

# General guidelines for invasive plant management based on comparative demography of invasive and native plant populations

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## Summary

1. General guidelines for invasive plant management are currently lacking. Population declines may be achieved by focusing control on demographic processes (survival, growth, fecundity) with the greatest impact on population growth rate. However, we often have little demographic information on populations in the early stages of an invasion when control can be most effective. Here we determine whether synthesis of existing demographic data on invasive and native plant populations can address this knowledge problem.
2. We compared population dynamics between invasive and native species using published matrix population models for 21 invasive and 179 native plant species. We examined whether the population growth rate responsiveness to survival, growth and fecundity perturbations varied between invasive and native species, and determined which demographic processes of invaders to target for reductions in population growth rate.
3. Invaders had higher population growth rates ( $\lambda$ ) than natives, resulting in differences in demographic processes. Perturbations of growth and fecundity transitions (elasticities) were more important for population growth of invaders, whereas perturbations of survival had greater importance for population growth of natives.
4. For both invasive and native species, elasticities of  $\lambda$  to survival increased with life span and decreased with  $\lambda$ ; while elasticities to growth and fecundity decreased with life span and increased with  $\lambda$ .
5. For long-lived invaders, simulated reductions in either survival, growth or fecundity transitions were generally insufficient to produce population declines, whereas multiple reductions in either survival + growth or survival + fecundity were more effective. For short-lived invaders, simulated reductions in growth or fecundity and all pairwise multiple reductions produced population declines.
6. *Synthesis and applications.* Life history and population growth rate of invasive species are important in the selection of control targets. For rapidly growing populations of short-lived invaders, growth and fecundity transitions should be prioritized as control targets over survival transitions. For long-lived invaders, simultaneous reductions in more than one demographic process, preferably survival and growth, are usually required to ensure population decline. These general guidelines can be applied to rapidly growing new plant invasions and at the invasion front where detailed demographic data on invasive species are lacking.

**Key-words:** comparative demography, elasticity, invasive plants, management, matrix models, population dynamics

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## Introduction

Management of invasive species aims to reduce population growth rate and consequently invasion speed, which can lead to reduction of the environmental and economic impacts of invaders (Pimentel *et al.* 2000). However, general guidelines for management of invasive plants are lacking, necessitating the construction and parameterization of population models for each new invader. The spread of the invader is best curbed by focusing control actions on the demographic processes that would result in the largest reduction in the population growth rate. Demographic processes here refer to the fundamental demographic rates: survival, growth and fecundity. Stage- or demographic rate-specific control of invasive plants is possible as biocontrol agents and some herbicides only attack certain life stages reducing survival, growth and/or fecundity transitions of those stages (Buckley *et al.* 2004; Gutierrez *et al.* 2005; Davis *et al.* 2006; Shea, Sheppard & Woodburn 2006). Here, we present the first review of the demography of invasive species, relative to native species, to determine whether there are general patterns based on demographic parameters that may be used to guide management efforts, and that can be incorporated into management strategies.

Matrix population models provide a tool for identification of the demographic processes with the greatest impact on population growth rates, enabling a better understanding of the population dynamics and potential management options for invasive species (Caswell 2001; Byers *et al.* 2002). A transition matrix (**A**) consists of matrix elements ( $a_{ij}$ ) which describe survival, growth and fecundity transitions from stage  $j$  to stage  $i$  during a certain period of time. Perturbation analyses of the demographic matrices, such as elasticity analysis, are used to determine which hypothetical changes in matrix elements ( $a_{ij}$ ) have the greatest effects on the deterministic population growth rate ( $\lambda$ ). The deterministic population growth rate denotes the asymptotic growth of the population, where  $\lambda > 1$  indicates an increasing population and  $\lambda < 1$  indicates a declining population. Perturbation analyses make a small change in each matrix element, holding all other elements constant to determine their potential effect on  $\lambda$ . Elasticities ( $e_{ij}$ ) indicate how a proportional change in each matrix element would affect  $\lambda$  (de Kroon *et al.* 1986; Caswell 2001). For both native and invasive plants, perturbations in demographic rates with small elasticities tend to have a small effect on  $\lambda$  (e.g. Ramula, Toivonen & Mutikainen 2007; Schutzenhofer & Knight 2007). For invasive species, elasticity analysis may thus be used to identify demographic transitions in the life cycle that would be appropriate control targets (Jongejans, Sheppard & Shea 2006).

The elasticities of native plant and animal taxa have been quantitatively reviewed and general patterns have emerged. For long-lived native plants, changes in survival transitions have the greatest influence on the population growth rates (i.e. survivorship has a high elasticity), while for short-lived native plants, changes in growth and fecundity transitions have the

greatest influence on the population growth rates (Silvertown, Franco & Menges 1996). Elasticity for fecundity typically increases with increasing  $\lambda$  (Silvertown *et al.* 1993, 1996; Franco & Silvertown 2004). These general patterns for native plants are consistent with those for animal taxa, such as birds (Sæther & Bakke 2000) and mammals (Heppell, Caswell & Crowder 2000). Invasive plants typically exhibit higher population performance in their invaded range than the native range (Hinz & Schwarzlaender 2004), and it is not known whether invasive plant species show similar elasticity patterns to those of native plant species.

Studies applying matrix population models to invasive plant species are now relatively common, enabling a quantitative synthesis of potential control targets for invaders. This synthesis will be particularly beneficial where urgent management strategies are needed for new invaders or species lacking detailed demographic data. Lack of demographic data is a common problem at the beginning of an invasion and at the invasion front where populations are rapidly increasing. Collection of demographic data is time-consuming and labour-intensive, and therefore ecologically informed control actions are often started long after the weed has been recognized as problematic. Initiating weed control at the beginning of an invasion may be critical for successful eradication of the weed (Simberloff 2003). A priori knowledge of potential control targets can also be used in selection of potentially effective biocontrol agents before their release. For instance, Davis *et al.* (2006) assessed the potential influence of four suggested biocontrol agents on the population growth of the biennial *Alliaria petiolata*, concluding that combinations of different biocontrol agents are probably required to successfully control the invader due to variation in the elasticity of  $\lambda$  to different demographic processes that are altered by the biocontrol agents.

The recent accumulation of matrix population models for invasive species and the long history of matrix population models for native species enable a quantitative comparison of population dynamics between invasive and native plant species. Based on species abundance data during succession, Meiners (2007) observed that the population dynamics of invasive plants are similar to those of native plants within a single community. However, we are not aware of any quantitative comparison between invasive and native plant species based on detailed demographic data on multiple species.

We used published demographic data for 21 invasive and 179 native plant species to compare their population dynamics in relation to life history. Further, we conducted simulations to identify the best management targets for invaders and to assess the reliability of management decisions based on an elasticity analysis. We first examine whether population growth rates of invasive and native species differ. We then determine whether elasticity patterns in relation to  $\lambda$  or plant life span differ between invasive and native species. Finally, we use simulations to define which demographic processes of invaders are the best potential targets for control.

## Methods

### THE DATA BASE

We conducted key word searches in the Web of Science (ISI) electronic data base (1975–2006) to find studies that had used a matrix population model for a terrestrial, invasive plant species in its invaded range, or a terrestrial native plant species. Additional studies were obtained by examining the latest issues of ecological journals and by including some unpublished data. The invasive status of the species was defined according to the respective publication. A study was included in the data base if it presented either one estimate of deterministic population growth rate ( $\lambda$ ), a transition matrix or an elasticity matrix for invasive species, or a transition matrix for native species. If the same invasive species occurred in many different publications, all publications providing additional demographic information were included in the data base to get an average measure of demography of the species (see Supplementary Material Appendix S1). For invaders with multiple studies per species (see Supplementary Material Appendix S1), the matrices were of the same dimensionality and therefore directly comparable across the studies (Enright, Franco & Silvertown 1995; Ramula & Lehtilä 2005). We corrected matrices for two invasive species to avoid an erroneous 1-year delay in the life cycle caused by the seed bank (Caswell 2001; see Supplementary Material Appendix S1). For native species with multiple studies of the same species, we randomly selected only one study to represent the species in question. The final data base consisted of 21 different invasive plant species with an elasticity matrix calculated from the mean of all matrices available for the given invader, and 179 different native plant species with each species' elasticity matrix calculated from the mean of all matrices in the chosen study (see Supplementary Material Appendix S1). All studies included here used a linear matrix population model. Such a linear model without density dependence is justified in describing population dynamics at low densities (e.g. at the beginning of an invasion). However, we note that if demographic rates are measured when plants are occurring at higher densities, the use of a linear model may incorrectly estimate  $\lambda$ .

### LIFE SPAN, POPULATION GROWTH RATE AND ELASTICITIES

To compare demographic properties between invasive and native species in relation to life history, we calculated life span for each species from the mean transition matrix using the methods described in Forbis & Doak (2004). For this method, all reproduction (sexual and asexual) was set to zero, starting from a population with one individual in the first non-seed stage in the matrix, and iterating population size until no individuals ( $\leq 0.01$  individuals) were left in the population. The life span was then determined as the number of years required to reach zero individuals. For eight species with a life span exceeding 1000 years, we set the life span to be 1000 years to produce biologically more realistic estimates. The method was modified for long-lived species with very low survival of the early life stages. In those cases where early survival was  $< 0.1$ , we started the calculation at the next larger life stage to avoid underestimating life span. When the transition matrix was unavailable or impossible to reconstruct, we used life span estimates provided by other studies (Loehle 1988; Franco & Silvertown 2004). We used the deterministic population growth rates ( $\lambda$ ) and deterministic elasticity values of  $\lambda$  reported, or we calculated elasticities of matrix elements based on the transition matrices according to Caswell (2001, equation 9-70).

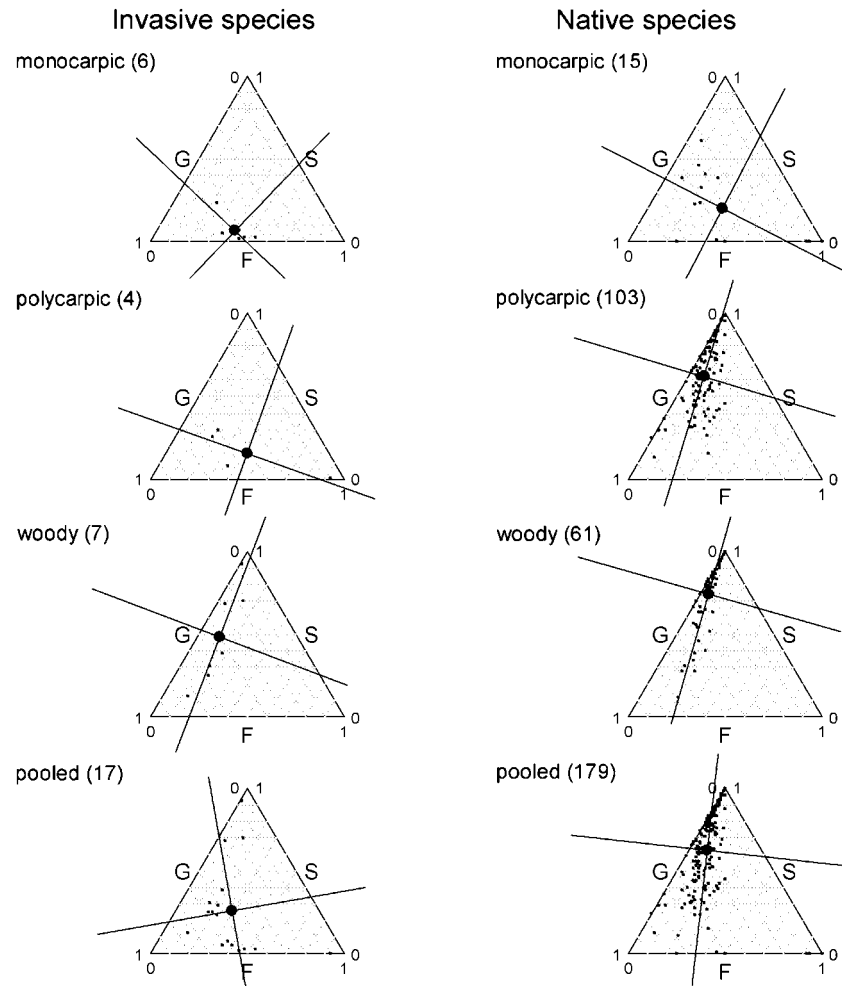
A transition matrix was unavailable for some invaders, while  $\lambda$  estimates were reported (see Supplementary Material Appendix S1). In those cases, we calculated an average of all reported  $\lambda$  values.

Elasticities of matrix elements describe the effect of a relative change in a matrix element on  $\lambda$ , summing to unity within a matrix (Caswell 2001). Due to the proportional nature of elasticities, they can be used to approximately compare the demography of different species (Silvertown *et al.* 1993, 1996). We chose to use elasticities of matrix elements instead of elasticities of underlying vital rates because relatively few publications reported vital rates. Elasticities of matrix elements generally produce qualitatively similar results and interpretations to those of elasticities of vital rates (Franco & Silvertown 2004). For each matrix, we grouped elasticities into survival, growth and fecundity components according to Silvertown *et al.* (1993). Survival consists of transitions staying in the same stage and shrinking in size (stasis and retrogression), growth consists of transitions from smaller to larger stages and clonal reproduction, and fecundity consists of sexual reproduction. We then used an ordination analysis to visually examine the distribution of these three main elasticity components for invasive and native species in relation to their life history. We classified species into monocarpic herbs that flower once during their lifetime, polycarpic herbs with multiple reproductive events during their lifetime, and woody species. Moreover, we examined the three main elasticity components in relation to  $\lambda$  and life span between the invasive and native species groups.

Few studies have assessed the success of management decisions based on an elasticity analysis in practice. This is probably because the management of species is rarely planned and evaluated systematically. To assess the potential reliability of management decisions based on the elasticity analysis, we conducted simulations for the 16 invasive species for which transition matrices were available (see Supplementary Material Appendix S1). Invaders for which just an elasticity matrix or  $\lambda$  estimates were available were omitted from the simulations. In the simulations, we reduced either survival (stasis and retrogression), growth or fecundity transitions for each invasive species by 10%, 20% ... 100% and examined the effect of these reductions on  $\lambda$ . As, for example, survival transitions occur in several life stages, multiple matrix elements in several life stages were reduced simultaneously. Reductions in multiple transitions allowed us to better assess the reliability of the elasticity analysis. Note that matrix elements representing growth always include a survival component and therefore reductions in growth transitions here also slightly reduced survival. Since many control actions indirectly reduce more than one demographic process simultaneously (Sheppard, Smyth & Swirepik 2001; Shea *et al.* 2005), we assessed the effects of such reductions on  $\lambda$  by reducing two demographic processes at a time. We reduced either survival + growth, survival + fecundity or growth + fecundity as described above.

### STATISTICAL ANALYSES

We used a two-way ANCOVA to examine  $\lambda$  values between invasive and native species with status (invasive vs. native) as an explanatory variable and life span as a covariate. The interaction term (status  $\times$  life span) was also included in the model. To improve the normality of the residuals,  $\lambda$  values were log-transformed. Due to greater variance of  $\lambda$  for invasive than native species, we modelled variances separately for both species groups using GROUP option in PROC MIXED procedure in SAS 9.1. This option is recommended to analyse data with heterogeneous variances as it uses group-specific variances for solving parameter estimates (Littell *et al.* 1996). Log-transformation for  $\lambda$  was unable to completely normalize the residuals



**Fig. 1.** Ordination of summed survival (S), growth (G) and fecundity (F) elasticities for 17 invasive and 179 native species in relation to life history. Principal axes show the average distribution of the elasticities in S-G-F space which altogether sum to one. Number of each species is given in parentheses.

and we therefore also conducted a nonparametric Wilcoxon test for  $\lambda$  values between invasive and native species.

In order to investigate the dependence of summed survival, growth and fecundity elasticities on demographic rates, we conducted ANCOVA tests with status and matrix dimension (small vs. large) as categorical explanatory variables, and life span and  $\lambda$  as continuous explanatory variables (covariates). Matrix dimension was included to control for possible differences in elasticity values caused by differential matrix dimensionality (Enright *et al.* 1995; Ramula & Lehtilä 2005). Division into small and large matrices (< 6 and  $\geq 6$  classes, respectively) was based on the median calculated from the whole data set. All possible interactions among the categorical and continuous variables were first included in the full model, resulting in 15 terms. We determined the best and simplest models according to Akaike's Information Criterion (AIC) and by omitting non-significant terms ( $P > 0.05$ ) from the full models starting from the least significant, highest order interaction term. Only the final models with the lowest AIC values are presented in the results. Fecundity elasticities were square root-transformed to normalize the residuals. For each model, we estimated the degrees of freedom using the Kenwardroger approximation.

Since the data set of invasive species contained one exceptionally high  $\lambda$  value ( $\lambda = 22.45$  for *Lespedeza cuneata*; see Appendix S1), which was approximately six times greater than the second highest  $\lambda$  for invasive species, we ran all the models with and without *Lespedeza* to explore the dependence of the results on that particular observation. Results for the elasticity analyses depended on the

inclusion of *Lespedeza*, which seemed to be an outlier that determined the direction of the relationships between elasticities and  $\lambda$ . To enable generalizations to be made for invaders, we primarily present results from all the statistical analyses without *Lespedeza* and when the results with *Lespedeza* differ, we report them separately in the text.

## Results

Population growth rates ( $\lambda$ ) of invasive species were significantly higher than those of native species (back-transformed least square mean = 1.47 and 1.05, respectively;  $F_{1,19} = 10.04$ ,  $P = 0.005$ , two-way ANCOVA and  $Z = 5.20$ ,  $P < 0.001$ , Wilcoxon test) even if *L. cuneata* with the extremely high  $\lambda$  value was excluded from the analysis. Population growth rates were unaffected by species life span ( $F_{1,20} = 0.65$ ,  $P = 0.429$ , two-way ANCOVA) and status  $\times$  life span interactions was also non-significant ( $F_{1,20} = 0.21$ ,  $P = 0.650$ , two-way ANCOVA).

The ordination analysis revealed that invasive species generally fell in the middle of the growth and fecundity axes, while native species usually occupied the area of the triangle where survival is more important than growth and fecundity (Fig. 1). This difference between invasive and native species was greatest for polycarpic herbs (Fig. 1).

Elasticities of  $\lambda$  to survival differed significantly between invasive and native species, with invasive species having smaller

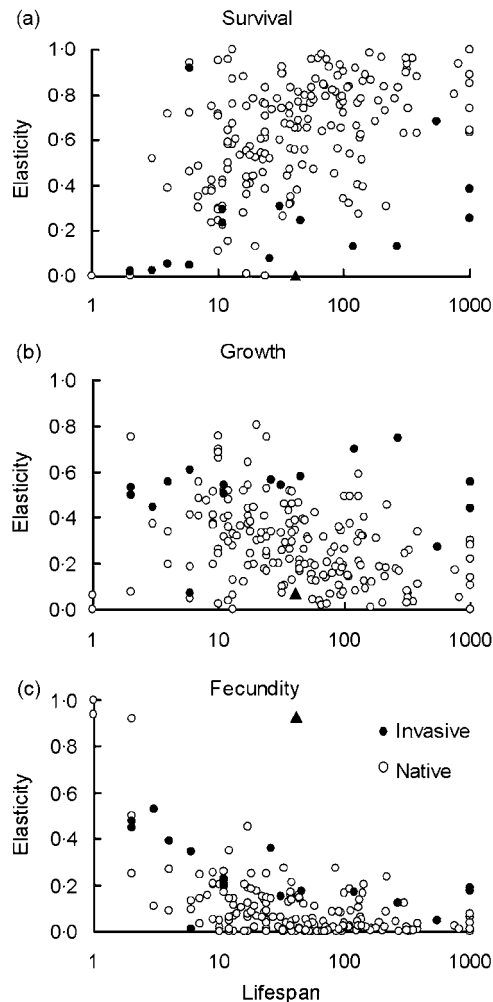
**Table 1.** Factors affecting summed elasticities for survival, growth and fecundity transitions of invasive and native plant species tested with an ANCOVA. Parameter estimates are calculated from the intercepts and slopes of the models, and indicate the magnitude and direction of the studied factors on elasticity

Factor	<i>F</i>	df/ddf	<i>P</i>	Parameter estimate	
Elasticity for survival					
Status	4.34	1/189	0.0387	Invasive	0.6551
				Native	0.9435
Life span	14.43	1/189	< 0.0001		0.0004
$\lambda$	41.18	1/189	< 0.0001		-0.3447
Dimension	8.79	1/189	0.0034	Small	0.9435
				Large	0.9610
Status $\times$ dimension	6.99	1/189	0.0089	Invasive small	0.6551
				Invasive large	0.9733
				Native small	0.9435
				Native large	0.9610
Elasticity for growth					
Life span	18.55	1/191	< 0.0001		-0.0009
$\lambda$	25.30	1/191	< 0.0001		0.1806
Life span $\times \lambda$	12.09	1/191	0.0006		0.0006
Elasticity for fecundity					
Life span	9.61	1/191	0.0022		-0.0002
$\lambda$	49.17	1/191	< 0.0001		0.2443
Dimension	10.81	1/191	0.0012	Small	0.0490
				Large	-0.0294

*F* and *P* values from ANCOVAs for different factors, df = numerator degrees of freedom, ddf = denominator degrees of freedom.

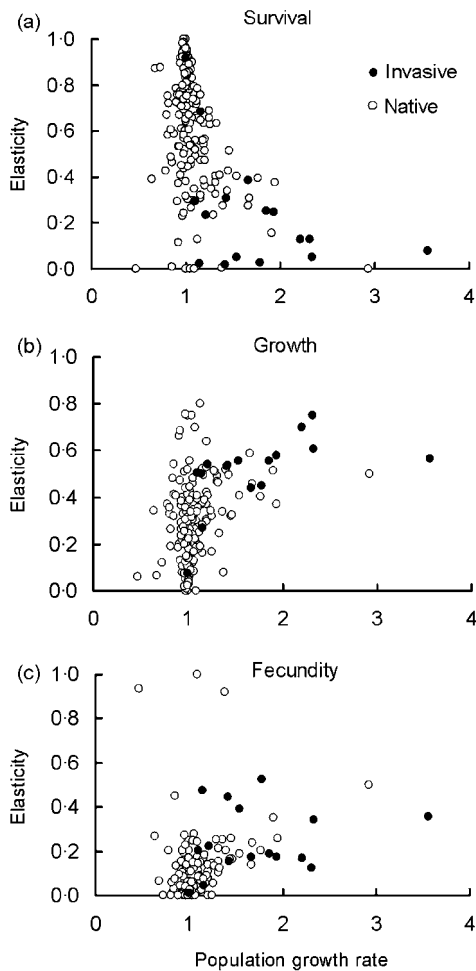
elasticity for survival than native species (Table 1). Matrix dimensionality differentially affected survival elasticities for invasive and native species (Table 1). For invasive species, survival elasticities were smaller for small matrices (< 6 classes) than large matrices, while for native species, survival elasticities were similar between small and large matrices (Table 1). For both species groups, elasticity for survival increased with increasing life span, while elasticity for growth and fecundity decreased with increasing life span (Table 1, Fig. 2), suggesting that short-lived and long-lived species are likely to respond differentially to management actions. Further, elasticity for survival decreased with increasing  $\lambda$  and elasticity for growth and fecundity increased with increasing  $\lambda$  (Table 1, Fig. 3). Matrix dimension affected fecundity elasticities, which for both species groups were greater for small than for large matrices (Table 1).

The inclusion of the invasive *Lespedeza cuneata* with the exceptionally high  $\lambda$  value in the elasticity analyses resulted in a highly significant status  $\times \lambda$  interaction for survival, growth and fecundity elasticities ( $P < 0.0001$ , for all ANCOVA tests), indicating that  $\lambda$  affects the elasticities of invasive and native species differentially. Visual inspection of the results showed that these differential responses were due to the elasticity values of *Lespedeza*, which determined the direction of the relationships between  $\lambda$  and elasticities for invasive species (see Supplementary Material Fig. S1).



**Fig. 2.** Relationship between the summed elasticities of main demographic processes and life span for invasive and native plants. For simplicity, the relationship for growth is shown without the effect of  $\lambda$  on life span. The invasive *Lespedeza cuneata* with an exceptionally high  $\lambda$  is indicated with a triangle.

Simulated reductions in survival, growth or fecundity transitions for invasive species confirmed that the  $\lambda$  values of short-lived invaders ( $\leq 11$  years) were more sensitive to reductions in growth and fecundity than those of long-lived invaders (Fig. 4b,c). Note that results for the long-lived *Lespedeza* with the exceptionally high  $\lambda$  are shown separately (see Supplementary Material Fig. S2). For short-lived invaders, on average 60–80% reduction in growth or fecundity was required to turn an increasing population into a declining population (Fig. 4b,c). For long-lived invaders, even if all fecundity or growth transitions were reduced by 100%,  $\lambda$  values declined close to 1, showing that the reductions in either fecundity or growth were an ineffective way to reduce the spread of long-lived invaders. For both short-lived and long-lived invaders, reductions in survival transitions (stasis and retrogression) tended to result in only minor declines in  $\lambda$ , and the populations were still maintained by growth and fecundity transitions as growth transitions included a survival component (Fig. 4a). For long-lived invaders, simultaneous reductions in survival



**Fig. 3.** Relationship between the summed elasticities of main demographic processes and population growth rate ( $\lambda$ ) for invasive and native plants. For simplicity, the relationship for growth is shown without the effect of life span on  $\lambda$ .

+ growth transitions reduced  $\lambda$  considerably more than simultaneous reductions in survival + fecundity or growth + fecundity, leading to a rapid decline of populations (Fig. 5). An exception was *Lespedeza*, in which simultaneous reductions in survival + growth had a negligible influence on  $\lambda$  (see Fig. S2). For short-lived invaders, simultaneous reductions in any two demographic processes reduced  $\lambda$  quite drastically, the most effective of which were reductions in fecundity + growth (Fig. 5).

## Discussion

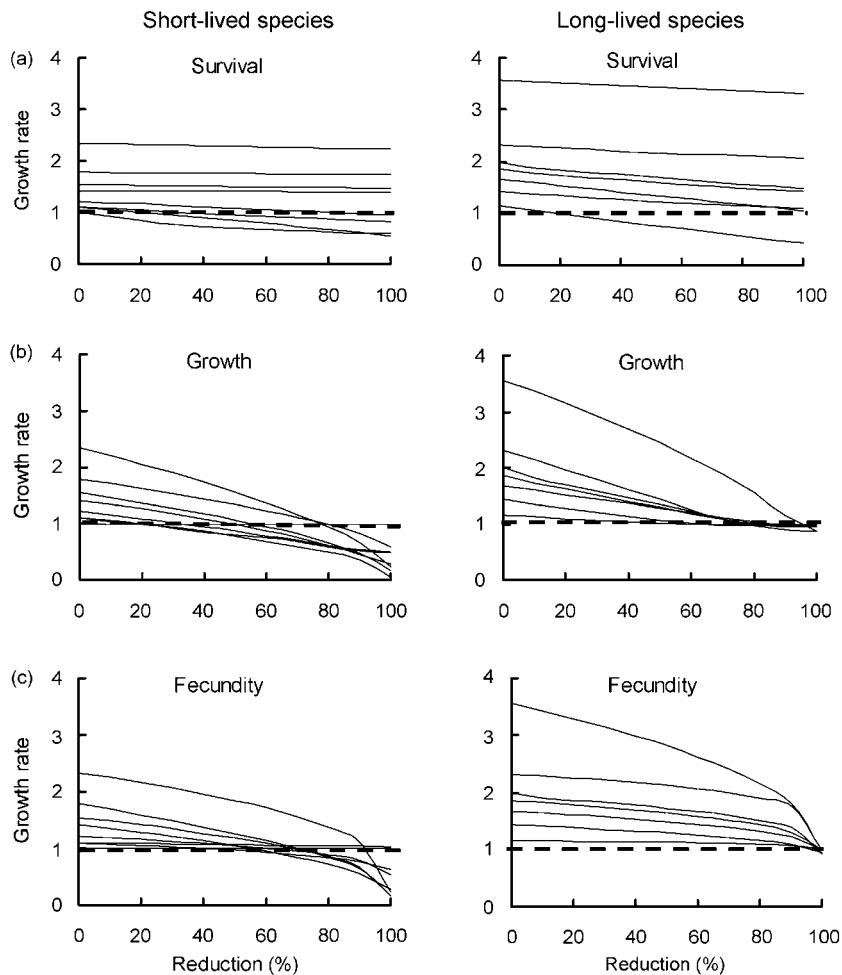
Based on the observed population dynamics of 21 invasive and 179 native plant species, we found that invasive species had higher population growth rates ( $\lambda$ ) than native species. Both our elasticity and simulation results show that the influence of reductions in survival, growth and fecundity rates on population dynamics depends on the life history of the species as well as the magnitude of  $\lambda$ , suggesting that knowledge

about life history and population growth rate can be used to inform invasive species management.

The higher population growth rates of invasive species might be due, in part, to the demographic rates of invaders being quantified during their exponential growth phase, whereas the demography of native species is more often quantified when species are showing stable or declining dynamics. In particular, population dynamics of common native species are often stabilized by plant density, which reduces demographic rates at high densities, preventing rapid growth (Freckleton *et al.* 2003). Many invasive species included in the present study are recent invaders, where populations are in the rapid expansion phase without strong density dependence. Similar to native species, plant density is likely to start to limit population growth of invaders later during the invasion process (Parker 2000), equalizing differences in  $\lambda$  between invasive and native species. Meiners (2007) compared population dynamics of common invasive and native species that had inhabited a plant community for more than 100 years, and found no difference in their population dynamics. Our results together with those of Meiners (2007) suggest that invasive plant species have higher population growth rates than native species only in the phase of a rapid expansion during the invasion process. In contrast to Meiners (2007), we found no difference in  $\lambda$  values in relation to life span of the species, indicating that populations of both short-lived and long-lived invaders are able to grow rapidly during the expansion phase.

Higher  $\lambda$  of invaders is likely to explain differences in the elasticities of  $\lambda$  between invasive and native species. Survival had a smaller elasticity for invasive than for native species. Ordination of the elasticities revealed that growth and fecundity elasticities tended to be greater for invasive than native species, suggesting that these two demographic processes are essential for the population dynamics of invaders. Similar to previous studies on native plants (Silvertown *et al.* 1996), we found that elasticities for growth and fecundity increased with increasing  $\lambda$ , while elasticities for survival decreased with increasing  $\lambda$  for both invasive and native species. Our results also suggest that for invasive species with exceptionally high  $\lambda$  values, some of these general relationships between elasticities and  $\lambda$  may be different from patterns for native species. More data on invaders with very high  $\lambda$  values would be required to examine their elasticity patterns in more detail. Dependence of elasticities on  $\lambda$  may partly explain among-population variation in the efficiency of control actions within invasive species. Shea *et al.* (2005) reported that a reduction in seed production was the optimal control strategy for a rapidly increasing *Carduus nutans* population, whereas a reduction in growth transitions was optimal for a slowly growing population of the same species.

Despite the differential  $\lambda$  and elasticity patterns between invasive and native species, we found that their elasticities for survival, growth and fecundity changed similarly in relation to life span. Elasticity of  $\lambda$  to fecundity and growth decreased with increasing life span, and elasticity of  $\lambda$  to survival increased with increasing life span. This indicates that for short-lived invaders, reductions in growth and/or fecundity

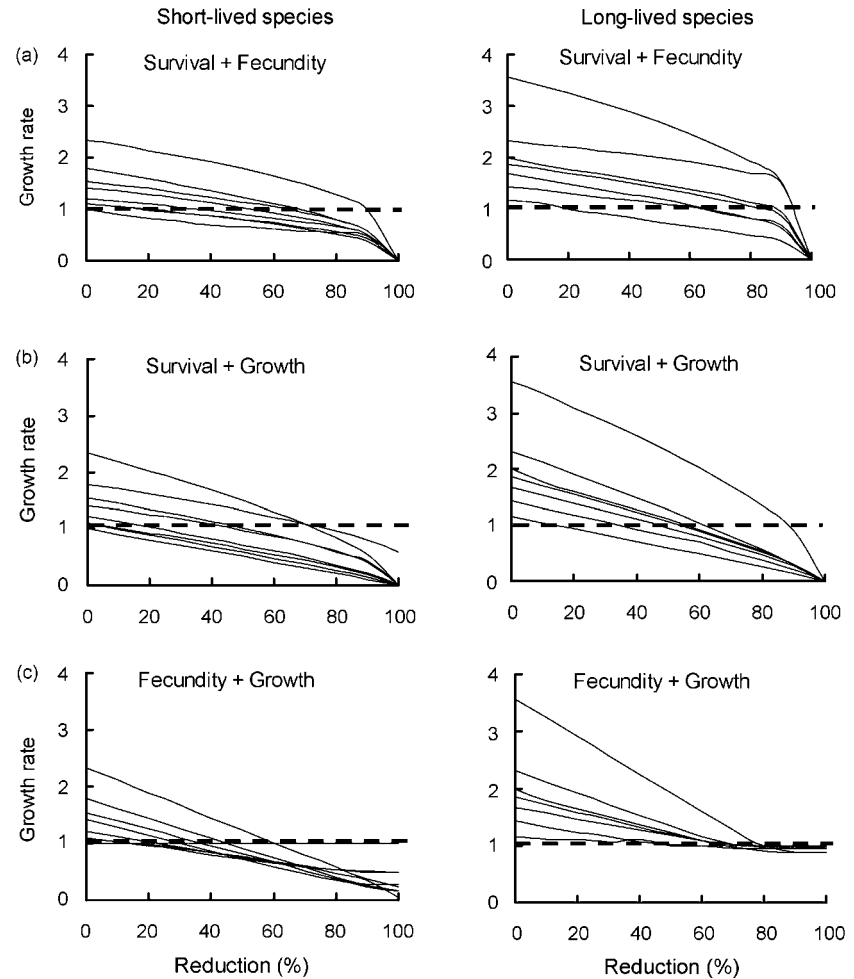


**Fig. 4.** Effects of simulated reductions in multiple survival, growth or fecundity transitions on population growth rate ( $\lambda$ ) for invasive plant species in relation to life history. Zero population growth ( $\lambda = 1$ ) is indicated with a dashed line. Short-lived species with life span  $\leq 11$  years arranged from the highest to lowest  $\lambda$  are: *Dipsacus sylvestris*, *Carduus nutans*, *Cirsium vulgare*, *Alliaria petiolata*, *Heracleum mantegazzianum*, *Centaurea maculosa*, *Rubus discolor*, *Prunus serotina*, and long-lived species are: *Agropyron cristatum*, *Pinus nigra*, *Cytisus scoparius*, *Molinia caerulea*, *Clidemia hirta*, *Parkinsonia aculeata*, *Ardisia elliptica*.

transitions would be the most efficient way to reduce plant invasion, while for long-lived invaders reductions in survival would be important. Our simulated reductions in survival, growth or fecundity revealed that smaller reductions in growth or fecundity were required for short-lived compared with long-lived invaders to turn increasing populations into declining populations ( $\lambda < 1$ ). For long-lived invaders, drastic reductions in growth or fecundity were often inadequate to considerably reduce  $\lambda$  and only led to slow declines of  $\lambda$ . This was because of high adult survival, which varied between 0.87–0.98, preventing  $\lambda$  from declining further. Therefore, simultaneous reductions in more than one demographic process, preferably survival and growth, are required to successfully control long-lived invaders. For both short-lived and long-lived invaders, control actions merely focusing on plant survival (stasis and retrogression) seem to be a relatively inefficient way to reduce the spread of the invader. It is important to note that as elasticity values for different demographic transitions vary, the influence of reductions in individual demographic transitions on  $\lambda$  depends on the life stage of the given species in which they occur. Therefore, reductions in some survival, growth or fecundity transitions reduce  $\lambda$  more than reductions in the others.

Specific demographic processes or their combinations can be reduced by selecting an appropriate management strategy. Survival can be reduced by chemical control (Shea *et al.* 2006) or biocontrol agents (Davis *et al.* 2006). Plant growth can be reduced using mechanical control such as mowing, grazing or slashing. For instance, clipping successfully reduced growth and fecundity of the invasive grass *Agropyron cristatum* (Hansen 2007). Further, biocontrol agents can slow down plant growth, preventing transitions to further stages (Shea *et al.* 2006). Fecundity can be reduced by burning or mowing plants before seed maturation (Emery & Gross 2005; Hansen 2007), or by using biocontrol agents that consume flowers or seeds (e.g. Buckley *et al.* 2004; Gutierrez *et al.* 2005; Davis *et al.* 2006; Shea *et al.* 2006). Many management strategies focusing on a specific demographic process also reduce other processes indirectly (Shea *et al.* 2005, 2006).

Overall, our results show that management actions focusing on demographic transitions with the greatest elasticity value generally have the greatest influence on  $\lambda$ , suggesting that elasticity analysis can be used to identify the best potential targets for management. Nevertheless, a simulation is required to assess the exact quantitative impact of a reduction on  $\lambda$ . To maximize the benefit of weed control, the costs of control



**Fig. 5.** Effects of simulated reductions in two demographic processes on population growth rate ( $\lambda$ ) for invasive plant species in relation to life history. Zero population growth ( $\lambda = 1$ ) is indicated with a dashed line. Short-lived species with life span  $\leq 11$  years arranged from the highest to lowest  $\lambda$  are: *Dipsacus sylvestris*, *Carduus nutans*, *Cirsium vulgare*, *Alliaria petiolata*, *Heracleum mantegazzianum*, *Centaurea maculosa*, *Rubus discolor*, *Prunus serotina*, and long-lived species are: *Agropyron cristatum*, *Pinus nigra*, *Cytisus scoparius*, *Molinia caerulea*, *Clidemia hirta*, *Parkinsonia aculeata*, *Ardisia elliptica*.

actions should also be taken into account. When costs are integrated with elasticities, controlling a demographic transition with the greatest elasticity value may be more costly than controlling a demographic transition with a smaller elasticity value (Baxter *et al.* 2006), leading to optimal management strategies which may not coincide with those determined by elasticity analysis alone. Costs of management vary with species and habitat, making generalizations at an economic level particularly difficult. Another important factor affecting the selection of an optimal life stage for control is the magnitude of the demographic transition in question. Transitions that naturally tend to be low for the given invader may not be the best option because such transitions may not be reduced much further.

In addition to life span and the magnitude of  $\lambda$ , elasticities for demographic transitions depend on matrix dimensionality. Small matrices often produce higher elasticity values for survival and fecundity than large matrices (Enright *et al.* 1995; Ramula & Lehtilä 2005). Here, matrix dimension varied a lot among species (see Appendix S1), and hence, elasticities for the main demographic processes are not strictly comparable among the species. In the present study, the small matrices (< 6 classes) of invasive species had smaller survival elasticities

than the small matrices of native species, which might have slightly underestimated the survival elasticities of invasive species in relation to those of native species. The fecundity elasticities of both species groups were greater for small than for large matrices. Since the data sets for both invasive and native species contain quite similar proportions of small matrices (53% and 46%, respectively), matrix dimensionality is unlikely to cause any bias in the comparison of fecundity elasticities between the species groups.

There are at least two limitations in the present study that may qualitatively affect the results of potential control targets. First, elasticities calculated here assume that populations are in their stable stage distributions. Unfortunately, it was impossible to examine the validity of this assumption because few studies reported observed stage distributions for populations. Secondly, the results are based on linear time invariant population models, which assume constant exponential population growth and ignore density dependence. Although a population may grow exponentially in the beginning of the invasion, density is likely to start to play a role in population dynamics later (Buckley & Metcalf 2005). Inclusion of density dependence may be particularly important for assessing the effects of biocontrol agents on population

dynamics for invaders (Buckley *et al.* 2005; Halpern & Underwood 2006). Moreover, demographic transitions do not remain constant but vary from year to year. It is well-known that elasticities produced by models ignoring density dependence and variation in demographic transitions sometimes differ from those produced by models taking these two factors into account (Benton & Grant 1996; Tuljapurkar, Horvitz & Pascarella 2003; Caswell & Takada 2004). When population dynamics are density-independent, which is often the case in new invasions, controlling growth and/or fecundity for short-lived invaders, and managing multiple demographic processes, preferably survival and growth, for long-lived invaders, seem to be the best options. However, our results should not be applied to density-dependent populations, as control actions focusing only on one life stage in a dense population may result in the relaxation of density dependence and rapid growth of earlier life stages (Parker 2000). The timing of management in a dense population is essential (Freckleton *et al.* 2003) because the relaxation of density dependence early in the growing season may lead to over-compensatory reproduction and subsequent rapid expansion of the population (Buckley *et al.* 2001). Furthermore, in the beginning of the invasion, there is often a lag phase when rapid population growth of invaders is inhibited (Sakai *et al.* 2001). Demographic studies conducted during this lag phase may produce management suggestions different from those presented here.

The current study provides general suggestions of the best potential targets for control actions in plant invasions where detailed demographic data are lacking. As populations of invasive species are growing at a higher rate than native species, their population dynamics differ from those of native species. High population growth rates are common in new invasions and at the front of invasion ranges where population dynamics are usually density-independent. Our results emphasize that the focus of control on survival, growth and/or fecundity transitions depends on species life history and the magnitude of the population growth rate. Therefore, differential management strategies are required for short-lived and long-lived invasive plants. As problematic invaders can generally be assumed to have high population growth rates, information merely on species life history (short-lived vs. long-lived) can be used to inform management, even in the absence of detailed knowledge on population growth rate. In rapidly growing populations of short-lived species, growth and fecundity transitions are better potential control targets than survival transitions, while the importance of survival increases with increasing life span. For long-lived invaders with high adult survival, simultaneous reductions in survival and growth are often required to turn increasing populations into declining populations.

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## Supplementary material

The following supplementary material is available for this article:

**Appendix S1.** The demographic properties of 21 invasive and 179 native plant species included in the study

**Fig. S1.** Relationship between the summed elasticities of main demographic processes and population growth rate ( $\lambda$ ) for invasive and native plants when the invasive *Lespedeza cuneata* is included.

**Fig. S2.** Effects of simulated reductions in multiple demographic transitions on population growth rate for the invasive *Lespedeza cuneata*.

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