

# The generality of management recommendations across populations of an invasive perennial herb

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**Abstract** Demographic models are widely used to produce management recommendations for different species. For invasive plants, current management recommendations to control local population growth are often based on data from a limited number of populations per species, and the assumption of stable population structure (asymptotic dynamics). However, spatial variation in population dynamics and deviation from a stable structure may affect these recommendations, calling into question their generality across populations of an invasive species. Here, I focused on intraspecific variation in population dynamics and investigated management recommendations generated by demographic models across 37 populations of a short-lived, invasive perennial herb (*Lupinus polyphyllus*). Models that relied on the proportional perturbations of vital rates (asymptotic elasticities) indicated an essential role for plant survival in long-term population dynamics. The rank order of elasticities for different vital rates (survival, growth, retrogression, fecundity) varied little among the 37 study populations regardless of population status (increasing or declining asymptotically).

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Summed elasticities for fecundity increased, while summed elasticities for survival decreased with increasing long-term population growth rate. Transient dynamics differed from asymptotic dynamics, but were qualitatively similar among populations, that is, depending on the initial size structure, populations tended to either increase or decline in density more rapidly than predicted by asymptotic growth rate. These findings indicate that although populations are likely to exhibit transient dynamics, management recommendations based on asymptotic elasticities for vital rates might be to some extent generalised across established populations of a given short-lived invasive plant species.

**Keywords** Demography · Elasticity · Invasive species · Management · Population model · Transient dynamics

## Introduction

Generating management recommendations for invasive species is of great interest in conservation biology. Demographic models based on vital rates, such as survival and fecundity of individuals, have been commonly used to guide the management of invasive plants (e.g., Parker 2000; Knight et al. 2008; McMahon and Metcalf 2008; Ramula et al. 2008;

Coutts et al. 2011; Pichancourt et al. 2012). For example, general guidelines derived from simple demographic models suggest that in the absence of density dependence, managing survival rather than fecundity may be a more efficient way to reduce local population growth for long-lived plant invaders, whereas the opposite is generally true for rapidly growing populations of short-lived invasive plants (Knight et al. 2008; Ramula et al. 2008). However, many of the current management guidelines for invasive plants are based on data from only a few populations per species (Knight et al. 2008; Ramula et al. 2008; but see Coutts et al. 2011). Because of this, they do not explicitly consider spatial variation in population dynamics which may affect management recommendations. As an example, McMahon and Metcalf (2008) observed considerable variation in population dynamics among populations of woody invaders, with clear consequences for management recommendations, and Parker (2000) found that management strategies for the invasive shrub *Cytisus scoparius* changed in relation to invasion history. This among-population variation in observed population dynamics may be partly due to differences in population growth rates, because the contribution of fecundity to population dynamics tends to increase with respect to that of survival with increasing population growth rate (Silvertown et al. 1993; de Kroon et al. 2000; Ramula et al. 2008).

In addition, current management guidelines of invasive plants are primarily based on long-term asymptotic population dynamics (e.g., Ramula et al. 2008; Knight et al. 2008), which assume that populations have already reached their stable stage or size structure. Given the fact that the observed stage structures differ from expected stable stage structures in many plant populations (e.g., Ramula and Lehtilä 2005; Williams et al. 2011), this assumption may not be realistic. In particular, invasive species, which tend to occur in disturbed habitats and often originate from a single seed, may rarely be in a stable stage structure. As a consequence, short-term transient dynamics might be more relevant than long-term asymptotic dynamics in guiding management of invaders (Ezard et al. 2010). Short-term transient dynamics describe changes in population size and structure in a period when the population growth rate may fluctuate from year to year before reaching its asymptote, the point at which stable dynamics can be used. Such fluctuations

may be caused by management actions, catastrophes, or natural disturbances (e.g., herbivores). For populations that deviate from the stable stage structure, asymptotic and transient methods may thus result in both quantitatively and qualitatively different predictions of population status (McMahon and Metcalf 2008; Ezard et al. 2010). For example, it has been shown that when colonisation begins from seed and adult stages are absent, asymptotic dynamics overestimates plant population densities in the short run (Iles et al. 2016), resulting in biased estimates of long-term densities. In general, differences between long-term asymptotic dynamics and short-term transient dynamics tend to be most pronounced in rapidly growing populations and in species with long generation times (Koons et al. 2005; Stott et al. 2010).

Here, I focused on intraspecific variation in population dynamics and investigated the generality of management recommendations generated by demographic models across 37 populations of an invasive perennial herb, *L. polyphyllus*. Demographic analyses were based on long-term asymptotic and short-term transient population dynamics in the absence of density dependence. I hypothesised that asymptotic elasticities would differ among populations depending on the magnitude of asymptotic population growth rate, and would thus highlight different aspects of the population dynamics as management targets. For example, I predicted that fecundity and growth would be important management targets in rapidly growing populations, while survival would be more important in slow-growing or declining populations. Moreover, I hypothesised that populations would exhibit qualitatively and quantitatively different transient dynamics, which would complicate management recommendations derived from asymptotic elasticities for controlling local population growth.

## Methods

### Study species and demographic data

The herbaceous *L. polyphyllus* invades different habitat types, from road verges to forest understoreys and wetlands (Timmins and Mackenzie 1995; Vyšniakienė et al. 2011; Meier et al. 2013; Ramula 2014), and in those places, is associated with a decline in local plant diversity (Valtonen et al. 2006; Ramula and

Pihlaja 2012) and arthropod abundance (S. Ramula and J. Sorvari, unpubl). The estimated lifespan of *L. polyphyllus* is a few years (S-L. Li, unpubl) and reproduction may take place during the second summer at earliest (Jauni and Ramula 2017). Flowers are pollinated by bumble bees (Haynes and Mesler 1984; Pohtio and Teräs 1995) and the species mainly reproduces from seed, although clonal reproduction is possible (Rapp 2009; Fremstad 2010; Li et al. 2016a). An individual plant is able to produce hundreds of seeds (Aniszewski et al. 2001; Ramula 2014) which are dispersed ballistically up to a few metres from the mother plant (Jantunen et al. 2005), but dispersal by humans is also common (Fremstad 2010). The species has a persistent seed bank (Timmins and Mackenzie 1995). In Finland, *L. polyphyllus* was introduced for ornamental purposes and has been spreading from the southern parts of the country northwards since the late 1800s (Fremstad 2010). It is primarily controlled by annually mowing stands before the seeds ripen.

I collected demographic data from 37 *L. polyphyllus* populations in a part of its introduced range in Finland by observing the survival, growth, and fecundity of mapped individuals on permanently marked study plots in 2010–2011 (more than 4000 individuals in total; see Ramula 2014 for details). The populations covered a latitudinal gradient of 448 km (mean pairwise distance  $\pm$  SD = 220.3  $\pm$  157.4 km) that may have reflected the invasion history of the species. Germination and seedling establishment were estimated separately from seed-sowing plots in each population ( $n = 3$  plots and 150 sown seeds per population). The majority of the study populations (25 out of 37) were located on road verges and wastelands, while the rest were located in forest understoreys and uncultivated former fields (Table S1 in Supplementary material). The populations were genetically differentiated when assessed in terms of 13 microsatellite loci (Li et al. 2016b).

#### Asymptotic and transient population dynamics

Using the demographic data from the two consecutive years, I constructed an integral projection model (IPM) for each population, in which survival, growth, and fecundity of individual plants were modelled as a continuous function of plant size (diameter  $\times$  height in cm with each vital rate

modelled separately; see Ramula 2014 for model details). The models were then discretised into  $50 \times 50$  matrices that included a seed bank (i.e. a stage describing seed survival and recruitment from the persistent seed bank), while clonal reproduction was ignored because of its low frequency in the study populations. Due to this discretisation, most methods that are used to analyse matrix population models can be applied to IPMs (Easterling et al. 2000; Merow et al. 2014).

To explore model outcomes based on long-term population dynamics and their implications in generating management recommendations, I calculated asymptotic elasticities from each IPM as in van Tienderen (1995) and decomposed them further into four underlying vital rates: survival, growth, retrogression (i.e. reversing back to previous sizes), and fecundity. This calculation approach takes into account covariances among demographic transitions within the same size class (van Tienderen 1995) and is recommended particularly for IPMs (Alden Griffith, unpubl). Asymptotic elasticities estimate how proportional perturbations in a given vital rate affect the long-term population growth rate ( $\lambda$ ), and they are commonly used to guide the management of different organismal groups (e.g., Silvertown et al. 1993; Heppell et al. 2000; Parker 2000; Franco and Silvertown 2004; Knight et al. 2008; Ramula et al. 2008). Vital rate elasticities may have negative values, meaning that an increase in this vital rate would decrease  $\lambda$  (Zuidema and Franco 2001). Moreover, from each IPM, I calculated the  $\lambda$  that describes the rate at which the population is predicted to increase or decline after it has reached its stable size structure. To facilitate comparison across populations, I scaled all elasticities to sum to one within each population. Moreover, as the asymptotic growth rates from the study period were not associated with population density (Ramula 2014), I assumed that population dynamics were density-independent.

To investigate whether management recommendations derived from asymptotic population dynamics can be applied to invasive populations that deviate from their stable size structure, I quantified transient dynamics. As transient dynamics depend on the length of the transient period (Stott 2016), I used standardised transient measures (transient density compared to predictions based on  $\lambda$  and case-specific

inertia) rather than direct perturbation analysis to compare transient dynamics among the study populations (see Stott 2016 for discussion on the pros and cons of different approaches). These standardised measures are independent of initial population sizes and asymptotic growth rates (Stott et al. 2011). Transient density describes population dynamics based on a specific initial size structure so that the initial density equals to one. Case-specific inertia describes population density of a given population structure relative to a population with stable growth rate and the same initial density, and correlates strongly with other indices of transient dynamics (Stott et al. 2011). Positive inertia values imply that a population increases (amplifies) at a faster rate than predicted by  $\lambda$ , while negative values imply that the population declines (attenuates) at a faster rate than predicted by  $\lambda$ . Case-specific inertia can be calculated for primitive matrices only, while transient density can be predicted also for imprimitive matrices that show non-stable population growth (Stott et al. 2012). For transient analysis, I started all 37 populations from the observed size structures that were standardised to sum to one and predicted dynamics for 20 years because most populations reached asymptotic dynamics after about 5–15 years (Fig. 4). An exception was population 32 in which transient dynamics lasted more than 20 years when the population initiated from seeds (Fig. 4b). Note that due to a lack of direct estimates of seed densities in the soil, I set the seed bank to its stable stage distribution of a given population (seed bank dominated population structure in all populations). To explore the sensitivity of model outcomes to seed bank density, I ran the models as above with the seed bank set to zero, but this did not qualitatively affect the results (not shown); only the outcomes from the model including the seed bank are presented. Transient dynamics are also sensitive to initial conditions (Stott et al. 2012; Stott 2016) and for comparison, I started the populations as entirely comprised of seeds (no individuals in other life stages were present), which is often the case in the beginning of the colonisation process for plant invaders. For example, *L. polyphyllus* has been used for landscaping in the introduced range (Fremstad 2010) and its seeds may have been transported e.g., via mowing machines. All demographic analyses were conducted in R (R Development Core Team 2016), and case-specific

inertia was calculated using the function *inertia* in the package *popdemo* of R.

### Statistical analyses

To explore vital rate elasticities in relation to long-term population growth rate, I ran Spearman rank correlations between the asymptotic elasticities summed separately for each vital rate (survival, growth, retrogression, fecundity) and  $\lambda$ . Since multiple analyses conducted with the same data set increase the probability of type I statistical error, I reduced this probability by adjusting the *P* values with a sequential Bonferroni correction.

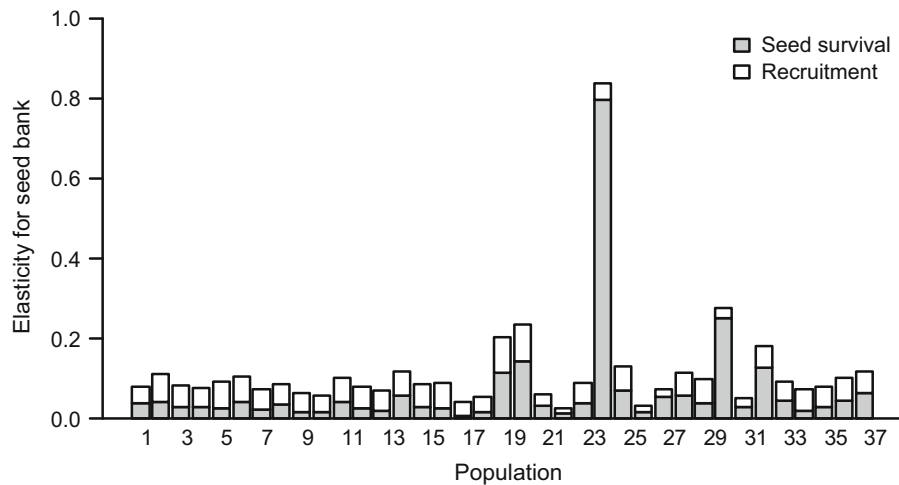
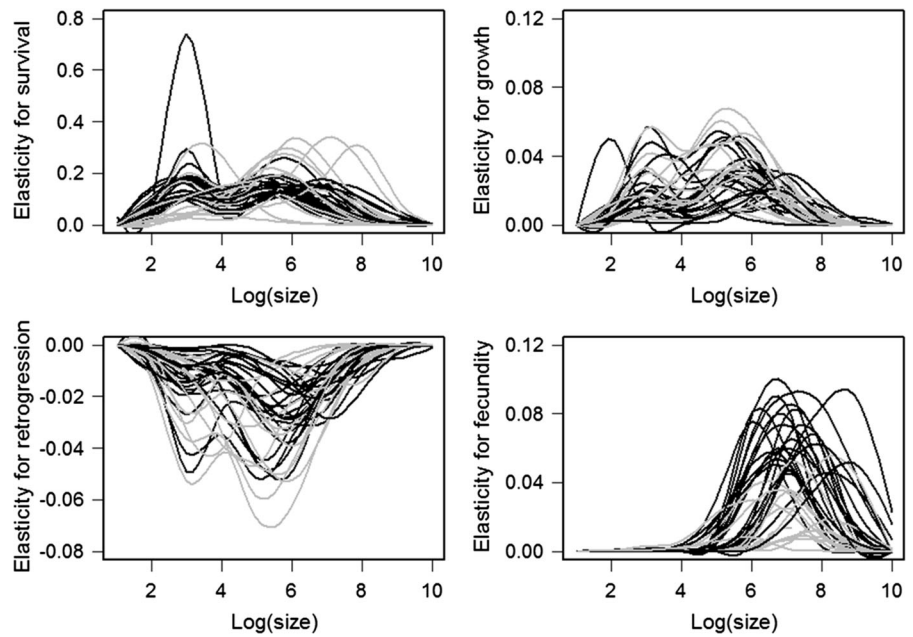
To examine the relationship between asymptotic and transient dynamics, I conducted a linear mixed model (the *lmer* function in R) with case-specific inertia as a response variable and  $\lambda$ , initial size structure with two categories (observed size structure, seeds only), and their interaction as fixed explanatory variables. Population was considered a random factor to account for the two inertia values per population. The response variable was logarithmically transformed to normalise residuals. The significance of the fixed variables was assessed using a model simplification based on a likelihood-ratio test fit with maximum likelihood.

## Results

### Asymptotic population dynamics

The asymptotic analyses predicted that most populations of *L. polyphyllus* would increase in the long term ( $\lambda > 1.0$  in 24 out of the 37 populations, Table S1). Overall, asymptotic elasticities showed surprisingly little variation in their rank order among the 37 study populations (Fig. 1), with the survival of established plants having the greatest elasticity in nearly all populations (Fig. S1 in Supplementary material). An exception was population 24 with the lowest population growth rate ( $\lambda = 0.52$ ) in which elasticity for seed survival in the seed bank dominated (Fig. 2). Based on visual assessment, declining populations tended to be more sensitive to changes in adult survival than increasing populations (Fig. 1). Summed elasticities for fecundity increased with increasing population growth rate, while summed elasticities for survival

**Fig. 1** Asymptotic elasticities for survival, growth, retrogression, and fecundity in relation to the size of *L. polyphyllus* individuals in 37 populations. Note that seed bank is not included in the survival and growth elasticities here (see Fig. 2 for seed bank elasticities). *Black lines* indicate increasing populations ( $\lambda > 1.0$ ) and *grey lines* indicate declining populations ( $\lambda < 1.0$ )



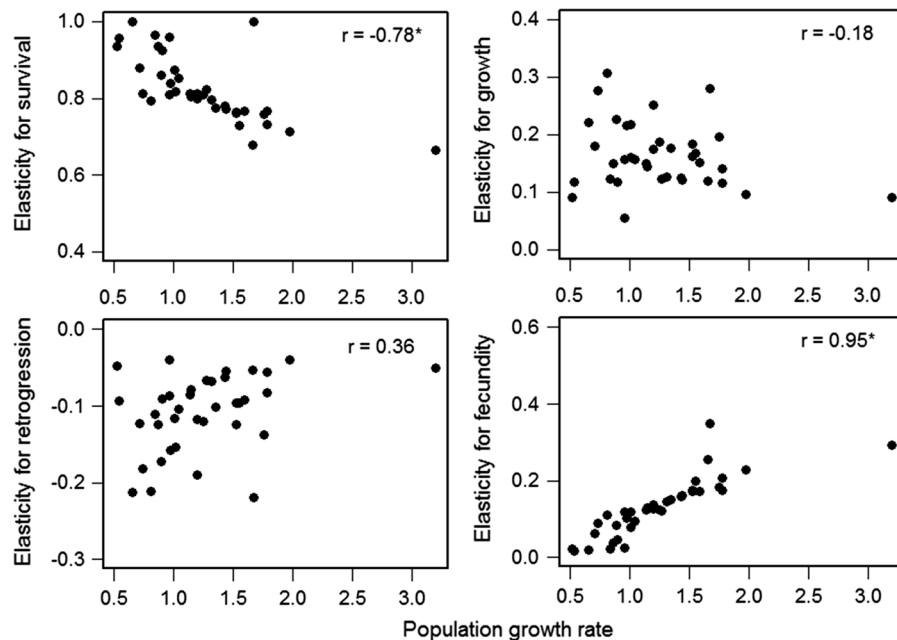
**Fig. 2** Summed asymptotic elasticities for the persistent seed bank consisting of seed survival and recruitment from the seed bank in the 37 populations of *L. polyphyllus*

declined with increasing population growth rate (Fig. 3). Elasticities summed separately for growth and retrogression were not statistically significantly associated with asymptotic population growth rate (Fig. 3).

Transient population dynamics

Populations showed diverse transient dynamics, with transient behaviour (amplification or attenuation) and

the length of the transient period depending on the initial population structure (Fig. 4). When the populations were started from the observed size structures, the transient analyses predicted that all of them would reach higher densities than predicted by  $\lambda$  before converging to their stable size structure in 5–10 years (Fig. 4a). However, inertia values were highly variable among populations (range 1.96–15.66; Table S1), indicating that population densities could be between about 2–16 times larger than predicted by  $\lambda$ . In



**Fig. 3** Asymptotic elasticities summed separately for survival, growth, retrogression, and fecundity in relation to the asymptotic population growth rate of *L. polyphyllus*. Each dot represents a population ( $n = 37$  populations). Shown are

Spearman's rank correlations ( $r$ ); statistically significant correlations ( $P < 0.05$ ) after a sequential Bonferroni correction are indicated with an asterisk

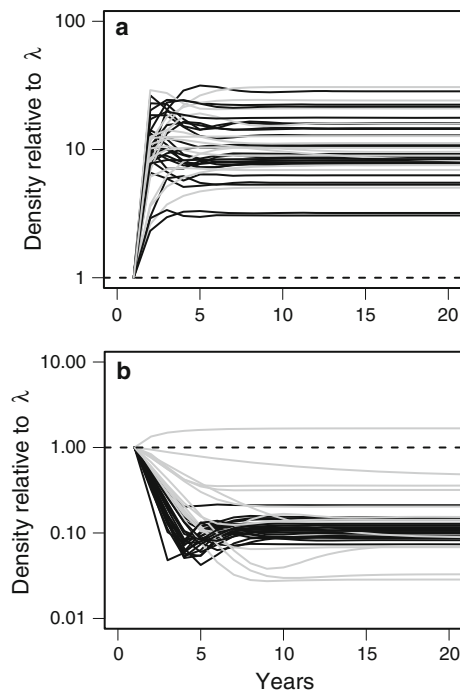
contrast, when the populations were started from seeds, the transient analyses predicted that all but one population with the lowest growth rate ( $\lambda = 0.52$ ) would decline in density compared to predictions based on  $\lambda$  before reaching asymptotic growth rate in 10–15 years (Fig. 4b). Inertia values below one (range 0.029–0.358) suggested that the populations could be about 3–36% of the size predicted by  $\lambda$ . These inertia values were not statistically significantly associated with the long-term population growth rate ( $\chi^2 = 3.064$ ,  $df = 1$ ,  $P = 0.080$ , slope =  $-0.233$  for  $\lambda$  and  $\chi^2 = 0.685$ ,  $df = 1$ ,  $P = 0.408$  for  $\lambda \times$  size structure interaction, a linear mixed model).

## Discussion

Population dynamics of a single invasive plant species may vary considerably in space (e.g., Parker 2000; Koop and Horvitz 2005; Ramula 2014), which may have critical ramifications for management. In particular, management recommendations based on asymptotic elasticities may exhibit among-population variation because of the associations of these

elasticities with population growth rate (e.g., Silvertown et al. 1993; Oostermeijer et al. 1996; de Kroon et al. 2000; Ramula et al. 2008). Such associations were found also in *L. polyphyllus*, for which fecundity elasticities increased and survival elasticities decreased with increasing population growth rate. Similar to observations in other short-lived perennials (e.g., Knight et al. 2008; Ramula et al. 2008), these findings emphasise the importance of fecundity transitions over other transitions in rapidly growing plant populations. Growth is generally important for increasing populations (Silvertown et al. 1993; de Kroon et al. 2000; Ramula et al. 2008). However, in the present study, summed elasticity for growth was not statistically significantly associated with  $\lambda$ , probably because growth was modelled independently of survival. In other words, the present study focused on independent vital rates, whereas many previous studies have used matrix elements that tend to be functions of multiple vital rates and that often include survival (e.g., Silvertown et al. 1993; Ramula et al. 2008, but see Franco and Silvertown 2004). One could of course question the reliability of management recommendations derived from asymptotic elasticities for vital





**Fig. 4** Transient dynamics of 37 populations of *L. polyphyllus* beginning from the observed size structures (**a**) and seeds only (**b**). *Black lines* indicate increasing populations ( $\lambda > 1.0$ ) and *grey lines* indicate declining populations ( $\lambda < 1.0$ ) based on the asymptotic dynamics. Initial population densities are scaled to equal to 1 and *dashed lines* denote asymptotic dynamics with stable population size structure

rates because they are by definition based on small perturbations and assume linear responses (de Kroon et al. 2000). However, asymptotic elasticities have been shown to apply for even larger perturbations of vital rates (de Kroon et al. 2000; Ramula et al. 2008), indicating that the outcomes of elasticity analysis tend to be qualitatively robust. It should be noted, though, that the present study does not incorporate management costs or efficacy that may change management recommendations (e.g., Baxter et al. 2006; Pichancourt et al. 2012; Kerr et al. 2016). Moreover, density dependence was ignored here, although it is likely to dampen the growth of dense invasions in the long term and, consequently, to affect management (Pardini et al. 2009; Ramula and Buckley 2010). Finally, the present study captured only a snapshot (2 years) of population dynamics and the underlying vital rates. Therefore, asymptotic elasticities estimated here may not guide weed management precisely if vital rates vary considerably over time (Tuljapurkar et al. 2003;

Haridas and Tuljapurkar 2005). In such a situation, stochastic elasticities that explicitly consider the temporal variability of vital rates are preferable over asymptotic elasticities for demographic studies (Tuljapurkar et al. 2003).

Despite the fact that vital rate elasticities were partially associated with the magnitude of asymptotic population growth rate in the present study, they showed surprisingly little variation in their rank order among the 37 study populations, with elasticity for survival being usually greater than elasticity for fecundity (Fig. 1). This result indicates that in the absence of density dependence and temporal variability of vital rates, a proportional reduction in survival would curb local population growth in the long run more than the same proportional reduction in fecundity. The prevention of seed production might, however, efficiently reduce population growth in the short term (i.e. in nonstable populations), when seed bank transitions are critical to populations (Ezard et al. 2010). Still, there was notable among-population variation in elasticities for survival across the size classes of *L. polyphyllus*, with the survival of the largest (adult) individuals being more important in declining populations ( $\lambda < 1.0$ ) than the survival of smaller plants. A similar pattern has been observed also for other perennial plants (e.g., Oostermeijer et al. 1996; Parker 2000). Importantly, the present study suggests that these management recommendations focusing on survival rather than on fecundity can be generalised across the populations of *L. polyphyllus* regardless of their status (increasing or declining asymptotically). This generality is in contrast with previous studies of invasive herbs and shrubs in which management recommendations tend to vary among populations of a species depending on habitat type or invasion stage (Parker 2000; McMahon and Metcalf 2008). Here, instead, the among-population variability of vital rate elasticities was small despite the fact that the 37 study populations represented four different habitat types (Table S1). Similarly, given the fact that the present sampling covered a latitudinal gradient of 448 km, and thus probably contained both relatively recent (a few years old) as well as more established invasions, invasion stage is also unlikely to explain the small degree of among-population variability of elasticities here. The study populations were also genetically differentiated (Li et al. 2016b), which is likely to increase rather than to reduce differences in

population dynamics given that genetic structure parallels phenotypic variation. The small variability of asymptotic elasticities for different vital rates across the 37 populations of *L. polyphyllus* might, however, be partially explained by species lifespan. *L. polyphyllus* is a short-lived perennial herb, with an estimated lifespan of only a few years (S-L. Li, unpubl), while other invasive plant species that exhibit considerable among-population variation in management recommendations are long-lived herbs or shrubs, with the estimated lifespan usually being decades (McMahon and Metcalf 2008). In order to confirm the possible effect of species lifespan on the spatial variability (or lack thereof) in management recommendations for an invasive plant species, more studies are required that take into consideration invaders with different lifespans.

In the present study, short-term population dynamics often differed from long-term population dynamics. The transient analysis revealed that all populations were predicted to reach higher densities relative to those predicted by  $\lambda$  when they were started from the observed size structures, while the opposite tended to be true when they were started from seeds. Higher densities compared to predictions based on  $\lambda$  imply that the populations tend to have higher initial reproductive values than expected (Koons et al. 2005). This could arise, for example, if the populations comprised of a larger proportion of flowering plants with high reproductive values and thus, a smaller proportion of seeds in the seed bank with low reproductive values than at the stable size structure. While the observed size structures above-ground generally matched quite well to the expected size structures, the visual inspection of the population size structures revealed that large plants were indeed slightly overrepresented in several populations (Ramula 2014, supplementary material). Such bias towards large (flowering) individuals with high reproductive values particularly in the beginning of the study period seems to be common in perennial plants, and probably results from a non-random sampling due to the fact that large individuals are usually easier to detect in the field than smaller vegetative plants (Williams et al. 2011). In contrast, lower transient densities compared to those predicted by  $\lambda$  when populations initiated from seeds have been reported also elsewhere (Iles et al. 2016) and are generally expected due to mortality before

reaching the reproductive stage. The only *L. polyphyllus* population that deviated from this pattern (and reached higher densities compared to predictions based on  $\lambda$ ) had the lowest asymptotic growth rate ( $\lambda = 0.52$ , Fig. 4b), suggesting that the seed bank buffered against a population decline in the short term. Regardless of the initial size structure, the rate of transient change (measured as case-specific inertia), however, varied among populations independently of  $\lambda$ . This observation echoes a previous comparative study among different plant species that found no relationship between short- and long-term population dynamics (Iles et al. 2016, but see Stott et al. 2010), indicating that vital rates contribute differentially to them and that both components may need to be considered separately when exploring population dynamics and different management options. In other words, asymptotic growth rate cannot be used to predict the rate of transient change. Since the present study utilised standardised transient measures, the findings on transient dynamics and their ramifications for management can be applied to short-lived plant invaders beyond the study species.

In summary, the present study demonstrates that asymptotic elasticities for vital rates (fecundity and survival in particular) change in relation to population growth rate. Despite this, the rank order of elasticities for main vital rates varied little across populations, suggesting that for already established populations of *L. polyphyllus*, asymptotic elasticities might be used to identify vital rates that are the best potential management targets. Moreover, there were little qualitative differences in transient dynamics among populations; depending on the initial size structure, populations tended to reach either higher or smaller densities compared to predictions based on  $\lambda$ . These results indicate that management recommendations might be to some extent generalised for a given short-lived invasive plant species, which could reduce the effort required for the collection of demographic data. However, the efficiency of the same management actions is likely to vary among populations due to differences in the magnitude of transient dynamics.

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### Compliance with ethical standards

**Conflict of interest** The author declares no conflict of interest.

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