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Using integral projection models to compare population dynamics of four closely related species

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Abstract Demographic processes, such as survival, growth, and reproduction, can inform us about invasion risk, extinction risk, and trade-offs in life history strategies. The population dynamics of four Amaranthaceae species in southern Illinois, USA were examined using integral projection models (IPMs) to determine whether vital rates reflect life history among these closely related species. Two of the species, *Amaranthus palmeri* and *Amaranthus tuberculatus*, are summer annuals and considered to be some of the most problematic agricultural weeds in the US Midwest. *Achyranthes japonica* is a relatively new invasive exotic species that primarily inhabits forests. *Iresine rhizomatosa*, is an endangered species in the study area, which also inhabits forests. Two populations of each species were studied from 2012 to 2014 in which height of individuals were measured and used as the state variable in the IPMs. The *Amaranthus* species and *Achyranthes japonica* had an estimated population growth rate >1, projecting increases in population size. By contrast, λ was <1 for *I. rhizomatosa*, projecting a decline in population size demonstrating its endangered status. Germination rates and seed viability were dependent on species and varied over time. Elasticity analyses showed that survival and growth contributed most to λ for the perennial species; whereas, for the annual species population dynamics were driven primarily by fecundity. Overall, *Achyranthes japonica* and the *Amaranthus* species show similar trends in demographic processes that align with their invasive nature and not with their life histories. Furthermore, this study demonstrates that more research on the competitive nature of *Achyranthes japonica* is needed.

Keywords Amaranthaceae · Demography · Exotic species · Invasive species · Matrix modeling

Introduction

The population dynamics of invasive species differs from that of endangered species. Some common characteristics that invasive species have include: broad-niched, self or wind pollination or non-specialized pollinators, rapid growth to reproductive maturity, high allocation of resources to reproduction, ability to spread rapidly, prolific vegetative reproduction, an ability to outcompete native species, and a rapid response to resource availability (Baker 1965; Bazzaz 1986; Simberloff et al. 1997; Sutherland 2004). Few invasive species possess all or most of these characteristics. Possession of these characteristics, however, does not necessarily mean that a plant will become invasive (Sakai et al. 2001). By contrast, rare and endangered species may exhibit life history characteristics associated with low fitness (Vitousek et al. 1996; Sakai et al. 2001).

Demographic processes, such as survival, growth, and reproduction, can inform us about invasion risk, extinction risk, and trade-offs in life history strategies. Demography links the processes that affect individuals to

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population and community level patterns (Merow et al. 2014). The diversity of life history characteristics associated with a species are the result of long evolutionary responses to natural selection over large scales. Studies of closely related species, such as species in the same family, may be informative in this respect (Boutin and Harper 1991).

The Amaranthaceae family contains important agricultural weeds, invasive exotics, and rare native plants. In the United States Midwest region, *Amaranthus palmeri* (S.) Watson and *Amaranthus tuberculatus* (Moq.) Sauer have been widely established as two of the prominent agricultural weeds. These species have many characteristics that make them very successful weeds including the ability to grow 2–3 m in height (Horak and Loughin 2000; Trucco and Tranel 2011) and extended seed germination and seedling emergence late into the row-crop growing season (Hartzler et al. 1999). *Achyranthes japonica* (Miq.) Nakai is a relatively recent introduction spreading across the Ohio River Valley. This perennial, C_3 herb is native to Korea, China and Japan (Sage et al. 2007; Choi et al. 2010; Evans and Taylor 2011; Schwartz et al. 2016). *Achyranthes japonica* is generally found in areas with some shade and moist soil. However, the species can also grow in drier areas in sun, and in densely shaded areas (Schwartz 2014). Dense patches of *Achyranthes japonica* have been found in bottomland forests, riverbanks, field edges, and in ditches and swales (Evans and Taylor 2011; Schwartz 2014; Schwartz et al. 2016). Apart from anecdotal observations, little has been reported on this species and only recently has an aggressive educational campaign been launched to learn more about this species. *Iresine rhizomatosa* Standl. is classified as endangered in Illinois and Maryland and is considered to be rare in Indiana (IDNR 1994; Gibson and Schwartz 2014). Despite its endangered and rare status, very little ecological work has been conducted on this species (Gibson and Schwartz 2014).

We conducted a demographic study to examine the population dynamics of four closely related species to determine which vital rate(s) contributed most to population growth rate to further understand whether the invasive status or the life history of a species is the driving force between the closely related species. We analyzed the population dynamics of each species from 2012 to 2014 using integral projection models (IPMs). The objective of this study was to evaluate the demographic patterns of each of the four species using an IPM to compare vital rates. The hypothesis was that the invasion status and not the life histories of the species would drive the demographic processes among these species.

Materials and methods

Study sites

Demographic observations were made at two sites per species across southern Illinois. The sites were located within 145 km of each other (Table 1). Variation occurred in environmental factors over the three-year study. In 2012, southern Illinois underwent a drought in which over the growing season (May–October) only 3.3 cm of rainfall occurred; whereas in 2013 and 2014, southern Illinois received 9.1 cm and 9.9 cm, respectively, of rainfall (National Weather Service records). In addition to the drought year that was experienced in 2012, there were also slightly higher mean temperatures in 2012 compared with 2013 and 2014. The mean growing season temperature in 2012 was 24 °C; whereas in 2013 and 2014, the mean growing season temperature was 22 °C both years.

Field methods

The two populations were monitored for three consecutive years (2012–2014) at each site. Within each population, ten 1-m^2 plots were established randomly in sites where the species was known to be present in April 2012. Populations of each species were pooled in an area of 200 m^2. Overall in 2012, we found, on average, 1334 individuals of *Achyranthes japonica* (density: 35 ± 4 individuals/m^2), 9564 individuals of *Amaranthus palmeri* (density: 77 ± 6 individuals/m^2), 11,002 individuals of *Amaranthus tuberculatus* (density: 106 ± 11 individuals/m^2), and 928 individuals of *I. rhizomatosa* (density: 9 ± 2 individuals/m^2). The density of individuals per m^2 was 29 ± 4 for *Achyranthes japonica*, 61 ± 5 for *Amaranthus palmeri*, 92 ± 9 for *Amaranthus tuberculatus*, 5 ± 1 for *I. rhizomatosa* the following year.

Seedlings were tagged and monitored by taking node counts every week throughout each growing season to determine plant size and the following years where applicable (i.e., the perennial *Achyranthes japonica* and *I. rhizomatosa*). Height measurements were taken at the various stages and used as the state variable. Adult plants were further classified into reproductive and non-reproductive plants. Individuals were followed for 3 years or until death. Demographic parameters were measured each year weekly from May to October. The difference in field season length depended on weather conditions and seedlings were monitored as soon as they emerged until after the first frost date of that year.

Flowering was recorded in October of each year: each plant was measured in terms of plant height, number of nodes and stems as well as the inflorescence length and

Table 1 Site characteristics for each species

Species	Site name	Location	Soil type[a]	Land cover	Mean temperature (°C)[b]	Mean precipitation (cm)[b]
Achyranthes japonica	Chestnut Hills	37°11′N 89°03′W	Menfro silt loam	Forest	22.9	7.5
Achyranthes japonica	Cypress Creek	37°17′N 89°06′W	Wheeling silt loam	Forest	22.9	7.5
Amaranthus palmeri	BRC: 9B	38°30′N 89°50′W	Bethalto silt loam	Agriculture field	24.5	8.6
Amaranthus palmeri	Rend Lake	38°07′N 88°54′W	Wynoose silt loam	Agriculture field	23.4	7.2
Amaranthus tuberculatus	BRC: T4	38°31′N 89°50′W	Bethalto silt loam	Agriculture field	24.5	8.6
Amaranthus tuberculatus	DeSoto	37°47′N 89°15′W	Hurst silt loam	Agriculture field	23.5	7.3
Iresine rhizomatosa	Beall Woods 1	38°20′N 87°49′W	Birds silt loam	Forest	23.9	8.3
Iresine rhizomatosa	Beall Woods 2	38°21′N 87°50′W	Birds silt loam	Forest	23.9	8.3

Data pooled over years

[a] Source: USDA Soil Survey (2015)

[b] Source: National Weather Service (2015)

number of inflorescences. Seed number per plant was determined by cleaning the seed to remove any chaff, then counting ten lots of 1000 seeds per sample per site per species (i.e., a total of 10,000 seeds per site which is equivalent to 20,000 seeds per species), and finally weighing the entire sample. The ten lots of 1000 seeds were averaged to determine the final seed count.

Seed viability and germination tests were conducted for each species at each site annually. To determine seed viability, seed bags containing 100 seeds each were buried in all plots, just below the soil surface at the end of each growing season and were retrieved at the beginning of the following growing season (Electronic Supplementary Material (ESM)). Germination tests were performed by hand seeding 10,000 seeds onto the soil surface in ten 1-m^2 plots for each field population in the fall and counting the number that germinated the following spring. The germination experiments resulted in an average germination rate of 86 ± 4.2 % for *Achyranthes japonica*, 12 ± 2.8 % for *Amaranthus palmeri*, 14 ± 2.2 % seeds for *Amaranthus tuberculatus*, and less than 1 ± 0.3 % for *I. rhizomatosa* (Table 2).

Data analysis

The implementation of IPMs requires calculating the integrals, which is most practically conducted by applying fine categorization (Crawley 2013; Metcalf et al. 2013). The limits of integration were determined from the variance of growth (described in Easterling et al. 2000). The maximum and minimum limits of integration was set by adding or subtracting three standard deviations of the growth increment based on the maximum and minimum observed sizes. Alternative statistical relationships for growth, survivorship, and fecundity as functions of plant size were calculated, then model selection methods based on the Akaike Information Criterion (AIC) were used to determine which provided the best fit to the data. Finally, for the analyses, we determined the population growth rate (λ), the P and F (Table 2) kernels, and the elasticity analysis. For all years, the survival function $s(z)$ was estimated by logistic regression of survival on size z (Fig. 1). Additionally, the mean number of offspring were estimated from the germination trials (see ESM) and was fitted using a Poisson linear regression on adult size ($P < 0.05$ for all years, Fig. 2). Models were fitted using the R package *IPMpack* (Metcalf et al. 2013), and the significance of nonlinear terms was tested using an ANOVA function with a χ^2 test statistic (Metcalf et al. 2013). Additionally, year effects were included in the model, but not site effects since preliminary analyses indicated that there was no significant difference among sites between species. The P and F kernels are shown separately (Fig. 3) and not as the full K kernel because the scales were so different and it was difficult to visualize together when the full kernel was implemented. Seasonal kernels were built, but there was no difference in the trends between the seasonal and pooled data kernels. Thus, the pooled kernels are shown.

Results

The population growth rates (λ) for *Achyranthes japonica*, *Amaranthus palmeri*, and *Amaranthus tuberculatus* were all close to or greater than one for each census period (Table 3). These values of λ indicate that the populations were growing. By contrast, *Iresine rhizomatosa*, however, had λ values less than one (2012: 0.53; 2013: 0.68) over both annual transitions indicating that the populations were in decline.

Table 2 Mean fecundity of *Achyranthes japonica*, *Amaranthus palmeri*, *Amaranthus tuberculatus*, and *Iresine rhizomatosa*

	Mean seeds/plant	Mean germination rate	Probability of		
			Seedling—Juvenile	Juvenile—Adult	Seed viability
Achyranthes japonica	331	0.86	0.67	0.72	0.93
Amaranthus palmeri	15,880	0.12	0.55	0.80	0.64
Amaranthus tuberculatus	63,441	0.14	0.48	0.77	0.71
Iresine rhizomatosa	1000	0.01	0.31	0.45	0.23

Measurements were averaged from 2012 to 2014 and pooled over sites per species. Overall, $n = 300$ plants/site (i.e., 2012 $n = 50$ plants/site, 2013 $n = 100$ plants/site, 2014 $n = 150$ plants/site)

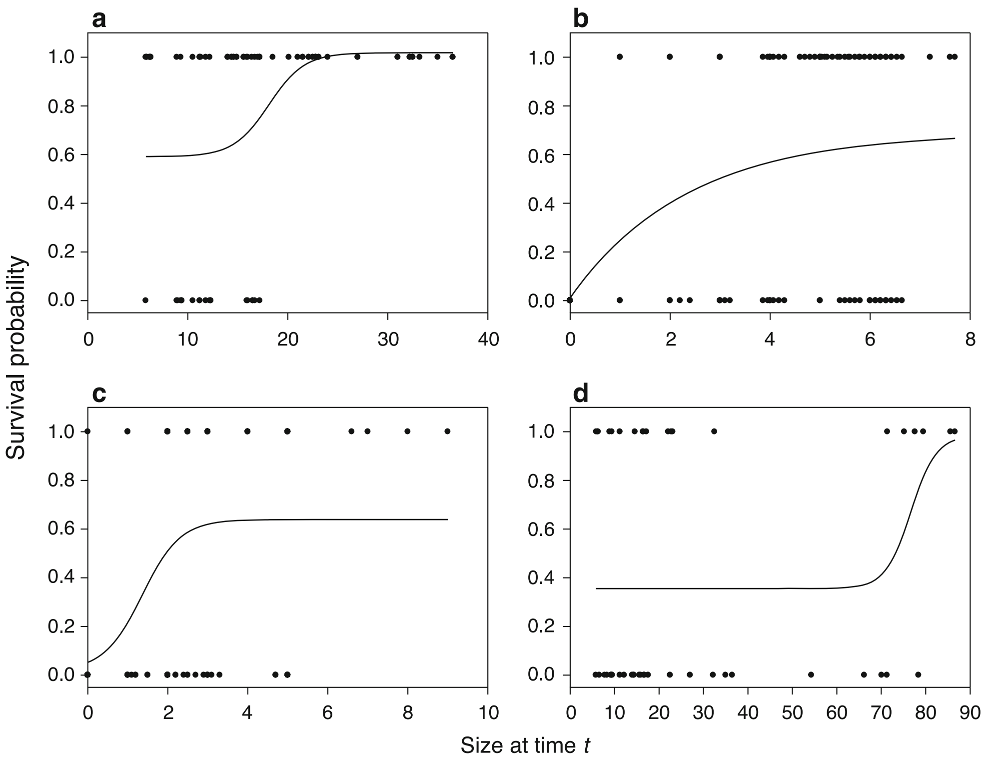

Fig. 1 Fitting of survival function based upon 2013–2014 data for **a** *Achyranthes japonica*, **b** *Amaranthus palmeri*, **c** *Amaranthus tuberculatus* and, **d** *Iresine rhizomatosa* grouped over two sites per species. The survival data are plotted (y-axis: 0 = death; 1 = survival) as a function of individual size x (plant height in cm). The x-axis scales are different among the panels. The *dots* represent the observed values and the lines represent the fitted values. The *fitted curve* for each panel is as follows: **a** $\log(s/(1 - s)) = 1.23 + 0.0156x$ ($P < 0.05$), **b** $\log(s/(1 - s)) = 0.23 + 0.044x$ ($P < 0.05$), **c** $\log(s/(1 - s)) = 1.06 + 0.0267x$ ($P < 0.05$), **d** $\log(s/(1 - s)) = 0.52 + 0.0012x$ ($P < 0.05$)

The P kernel for *Achyranthes japonica* shows that size at $t + 1$ is not related to size at t, meaning that the small plants are expected to grow a lot and the large plants shrunk (Fig. 3a). The two *Amaranthus* species again showed a similar result in that survivorship increased with the growth of the plant (i.e., larger plants had a high survivorship) (Fig. 3b, c). The endangered *I. rhizomatosa* had a similar P kernel to *Achyranthes japonica* in terms of relatively little growth that occured from 1 year to the next and that large-sized reproductive individuals had the highest survivorship probabilities (Fig. 3d). Juvenile plants seem to have the lowest survivorship. The *Amaranthus* species, however, can reproduce over a wide range of plant sizes; whereas, *I. rhizomatosa* needs to be large in size to reproduce.

In this study, the survival/growth functions made a greater contribution to λ than the fecundity function. The elasticity values varied among species and the *Amaranthus* species showed similar results (Fig. 4). *Achyranthes japonica* and the *Amaranthus* species had higher values,

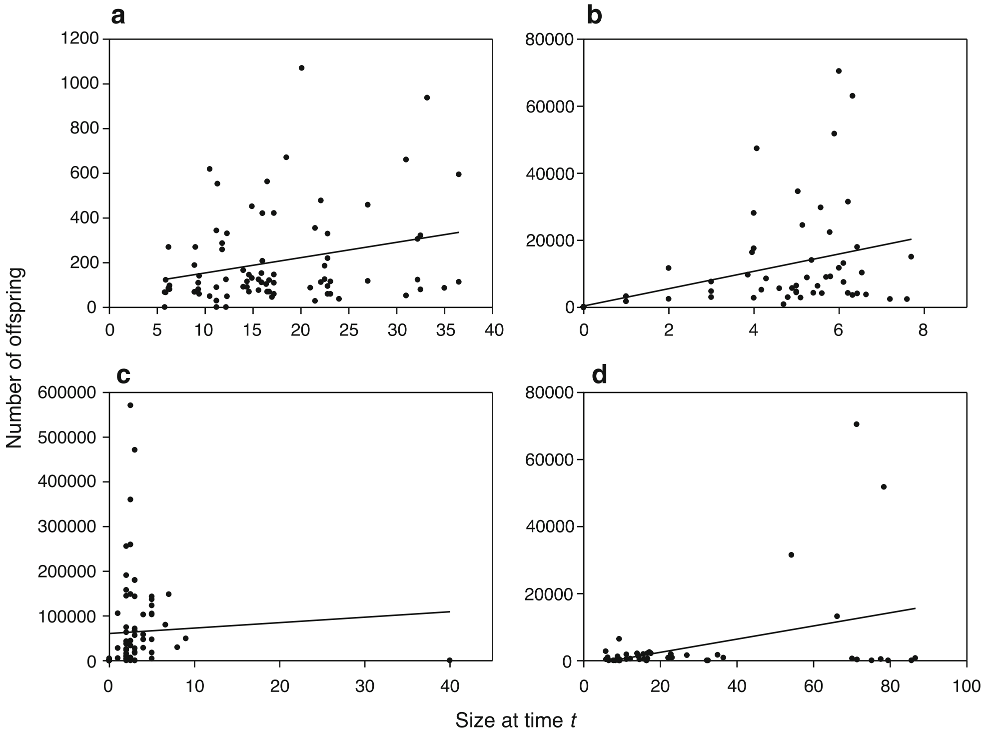

Fig. 2 Number of offspring as a function of individual size [plant height (cm)], along with the fitted linear regression for the mean number of offspring for **a** *Achyranthes japonica*, **b** *Amaranthus palmeri*, **c** *Amaranthus tuberculatus*, and **d** *Iresine rhizomatosa*. Data pooled over years. The *fitted line* for each panel is as follows: **a** $y = 85.77 + 0.6861x$ ($R^2 = 0.609$), **b** $y = 4.45 + 0.0026x$ ($R^2 = 0.247$), **c** $y = 48{,}000 + 0.0012x$ ($R^2 = 0.027$), **d** $y = 0.143 + 0.0197x$ ($R^2 = 0.157$). The *x*- and *y*-axis scales are different among the panels. The *dots* represent the observed values and the *lines* represent the fitted values

than *I. rhizomatosa*, for the growth and survival transitions of small and intermediate-sized individuals. *Iresine rhizomatosa*, however, had high elasticity values for the growth and survival transitions of largest sized individuals had the best chance of survival compared with small, young individuals. The elasticity values are shown for only 2013–2014 because the pattern was similar the prior year.

Discussion

The four closely related Amaranthaceae species showed similar IPM outputs related to life cycle or invasiveness. The two perennial species both had similar *P* and *F* kernels showing that the largest plants were the drivers of survival. The annual weedy *Amaranthus* species and the perennial *Achyranthes japonica*, the invasive species, were similar in survival from time *t* to time *t* + 1 and in fecundity, although they differ in their life histories. The similarities between the invasive species and the annual life forms provide insight into management and conservation efforts. According to our results, the small-sized to intermediate-sized individuals are the most critical for controlling populations of the invasive species, which corresponds with several other studies (especially in agriculture) (Horak and Loughin 2000; Zimdahl 2004; Trucco and Tranel 2011). This early growth stage is imperative to the survival of the endangered species as well. Understanding the dynamics of these species individually can only enhance our knowledge when comparing species within a family and projecting the rate of population growth. This knowledge allows land managers to be pre-warned about life-stage sensitivity of a potential new invasive species coming into an area. Thus, this knowledge allows some time to develop an appropriate management plan.

There were however, differences in seedling density, survivorship, and fecundity between species and years. This response could be due, in part, to varying environmental factors. In 2012, southern Illinois underwent a drought in which over the growing season (May–October) only 3.3 cm of rainfall occurred; whereas in 2013 and 2014, southern Illinois received 9.1 and 9.9 cm, respectively (National Weather Service 2015). In addition to the drought year that was experienced in 2012, there were also higher mean temperatures in 2012 compared with 2013 and 2014. The mean growing season temperature in 2012 was

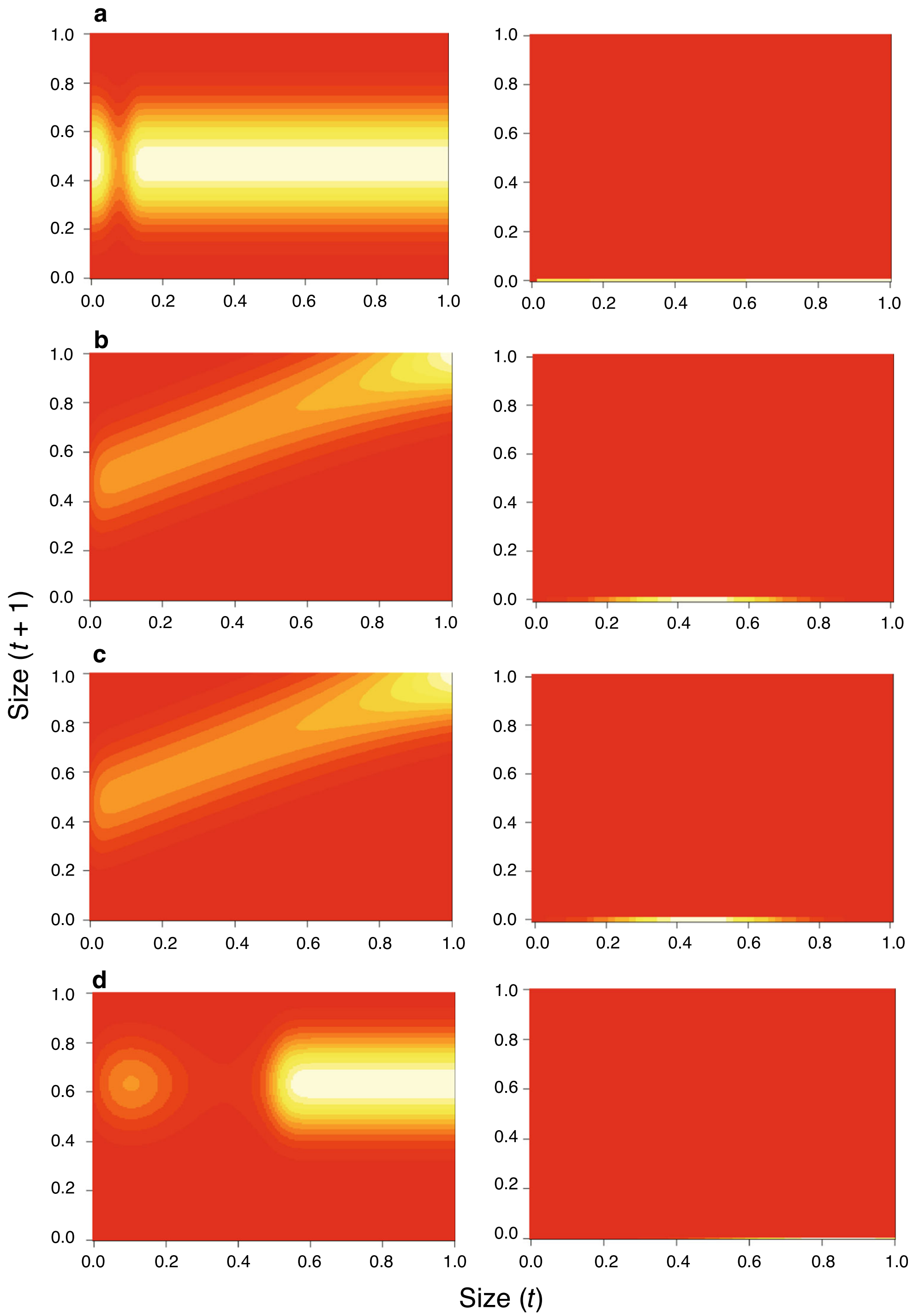

Fig. 3 The *P* (*left panel*) and *F* (*right panel*) kernels for **a** *Achyranthes japonica*, **b** *Amaranthus palmeri*, **c** *Amaranthus tuberculatus*, and **d** *Iresine rhizomatosa* from 2013 to 2014. The *lighter areas* indicate the more likelihood of transition

24 °C; whereas in 2013 and 2014, the mean growing season temperature was 22 °C both years. The small individuals were susceptible to drought, especially for *I. rhizomatosa*. Thus, reallocation of plant resources for survival, in terms of vegetative and root growth, rather than fecundity likely occurred during these periods of environmental stress (Grime 1979). Temperature is an important ecological factor in determining species growth and productivity. For example *Amaranthus palmeri* and *Amaranthus tuberculatus* exhibit their highest germination rate of 30 and 50 %, respectively, when mean air temperatures are at 25 °C (Guo and Al-Khatib 2003).

Table 3 Lambda values (λ) for the period 2012–2014 for all species

	λ	
	2012–2013	2013–2014
Achyranthes japonica	1.37	1.79
Amaranthus palmeri	1.15	1.22
Amaranthus tuberculatus	0.97	1.18
Iresine rhizomatosa	0.53	0.68

Pooled over sites. Overall, $n = 300$ plants/site (i.e., 2012 $n = 50$ plants/site, 2013 $n = 100$ plants/site, 2014 $n = 150$ plants/site)

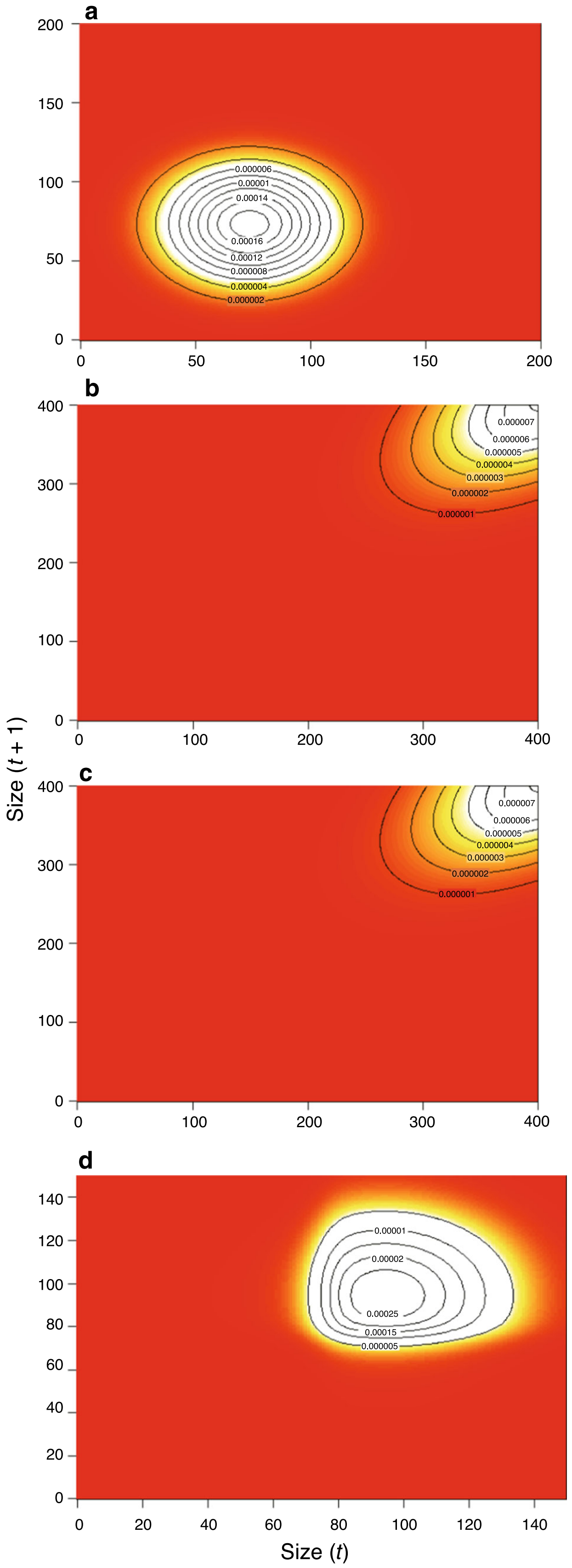

Fig. 4 Elasticity surfaces for the integral projection model fitted ▶ **a** *Achyranthes japonica*, **b** *Amaranthus palmeri*, **c** *Amaranthus tuberculatus*, and **d** *Iresine rhizomatosa* from 2013 to 2014. The *x*- and *y*-axis scales [plant height (cm)] are different among the panels. The *lighter areas* indicate the importance of reproduction and transitions of individuals into the reproductive size classes (the smaller size in year $t + 1$ than in year t indicates production of offspring) to λ

Habitat type and management strongly influences plant performance (Schwartz et al. 2016). Although causes of mortality were not recorded, disturbances such as flooding, herbicide drift, herbivory, and general human traffic resulted in high mortality of individuals at some sites. Furthermore, the endangered status of *I. rhizomatosa* is enhanced by anthropogenic disturbances. These types of disturbances have also increased seedling mortality for other endangered species, such as *Mammillaria gaumeri* (Britton & Rose) Orcutt, by altering the composition of the surrounding plant community and fragmenting its already restricted habitat (Ferrer-Cervantes et al. 2012).

The population growth rate for three of the study species was greater than one, which was expected for agricultural weeds and an invasive species. Lower lambdas (λ), as seen in the *I. rhizomatosa* populations, during some years can be attributed partially to the higher mortality of individuals in those years, which relates to its endangered status. For example, in 2012, there was a higher mortality, than in other years, for all species due to the extreme drought in southern Illinois. In the following years, the population remained more stable than in the previous year.

Elasticity analysis on the whole IPM kernel includes survival, growth, and reproduction and has been used to separate these demographic functions to λ from different size classes (Easterling et al. 2000). In general, the vital rates are affected by λ the most due to the larger proportion of the stable stage distribution. However, this is altered by the assumption that smaller plants contribute almost no recruits to the next generation (Childs et al. 2004). The elasticity values in this study show that population growth of *I. rhizomatosa* and the *Amaranthus* species depends strongly on the retention and survival of larger individuals; whereas, growth of *Achyranthes japonica* populations are affected most by demography of smaller individuals. Our current knowledge of *Achyranthes japonica* and *I. rhizomatosa* demography is limited to two sites with different data on growth, survival, and fecundity (Gibson and Schwartz 2014; Schwartz et al. 2016). There continues to be a need to more widely measure and model the demography of these closely related species to make generalizations about vital rates.

As this study demonstrates, the invasive nature of a species and not its life history is a driving factor of population growth rate. Furthermore, this study provides insight into the population dynamics of four closely related species in which two of the species are poorly studied. More research is needed on the population dynamics of these species and how these closely related species interact with one another. Using more sites across different states would greatly add to what little information is known about the population dynamics of these species, especially *Achyranthes japonica* and *I. rhizomatosa*.

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