The influence of time since introduction on the population growth of introduced species and the consequences for management

Hiroyuki Yokomizo1 · Takenori Takada2 · Keiichi Fukaya3 · John G. Lambrinos4

Introduction

Demographic processes drive the population growth and spread of invasive species (Rejmanek and Richardson 1996; Sakai et al. 2001). As a consequence, the design of optimal management strategies should take into account the species and context dependent demography of invasive populations (Taylor and Hastings 2004; Ramula et al. 2008). For example, elasticity analysis of the components of demographic rates (stasis, fecundity, growth) has been used to identify the most important life stages and demographic transitions to target during management (Ramula et al. 2008). A complicating factor for these efforts is the potential for demographic rates to change over the time course of an invasion. Several factors potentially change the demography, vital rates, and population growth of introduced populations both relative to populations in the native range and over time as invasions progress (Lambrinos 2004; Strayer et al. 2006; Flory and D’Antonio 2015; Iacarella et al. 2015). Empirical and theoretical evidence exists for at least three broad mechanisms driving these changes: founder effects, novel environmental interactions, and adaptive evolution.

Founder effects at the start of an invasion or along an invasion front can create Allee effects or alter patterns of genotypic and phenotypic diversity that in turn influence

Abstract

Several processes likely act to change the demographic rates of introduced species over time, and this changing demography could influence the optimal management of invasive populations. Optimal management strategies should be derived based on the demography. However, we have a poor understanding of the degree to which the demography of introduced species changes following initial introduction. We used published matrix population models of introduced plant populations to test how population growth rate and elasticity change with time since introduction. We did not find a significant relationship between population growth rate and time since introduction. However, elasticity to stasis increased while elasticity to growth decreased with time since introduction. Broadly, as time since introduction progressed the elasticities of the introduced plant populations became more similar to those that have been reported for native species. These results suggest that the optimal management strategy should be derived incorporating elasticity through time, especially when the time scope of management is long or the available demographic data were obtained in the past.

Keywords

Elasticity · Invasive plants · Management · Matrix models · Population growth rate · Time since introduction

Electronic supplementary material

The online version of this article (doi:10.1007/s10144-017-0581-6) contains supplementary material, which is available to authorized users.

Hiroyuki Yokomizo is the recipient of the 8th Population Ecology Young Scientist Award.

Hiroyuki Yokomizo
hiroyuki.yokomizo@nies.go.jp

1 Center for Health and Environmental Risk Research, National Institute for Environmental Studies, Onogawa 16-2, Tsukuba 305-8506, Japan

2 Graduate School of Environmental Science, Hokkaido University, Sapporo 060-0810, Japan

3 The Institute of Statistical Mathematics, 10-3 Midori-cho, Tachikawa, Tokyo 190-8562, Japan

4 Department of Horticulture, Oregon State University, Corvallis, OR 97331, USA
vital rates (Taylor and Hastings 2005; Forsman 2014). These founding events are typically thought to reduce fitness and population growth during the early stages of an invasion, although the overall influence of founding processes on invasive population dynamics is complex and broadly not well understood (Dlugosch et al. 2015). For example, the reduced molecular genetic variation frequently observed in founding populations does not necessarily correspond to levels of quantitative fitness related trait variation, which in some cases can increase following bottlenecks or shift to more advantageous allelic compositions (Facon et al. 2011; Stapley et al. 2015). Founder effects can also be relatively transient as population growth or additional immigration mitigate Allee effects, alter other density dependent processes such as intraspecific competition, buffer populations from stochastic effects, or increase levels of potentially adaptive variation (Antonovics and Levin 1980; Kanarek et al. 2015).

Introduced populations encounter a range of novel environmental conditions that potentially alter demographic rates (novel environmental interactions). One of the most salient hypotheses for the demographic success of invasive populations is the absence of coevolved natural enemies in the introduced range (Keane and Crawley 2002). A wide range of other abiotic and biotic factors can also potentially influence the population dynamics of introduced species including unique or fluctuating abiotic conditions (Davis et al. 2000; Gerhardt and Collinge 2007; Guisan et al. 2014), interactions with native communities (Maron and Vilà 2001; Callaway and Ridenour 2004), and direct or indirect interactions with other introduced species (Simberloff and Holle 1999; Meza-Lopez and Siemann 2015). In aggregate, the influence of novel environments on the growth of introduced populations is complex and has resisted generalization. For example, while there is relatively strong evidence that invasive plant populations experience reduced natural enemy loads and damage, there is far less evidence that this translates into enhanced performance or explains their demographic success (Chun et al. 2010; Heger and Jeschke 2014).

Adaptive evolution in life history could either increase or decrease the growth rate of introduced populations. One frequently invoked hypotheses in plants is that the absence of specialist predators and pathogens drive selection for increased competitive ability in the invader: the evolution of increased competitive ability (EICA) hypothesis (Blossey and Notzold 1995). Empirical evidence for this hypothesis is equivocal, and has been hampered by methodological limitations (Felker-Quinn et al. 2013; Colautti and Lau 2015). Contrastingly, other selective pathways can act to reduce invasive population growth. Increasing abundance of invasive populations can act as a selective agent on native species, which in turn have negative feedbacks on invader population growth. There is evidence that native species have evolved to feed on and better compete with introduced species (Strauss et al. 2006; Strayer et al. 2006; Berthon 2015), although few studies have linked these changes to feedbacks on invader fitness or population growth.

There may be no general pattern to the changing demographic characteristics of introduced populations over time given the context and species specific nature of the forces acting on vital rates. On the other hand, the type and nature of the forces influencing demography might vary predictably over the time course of invasion. Factors such as enemy release that favor high population growth rate could predominate during the early stages of an invasion, while factors such as evolution in native natural enemies that favor reduced population growth could predominate during later stages. This would drive broad comparative differences in demographic traits between younger and older introduced populations. Only a few studies have explicitly tested how the invasion process alters demography across a large number of species, and these have primarily compared introduced populations to native counterparts. Moreover, the aggregate results have been equivocal. For example, Ramula et al. (2008) compared matrix population models of 21 invasive and 179 native plant populations and found that invaders had higher population growth rates and different transition elasticities compared to natives. Parker et al. (2013) compared population data from both the native and introduced range of 53 introduced species and found that while species (particularly plants) generally performed better in the introduced range, more than half of the species in their study performed similarly in both ranges. In addition, there was no effect of time since introduction on the degree of performance difference between ranges.

Optimal management strategies in the current time step need to take into account future population dynamics (e.g., Yokomizo et al. 2009, 2014). Hence if the vital rates of demographic processes or their elasticities commonly change over time since introduction, then management actions would need to be equally as dynamic. Moreover, if management decisions are based on demographic data taken a long time ago, any subsequent demographic change might make the management decision sub-optimal. However, most studies on optimal management do not incorporate changing vital rates or time since introduction dependent transition probabilities.

While we have strong evidence that a range of processes likely act to change the demographic rates of introduced species over time, it is unclear if these result in general patterns of demographic change as invasions progress, or if time since invasion should be considered when developing optimal control strategies. In this study we used published matrix population models of introduced plant
populations to describe how population growth rate and elasticity to demographic processes change with time since introduction.

**Method**

**Study and matrix selection**

We used keyword searches in the Web of Science (ISI), Google Scholar, and the COMPADRE (Salguero-Gómez et al. 2015; http://www.compadredb.org) databases to find published matrix population models for vascular plant populations in an introduced range. We limited matrices to those that were parameterized using field collected data of geographically distinct populations over a defined time period. We excluded matrices derived from populations under greenhouse or environmentally controlled conditions and matrices that were parameterized using an amalgam of literature derived data from disparate populations and times. Some matrices contained a few matrix element or vital rate parameters that were estimated using expert knowledge or literature values. We included these matrices in our database if the approximated or literature derived values were based on dynamics observed in the invasive range of the species and the majority of parameters in the model were derived from direct field observations of specific populations. In addition, some matrices were parameterized using mean matrix element or vital rate across several study populations. We included these matrices as long as the populations used to generate the mean matrix element or vital rate were within the same geographic area and studied at the same time. Several studies explicitly tested the role of natural enemies on population dynamics through competitor or predator exclusions. In these cases we selected only matrices based on un-manipulated control populations. We used values of population growth rate from literature without obtaining their projection matrix for some species. We excluded COMPADRE data in which the largest maximum stage-specific survival was larger than one.

**Time since introduction and range definition**

We defined the native or introduced status of populations relative to the eight terrestrial biogeographic realms. We used a combination of published observations and historical accounts, to identify the earliest confirmed date of introduction into a biogeographic realm for each species. In some cases this date was well documented, but in others introduction pathways and timing were less clear. In some cases minimum time since introduction could only be inferred by the first recorded herbarium record. In other cases we approximated time since introduction to the nearest decade when rough introduction estimates were available. For example, *Raphanus sativus* and *Tragopogon dubius* are known to have been introduced in the “mid-1800s” and early “1900s”; in our database we set their respective introduction dates as 1850 and 1900.

**Calculating population growth rate (λ) and elasticity**

We calculated population growth rate (λ) for each of our compiled matrices. For many species this resulted in multiple λ values reflecting different populations and time periods (both within and across studies). We calculated the arithmetic mean of λ and each element of the elasticity matrices for populations within the same biogeographic realm and within the same time since introduction. We calculated the geometric mean of λ when we have λ for consecutive years within the same decade in the same populations. As noted above, some published matrices were based on average matrix elements or vital rates across several study populations.

Elasticity describes the relative effects of changing matrix elements or vital rates on λ. The sum of elasticities within a matrix is one (Caswell 2001). We obtained elasticities to each matrix element and categorized it into S (stasis), F (fecundity), or G (growth). The diagonal elements, which indicate that a status does not change during 1 year, were categorized into S (stasis). The other elements which indicate the transition to the state of seed or seed bank were categorized into F (fecundity). If the projection matrix did not include the state of seed or seed bank, the elements of the smallest size were categorized into F (fecundity). The other elements were categorized to G (growth). G (growth) includes progression, retrogression, clonal growth and recruitment of juveniles or seedlings from current seed production. Other studies such as Silvertown et al. (1993) and Ramula et al. (2008) categorized retrogression into S and recruitment of juveniles or seedlings from current seed production into G. We categorized matrix elements differently because it was difficult to distinguish among retrogression, clonal growth and recruitment of juveniles or seedlings from current seed production.

We obtained population growth rates for 47 species (57 populations). Those 57 populations consisted of 35 forbs, 10 shrubs, 8 trees, 2 graminoids, 1 succulent, 1 vine populations as growth forms; in terms of life cycles the populations consisted of 10 annuals, 6 biennials, and 41 perennials (Table S1 in Electronic Supplementary Material (ESM)). We also obtained elasticities for 34 species (43 populations) with time since introduction. Those 43 populations consisted of 28 forbs, 8 shrubs, 5 trees, 1 graminoid, 1 succulent, as growth forms, and 6 annuals, 5 biennials, 32 perennials as life cycles (Table S1 in ESM).
Statistical analysis

To investigate the relationship between time since introduction and population growth rate we conducted a linear regression analysis in which years since introduction was regressed on log transformed growth rate. Matrix dimension is known to affect elasticities (Ramula et al. 2008; Salguero-Gómez and Plotkin 2010) so we analyzed dependences of the elasticities on population growth rate on both time since introduction and matrix dimension using Dirichlet regression models. Dirichlet regression is used to analyze a set of bounded variables whose sum is constant such as proportion and probability (e.g., Adler et al. 2014). It is appropriate to analyze variation in elasticities as well, since elasticities sum to one. Six models with different sets of explanatory variables were fitted for analysis of elasticities. Three models of elasticities were (1) intercept only (null model), (2) years since introduction (linear model), (3) years since introduction and its square (quadratic model). In addition, we considered three additional models that included matrix dimension added as an explanatory variable to the three models. Akaike’s Information Criterion (AIC) and Bayesian information criterion (BIC) were used to compare these models. All analyses were conducted in R 3.3.1 software (R Development Core Team 2016) where lm() function is used for the former analysis and DirichReg() function in DirichletReg package (Maier 2015) is used to the latter.

In our data set, multiple populations of the same species are included (4 populations for 2 species and 2 populations for 3 species). We also conducted additional analysis to use only one data point for each species to remove the dependence of the multiple data points for one species (there are 128 cases for the data set) (see Table S2 in ESM).

Results

The linear regression analysis of logarithmic population growth log $\lambda$, against years since introduction was not statistically significant ($F_{1,55} = 0.327$, $P = 0.570$) (Fig. 1). We did not find any significant relationship between logarithmic population growth rate and time since introduction even when we analyzed the relationship for each growth form (forb, shrub, tree) separately (results are not shown).

Among the six Dirichlet regression models we examined for elasticities, the linear model, which includes years since introduction and matrix dimension as explanatory variables, had the minimum value of AIC and BIC (Table 1). Parameter estimates of this best-fitted model are shown in Table 2. The result indicates that years since introduction significantly influence elasticities. Elasticity to G decreases with time since introduction (Fig. 2). Elasticity to F is almost constant with time since introduction and relatively smaller than that of S and G (Fig. 2). The precision decreases with time since introduction (solid line in Fig. 2). This means that elasticities tend to be less concentrated around the conditional mean as the time since introduction increases.

The result of model selection indicates that matrix dimension also significantly influences elasticities. Elasticity to S increases with matrix dimension while elasticity to F decreases with matrix dimension (Fig. 3). Elasticity to G is almost constant with matrix dimension (Fig. 3). The precision of the Dirichlet distribution increases with matrix dimension (solid line in Fig. 3). Hence, the elasticities of smaller matrices tend to have lower precision, which means that the values of elasticities are more likely to deviate from the conditional means than those of larger matrices.

Additional analysis to remove the dependence of the multiple data points for one species concluded that the best model selected by AIC does not change and includes both years since introduction and matrix dimension. On the other hand, the best model selected by BIC in 71.9% of the cases includes only years since introduction and the best model in 28.1% of the cases includes both years since introduction and matrix dimension (see Table S2 in ESM). Based on the best models selected by AIC and BIC, it is reasonable to consider that elasticities change with time since introduction.
Discussion

We used published matrix population models of introduced plant populations to describe how population growth rate and elasticity change with time since introduction. While we did not find a significant relationship between population growth rate and time since introduction, we did observe an overall shift in the relative importance of the components of demographic processes. Elasticity to stasis increased with time since introduction, while elasticity to growth decreased with time since introduction. These shifts imply that optimal management strategies should incorporate changing elasticity through time, especially when the time scope of management is long or the available demographic data were obtained in the past.

Our inability to detect an overall influence of time since introduction on population growth is likely partly a result of the diverse life histories of the species in our dataset. A better approach would be to standardize introduced population

Table 1 AIC and BIC values of the six fitted Dirichlet models testing the relationship between time since introduction and summed stasis (S), fecundity (F), and growth (G) elasticities on population growth for introduced plant populations

| Models                   | AIC    | BIC    |
|--------------------------|--------|--------|
| Without matrix dimension |        |        |
| Null model               | −129.3 | −124.0 |
| Linear model             | −149.6 | −139.1 |
| Quadratic model          | −148.4 | −132.5 |
| With matrix dimension    |        |        |
| Null model               | −140.4 | −129.8 |
| Linear model             | −155.7 | −139.8 |
| Quadratic model          | −153.9 | −132.8 |

Table 2 The effect of time since introduction of plant populations and matrix dimension on summed elasticities on population growth for (1) stasis, (2) fecundity and (3) growth of the best-fitted model (linear model with matrix dimension) with Dirichlet regression

|                      | Estimate | SE     | Z     | P    |
|----------------------|----------|--------|-------|------|
| (1) Stasis           |          |        |       |      |
| Intercept            | −1.052   | 0.5589 | −1.883| 0.0597|
| Time since introduction | −0.003278 | 0.002134 | −1.536 | 0.1244|
| Matrix dimension     | 0.3325   | 0.08546 | 3.890 | 0.0001|
| (2) Fecundity        |          |        |       |      |
| Intercept            | −0.5553  | 0.4818 | −1.152| 0.2491|
| Time since introduction | −0.004695 | 0.001658 | −2.832 | 0.00463|
| Matrix dimension     | 0.1124   | 0.08087 | 1.390 | 0.1645|
| (3) Growth           |          |        |       |      |
| Intercept            | 0.2130   | 0.5676 | 0.375 | 0.7075|
| Time since introduction | −0.006136 | 0.001694 | −3.622 | 0.000292|
| Matrix dimension     | 0.2769   | 0.08916 | 3.106 | 0.001899|

Fig. 2 Relationship between time since introduction and summed stasis (S), fecundity (F), and growth (G) elasticities on population growth for introduced plant populations. Elasticities are calculated from published population projection matrices. Dashed, dotted and dot-and-dash line indicates the Dirichlet regression lines for the elasticity of S, F and G, respectively. Bold line shows precision of the Dirichlet distribution, which is defined as the sum of all parameters of the Dirichlet distribution conditional on years since introduction and matrix dimension; the lower precision value indicates each elasticity value deviates largely from its expected value with higher probability. Mean value of matrix dimensions (4.60) is used on the plots

Fig. 3 Relationship between matrix dimensions and summed stasis (S), fecundity (F), and growth (G) elasticities on population growth for introduced plant populations. Dashed, dotted and dot-and-dash line indicates the Dirichlet regression lines for the elasticity of S, F and G, respectively. Bold line shows precision of the Dirichlet distribution conditional on years since introduction and matrix dimension. Mean value of time since introduction (160.65) is used on the plots
growth rates relative to that of conspecific populations in the native range. We were unable to do that in this study because of the lack of matrix population models for species in both the native and introduced ranges. Of the 47 species in our dataset only five had published models that we could obtain population growth rates for populations in both the native and introduced ranges. In addition, incomplete sampling and inherent differences in environmental and spatial clines within the respective ranges can also complicate performance comparisons between native and introduced populations (Colautti and Lau 2015). The accumulation of long-term demographic data of introduced meta-populations, as well as broader spatial and temporal coverage of demographic data for populations in both native and introduced ranges is needed to better understand how introduced population dynamics change over time. For some species, considerable time has passed since the study from which we obtained matrix models was conducted. New research to collect contemporary population data could allow the creation of more longitudinally structured datasets, which would be useful for testing how population growth and other demographic parameters change over time.

Beyond this methodological constraint, the high spatial and temporal variability of invader-environment interactions, as well as their highly species and context specific nature likely also act to obscure any general influence of time since invasion on population growth rate. For example, available data suggest no consistent pattern to how invasive plant-soil feedbacks influence individual performance or population growth, and the nature of these feedbacks is partly dependent on the growth form of the invader (Suding et al. 2013; Meisner et al. 2014). Similarly, the relative influence of positive and negative selective pressures on invader population growth reflects complex eco-evolutionary feedbacks that vary in space and time. A good example comes from Alliaria petiolata populations invading North America. Evans et al. (2016) demonstrate how shifts in the relative strengths of interspecific and intraspecific competition drive selective pressure on population growth rate of A. petiolata. Initially and along the low density leading front of the invasion, production of the allelochemical sinigrin enhances the survival of juvenile life stages facing high levels of interspecific competition. As the density of A. petiolata increases, natural selection shifts to favor reduced sinigrin production due to the intense intraspecific competition among seedlings, but with a tradeoff of reduced per capita juvenile survival. As a consequence, young A. petiolata populations at the leading front of the invasion have the highest stochastic growth rate, while older populations have lower or even negative stochastic population growth (Evans et al. 2016). In addition, the success of A. petiolata in North America has been strongly linked to the over-abundance of white-tailed deer, which preferentially suppress native competitors and create disturbed conditions that favor A. petiolata. In a long-term deer exclusion study A. petiolata population had high annual population growth in the presence of deer, but negative population growth when deer were excluded (Kalisz et al. 2014).

We did find that time since introduction significantly shifted the relative importance of the demographic processes, with the elasticity to growth decreasing and that of stasis increasing with time since introduction. This pattern is similar to those reported by Ramula et al. (2008) who performed a comparative elasticity analysis of invasive and native species using published matrix population models. They found that native and invasive species differed in their elasticities; invasive species had lower average elasticity to survivorship and higher average elasticity to growth compared to native species (Ramula et al. 2008). Our observed increase in S and decrease in G with time since introduction suggests that the elasticities to fundamental demographic processes of introduced species may become more similar to those of native species through time since introduction. However, we need to note that we categorized S, F, G partially differently than Ramula et al. (2008). Ramula et al. (2008) categorized retrogression into S and recruitment of juveniles or seedlings from current seed production into F, while we categorized them into G due to inadequate information and therefore, the value of G tends to be greater than that of Ramula et al. (2008). It is also possible that the apparent convergence in elasticities between native and introduced species could simply reflect unequal sampling of population age distributions of the two ranges: many of the data for native species may have been collected from more established populations compared to the data for introduced species.

Elasticity to fecundity, F, did not change as much through time since introduction. This might reflect a lack of data for populations that have recently been introduced because fecundity related processes may exert a relatively strong influence during the initial introduction stages. There is theoretical and empirical evidence that reduced intraspecific competition along the low density front of an invasion can select for traits such as fecundity that contribute to increased population growth and spread rate (Hastings et al. 2005; Perkins et al. 2013; Williams et al. 2016). We need more data of alien species at the early stage of introduction to detect any changes in elasticity to fecundity (F), although these types of data are usually not obtained until later in the invasion process and then often only if the species has become a management problem.

Analyses using vital rates rather than matrix elements are useful to avoid dependencies between survival, growth and fecundity and for providing practical insights on the management of invasive species. However we could not use...
vital rates in this study because we lacked direct information about vital rates for most of the species in our database. Since vital rates or matrix elements are not uniformly variable, elasticity analyses that incorporate this variation could be useful for developing species-specific management strategies (Zuidema and Franco 2001). We also did not consider the influence of phylogenetic relationship among species. Population characteristics may be more similar among related species compared to those of phylogenetically more distant species, which may introduce a bias in our inference. However, as far as we know, Dirichlet regression analysis that accounts for phylogenetic dependence is not available yet. One possible approach is to incorporate the phylogenetic relationships using phylogenetic generalized least squares (PGLS) regression (e.g., Adler et al. 2014), but this cannot deal with the interdependence between the elasticities differently from Dirichlet regression.

Our observed shifts in S, F, G elasticities suggest that control efforts targeted at reducing transitions to larger size classes or clonal growth should be more effective in relatively new invasive populations. However even if targeting reduced growth is optimal in the short term, it may not always remain the case over a longer time scope of management due to change in the elasticities. A range of management tools and approaches are available that each target specific demographic processes of invasive populations. Consequently, management strategies, either by design or accident, often reduce specific matrix elements that correspond to S (stasis), F (fecundity) or G (growth) (Ramula et al. 2008). For example, strategies designed to minimize the current environmental impact of invasion or to facilitate a restoration goal typically target established individuals through techniques such as mowing, grazing or clipping. These approaches reduce transitions to larger classes and reduce G. In other instances, management strategies are specifically design to reduce F. For example, burning or mowing plants before seed maturation or biocontrol agents that consume flowers or seeds (e.g., Buckley et al. 2004; Davis et al. 2006; Gutierrez et al. 2005; Shea et al. 2006). Strategies reducing seed production could also reduce G because we categorized the matrix elements where seeds grow into the second classes from current seed productions into G.

We need to choose management measures that take into account the stage specific cost of management in addition to elasticities (e.g., Baxter et al. 2006) and it may not always be optimal to invest in management measures to reduce larger elasticities. For example, Buhle et al. (2005) used a bioeconomic approach to find the optimal strategy for controlling invasive oyster drills (Ocinebrellus inornatus). They found that targeting adult survival was optimal even though its population elasticity was lower than targeting juvenile stages that contributed to fecundity because of the markedly cheaper cost of controlling adults. However, this strategy was not optimal during periods of peak reproduction suggesting that time dependent changes in population growth rate or demographic processes will shift the optimal control strategy. Hastings et al. (2006) found that a time varying strategy that switched from removing the stage with the highest reproductive value per unit cost to the stage that contributes most to next season’s population per unit cost was more optimal than a fixed strategy.

It is difficult to derive the optimal management effort strategy precisely incorporating the change in elasticity because the precision of the regression was not enough to predict change in elasticities. However, our findings suggest that incorporating changes in elasticity could improve the effectiveness of management guidelines especially for long time scopes of management. Our results also indicate that management decisions based on old demographic data could lead to sub-optimal management due to change in elasticities.

Acknowledgements We thank Dr. Gaku Takimoto and two anonymous reviewers for their constructive comments. This work was supported by JSPS KAKENHI Grant Numbers 26291087 and 15H04418.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References
Adler PB, Salguero-Gomez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M (2014) Functional traits explain variation in plant life history strategies. Proc Natl Acad Sci 111:740–745
Antonovics J, Levin DA (1980) The ecological and genetic consequences of density-dependent regulation in plants. Annu Rev Ecol Syst 11:411–452
Baxter PWJ, McCarthy MA, Possingham HP, Menkhorst PW, McLean N (2006) Accounting for management costs in sensitivity analyses of matrix population models. Conserv Biol 20:893–905
Berthon K (2015) How do native species respond to invaders? Mechanistic and trait-based perspectives. Biol Inv 17:2199–2211
Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889
Buckley YM, Rees M, Paynter Q, Lonsdale M (2004) Modelling integrated weed management of an invasive shrub in tropical Australia. J Appl Ecol 41:547–560
Buhle ER, Margolis M, Ruesink JL (2005) Bang for buck: cost-effective control of invasive species with different life histories. Ecol Econ 52:355–366
Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Front Ecol Environ 2:436–443

Caswell H (2001) Matrix population models, 2nd edn. Sinauer Associates, Sunderland

Chun YJ, van Kleunen M, Dawson W (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. Ecol Lett 13:937–946

Colautti RI, Lau JA (2015) Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. Mol Ecol 24:1999–2017

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Davis AS, Landis DA, Nuzzo V, Blossey B, Gerber E, Hinz HL (2006) Demographic models inform selection of biocontrol agents for garlic mustard (Alliaria petiolata). Ecol Appl 16:2399–2410

Dlugosch KM, Anderson SR, Braasch J, Cang FA, Gillette HD (2015) The devil is in the details: genetic variation in introduced populations and its contributions to invasion. Mol Ecol 24:2095–2111

Evans JA, Lankau RA, Davis AS, Raghu S, Landis DA (2016) Soil-mediated eco-evolutionary feedbacks in the invasive plant Alliaria petiolata. Funct Ecol 30:1053–1061

Facon B, Hulbauer RA, Tayeh A, Loiseau A, Lombaert E, Vitalis R, Guillemaud T, Lundgren JG, Estoup A (2011) Inbreeding depression is purged in the invasive insect Harmonia axyridis. Current Biol CB 21:424–427

Felker-Quinn E, Schweitzer JA, Bailey JK (2013) Meta-analysis reveals evolution in invasive plant species but little support for evolution of increased competitive ability (EICA). Ecol Evol 3:739–751

Flory SL, D’Antonio CM (2015) Taking the long view on the ecologi cal effects of plant invasions. Am J Bot 102:817–818

Forsman A (2014) Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. Proc Natl Acad Sci 111:302–307

Gerhardt F, Collinge SK (2007) Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. Ecol Appl 17:922–933

Guisan A, Petitpierre B, Jack H, Artaxo P, Guillemaud T, Lundgren JG, Estoup A, Micol E, Aimé C (2016) Spatial distribution of invasive species. PLoS One 11:e0153566

Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA, Moore K, Taylor C, Thomson D (2005) The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 8:91–101

Hastings A, Hall RJ, Taylor CM (2006) A simple approach to optimal control of invasive species. Theor Popul Biol 70:431–435

Heger T, Jeschke JM (2014) The enemy release hypothesis as a hierarchy of hypotheses. Oikos 123:741–750

Iacarella JC, Mankiewicz PS, Ricciardi A (2015) Negative competitive effects of invasive plants change with time since invasion. Ecosphere 6:1–14

Kalisz S, Spigler RB, Horvitz CC (2014) In a long-term experimental demographic study, excluding ungulates reversed invader’s explosive population growth rate and restored natives. Proc Natl Acad Sci 111:4501–4506

Kanarek AR, Webb CT, Barfield M, Holt RD (2015) Overcoming Allee effects through evolutionary, genetic, and demographic rescue. J Biol Dynam 9:15–33

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Lambinos JC, Stow CA, Lamberson MJ, Paton WJ, Polunin NV, Thompson K (2009) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Maier MJ (2015) DirichletReg: Dirichlet regression in R. R package version 0.6–3. http://dirichletreg.r-forge.r-project.org/. Accessed 19 Apr 2017

Maron JL, Vilà M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373

Meissner A, Hol WHG, de Boer W, Krumins JA, Wardle DA, van der Putten WH (2014) Plant–soil feedbacks of exotic plant species across life forms: a meta-analysis. Biol Rev 16:2551–2561

Meza-Lopez MM, Siemann E (2015) Experimental test of the invasion meltdown hypothesis: an exotic herbivore facilitates an exotic plant, but the plant does not reciprocally facilitate the herbivore. Freshw Biol 60:1475–1482

Parker JD, Torchin ME, Hulbauer RA, Lemoine NP, Alca B, Blumenthal DM, Bossdorf O, Byers JE, Dunn AM, Heckman RW, Hejda M (2013) Do invasive species perform better in their new ranges? Ecology 94:985–994

Perkins AT, Phillips BL, Baskett ML, Hasting A (2013) Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. Ecol Lett 16:1079–1087

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ Accessed 19 Apr 2017

Ramula S, Knight TM, Burns JH, Buckley YM (2008) General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. J Appl Ecol 45:1124–1133

Rejmánek M, Richardson DM (1996) What Attributes make some plant species more invasive? Ecology 77:1655–1661

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O’Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive specie. Ann Rev Ecol Syst 32:305–332

Salguero-Gómez R, Plotkin JB (2010) Matrix dimensions bias demographic inferences: implications for comparative plant demographic. Am Nat 176:710–722

Salguero-Gómez R, Jones OR, Archer CR, Buckley YM, Che-Castaldo J, Caswell H Hodgson D, Scheuerlein A, Conde DA, Brinks E, de Buhr H, Farack C, Gottschalk F, Hartmann A, Henning A, Hoppe G, Rümer G, Runge J, Ruoff T, Wille J, Zeh S, Davison R, Vierdeg D, Baudisch A, Altwegg D, Colchero F, Dong M, de Kroon H, Lebrandon JD, Metcalf CJE, Neel MM, Parker IM, Takada T, Valverde T, Vélez-Espino LA, Wardle GM, Franco M, Vauel JW (2015) The COMPADRE plant matrix database: an open online repository for plant demography. J Ecol 103:202–218

Shea K, Sheppard A, Woodburn T (2006) Seasonal life-history models for the integrated management of the invasive weed thistling Carduus nutans in Australia. J Appl Ecol 43:517–526

Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous species. J Ecol 81:465–476

Simberloff D, Holle BV (1999) Positive interactions of nonindigenous species: Invasional meltdown? Biol Inv 1:21–32

Stanley J, Santure AW, Dennis SR (2015) Transposable elements as agents of rapid adaptation may explain the genetic paradox of invasive species. Mol Ecol 24:2241–2252

Stauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol Lett 9:357–374
Strayer DL, Eviner VT, Jeschke LM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21:645–651

Suding KN, Harpole WS, Fukami T, Kulmatiski A, MacDougall AS, Stein C, van der Putten WH (2013) Consequences of plant–soil feedbacks in invasion. J Ecol 101:298–308

Taylor CM, Hastings A (2004) Finding optimal control strategies for invasive species: a density-structured model for Spartina alterniflora. J Appl Ecol 41:1049–1057

Taylor CM, Hastings A (2005) Allee effects in biological invasions. Ecol Lett 8:895–908

Williams JL, Kendall BE, Levine JM (2016) Rapid evolution accelerates plant population spread in fragmented experimental landscapes. Science 353:482–485

Yokomizo H, Possgim HP, Thomas MB, Buckley YM (2009) Managing the impact of invasive species: the value of knowing the impact-density curve. Ecol Appl 19:376–386

Yokomizo H, Coutts SR, Possgim HP (2014) Decision science for effective management of populations subject to stochasticity and imperfect knowledge. Popul Ecol 56:41–53

Zuidema PA, Franco M (2001) Integrating vital rate variability into perturbation analysis: an evaluation for matrix population models of six plant species. J Ecol 89:995–1005