of native macrophytes on *A. vesiculosa* abundance ($P = 0.237$). Notably, *A. vesiculosa* was also absent from the majority (c. 80%) of quadrats in which no native macrophytes were recorded ($n = 108$).

Population fecundity

A marked decline was observed in both the number of flowering *A. vesiculosa* individuals and the number of apical branches per individual in response to increasing percentage cover of native macrophytes ($P = 0.003$ and< 0.001, respectively). The main effect of water depth was not significant for either of these factors ($P = 0.882$ and 0.691, respectively). Flower and apical branch production was approximately 50 and 15 times higher, respectively, in individuals from the shallow, open waters of

Table 2 Morphological characteristics and population ecology of *Aldrovanda vesiculosa* from four different microsites in the Meadow Creek catchment, Virginia, United States. A: In the shallow water of a braided creek, heavily shaded by dense stands of *Peltandra virginica*(Location 8); B: In deeper water at the fringe of a large, open lake, growing with *Utricularia inflata* among *Carex festucacea* and *Peltandra virginica* (Location 9); C: In a shallow swampy area adjacent to the main creek channel, among *Carex alata, Carex lurida, Nuphar advena, Sagittaria latifolia* and *Typha latifolia* (Transect 4); D: In shallow, predominantly open water with *Utricularia purpurea* and *Utricularia inflata* among scattered *Peltandra virginica, Nuphar advena*, and *Nymphaea odorata* ssp. *odorata* (Transect 1). Data are presented as mean ± one standard error where possible, with four quadrats and 100 individuals assessed for each location. Annotated lettering indicates statistical significance between locations for each parameter ($P < 0.05$)

	Microhabitat			
	A	B	C	D
Microhabitat characteristics				
Native macrophyte cover (%)	90.7 ± 1.2a	69.5 ± 6.3b	43.2 ± 4.1c	5.3 ± 9.2d
Aldrovanda vesiculosa cover (%)	23.7 ± 4.1a	5.0 ± 2.2b	56.5 ± 11.6c	83.1 ± 9.0d
Depth (cm)	23.6 ± 3.1	47.3 ± 0.7	34.1 ± 5.0	26.5 ± 0.5
Water chemistry				
NH_4-N (mg L^{-1})	0.12	0.08	0.10	0.08
NO_3-N (mg L^{-1})	0.32	0.23	0.25	0.24
Total phosphorus (mg L^{-1})	0.26	0.16	0.49	0.18
Dissolved oxygen (mg L^{-1})	8.59	9.52	8.25	9.14
Total organic carbon (mg L^{-1})	10	7.6	7.8	7.2
pH	5.81	6.27	5.72	5.70
Aldrovanda vesiculosa individuals				
Length (mm)	64.3 ± 3.8a	101.1 ± 7.3b	122.7 ± 5.6c	147.1 ± 4.0d
Width (mm)	11.9 ± 0.4a	12.4 ± 0.3a	16.2 ± 0.2b	18.6 ± 0.2c
Number of apical branches	0.2 ± 0.1a	1.3 ± 0.2b	2.2 ± 0.5c	3.0 ± 0.4c
Percentage of individuals in flower	0.1 ± 0.1a	0.1 ± 0.1a	2.2 ± 0.2b	4.9 ± 0.5c
Leaves per whorl	6.8 ± 0.1a	7.0 ± 0.1a	7.3 ± 0.1b	7.5 ± 0.1b
Number of whorls	16.1 ± 0.7a	20.9 ± 0.6b	22.3 ± 0.6c	28.5 ± 0.3d
Internode length (mm)	4.0 ± 0.1a	5.0 ± 0.1b	5.4 ± 0.1c	5.2 ± 0.1c
Trap size (mm)	1.9 ± 0.1a	2.0 ± 0.1a	4.6 ± 0.1b	5.6 ± 0.1c
Total number of traps	102.8 ± 7.3a	121.4 ± 5.0b	163.8 ± 5.1c	212.1 ± 3.0d
Whorls with prey per individual (%)	15.7 ± 2.4a	20.2 ± 4.7b	25.1 ± 4.3c	36.5 ± 8.7d

Location 1 than in the heavily vegetated Location 8 (Table 2). Flowering success throughout the study site appeared poor, with only 98 fertile fruit recorded (*c.* 10% of flowers recorded). However, the majority of fertile fruit were collected from Transect 1 (42), Transect 2 (18), and Transect 4 (14). Seed set was low, ranging from one to nine seeds per fruit (mean 5.7 ± 0.9), and did not vary significantly between transects ($P = 0.633$). Seed fill was also relatively low (45.2 ± 6.4%).

No *A. vesiculosa* seeds were recovered from sediment samples. Sediment seed bank assays yielded 143 seeds of at least 10 species, predominantly *Carex lurida* (72 seeds), *C. aquatilis* (66), *Nymphaea odorata* ssp. *odorata* (42), *C. festucacea* (22) and *C. alata* (20). Seeds of additional species retrieved included *Nuphar advena* (8), *Peltandra virginica* (6), *Commelina virginica* (4), *Iris virginica* (2) and *Eriocaulon decangulare*(1). Thirty-six retrieved seeds could not be identified.

The viability of *A. vesiculosa* seeds in experimental sediment persistence trials (as indicated by seed fill) declined rapidly from 100% to 65 ± 5% and 38 ± 4%

after 3 and 6 months of burial in *ex situ* cultivation tanks, respectively. All seeds remaining at the end of the experiment were determined to be viable. The majority of non-viable seeds appeared rotten or had suffered fungal attack, and exhibited a black, spongy endosperm containing fungal hyphae.

No intact seeds were recovered from bird faeces during experimental feeding trials, and no seeds were recovered from food or water bowls to indicate regurgitation within the 24 h period. Several large *A. vesiculosa* seed coat fragments (0.2–0.3 mm) were recovered at 90 min, followed by numerous minute fragments (<0.1 mm) recovered between 3–8 h. A single intact Cyperaceae seed was recovered after 30 min, possibly originating from the *Scirpus*sp. surrounding the enclosure. All plastic markers were recovered intact after 8 h.

Morphological characteristics

All measured morphological characteristics varied significantly between transects ($P < 0.05$), with Transect 1

harbouring the largest and most vigorous individuals (Table 2). In addition to exhibiting markedly increased average length and width, plants at Transect 1 possessed the highest average number of whorls, leaves per whorl, trap size and number of traps per individual. A significant negative monotonic relationship was evident between the length, width, number of whorls, trap size and total number of traps per individual in response to increasing cover of native macrophytes ($P < 0.01$ in all cases). No relationship was evident between measured morphological characteristics and water depth.

Water chemistry

Water chemistry analysis indicated that all four sampled microsites were probably dystrophic (*sensu* Smith, Tilman & Nekola, 1999), and display nutrient concentrations indicating that they are likely to be meso-eutrophic (Table 2). Waters were acidic, rich in organic carbon and contained moderate-low concentrations of NH_4-N, NO_3-N and total P.

Weed risk assessment

A revision of the predicted invasiveness risk level for *A. vesiculosa* against the USAqWRA criteria resulted in a score of 29 (Appendix S1). This suggests the species possesses a low invasiveness risk level (determined by a threshold score of 31), and supports the existing *a priori* classification of *A. vesiculosa* as a 'non-invader'.

Discussion

Here, we present the first large-scale analysis of population ecology for the globally endangered *Aldrovanda vesiculosa* and provide the first evidence of a link between fecundity and microhabitat in this species. Results indicate that the growth and fecundity of *A. vesiculosa* are highly responsive to both biotic and abiotic habitat factors and that the species possesses a limited capacity to compete with native North American aquatic plants. The most significant factors influencing growth and fecundity included water depth and competition from emergent and floating macrophytes, with water chemistry and the abundance of invertebrate prey also likely to play a significant role in determining microhabitat suitability. A strong increase in plant performance was evident along a habitat suitability gradient, with the highest average values for all measured morphological and reproductive characters recorded from shallow areas where competition from native macrophytes was limited. Most significantly, although sexual reproduction was limited across the entire study site, the number of flowering individuals in these locations was up to 50 times higher than in deeper or heavily vegetated microhabitats. A high rate of apical branching is indicative of the suitability of growing conditions for *A. vesiculosa* (Kamiński, 1987a; Adamec, 1999), and the highest rates of apical branching were observed in areas where competition was limited. Previous studies have suggested that optimal irradiance for *A. vesiculosa* growth is around 30−50% of incident sunlight, with the species' growth significantly reduced in more heavily shaded conditions (Adamec, 1997, 1999; Adamec & Kovářová, 2006). As the production of flowers and apical branches was not responsive to water depth, it would appear that competition is one of the most significant constraints on reproductive success in *A. vesiculosa*.

Although *A. vesiculosa* was present throughout the study site in areas of different water depth and in various vegetation assemblages, results from this study support the previously reported propensity of *A. vesiculosa* to favour shallow dystrophic waters harbouring loose, open assemblages of emergent and floating macrophytes (*sensu* Kamiński, 1987a; Adamec, 1999; Adamec & Lev, 1999). All measured morphological characters were greatest in the shallow and predominantly open waters of Transect 1, where *A. vesiculosa* grew with native submerged aquatic carnivorous plants (*Utricularia purpurea* and *U. inflata*) among scattered *Peltandra virginica*, *Nuphar advena*, and *Nymphaea odorata* ssp. *odorata*. *Aldrovanda vesiculosa* was rarely present at high percentage cover (>70%) in areas of deep water or high native macrophyte cover, with the exception of several slowly flowing deeper areas (50−80 cm) where the species grew in open water among the floating leaves of *Nymphaea odorata* ssp. *odorata*. Water depth has been previously reported as a significant determinant of habitat suitability in *A. vesiculosa* (Adamec, 1999; Adamec & Lev, 1999). In this study, the species exhibited an optimum response to water depth, and was consistently recorded from shallow water (10−50 cm deep). Although shallower habitats (<10 cm) may exhibit suitable water chemistry conditions, studies suggest that these areas may be more prone to water level fluctuations and encroachment from emergent macrophytes or terrestrial plants (Adamec, 1999, 2005).

High competition also appears to limit the abundance and growth of *A. vesiculosa*, with both the size and number of individuals decreasing with a corresponding increase in the percentage cover of native macrophytes. The pooled cover of native macrophytes displayed a

contrasting trend in response to water depth, and the effect of water depth on *A. vesiculosa* abundance was independent of the effect of native macrophyte cover. The poor performance of *A. vesiculosa* in heavily vegetated areas is likely to result from limited irradiance at water level, reduced surface water temperature and altered water chemistry (particularly pH and reduced CO_2 concentration); all these are regarded as critical parameters in the species' optimum growth (Kamiński, 1987a,b; Adamec, 1997, 1999; Cross, 2012a). However, dense strands of floating and emergent taxa are also likely to provide physical obstruction, limiting both the clonal growth of *A. vesiculosa* and its local dispersal by wind or water movement. A high concentration of CO_2 in particular is regarded as crucial for optimal growth in *A. vesiculosa*, and is generally associated with shallow acidic waters with deep organic sediments (Adamec, 1997, 1999, 2005). However, it is also likely that the propensity for *A. vesiculosa* to occur in shallow areas may be a result of reduced water currents in these habitats, a factor likely to be important for rootless submerged aquatic plants. Field growth trials indicate that prey capture and a degree of eutrophication significantly increase growth rate in *A. vesiculosa*, with significantly higher growth rates observed at a meso-eutrophic site with high prey availability than at an oligo-mesotrophic site with low prey availability (Adamec & Kovářová, 2006). The strong correlation between growth and flowering with prey capture in this study in microsites with similar nutrient status suggests that higher rates of prey capture are beneficial for both development and fecundity in *A. vesiculosa*.

Clonal aquatic plants with extensive lateral spread exhibit some of the lowest rates of sexual reproductive output (Herben, Šerá & Klimešová, 2014), and it is perhaps unsurprising therefore that the production of flowers and successful seed set in *A. vesiculosa* were low across the entire study site. Similarly, low levels of floral success and seed set have been previously reported for the species (Nakano, 1992; Adamec & Tichý, 1997; Adamec, 1999; Cross, 2012a). No *A. vesiculosa* seeds were recovered from the sediment seed bank. A seed survival rate of less than 40% after 6 months under experimental conditions suggests that very few seeds are likely to persist in the sediment seed bank between seasons. This low survival rate, combined with the limited seed set and a low seed viability observed, indicates that sexual reproduction is unlikely to play a major role in the interseasonal persistence of *A. vesiculosa* at the study site. However, the recovery of a native *A. vesiculosa* population at Lake Baláta-tó, Hungary, following drying of the lake in 2003 appears to have been from seeds (L. Adamec, unpubl. data), suggesting that seed bank development may be variable between populations or dependent upon as yet unknown environmental factors.

The dispersive capacity of *A. vesiculosa* warrants further research. In order for propagules to disperse and establish at new locations, they must possess the capacity to survive dispersal conditions (Santamaría, 2002). For endozoochorous (internal) transport by waterbirds, this implies a capacity to withstand the chemical and mechanical processes within the avian gut for a suitable period of time (Claussen *et al.*, 2002; Figuerola & Green, 2002; Santamaría, 2002). Vegetative tissue in *A. vesiculosa* is thin and easily fragmented, and thus it would appear unlikely that vegetative propagules (e.g. stem fragments and turions) possess this capacity (see Claussen *et al.*, 2002). Preliminary evidence from this study suggests that seeds also do not survive internal bird gut transport, with all seeds entirely or partially digested. Although our experiment was not replicated due to the availability of only a single *Anascastanea* individual, previous studies have also drawn conclusions regarding the digestibility of aquatic plant seeds from only a single experimental bird (Smits, Van Ruremonde & Van Der Velde, 1989; Camenisch & Cook, 1996). It would appear likely, based on the available evidence, that dispersal in *A. vesiculosa*, at least at local scales, is facilitated by either hydrochory or exozoochory. Anecdotal evidence suggests that the movement of beavers may have facilitated the upstream spread of *A. vesiculosa* in Meadow Creek, with downstream dispersal occurring predominantly during flood events following winter ice melt, and individuals blown by wind into shallow littoral areas (*sensu* Adamec, 1995; Adamec & Lev, 1999). Adamec (1999) observed ducks grazing on free-floating *A. vesiculosa* turions at naturalised locations in Europe, and suggested that, in addition to waterbirds, the movement of larger animals such as deer in the littoral zone may also spread vegetative propagules. The deliberate or accidental movement of *A. vesiculosa* plants or fragments by anthropogenic means (particularly through recreational activities such as boating) is also plausible. However, empirical evidence to implicate any particular dispersive mechanism in the movement of *A. vesiculosa* between suitable habitats is lacking.

Population ecology data from this study, combined with the results of previously published studies of ecology and biology in *A. vesiculosa* (e.g. Adamec & Lev, 1999), suggest that the species possesses a low invasiveness risk level and support the existing *a priori* classification of *A. vesiculosa* as a 'non-invader' (Gordon *et al.*,

2012). Although the species is a rapidly growing clonal submerged macrophyte and therefore possesses the capacity to proliferate quickly in areas of suitable habitat (Adamec, 1999), the species' ability to attain optimal growth appears significantly constrained by its stenotopic ecology to small microhabitats (tens to hundreds of m^2; Adamec, 2005). Our study did not assess species-specific competitive interactions, and we acknowledge that the pooling of native macrophytes into a single variable may overlook the occupation of different niches by these taxa along the water depth gradient. However, all measured growth parameters for *A. vesiculosa* displayed significant responsiveness to biotic and abiotic factors, and data provided no evidence to suggest *A. vesiculosa* poses a competitive threat to native aquatic plants. Carnivorous macrophytes from the genus *Utricularia* are perhaps the most likely group to be affected by the naturalisation of *A. vesiculosa* in any given habitat, given the similar reliance of these taxa on carnivory for survival. However, these taxa are commonly found growing sympatrically throughout the natural range of *A. vesiculosa* (Kamiński, 1987a; Adamec, 1995; Vilkonis, 2004; Cross, 2012a), and the frequent co-occurrence of *A. vesiculosa* with *Utricularia geminiscapa, U. inflata, U. purpurea* and *U. macrorhiza* in the study area suggests that the two genera may occupy slightly different niches within a common microhabitat. No negative effects on native aquatic *Utricularia* or other aquatic plants have been documented 10 years after naturalisation of *A. vesiculosa* in the Czech Republic (e.g. Adamec & Lev, 1999; Adamec, 2005), and experimental and field trials suggest that *A. vesiculosa* and aquatic *Utricularia* may possess different growth strategies and prey selectivity (Adamec & Kovářová, 2006; Adamec, Sirova & Vrba, 2010). Future studies should examine the potential competitive relationships between *A. vesiculosa* and *Utricularia* in greater detail.

While *A. vesiculosa* does not appear to represent a competitive threat to native aquatic plants, the species' impact on native aquatic invertebrate communities may be significant. With up to *c.* 40% of traps containing captured prey in suitable microhabitats, and approximately 200 traps per individual in these areas, it is evident that large numbers of invertebrates are captured. Although *A. vesiculosa* has been reported to preferentially capture mosquito larvae (Cross, 2012a), and may therefore be beneficial in controlling mosquitos, the impact of the species on native aquatic fauna requires further study. Additionally, although *A. vesiculosa* possesses a low biomass, the constant senescence of basal whorls as individuals grow from the apical end may increase sedimentation in areas where the species is particularly abundant.

In the face of continuing decline of *A. vesiculosa* throughout its natural range, management initiatives should focus on the conservation of suitable habitat and the repatriation of populations into rehabilitated areas. In particular, focus should be placed on the determination and ongoing management of specific microhabitats that provide optimal conditions for the species' growth and reproduction. Data from this study support previous conclusions that *A. vesiculosa* possesses little capacity to become invasive (e.g. Adamec & Lev, 1999), and does not appear to compete significantly with other aquatic macrophytes. However, further research is required to elucidate the potentially cryptic impacts of *A. vesiculosa* on ecosystem functioning, in particular its effect on local invertebrate communities. If these impacts prove to be minor, carefully managed assisted dispersal in some regions may represent a viable conservation tool given the apparent lack of genetic variation present between *A. vesiculosa* populations globally (Maldonado San Martin *et al.*, 2003; Elansary, Adamec & Storchova, 2010). Introductions at a number of locations where *A. vesiculosa* historically did not occur in Europe appear to have resulted in stable, persistent populations (Adamec & Lev, 1999; Adamec, 2005; Cross, 2012a), and may offer places of refuge to a species which otherwise appears to be on a trajectory towards extinction.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Weed risk assessment score for *Aldrovanda vesiculosa*, following the United States Aquatic Weed Risk Assessment (USAqWRA) questions and score guidance of Gordon *et al.* (2012).