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1 For Biological Invasions

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4 **The generality of management recommendations across populations of an invasive**  
5 **perennial herb**

6

7 Satu Ramula

8

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10 Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland.

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17 Corresponding author:

18 Satu Ramula

19 Section of Ecology, Department of Biology, University of Turku

20 FI-20014 Turku, Finland

21 Tel: +358 2 333 5717

22 E-mail: satu.ramula@utu.fi

23

24

25 Running title: The generality of management recommendations

26 **Abstract** Demographic models are widely used to produce management recommendations  
27 for different species. For invasive plants, current management recommendations to control  
28 local population growth are often based on data from a limited number of populations per  
29 species, and the assumption of stable population structure (asymptotic dynamics). However,  
30 spatial variation in population dynamics and deviation from a stable structure may affect  
31 these recommendations, calling into question their generality across populations of an  
32 invasive species. Here, I focused on intraspecific variation in population dynamics and  
33 investigated management recommendations generated by demographic models across 37  
34 populations of a short-lived, invasive perennial herb (*Lupinus polyphyllus*). Models that  
35 relied on the proportional perturbations of vital rates (asymptotic elasticities) indicated an  
36 essential role for plant survival in long-term population dynamics. The rank order of  
37 elasticities for different vital rates (survival, growth, retrogression, fecundity) varied little  
38 among the 37 study populations regardless of population status (increasing or declining  
39 asymptotically). Summed elasticities for fecundity increased, while summed elasticities for  
40 survival decreased with increasing long-term population growth rate. Transient dynamics  
41 differed from asymptotic dynamics, but were qualitatively similar among populations, that is,  
42 depending on the initial size structure, populations tended to either increase or decline in  
43 density more rapidly than predicted by asymptotic growth rate. These findings indicate that  
44 although populations are likely to exhibit transient dynamics, management recommendations  
45 based on asymptotic elasticities for vital rates might be to some extent generalised across  
46 established populations of a given short-lived invasive plant species.

47

48 **Keywords** Demography, Elasticity, Invasive species, Management, Population model,  
49 Transient dynamics

50

## 51 **Introduction**

52 Generating management recommendations for invasive species is of great interest in  
53 conservation biology. Demographic models based on vital rates, such as survival and  
54 fecundity of individuals, have been commonly used to guide the management of invasive  
55 plants (e.g., Parker 2000; Knight et al. 2008; McMahon and Metcalf 2008; Ramula et al.  
56 2008; Coutts et al. 2011; Pichancourt et al. 2012). For example, general guidelines derived  
57 from simple demographic models suggest that in the absence of density dependence,  
58 managing survival rather than fecundity may be a more efficient way to reduce local  
59 population growth for long-lived plant invaders, whereas the opposite is generally true for  
60 rapidly growing populations of short-lived invasive plants (Knight et al. 2008; Ramula et al.  
61 2008). However, many of the current management guidelines for invasive plants are based on  
62 data from only a few populations per species (Knight et al. 2008; Ramula et al. 2008; but see  
63 Coutts et al. 2011). Because of this, they do not explicitly consider spatial variation in  
64 population dynamics which may affect management recommendations. As an example,  
65 McMahon and Metcalf (2008) observed considerable variation in population dynamics  
66 among populations of woody invaders, with clear consequences for management  
67 recommendations, and Parker (2000) found that management strategies for the invasive shrub  
68 *Cytisus scoparius* changed in relation to invasion history. This among-population variation in  
69 observed population dynamics may be partly due to differences in population growth rates,  
70 because the contribution of fecundity to population dynamics tends to increase with respect to  
71 that of survival with increasing population growth rate (Silvertown et al. 1993; de Kroon et  
72 al. 2000; Ramula et al. 2008).

73 In addition, current management guidelines of invasive plants are primarily based on  
74 long-term asymptotic population dynamics (e.g., Ramula et al. 2008; Knight et al. 2008),  
75 which assume that populations have already reached their stable stage or size structure. Given

76 the fact that the observed stage structures differ from expected stable stage structures in many  
77 plant populations (e.g., Ramula and Lehtilä 2005; Williams et al. 2011), this assumption may  
78 not be realistic. In particular, invasive species, which tend to occur in disturbed habitats and  
79 often originate from a single seed, may rarely be in a stable stage structure. As a  
80 consequence, short-term transient dynamics might be more relevant than long-term  
81 asymptotic dynamics in guiding management of invaders (Ezard et al. 2010). Short-term  
82 transient dynamics describe changes in population size and structure in a period when the  
83 population growth rate may fluctuate from year to year before reaching its asymptote, the  
84 point at which stable dynamics can be used. Such fluctuations may be caused by management  
85 actions, catastrophes, or natural disturbances (e.g., herbivores). For populations that deviate  
86 from the stable stage structure, asymptotic and transient methods may thus result in both  
87 quantitatively and qualitatively different predictions of population status (McMahon and  
88 Metcalf 2008; Ezard et al. 2010). For example, it has been shown that when colonisation  
89 begins from seed and adult stages are absent, asymptotic dynamics overestimates plant  
90 population densities in the short run (Iles et al. 2016), resulting in biased estimates of long-  
91 term densities. In general, differences between long-term asymptotic dynamics and short-  
92 term transient dynamics tend to be most pronounced in rapidly growing populations and in  
93 species with long generation times (Koons et al. 2005; Stott et al. 2010).

94         Here, I focused on intraspecific variation in population dynamics and investigated  
95 the generality of management recommendations generated by demographic models across 37  
96 populations of an invasive perennial herb, *Lupinus polyphyllus*. Demographic analyses were  
97 based on long-term asymptotic and short-term transient population dynamics in the absence  
98 of density dependence. I hypothesised that asymptotic elasticities would differ among  
99 populations depending on the magnitude of asymptotic population growth rate, and would  
100 thus highlight different aspects of the population dynamics as management targets. For

101 example, I predicted that fecundity and growth would be important management targets in  
102 rapidly growing populations, while survival would be more important in slow-growing or  
103 declining populations. Moreover, I hypothesised that populations would exhibit qualitatively  
104 and quantitatively different transient dynamics, which would complicate management  
105 recommendations derived from asymptotic elasticities for controlling local population  
106 growth.

107

## 108 **Methods**

### 109 *Study species and demographic data*

110 The herbaceous *Lupinus polyphyllus* invades different habitat types, from road verges to  
111 forest understoreys and wetlands (Timmins and Mackenzie 1995; Vyšniauskiene et al. 2011;  
112 Meier et al. 2013; Ramula 2014), and in those places, is associated with a decline in local  
113 plant diversity (Valtonen et al. 2006; Ramula and Pihlaja 2012) and arthropod abundance (S.  
114 Ramula and J. Sorvari, unpubl). The estimated lifespan of *L. polyphyllus* is a few years (S-L.  
115 Li, unpubl) and reproduction may take place during the second summer at earliest (Jauni and  
116 Ramula 2017). Flowers are pollinated by bumble bees (Haynes and Mesler 1984; Pohtio and  
117 Teräs 1995) and the species mainly reproduces from seed, although clonal reproduction is  
118 possible (Rapp 2009; Fremstad 2010; Li et al. 2016a). An individual plant is able to produce  
119 hundreds of seeds (Aniszewski et al. 2001; Ramula 2014) which are dispersed ballistically up  
120 to a few metres from the mother plant (Jantunen et al. 2005), but dispersal by humans is also  
121 common (Fremstad 2010). The species has a persistent seed bank (Timmins and Mackenzie  
122 1995). In Finland, *L. polyphyllus* was introduced for ornamental purposes and has been  
123 spreading from the southern parts of the country northwards since the late 1800s (Fremstad  
124 2010). It is primarily controlled by annually mowing stands before the seeds ripen.

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

136

### 137 *Asymptotic and transient population dynamics*

138 Using the demographic data from the two consecutive years, I constructed an integral  
139 projection model (IPM) for each population, in which survival, growth, and fecundity of  
140 individual plants were modelled as a continuous function of plant size (diameter  $\times$  height in  
141 cm with each vital rate modelled separately; see Ramula 2014 for model details). The models  
142 were then discretised into 50  $\times$  50 matrices that included a seed bank (i.e. a stage describing  
143 seed survival and recruitment from the persistent seed bank), while clonal reproduction was  
144 ignored because of its low frequency in the study populations. Due to this discretisation, most  
145 methods that are used to analyse matrix population models can be applied to IPMs (Easterling  
146 et al. 2000; Merow et al. 2014).

147 To explore model outcomes based on long-term population dynamics and their  
148 implications in generating management recommendations, I calculated asymptotic elasticities  
149 from each IPM as in van Tienderen (1995) and decomposed them further into four underlying

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

164         To investigate whether management recommendations derived from asymptotic  
165 population dynamics can be applied to invasive populations that deviate from their stable size  
166 structure, I quantified transient dynamics. As transient dynamics depend on the length of the  
167 transient period (Stott 2016), I used standardised transient measures (transient density  
168 compared to predictions based on  $\lambda$  and case-specific inertia) rather than direct perturbation  
169 analysis to compare transient dynamics among the study populations (see Stott 2016 for  
170 discussion on the pros and cons of different approaches). These standardised measures are  
171 independent of initial population sizes and asymptotic growth rates (Stott et al. 2011).  
172 Transient density describes population dynamics based on a specific initial size structure so  
173 that the initial density equals to one. Case-specific inertia describes population density of a  
174 given population structure relative to a population with stable growth rate and the same initial



175 density, and correlates strongly with other indices of transient dynamics (Stott et al. 2011).  
176 Positive inertia values imply that a population increases (amplifies) at a faster rate than  
177 predicted by  $\lambda$ , while negative values imply that the population declines (attenuates) at a  
178 faster rate than predicted by  $\lambda$ . Case-specific inertia can be calculated for primitive matrices  
179 only, while transient density can be predicted also for imprimitive matrices that show non-  
180 stable population growth (Stott et al. 2012). For transient analysis, I started all 37 populations  
181 from the observed size structures that were standardised to sum to one and predicted  
182 dynamics for 20 years because most populations reached asymptotic dynamics after about 5-  
183 15 years (Fig. 4). An exception was population 32 in which transient dynamics lasted more  
184 than 20 years when the population initiated from seeds (Fig. 4b). Note that due to a lack of  
185 direct estimates of seed densities in the soil, I set the seed bank to its stable stage distribution  
186 of a given population (seed bank dominated population structure in all populations). To  
187 explore the sensitivity of model outcomes to seed bank density, I ran the models as above  
188 with the seed bank set to zero, but this did not qualitatively affect the results (not shown);  
189 only the outcomes from the model including the seed bank are presented. Transient dynamics  
190 are also sensitive to initial conditions (Stott et al. 2012; Stott 2016) and for comparison, I  
191 started the populations as entirely comprised of seeds (no individuals in other life stages were  
192 present), which is often the case in the beginning of the colonisation process for plant  
193 invaders. For example, *L. polyphyllus* has been used for landscaping in the introduced range  
194 (Fremstad 2010) and its seeds may have been transported e.g., via mowing machines. All  
195 demographic analyses were conducted in R (R Development Core Team 2016), and case-  
196 specific inertia was calculated using the function *inertia* in the package *popdemo* of R.

197

198 *Statistical analyses*

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

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

212

## 213 **Results**

### 214 *Asymptotic population dynamics*

215 The asymptotic analyses predicted that most populations of *L. polyphyllus* would increase in  
216 the long term ( $\lambda > 1.0$  in 24 out of the 37 populations, Table S1). Overall, asymptotic  
217 elasticities showed surprisingly little variation in their rank order among the 37 study  
218 populations (Fig. 1), with the survival of established plants having the greatest elasticity in  
219 nearly all populations (Fig. S1 in Supplementary material). An exception was population 24  
220 with the lowest population growth rate ( $\lambda=0.52$ ) in which elasticity for seed survival in the  
221 seed bank dominated (Fig. 2). Based on visual assessment, declining populations tended to be  
222 more sensitive to changes in adult survival than increasing populations (Fig. 1). Summed  
223 elasticities for fecundity increased with increasing population growth rate, while summed  
224 elasticities for survival declined with increasing population growth rate (Fig. 3). Elasticities

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

227

### 228 *Transient population dynamics*

229 Populations showed diverse transient dynamics, with transient behaviour (amplification or  
230 attenuation) and the length of the transient period depending on the initial population  
231 structure (Fig. 4). When the populations were started from the observed size structures, the  
232 transient analyses predicted that all of them would reach higher densities than predicted by  $\lambda$   
233 before converging to their stable size structure in 5-10 years (Fig. 4a). However, inertia  
234 values were highly variable among populations (range 1.96-15.66; Table S1), indicating that  
235 population densities could be between about 2-16 times larger than predicted by  $\lambda$ . In  
236 contrast, when the populations were started from seeds, the transient analyses predicted that  
237 all but one population with the lowest growth rate ( $\lambda = 0.52$ ) would decline in density  
238 compared to predictions based on  $\lambda$  before reaching asymptotic growth rate in 10-15 years  
239 (Fig. 4b). Inertia values below one (range 0.029-0.358) suggested that the populations could  
240 be about 3-36% of the size predicted by  $\lambda$ . These inertia values were not statistically  
241 significantly associated with the long-term population growth rate ( $\chi^2 = 3.064$ ,  $df = 1$ ,  $P =$   
242  $0.080$ , slope =  $-0.233$  for  $\lambda$  and  $\chi^2 = 0.685$ ,  $df = 1$ ,  $P = 0.408$  for  $\lambda \times$  size structure interaction,  
243 a linear mixed model).

244

### 245 **Discussion**

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

250 elasticities with population growth rate (e.g., Silvertown et al. 1993; Oostermeijer et al. 1996;  
251 de Kroon 2000; Ramula et al. 2008). Such associations were found also in *L. polyphyllus*, for  
252 which fecundity elasticities increased and survival elasticities decreased with increasing  
253 population growth rate. Similar to observations in other short-lived perennials (e.g., Knight et  
254 al. 2008; Ramula et al. 2008, these findings emphasise the importance of fecundity transitions  
255 over other transitions in rapidly growing plant populations. Growth is generally important for  
256 increasing populations (Silvertown et al. 1993; de Kroon et al. 2000; Ramula et al. 2008).  
257 However, in the present study, summed elasticity for growth was not statistically significantly  
258 associated with  $\lambda$ , probably because growth was modelled independently of survival. In other  
259 words, the present study focused on independent vital rates, whereas many previous studies  
260 have used matrix elements that tend to be functions of multiple vital rates and that often  
261 include survival (e.g., Silvertown et al. 1993; Ramula et al. 2008, but see Franco and  
262 Silvertown 2004). One could of course question the reliability of management  
263 recommendations derived from asymptotic elasticities for vital rates because they are by  
264 definition based on small perturbations and assume linear responses (de Kroon et al. 2000).  
265 However, asymptotic elasticities have been shown to apply for even larger perturbations of  
266 vital rates (de Kroon et al. 2000; Ramula et al. 2008), indicating that the outcomes of  
267 elasticity analysis tend to be qualitatively robust. It should be noted, though, that the present  
268 study does not incorporate management costs or efficacy that may change management  
269 recommendations (e.g., Baxter et al. 2006; Pichancourt et al. 2012; Kerr et al. 2016).  
270 Moreover, density dependence was ignored here, although it is likely to dampen the growth  
271 of dense invasions in the long term and, consequently, to affect management (Pardini et al.  
272 2009; Ramula and Buckley 2010). Finally, the present study captured only a snapshot (two  
273 years) of population dynamics and the underlying vital rates. Therefore, asymptotic  
274 elasticities estimated here may not guide weed management precisely if vital rates vary

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

278         Despite the fact that vital rate elasticities were partially associated with the  
279 magnitude of asymptotic population growth rate in the present study, they showed  
280 surprisingly little variation in their rank order among the 37 study populations, with elasticity  
281 for survival being usually greater than elasticity for fecundity (Fig. 1). This result indicates  
282 that in the absence of density dependence and temporal variability of vital rates, a  
283 proportional reduction in survival would curb local population growth in the long run more  
284 than the same proportional reduction in fecundity. The prevention of seed production might,  
285 however, efficiently reduce population growth in the short term (i.e. in nonstable  
286 populations), when seed bank transitions are critical to populations (Ezard et al. 2010). Still,  
287 there was notable among-population variation in elasticities for survival across the size  
288 classes of *L. polyphyllus*, with the survival of the largest (adult) individuals being more  
289 important in declining populations ( $\lambda < 1.0$ ) than the survival of smaller plants. A similar  
290 pattern has been observed also for other perennial plants (e.g., Oostermeijer et al. 1996;  
291 Parker 2000). Importantly, the present study suggests that these management  
292 recommendations focusing on survival rather than on fecundity can be generalised across the  
293 populations of *L. polyphyllus* regardless of their status (increasing or declining  
294 asymptotically). This generality is in contrast with previous studies of invasive herbs and  
295 shrubs in which management recommendations tend to vary among populations of a species  
296 depending on habitat type or invasion stage (Parker 2000; McMahon and Metcalf 2008).  
297 Here, instead, the among-population variability of vital rate elasticities was small despite the  
298 fact that the 37 study populations represented four different habitat types (Table S1).  
299 Similarly, given the fact that the present sampling covered a latitudinal gradient of 448 km,

300 and thus probably contained both relatively recent (a few years old) as well as more  
301 established invasions, invasion stage is also unlikely to explain the small degree of among-  
302 population variability of elasticities here. The study populations were also genetically  
303 differentiated (Li et al. 2016b), which is likely to increase rather than to reduce differences in  
304 population dynamics given that genetic structure parallels phenotypic variation. The small  
305 variability of asymptotic elasticities for different vital rates across the 37 populations of *L.*  
306 *polyphyllus* might, however, be partially explained by species lifespan. *Lupinus polyphyllus* is  
307 a short-lived perennial herb, with an estimated lifespan of only a few years (S-L. Li, unpubl),  
308 while other invasive plant species that exhibit considerable among-population variation in  
309 management recommendations are long-lived herbs or shrubs, with the estimated lifespan  
310 usually being decades (McMahon and Metcalf 2008). In order to confirm the possible effect  
311 of species lifespan on the spatial variability (or lack thereof) in management  
312 recommendations for an invasive plant species, more studies are required that take into  
313 consideration invaders with different lifespans.

314         In the present study, short-term population dynamics often differed from long-term  
315 population dynamics. The transient analysis revealed that all populations were predicted to  
316 reach higher densities relative to those predicted by  $\lambda$  when they were started from the  
317 observed size structures, while the opposite tended to be true when they were started from  
318 seeds. Higher densities compared to predictions based on  $\lambda$  imply that the populations tend to  
319 have higher initial reproductive values than expected (Koons et al. 2005). This could arise,  
320 for example, if the populations comprised of a larger proportion of flowering plants with high  
321 reproductive values and thus, a smaller proportion of seeds in the seed bank with low  
322 reproductive values than at the stable size structure. While the observed size structures  
323 aboveground generally matched quite well to the expected size structures, the visual  
324 inspection of the population size structures revealed that large plants were indeed slightly

325 overrepresented in several populations (Ramula 2014, supplementary material). Such bias  
326 towards large (flowering) individuals with high reproductive values particularly in the  
327 beginning of the study period seems to be common in perennial plants, and probably results  
328 from a non-random sampling due to the fact that large individuals are usually easier to detect  
329 in the field than smaller vegetative plants (Williams et al. 2011). In contrast, lower transient  
330 densities compared to those predicted by  $\lambda$  when populations initiated from seeds have been  
331 reported also elsewhere (Iles et al. 2016) and are generally expected due to mortality before  
332 reaching the reproductive stage. The only *L. polyphyllus* population that deviated from this  
333 pattern (and reached higher densities compared to predictions based on  $\lambda$ ) had the lowest  
334 asymptotic growth rate ( $\lambda = 0.52$ , Fig. 4b), suggesting that the seed bank buffered against a  
335 population decline in the short term. Regardless of the initial size structure, the rate of  
336 transient change (measured as case-specific inertia), however, varied among populations  
337 independently of  $\lambda$ . This observation echoes a previous comparative study among different  
338 plant species that found no relationship between short- and long-term population dynamics  
339 (Iles et al. 2016, but see Stott et al. 2010), indicating that vital rates contribute differentially  
340 to them and that both components may need to be considered separately when exploring  
341 population dynamics and different management options. In other words, asymptotic growth  
342 rate cannot be used to predict the rate of transient change. Since the present study utilised  
343 standardised transient measures, the findings on transient dynamics and their ramifications  
344 for management can be applied to short-lived plant invaders beyond the study species.

345         In summary, the present study demonstrates that asymptotic elasticities for vital rates  
346 (fecundity and survival in particular) change in relation to population growth rate. Despite  
347 this, the rank order of elasticities for main vital rates varied little across populations,  
348 suggesting that for already established populations of *L. polyphyllus*, asymptotic elasticities  
349 might be used to identify vital rates that are the best potential management targets. Moreover,

350 there were little qualitative differences in transient dynamics among populations; depending  
351 on the initial size structure, populations tended to reach either higher or smaller densities  
352 compared to predictions based on  $\lambda$ . These results indicate that management  
353 recommendations might be to some extent generalised for a given short-lived invasive plant  
354 species, which could reduce the effort required for the collection of demographic data.  
355 However, the efficiency of the same management actions is likely to vary among populations  
356 due to differences in the magnitude of transient dynamics.

357

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363

### 364 **Compliance with Ethical Standards**

365 The author declares no conflict of interest.

366

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494 Figure legends

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496 **Fig. 1** Asymptotic elasticities for survival, growth, retrogression, and fecundity in relation to  
497 the size of *Lupinus polyphyllus* individuals in 37 populations. Note that seed bank is not  
498 included in the survival and growth elasticities here (see Fig. 2 for seed bank elasticities).

499 Black lines indicate increasing populations ( $\lambda > 1.0$ ) and grey lines indicate declining  
500 populations ( $\lambda < 1.0$ )

501

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

504

505 **Fig. 3** Asymptotic elasticities summed separately for survival, growth, retrogression, and  
506 fecundity in relation to the asymptotic population growth rate of *Lupinus polyphyllus*. Each  
507 dot represents a population (n = 37 populations). Shown are Spearman's rank correlations (r);  
508 statistically significant correlations ( $P < 0.05$ ) after a sequential Bonferroni correction are  
509 indicated with an asterisk

510

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

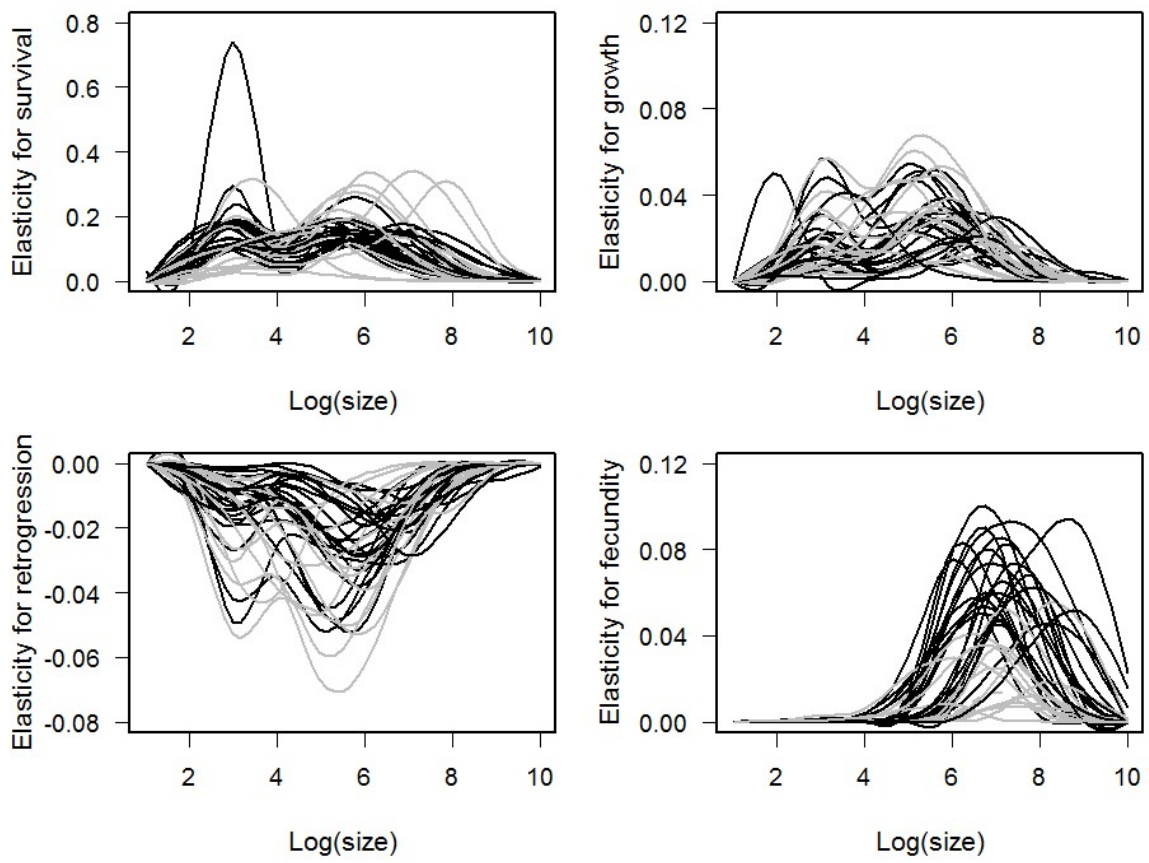


Fig. 1

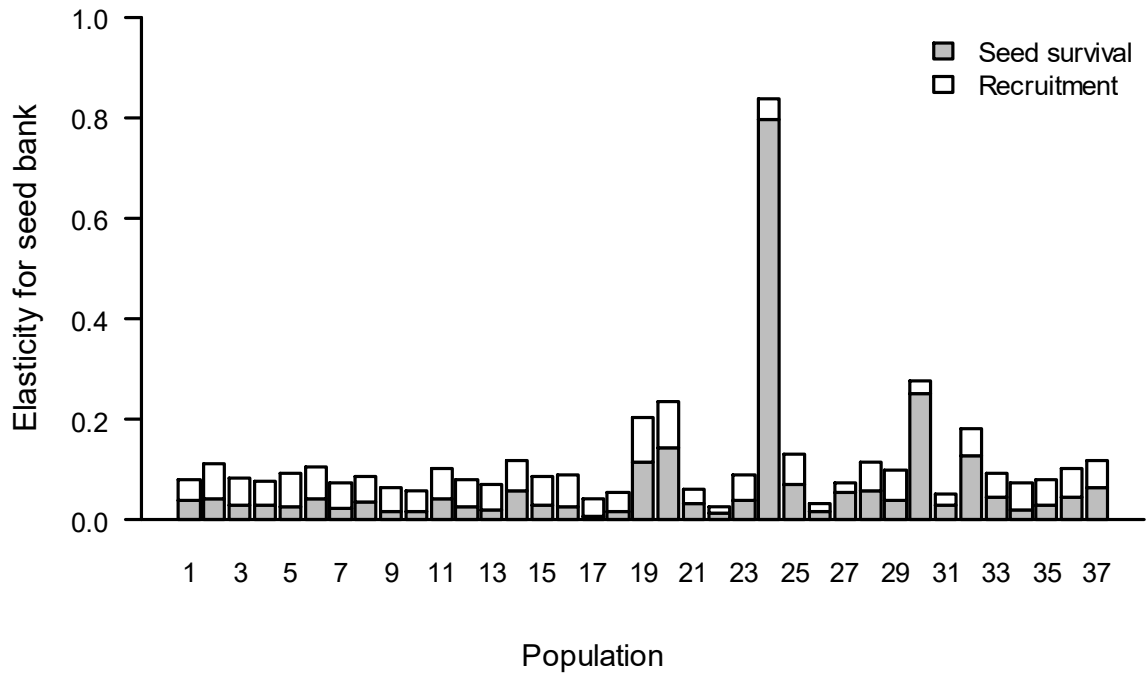


Fig. 2



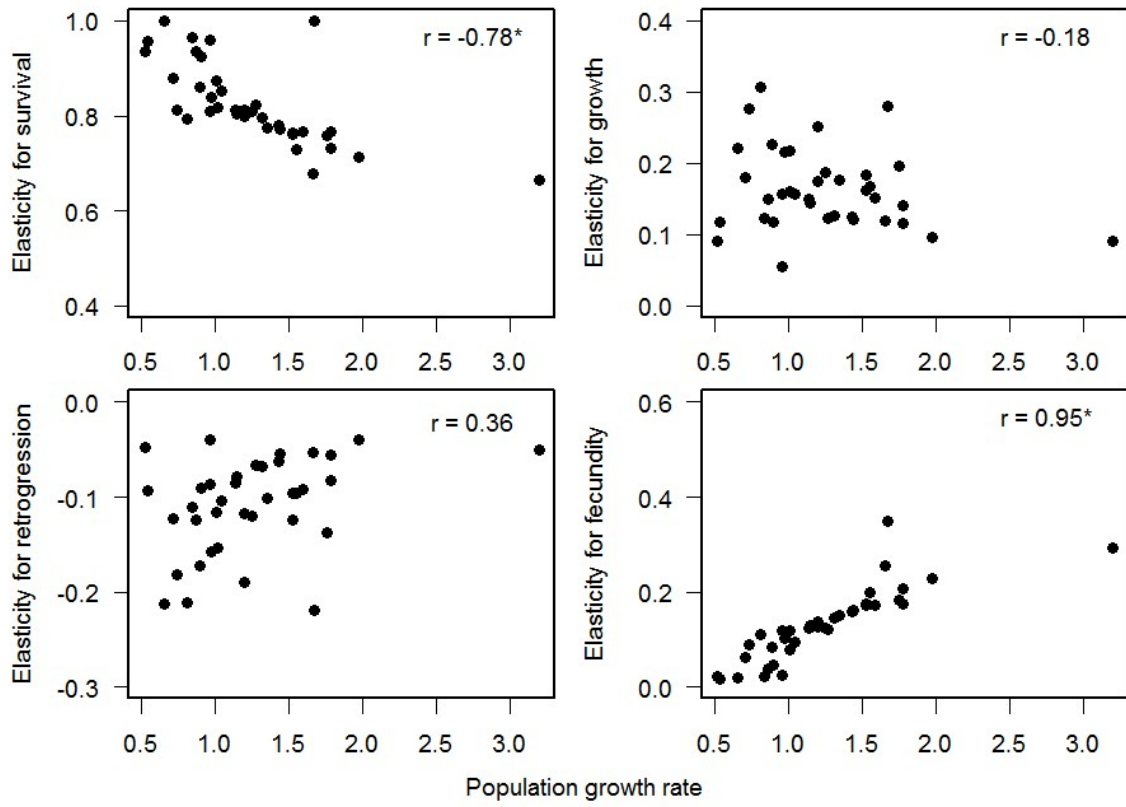


Fig. 3

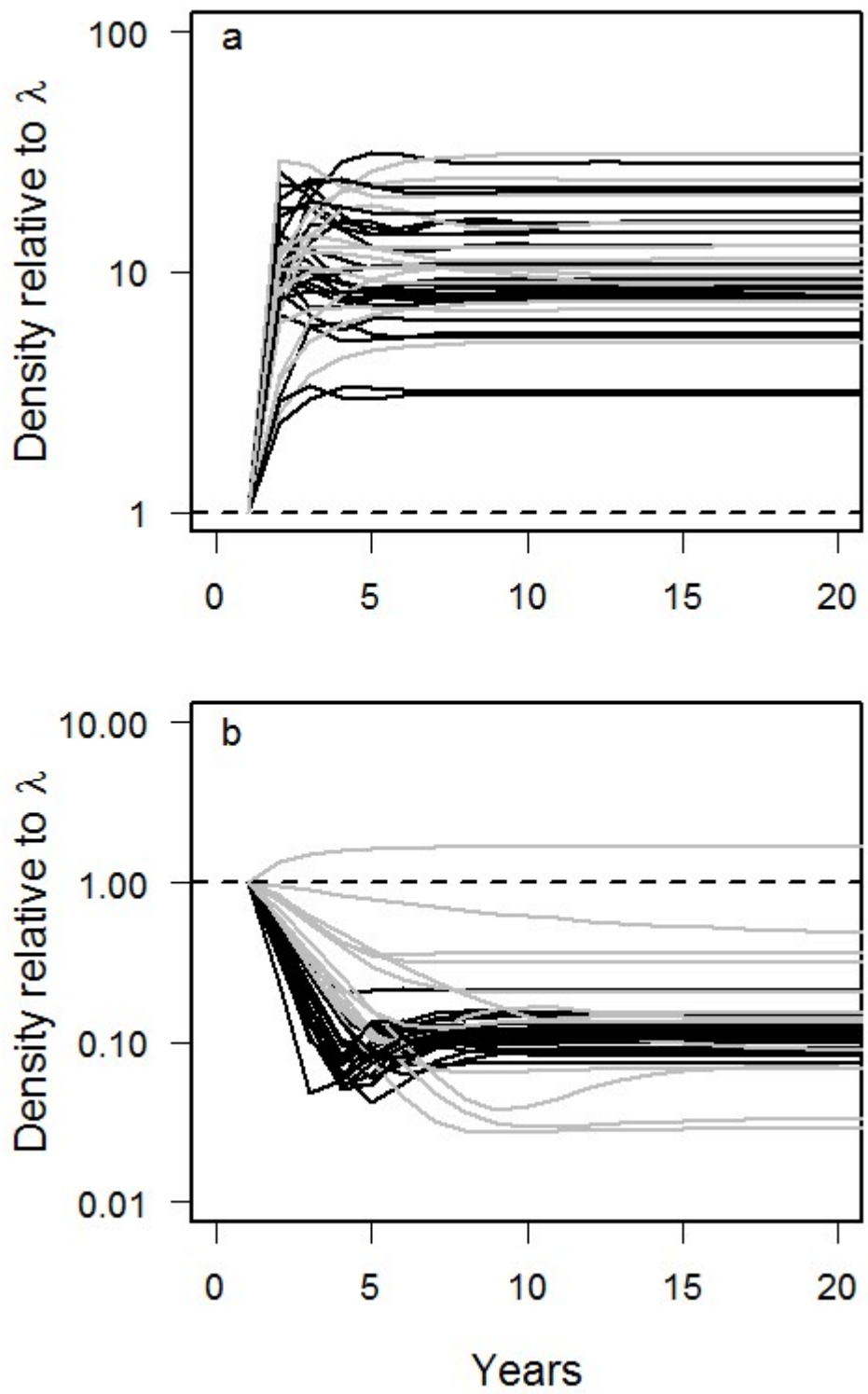


Fig. 4