

REVIEW

Advancing population ecology with integral projection models: a practical guide

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Summary

1. Integral projection models (IPMs) use information on how an individual's state influences its vital rates – survival, growth and reproduction – to make population projections. IPMs are constructed from regression models predicting vital rates from state variables (*e.g.* size or age) and covariates (*e.g.* environment). By combining regressions of vital rates, an IPM provides mechanistic insight into emergent ecological patterns such as population dynamics, species geographic distributions or life-history strategies.

2. Here, we review important resources for building IPMs and provide a comprehensive guide, with extensive R code, for their construction. IPMs can be applied to any stage-structured population; here, we illustrate IPMs for a series of plant life histories of increasing complexity and biological realism, highlighting the utility of various regression methods for capturing biological patterns. We also present case studies illustrating how IPMs can be used to predict species' geographic distributions and life-history strategies.

3. IPMs can represent a wide range of life histories at any desired level of biological detail. Much of the strength of IPMs lies in the strength of regression models. Many subtleties arise when scaling from vital rate regressions to population-level patterns, so we provide a set of diagnostics and guidelines to ensure that models are biologically plausible. Moreover, IPMs can exploit a large existing suite of analytical tools developed for matrix projection models.

Key-words: demography, elasticity, life history, matrix projection model, population growth rate, population projection model, sensitivity, stage structure, vital rates

Introduction

Demography underpins many contemporary challenges in ecology. From understanding species' distributions to the fate of biodiversity under climate change, demography links the processes that affect individuals to population- and community-level patterns (*e.g.* Adler, Ellner & Levine 2010). Integral projection models (IPMs; Easterling, Ellner & Dixon 2000) have emerged as a powerful tool for quantifying how the vital

rates of individuals (*i.e.* survival, growth and fecundity) govern such higher-level properties, partly because they rely on the flexibility and simplicity of regression models. IPMs provide a mechanistic approach to understanding and linking biological processes across scales, which permits evaluation of the biological plausibility of models at each step of the analysis to make robust predictions (Fig. 1).

Building IPMs typically begins by obtaining longitudinal data describing individuals' vital rates. The minimum data required for an IPM consists of two censuses of individual state and fate (typically for estimation of survival and growth and optionally fecundity; Appendix S1–S7). The fundamental

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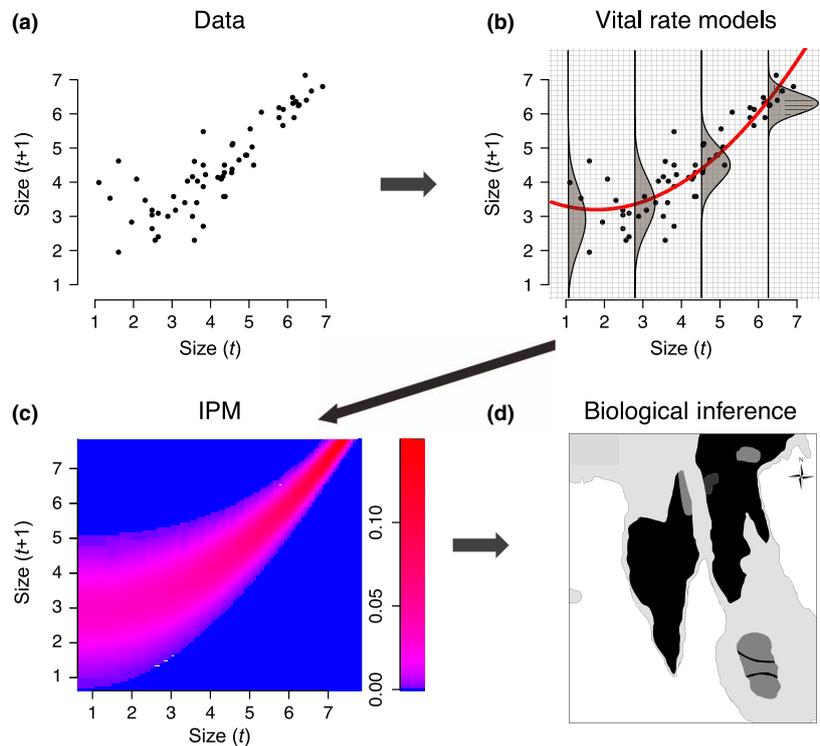


Fig. 1. Workflow for Integral projection models (IPMs). Regression is used to link demographic observations to biological inference. (a) A typical relationship between an individual's size in successive time intervals ($g(z'|z)$). (b) The expected size at time $t + 1$ is modelled using a quadratic regression (red line) of size at time t . The variance is modelled as a decreasing linear function of size at time t and illustrated with density functions for four initial sizes. A grid is overlaid on these continuous regression functions to perform the integration (using the midpoint rule) necessary for an IPM. (c) The discretized IPM kernel, derived from combining the growth model (b) with a survival and fecundity model, depicted as a heat map. (d) Projecting IPMs across a landscape to produce a habitat suitability map (Appendix S1-S7).

building blocks of IPMs are regression models that relate the state of an individual (e.g. size, age and location) to its vital rates. The regressions may also include additional biotic or abiotic covariates that explain variation in vital rates beyond the effects of individual state (Appendix S1,F; Dahlgren & Ehrlén 2009; Adler, Ellner & Levine 2010; Dalglish *et al.* 2011; Nicolè *et al.* 2011). In this way, IPMs can link observations of an individual (Fig. 1a) to variation in vital rates among individuals (Fig. 1b) to project population dynamics (Fig. 1c) and emergent biological patterns such as fitness landscapes (Appendix S1,G) or range limits (Appendix S1,F; Fig. 1d).

Previous work has highlighted some of the strengths of IPMs as they compare to matrix population models (MPMs; cf. Caswell 2001; Easterling, Ellner & Dixon 2000; Ellner & Rees 2006; Coulson 2012; Ozgul *et al.* 2012). A primary difference between the two frameworks is that MPMs assume that individuals occupy discrete stages, whereas IPMs naturally accommodate both discrete and continuous state variables (e.g. Childs *et al.* 2003; Jacquemyn, Brys & Jongejans 2010; Yule, Miller & Rudgers 2013). For some organisms, it is natural to divide the life cycle into discrete components (e.g. insects with particular instars), but for many others using a continuous state variable is more appropriate (e.g. size). The artificial discretization imposed by MPMs can have substantial effects on demographic predictions because it ignores variability

among individuals within each stage (Easterling, Ellner & Dixon 2000; Salguero Gómez & Plotkin 2010). IPMs are usually parameterized with simple regressions, whereas MPMs typically estimate probabilities from observed transitions (but see Morris & Doak 2002). The vital rate regressions that underlie IPMs require many fewer parameters than MPMs when fitted to the same data (Ellner & Rees 2006; Ramula, Rees & Buckley 2009). For example, rather than estimating multiple matrix elements corresponding to stasis, shrinkage and growth (e.g. Evans, Holsinger & Menges 2010), one can fit a single regression for these dynamics. Such regressions can avoid overfitting to sparsely sampled transitions (Ramula, Rees & Buckley 2009; Dahlgren, García & Ehrlén 2011). Regression modelling allows vital rates to be estimated at any value of the state variable, which allows IPMs to describe state transitions at very high resolution. IPM predictions are thus only as good as the parametric assumptions and inferred transitions from vital rate regressions.

Here, we emphasize how IPMs enable mechanistic insight into population-level patterns by modelling the ecological factors influencing vital rates. We attempt to make applications of IPMs to ecology and evolution, specifically more complex examples, more transparent. There is a growing body of work on IPMs in animal populations (e.g. Coulson, Tuljapurkar & Childs 2010; Ozgul *et al.* 2010; Coulson 2012), but here, we focus on building IPMs for plants and note that our discussion

readily applies to other organisms. To do this, we describe how to build each component of an IPM for a series of increasingly complex life histories and provide extensive R code (R Core Team 2013) for a series of case studies in seven appendices. We discuss diagnostic tools for IPMs and provide advice for building biologically complex IPMs.

How to build an IPM

The core of an IPM is the *kernel* – a function that describes how the state of an individual at one time dictates its state and that of its offspring at some future time. Individuals can be characterized in terms of one or more state variables that explain variation in vital rates; often the state variable is some measure of size (hereafter, we simply refer to size: e.g. basal rosette area for herbs or body length for mammals).

The kernel describes how the size (z) distribution of individuals at time t , $n_t(z)$, changes over one time step. Time step length is chosen to reflect the life cycle or census interval, for example, 1 year for long-lived organisms or seasons for short-lived organisms. The integral of $n_t(z)$ over a size interval I ($\int_I n_t(z) dz$) represents the number of individuals in that interval. The kernel, $K(z', z)$, maps this size distribution at time t to a size distribution at time $t + 1$ (one time step later) by describing how individuals survive, change in state (e.g. grow or shrink) and reproduce:

$$n_{t+1}(z') = \int_{\Omega} K(z', z) n_t(z) dz \quad \text{eqn 1}$$

where z' indicates size at $t + 1$ and Ω denotes the possible range of individual sizes (see ‘Analyzing the model’). The integral in eqn (1) performs a sum over all possible ways (survival, growth and reproduction) of changing from size z at time t to size z' at time $t + 1$.

DECOMPOSING THE KERNEL: VITAL RATES

To construct the kernel $K(z', z)$, one must first explore how vital rates change with individual state. For most organisms, the kernel can be split into a *survival/growth kernel*, P , and a *fecundity kernel*, F , such that $K(z', z) = P(z', z) + F(z', z)$. The survival/growth kernel describes the probability that an individual survives the census interval, and if so, the probability distribution for the size it might become. The fecundity kernel describes the number of offspring produced by reproductive individuals during the census interval, and the size distribution of those new offspring. Below, we illustrate how to construct a kernel from vital rate functions using five models for perennial plants with life histories of increasing complexity. In the next section (Regressions), we discuss how to parameterize these vital rate functions using regression models.

Example 1: A long-lived perennial plant with no seedbank

We begin by modelling the life history of a long-lived perennial plant. We assume that once seeds germinate, individuals grow

until they are large enough to produce seeds, after which they continue to reproduce until they die. Growth, fecundity and survival are all size-dependent. In the simplest case, the survival/growth kernel is given by $P(z', z) = s(z) g(z'|z)$. The survival function, $s(z)$, depends on the size of an individual at time t and describes the probability that an individual will survive to $t + 1$. The growth function, $g(z'|z)$, describes the probability density of size z' that an individual of size z can grow to during one time step, conditional on having survived. In perennial plants, with individuals censused before seeds are released (a ‘pre-reproductive’ census), the fecundity kernel commonly distinguishes total seed production from all sources of seed loss (e.g. predation, dispersal to an unsuitable habitat). If the sources of seed loss are unknown, it is common to use an establishment probability, p_{estab} , as a ‘black box’ that describes the ratio of recruits observed at $t + 1$ compared with the seeds produced at t (Metcalfe *et al.* 2008). The fecundity kernel can be modelled as $F(z', z) = p_{\text{flower}}(z) f_{\text{seeds}}(z) p_{\text{estab}} f_{\text{recruit size}}(z')$, where $p_{\text{flower}}(z)$ is the probability of flowering as a function of individual size z , $f_{\text{seeds}}(z)$ describes the number of seeds produced as a function of individual size, and $f_{\text{recruit size}}(z')$ describes the size distribution of recruits observed at time $t + 1$. Taken together, $p_{\text{flower}}(z)$, $f_{\text{seeds}}(z)$ and p_{estab} describe the production of recruits, which follow the size distribution $f_{\text{recruit size}}(z')$.

This example exhibits a few generalities that will recur in subsequent examples. The survival/growth and fecundity kernels each have two components, which we term the *individual component* and a *size redistribution component*. The individual components are typically only functions of z (e.g. survival, flowering probability and seed number) and describe the number or proportion of individuals that follow the size redistribution component. Size redistribution components are functions of z' (and optionally z), because they describe the size of individuals in the next year (e.g. growth and recruit size distribution).

Example 2: Monocarpic perennial plant

The life cycle of monocarpic perennials is slightly more complex because flowering is fatal (Rees & Rose 2002; Metcalfe *et al.* 2008; Rees & Ellner 2009). Distinguishing death due to flowering from other sources of mortality is necessary because flowering-related death has a positive effect on populations (if a sufficient number of seeds are produced), while death before flowering has a negative effect on populations. For a pre-reproductive census, the survival/growth kernel is given by $P(z', z) = s(z) [1 - p_{\text{flower}}(z)] g(z'|z)$. The individual component of $P(z', z)$ has two parts: one part due to flowering ($p_{\text{flower}}(z)$) and one part for vegetative individuals ($s(z)$). Fecundity is modelled as in Example 1.

Example 3: Perennial plant with seedbank

IPMs can also handle complex life histories using discrete stages, such as a seedbank. In this case, we assume that all seeds in the seedbank are demographically equivalent, regardless of

their size or age. Ramula, Rees & Buckley (2009) described an IPM incorporating a seedbank for perennial herbs, with plants censused before reproduction, which we illustrate here. Incorporating a discrete state for seed dynamics requires an additional equation to describe the number of seeds in the seedbank. We can construct this as follows: let B_t denote the number of seeds in the seedbank at time t , $s_{\text{seed surv}}$ denote the survival probability of seeds in the seedbank over one time step, $s_{\text{recruit bank}}$ denote the probability of recruiting from the seedbank, and $s_{\text{recruit direct}}$ denote the probability of skipping the seedbank and recruiting. Then, number of seeds in the seedbank at $t + 1$ is given by:

$$\underbrace{B_{t+1}}_{\text{total seeds in seed bank}} = \underbrace{B_t s_{\text{seed surv}} (1 - s_{\text{recruit bank}})}_{\text{seeds remaining in seed bank}} + \underbrace{\int_{\Omega} p_{\text{flower}}(z) f_{\text{seeds}}(z) (1 - s_{\text{recruit direct}}) n_t(z) dz}_{\text{new seeds to seed bank}} \quad \text{eqn 2}$$

The term $[B_t s_{\text{seed surv}} (1 - s_{\text{recruit bank}})]$ describes the number of seeds that will remain in the seedbank until the next year: the total number of seeds already in the seedbank (B_t) is reduced by those lost to mortality ($s_{\text{seed surv}}$) and those lost to recruitment ($1 - s_{\text{recruit bank}}$). The term $[\int_{\Omega} p_{\text{flower}}(z) f_{\text{seeds}}(z) (1 - s_{\text{recruit direct}}) n_t(z) dz]$ describes the number of new seeds entering the seedbank as the product of the number of new seeds produced and the proportion that go directly to the seedbank ($1 - s_{\text{recruit direct}}$).

Equation 2 is linked to the following continuous stage model, which describes the dynamics of the established individuals:

$$\underbrace{n(z')}_{\text{size distribution next year}} = \underbrace{B_t s_{\text{recruit bank}} f_{\text{recruit size}}(z')}_{\text{recruits from seed bank}} + \underbrace{\int_{\Omega} [P(z, z') + F(z, z')] n_t(z) dz}_{\text{transitions in continuous stages and recruits skipping seed bank}} \quad \text{eqn 3}$$

The term $[B_t s_{\text{recruit bank}} f_{\text{recruit size}}(z')]$ describes the number and size distribution of recruits germinating from the seedbank, that is, the total number of seeds in the seedbank (B_t) multiplied by the proportion that recruit ($s_{\text{recruit bank}}$), with the new recruits distributed according to the size distribution ($f_{\text{recruit size}}(z')$). The fecundity kernel inside the integral describes the number of recruits arising from seeds that skip the seedbank: $F(z', z) = p_{\text{flower}}(z) f_{\text{seeds}}(z) s_{\text{recruit direct}} f_{\text{recruit size}}(z')$. The function $F(z', z)$ differs from the two previous examples only by the inclusion of $s_{\text{recruit direct}}$, which is incorporated in the individual component and reduces the total number of seeds establishing next year by the proportion that go into the seedbank. Any appropriate kernel for $P(z', z)$ can be used. For an iteroparous herb, Ramula, Rees & Buckley (2009) used $P(z', z) = s(z) g(z'|z)$, exactly as described in Examples 1 and 2. Operationally, adding a discrete seedbank is straightforward: it adds an extra row and column to the discretized kernel (top-most row and left-most column in Fig. 1c), whose values are given by eqn (2) (Appendix S1,C; Hesse, Rees & Müller Schärer 2008).

Example 4: Perennial plant with multiple discrete stages

In Example 3, seedlings were part of the continuous stage (eqn 3), but in some cases, it is better to assign seedlings to a separate, discrete class (S_t) if their vital rates have different size dependence than larger individuals. For a model of the forest herb *Actaea spicata* (Ranunculaceae; Appendix S1,F), seedlings were treated as a discrete class because seedling survival was lower than expected based on their size (Dahlgren & Ehrlén 2009, 2011). This IPM is described with the following three equations:

$$B_{t+1} = \int_{\Omega} p_{\text{flower}}(z) f_{\text{fruit}}(z) f_{\text{seeds/fruit}} n_t(z) dz \quad \text{eqn 4}$$

$$S_{t+1} = p_{\text{estab}} B_t \quad \text{eqn 5}$$

$$n_{t+1}(z') = s_{\text{seed surv}} f_{\text{recruit size}}(z') S_t + \int_{\Omega} s(z) g(z'|z) n_t(z) dz \quad \text{eqn 6}$$

A seedbank (eqn 4) accounts for the fact that underground germination occurs 1 year after seed release and above-ground recruitment 1 year later. Equation 4 differs from the seedbank in eqn 2 in that all seeds go into the seedbank and seeds cannot stay in the seedbank. Equation 4 also differs from eqn 2 in that the number of seeds is modelled as a function of size in eqn 2, whereas here, the number of fruits is modelled as a function of size ($f_{\text{fruit}}(z)$), with this multiplied by the average number of seeds per fruit ($f_{\text{seeds/fruit}}$). Seeds that survive and germinate (p_{estab}) become seedlings (S_t) for 1 year (eqn 2), and if they survive ($s_{\text{seedling surv}}$), establish the following year with the size distribution given by $f_{\text{recruit size}}(z')$ (eqn 6). The dynamics of established individuals is described by eqn 6, which is directly analogous to eqn 3.

Example 5: Perennial plant with multiple discrete stages and environmental covariates

Vital rate functions can readily accommodate covariates, such as environmental conditions, that help to predict individuals' vital rates above and beyond the state variable. For the model in Example 4, two modifications were needed to capture population dynamics in Dahlgren & Ehrlén (2009, 2011); Appendix S1,F). They included the effect of soil potassium concentration (K_{conc}) on growth (replacing $g(z'|z)$ with $g(z'|z, K_{\text{conc}})$) and the effect of fruit predation (p_{pred}) on the number of seeds produced per individual (replacing $f_{\text{fruit}}(z)$ with $f_{\text{fruit}}(z, p_{\text{pred}})$). This enabled them to model the temporal dynamics as a function of changes in soil potassium concentration due to the successional dynamics of spruce forests (details in Appendix S1,F). The functional forms of all vital rate functions were determined by regression and are shown in Table 1.

Table 1. Model components used by the IPM for a perennial plant (*Actaea spicata*) with multiple discrete stages in Examples 4 and 5 and Appendix S1,F. z is the size of an individual at time t and z' is size at time $t + 1$

Model component	Function
Vital rates	
Survival ($s(z)$)	$\text{logit}(s) = -1.39 + 0.49 z$
Growth ($g(z', z)$)	$z' = 2.13 + 0.71 z + 0.013 K_{\text{conc}}$ $\sigma^2 = 1.25$
Flowering (p_{flower})	$\text{logit}(p_{\text{flower}}) = -9.90 + 1.18 z$
Fruit number ($f_{\text{fruit}}(z)$)	$\text{log}(f_{\text{fruit}}) = 0.31 + 0.28 z$
Seed number ($f_{\text{seeds/fruit}}(p_{\text{pred}})$)	$f_{\text{seeds/fruit}} = 0.39 p_{\text{pred}} + 9.26$ $(1 - p_{\text{pred}})$
Germination (p_{estab})	$p_{\text{estab}} = 0.0062$
Seedling survival ($s_{\text{seed surv}}$)	$s_{\text{seed surv}} = 0.24$
Seedling size ($f_{\text{recruit size}}$)	$f_{\text{recruit size}}$: mean = 3.08, s.d. = 1.45
Covariates	
Potassium concentration (K_{conc})	$K_{\text{conc}} = 1.72 \exp(3.01 - 0.53 * p_{\text{spruce}})$
Proportion spruce (p_{spruce})	$p_{\text{spruce}} = 1 / (1 + \exp(-0.09t + 5))$
Proportion fruits predated (p_{pred})	$p_{\text{pred}} = 0.2$

IPM, integral projection models.

A wide range of life histories can be incorporated into an IPM by including more complex discrete (e.g. seedbank and seedlings; Appendix S1,F) or continuous stages (e.g. clonally produced individuals; Appendix S1,B) and partitioning the kernel into the appropriate vital rate functions. We expect that models with multiple discrete and continuous stages represent the future of IPMs; for example, Jacquemyn, Brys & Jongejans (2010) used three discrete stages and two continuous stages to describe the following life cycle of a perennial orchid: protocorm → tuber → non-flowering plants (of various sizes) → flowering rosette (of various sizes) → protocorm; the third discrete stage being dormant plants. Ultimately, the limit to model complexity is data availability. Fortunately, one can determine whether the data are sufficient to parameterize a

particular vital rate model using the tried and tested methods of regression.

In principal, describing the life history for animal populations is conceptually the same as for plants because populations are governed by survival, growth and reproduction (e.g. Coulson, Tuljapurkar & Childs 2010; Bruno *et al.* 2011; Childs *et al.* 2011; Wallace, Leslie & Coulson 2012). Animal IPMs may be moderately high dimensional, as individual performance is influenced by multiple developmental stages (Ozgul *et al.* 2012), sex (Schindler *et al.* 2013), and vital rates vary with age as well as body size (Ozgul *et al.* 2010; Coulson *et al.* 2011). In animal populations, data on the dependence of offspring size on parental size may be more readily available, enabling slightly more complex fecundity models (e.g. $f_{\text{recruit size}}(z'|z)$).

REGRESSIONS

Most of the strengths of IPMs are strengths of regressions. The simplicity of regression facilitates an iterative approach to modelling, allowing researchers to move between data, vital rate models and population-level predictions in order to arrive at robust IPMs. Here, we provide a brief description of the most common vital rate regressions, shown in Table 1, and provide more detailed discussion in Appendix S1,D. While we focus on the simplest case – modelling vital rates as a function of a single state variable – strength lies in incorporating other predictors. These predictors could include additional state variables such as age (Childs *et al.* 2003; Ellner & Rees 2006), sex, infection status (Bruno *et al.* 2011), or genotype (Coulson *et al.* 2011) or covariates such as successional stage (Metcalf, McMahon & Clark 2009a; Metcalf *et al.* 2009b), trait differences (e.g. specific leaf area), abiotic environments (Appendix S1,F; Dahlgren & Ehrlén 2009; Dalglish *et al.* 2011, Nicolè *et al.* 2011), time-lags (Kuss *et al.* 2008) or competition (Adler, Ellner & Levine 2010). Importantly, if vital rate functions include covariates (e.g. environmental conditions; Appendix

Table 2. Analyses illustrated in Appendices to this paper

Appendix	Title	Life History	Vital Rate Model Features	IPM Analysis	Biological inference
S1,A	A simple IPM	Long-lived perennial	Compare growth models; Correct eviction	λ ; Sensitivity; Elasticity; Life-history diagnostics	Functional form of growth models
S2,B	Fecundity models	Long-lived perennial, clonal	Compare state variables, vital rate complexity; Clonal reproduction	λ ; Parameter sensitivity; Elasticity decomposition	Life cycle construction
S3,C	IPMs for complex life cycles	Perennial herb, seedbank, dormancy	Complex fecundity; Discrete stages	Life table response experiment	Understanding differences among populations
S4,D	Regression techniques	Canopy trees	Regression techniques; Sample size issues; Missing Fecundity	Passage time; Life expectancy	Uncertainty in population statistics
S5,E	Stochastic IPMs	Simulated; Canopy trees	Compound matrices to describe environmental transitions	Transient dynamics; Stochastic λ ; Passage time; Life expectancy	Response to variable environment
S6,F	Demography-based Niche Models	Perennial herb	Discrete stages; Including environmental covariates	λ ; Transient dynamics	Mapping current and future distribution
S7,G	Evolutionary demography of monocarps	Monocarpic perennial	Density dependence	R_0 ; Stochastic environment; Adaptive dynamics	Evolutionarily stable flowering strategies

S1,F), a different kernel is built for each unique set of covariates, which assumes that all individuals experience the same environment.

Survival ($s(z)$)

Survival data are binomial, with the possible outcomes either death (0) or survival (1), so it is modelled with logistic regression (a generalized linear model with a binomial link function).

Growth ($g(z'|z)$)

Growth is often modelled with a linear regression, which is taken as the mean of normal (or log-normal) distribution. The linear regression describes the expected size at the next census, while the normal distribution describes the range of possible sizes about this expectation (Fig. 1b). The variance of the normal distribution is often taken to be equal to the variance of the residuals from the linear regression. Figure 1b,c shows a model where the variance increases linearly with size, fit using generalized least squares regression.

Probability of life-history transition (e.g. flowering) ($p_{\text{flower}}(z)$)

As with survival, life-history transition data are typically binary, thus logistic regression is used. Such transitions might include flowering or transitioning between discrete stages (e.g. between protocorms and tubers in orchids or metamorphosis in arthropods).

Offspring number ($f_{\text{seeds}}(z)$)

The number of offspring is typically treated as count data and modelled using Poisson regression (a generalized linear model with a log link function) (Easterling, Ellner & Dixon 2000). For plants, proximate measures of the total offspring number are often used: for example, one can model the number of flowering rosettes and multiply by the average number of seeds per rosette (Salguero-Gómez *et al.* 2012).

Establishment probability (p_{estab})

Many vital rates that enter the individual component of the kernel, such as germination or recruitment probability, are commonly modelled as constants either because they are size-independent or there are insufficient data to determine the size dependence.

Recruit size distribution ($f_{\text{recruit}}(z'|z)$)

When parentage is unknown (common in plant studies), it is common to model the size distribution of recruits as a normal or log-normal distribution fit to the sizes of recruits at $t + 1$ (Ellner & Rees 2006). For vegetative or asexual reproduction, or when parentage is known, offspring size is modelled as a function of maternal size using linear regression (Easterling, Ellner & Dixon 2000, Coulson *et al.* 2011, Appendix S1,B).

ANALYSING THE MODEL

To build a kernel, the regression functions (Table 1) are combined according to the life history (see 'Decomposing the kernel: Vital rates'). The kernel is used to project the size distribution forward in time by integrating eqn 1. To do so, the user must specify the limits of integration (Ω in eqn 1). Limits typically span values much smaller and larger than the observed individuals (Easterling, Ellner & Dixon 2000; Williams, Miller & Ellner 2012). Generally, minor changes to Ω should leave long-term dynamics unaffected because individuals will rarely be recruited at, or survive to, such sizes, respectively (Appendix S1,B,C).

Numerical integration methods are used with IPMs because kernel functions are often complex and not analytically integrable. Numerical methods discretize the kernel, which generates a large matrix (Easterling, Ellner & Dixon 2000; Zuidema *et al.* 2010). The most commonly used integration method is the midpoint rule and evaluates the kernel at mesh points (cell centres) on an evenly spaced grid (Fig. 2; Easterling, Ellner & Dixon 2000). The grid dimension is typically between 50 and 200; it should be chosen such that the resulting eigenvalues/vectors are not sensitive to grid size (Appendix S1,B,C; Zuidema *et al.* 2010).

Integral projection models and matrix projections models (MPMs) are similar objects mathematically (Fig. 2), which means that many of the tools developed for MPMs are easily transferable to IPMs. When a cell-based integration method is used, such as the 'midpoint rule,' the discretized kernel can be thought of as an MPM with a very large number of stages (Easterling, Ellner & Dixon 2000, Ellner & Rees 2006). An IPM matrix is obtained solely for numerical integration, and boundaries between matrix elements have no biological basis. Analytical tools for IPMs are based on the same types of analyses used for MPM and hence predict the same population statistics (Appendix S1,A–G; Caswell 2001; Morris & Doak 2002; de Kroon, van Groenendael & Ehrlén 2000):

1. The size distribution and population growth rate (λ) to which a population converges in the absence of perturbation (i.e. if the demographic transitions do not change), can be extracted directly from eigenanalysis of the discretized kernel. The 'stable size distribution' is defined by the right eigenvector of the matrix, and the 'asymptotic growth rate' by the largest eigenvalue. The corresponding reproductive value, or contribution to long-term population size for each size, is defined by the left eigenvector.

2. Asymptotic analyses may describe general characteristics of a population, but may poorly predict short-term dynamics. Transient dynamics are important when the population differs from the stable distribution (Williams *et al.* 2011). These changes can be simply quantified by projecting the population forward in time via matrix multiplication, starting from the initial size distribution and the discretized kernel (Appendix S1, A). One can determine whether transient dynamics are important using the damping ratio (ρ) (i.e. the ratio between the first and second eigenvalues) to describe the time-scale of transient dynamics (Caswell 2001).

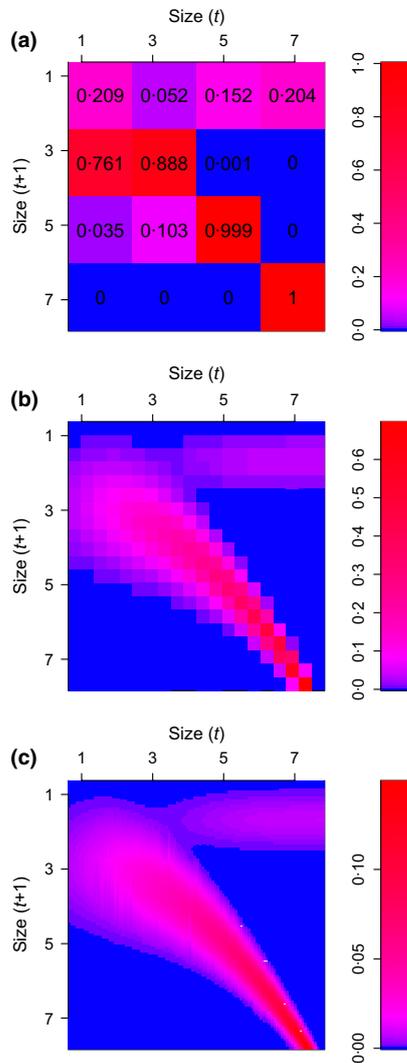


Fig. 2. Integral projection models (IPMs) and matrix projection models are at opposite ends of a continuum. Population projection models are shown for a long-lived herbaceous perennial plant, using the same vital rate regressions (Nicolè *et al.* 2011). These discretized kernels have been constructed from the IPM in Appendix S1,A, but discretized at different resolutions. When integration is performed using the midpoint rule, as is typically done, the distinction between MPMs or IPMs is blurred because the discretized IPM kernel can be interpreted as matrix of transition probabilities. The only further distinction between MPMs and IPMs is that MPMs typically use observations to directly parameterize the transition probabilities, whereas IPMs infer the transition probabilities based on vital rate regressions. (a) A four-stage projection model, for example, representing seedlings, juveniles, small adults and large adults. Survival and growth occur along the diagonal and sub-diagonal, and fecundity is captured in the top row. This coarse discretization corresponds to using step functions for vital rate models. Choosing a coarse resolution makes the assumption that all individuals in a particular stage are identical. (b) A 20-stage projection model better captures variability among individuals (e.g. fecundity varies among the top five rows, compared with the single row in (a)). If built from observed transitions (typical MPMs), such resolution requires a large amount of data, however when inferring transitions (IPMs) this resolution is rather coarse. (c) A 100-stage projection model. A discretization of the kernel at this high resolution is typically labelled an IPM. IPMs thus preserve the understanding gained by modelling the vital rates as a function of continuous state variables by performing the projection at a higher resolution.

3. Using Markov chain theory, models of structured populations can be extended to incorporate stochastic changes in vital rates over time (Tuljapurkar 1990). These have proven powerful for exploring evolutionary dynamics (evolutionarily stable strategies; Appendix S1,G; Childs *et al.* 2004; Rees *et al.* 2006; Ellner & Rees 2007), management questions (risk of extinction; Fieberg & Ellner 2001; Morris & Doak 2002) and predicting environmental responses (Fieberg & Ellner 2001; Morris & Doak 2002).

4. Sensitivity and elasticity (proportional sensitivity) analyses can determine how different parts of the kernel influence population statistics (de Kroon, van Groenendael & Ehrlén 2000; Caswell 2001). These analyses can illustrate the relative importance of different transitions, showing in a continuous ‘landscape’ which vital rates and which size ranges contribute most to λ or other population statistics (Appendix S1,A,B). Sensitivity and elasticity values can be used to estimate selection gradients in evolutionary studies (Caswell 2001) or to compare effects of different management options in conservation planning (Morris & Doak 2002). Methods exist to estimate sensitivity of an array of population characteristics in the context of transient dynamics (Caswell 2007; Haridas & Tuljapurkar 2007) and stochastic dynamics.

5. Another strength of IPMs is the ability to explore vital rate parameter sensitivity (Appendix S1,B). Distinct from transition sensitivities (as above), for example, the sensitivity of λ to growth regression parameters can be used to investigate the effects of changes in individual growth rate across all stages simultaneously (intercept), or in a manner that favours larger individuals over smaller individuals (slope).

6. Many other population statistics are readily calculated from IPM matrices, such as passage times to life-history events (e.g. maturation; Fig. 3c), life expectancy (Fig. 3d), net reproductive rate (R_0) or generation length (Appendix S1,A; Caswell 2001; Smallegange & Coulson 2013).

IPM Diagnostics

In this section, we highlight some common issues encountered when building regressions, and using IPMs, and suggest solutions.

VITAL RATE MODEL DIAGNOSTICS

Though typically limited by the available data, in principle one must choose how to decompose the life cycle into vital rate functions. Capturing more biological detail with more vital rate functions or parameters comes at the expense of requiring more data. For example, the transition from seeds to new recruits can be modelled simply using parent-seedling ratios, thereby ignoring processes that affect establishment (p_{estab} , as above; Appendix S1,A). Alternatively, the same reproductive process can be represented in greater detail by modelling the probability of reproduction, number of reproductive structures, number of propagules per reproductive structure, germination probability and seedling survival probability (Appendix S1,B,C; Yang *et al.* 2011; Salguero-Gómez *et al.* 2012).

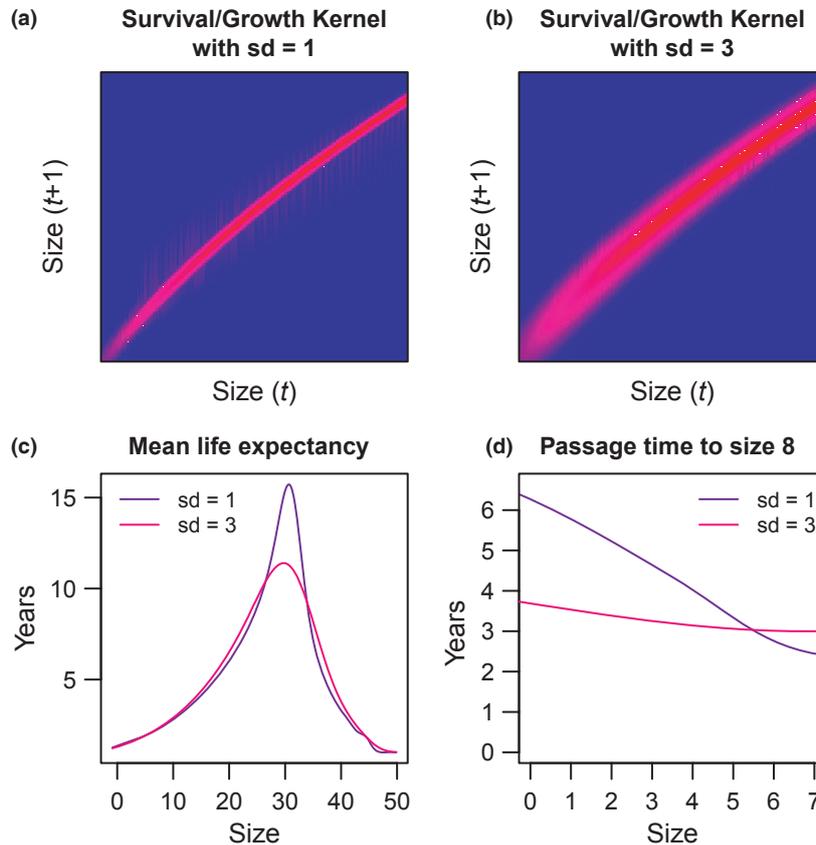


Fig. 3. A comparison of population inference due to differences in the variance in individual growth. Growth models were fit to simulated data where the standard deviation of the fits was set at 1 and 3. This leads to (a–b) different survival/growth kernels, (c) different life expectancy patterns and (d) different passage time patterns.

Ideally, the level of biological detail is chosen based on the importance of life-history transitions and the biological questions at hand.

The choice of state variable is also fundamentally important. For example, size can be measured in a variety of ways, thus it is worth exploring how vital rates vary in response to the choice of state variable, or transforming the state variable to emphasize certain parts of the state variable range (Appendix S1,B). Typically, the state variable that best differentiates the size dependence of fecundity and survival is chosen.

Even if vital rate models have a good statistical fit, they may not be biologically reasonable for all values of the state variable (Appendix S1,D). For example, in large-scale demographic studies, data are typically missing for some values of the state variable or covariates, and it is important to check whether interpolated estimates are reasonable for unobserved cases. For example, in Fig. 1b, we can reasonably predict growth transitions for any individual across the range of sizes if we believe the growth regression is satisfactory. As another example of evaluating biological plausibility, consider survival models for long-lived canopy trees (Appendix S1,D). If mortality of large individuals is not observed (a common issue), a standard logistic regression can reach the asymptote of 1 and predict that those individuals are effectively immortal. A hierarchical model can provide a more biologically realistic survival estimate by

borrowing strength from other, better sampled groups. If collecting more data at the extreme values of size is not possible, one could set a maximum survival probability based on prior expectations of the species' life span. Life expectancy can be explicitly calculated from the discretized kernel to check that these expectations are met (Appendix S1,A).

Accurately modelling variance is important, as this can have a strong influence on projections. Although the expected growth of an individual is based on the fitted model (e.g. the regression of increment on size), the realized growth is a probability distribution around that expectation (Figs 1b and 3). The probability distributions shown vertically in Fig. 1b illustrate how size at time t determines the possible sizes that an individual might attain at time $t + 1$. A large variance around the expected growth indicates that many individuals grow faster or slower than the expected amount. Because of Jensen's inequality, increasing the variance of growth can change the mean population growth rate (higher or lower, depending on the shape of the individual growth model) and lead to different passage times and life expectancies (Fig. 3). Describing the variation among the potential future sizes does not explain the variation in future sizes directly, but characterizes the magnitude of process (and observation) uncertainty and describes heterogeneity among individuals (cf. Clark 2003). Estimating variance is thus biologically important (Clark 2003).

It is important to consider how the predictions of the vital rate model interact with one another to influence population statistics. For example, if the mean growth curve described by $g(z'|z)$ is always greater than the 1:1 (or the $z' = z$) line, surviving individuals can grow indefinitely (Appendix S1,A). If large individuals survive with a high probability, there is effectively no upper limit on size. Conversely, the point where $g(z'|z)$ crosses the 1:1 line identifies the asymptotic mean maximum size for individuals (conditional on survival). If unconstrained growth is unrealistic and produces extreme population projections (i.e. unrealistically large individuals in the stable population distribution), one should check whether the data support alternative models that reduce growth or senescence for large individuals (e.g. fitting a negative quadratic term in the growth and/or survival function in Appendix S1,B,D). Alternatively, parameters can be adjusted based on prior knowledge.

Vital rate regression models facilitate parsimonious and statistically grounded modelling of uncertainty in IPMs. Uncertainty in regression parameter estimates can be propagated to population statistics simply by (bootstrap) sampling from the estimated parameter distributions and recalculating kernels and population statistics (e.g. Ellner & Rees 2006; Jongejans, Sheppard & Shea 2006). Regression models draw inference across a continuous state variable, meaning that the shape of that predictive vital rate function can be influenced by outliers, sampling bias and other features of the model, making uncertainty analyses particularly critical. Uncertainty in parameter values may be used as a proxy for temporal variability in stochastic simulation models if uncertainty likely derives from temporal, rather than spatial, variability. Uncertainty analysis can also be used in conjunction with sensitivity analysis to understand the implications of uncertainty on population statistics (cf. Buckley *et al.* 2005; Hegland, Jongejans & Rydgren 2010). In Appendix S1,D, we discuss in more detail how model structure and sample size can influence population inference.

KERNEL DIAGNOSTICS

Once the kernel is specified, it is important to evaluate whether population statistics are affected by the choice of integration method and size limits (Metcalfe *et al.* 2013; Ω in eqn 1), and whether those statistics correspond to observed (or expert opinion) population characteristics. When discretizing the kernel, the grid resolution should be sufficiently high to accurately characterize the topography of the kernel, avoiding grid cells that large enough to average over peaks and valleys. When this is done, using the midpoint rule for integration should be sufficient. However, the midpoint rule can be impractical for slow-growing species (e.g. trees) that require extremely large matrices (Zuidema *et al.* 2010). Any of a number of numerical integration methods can be used, the details of which are beyond the scope of this guide.

A common problem that can result from a poor choice of size limits is the unintentional 'eviction' of individuals, which leads to underestimation of survival (Appendix S1,A; Dalglish *et al.* 2011; Williams, Miller & Ellner 2012). Because the growth and recruit size distributions are probability densities

than can extend to $\pm\infty$, predicted values can fall outside of the size range chosen for the IPM, causing individuals to be 'evicted' from the model. Detecting eviction is straightforward: the predicted values of size-specific survival (for growth) and size-specific establishment (for reproduction) should equal the column sums of the discretized survival/growth and fecundity kernels, respectively. If the column sums are lower than the predicted values, individuals will be evicted from projections. One can resolve eviction either by transforming the data or using non-Gaussian distributions, so that transitions are not predicted beyond the range of the models (Williams, Miller & Ellner 2012). Eviction can also be resolved by expanding the size range in the model to include sizes that were previously evicted, or adding discrete size classes at the extremes of the size range that include all individuals predicted at sizes beyond the extremes with an upper/lower bound on the transition probability (Appendices A, F; Williams, Miller & Ellner 2012).

Ecologists are likely to have substantial prior knowledge about population statistics that are easy to obtain from any IPM, which can help to diagnose the plausibility of a model. For example, populations in a stable environment can be expected to have an asymptotic growth rate close to 1 (between 0.95 and 1.05 for the forest herb modelled in Appendix S1,F). In contrast, populations in unstable (abiotic or biotic) environments can be expected to have growth rates different from 1. As a second example, the majority of established individuals in stable populations of long-lived species would typically be large. In contrast, increasing populations of short-lived species with high adult mortality rates compensated by high rates of recruitment should be composed mainly of smaller individuals. As a third example, in populations with high reproductive output but low juvenile survival rates, reproductive value would be expected to increase dramatically with size, such that a large reproductive individual of a long-lived species may have a reproductive value that is several orders of magnitude higher than that of a juvenile. In contrast, in a population where large individuals have a high risk of mortality, reproductive values would not be expected to differ much between individuals of different size. In short, the practitioner should rely on the fundamentals of comparative demography.

Many other model diagnostics are equivalent to those used for MPMs; hence, the vast literature on MPM construction also applies to IPMs (Caswell 2001; Morris & Doak 2002). For example, the projected timing of critical life-history events such as age at first reproduction, generation time and mean life expectancy should match observations should be consistent with field data or conventional knowledge (Fig. 3; Caswell 2001). Also, calculating confidence (credible) intervals on population statistics from bootstrap analysis (posterior samples) is critical to determine whether the IPM reasonably narrows down the range of possible population dynamics (Alvarez-Buylla & Slatkin 1994). Understanding the range of possible predictions is particularly important for IPMs because demographic transitions are interpolated from vital rate regressions and estimates of uncertainty help quantify the quality of that interpolation.

Biological challenges for IPMs

Integral projection models enable biologists to address old but important questions in a new, mechanistically informed manner. Below, we highlight some promising biological advances made possible by IPMs and discuss their inherent challenges to highlight avenues for future research.

Much of the theoretical development and application of IPMs have taken place in the context of plant populations and although extension to animal is typically straightforward, some unique challenges may exist when modelling animal populations. The larger number of potential state variables relevant for animals, compared with plants, could necessitate more sophisticated techniques of numerical integration, as the commonly used midpoint rule will be inefficient for high dimensional integrals. One area where IPMs could make an important contribution is in the development of demographic models structured by sex (Schindler *et al.* 2013), behavioural (e.g. date of egg laying) or physiological (e.g. immune function) measures of state. Longitudinal physiological data from field populations are starting to become available (e.g. Nussey *et al.* 2011), which paves the way for data-driven models that link physiology and population dynamics. The theory for such models is already well worked out (Ellner & Rees 2006), though significant practical challenges need to be overcome. Missing data in animal populations often presents challenges, and imputing state variables using hierarchical models may be necessary (cf. Colchero, Jones & Rebke 2012).

Implicit and explicit spatial population dynamics can be included in IPMs by bringing together local demography and dispersal (Jongejans, Skarpaas & Shea 2008). One way of incorporating spatial structure of multiple populations into a traditional matrix model is to build a 'mega-matrix' model, wherein each submatrix represents a different population and dispersal is captured by transitions among the submatrices (Hunter & Caswell 2005). Neighbourhood-specific competitive interactions can also be captured with spatially implicit models (Adler, Ellner & Levine 2010; Adler, Dalgleish & Ellner 2011). By modelling vital rates as a function of environment (e.g. precipitation), IPMs can be used to forecast the spatial distribution of population dynamics (Appendix S1,F). Spatially explicit IPMs also borrow from traditional matrix model approaches: Jongejans *et al.* (2011) combined the IPM framework with integrodifference equation models for spread in discrete time and homogeneous space (Neubert & Caswell 2000). If spatial heterogeneity is important, a simulation approach can be used to redistribute individuals at each time step among populations based on a dispersal kernel (Record 2010).

Integral projection models can produce proxies for fitness, such as population growth rates given phenotype differences; this application falls at the nexus between evolutionary biology and ecology. At a scale that could be referred to as 'meso-evolutionary' – that is, models of a single species, with implicit, relatively simple genetics, stochastic IPMs have been used to successfully predict the evolutionarily stable life-history strategies for maturation and offspring size: projections often closely resemble trait distributions observed in natural populations

(Appendix S1,D; Rees & Rose 2002; Metcalf, Rose & Rees 2003; Metcalf & Pavard 2007; Childs *et al.* 2011; Miller *et al.* 2012). IPMs have also been used to understand short-term eco-evolutionary dynamics of population size distributions, genotype distributions and other state variables in response to environmental change (Coulson, Tuljapurkar & Childs 2010; Coulson 2012; Smallegange & Coulson 2013). Extending the power of these evolutionary analyses will require the incorporation of additional state variables. The introduction of two-sex IPMs could be used to describe the complexities of frequency dependence. More realistic representations of the quantitative genetic structure underlying traits are another challenging but important direction.

Density dependence may be difficult to quantify at the individual level but models without density dependence can result in unrealistic projections of stage structure (Appendix S1,G; Metcalf, Rose & Rees 2003; Hesse, Rees & Müller Schärer 2008; Dahlgren & Ehrlén 2009; Eager *et al.* 2013). A recently developed approach that can incorporate density dependence relies on using a time-series of the population size distribution to constrain projections (Ghosh, Gelfand & Clark 2012). Future IPM research would benefit from a synthesis of population-level data (repeated observations of state distributions) to improve the accuracy of projections while using individual-level data to understand how underlying vital rates relate to state transitions (Ellner 2012).

IPMs are useful for understanding population-level patterns that could not be inferred from data on survival, growth and fecundity, or models of these vital rates alone. The ease of incorporating biotic and abiotic factors into vital rate models places demography in an ecological context. This leads to a more mechanistic understanding of populations and potentially better predictions of population dynamics – both in ecological and evolutionary terms (Smallegange & Coulson 2013). IPMs offer ecologists a powerful workflow – from data, through vital rate models, to population inference – with every step of IPM development requiring hypotheses, diagnostics and ecological understanding.

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References

- Adler, P.B., Dalgleish, H.J. & Ellner, S.P. (2011) Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology*, **100**, 478–487.
- Adler, P.B., Ellner, S.P. & Levine, J.M. (2010) Coexistence of perennial plants: an embarrassment of niches. *Ecology Letters*, **13**, 1019–1029.
- Alvarez-Buylla, E.R. & Slatkin, M. (1994) Finding confidence limits on population growth rates: three real examples revised. *Ecology*, **75**, 255–260.

- Bruno, J., Ellner, S., Vu, I., Kim, K. & Harvell, C. (2011) Impacts of aspergillosis on sea fan coral demography: modeling a moving target. *Ecological Monographs*, **81**, 123–139.
- Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H. & Rees, M. (2005) Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, **42**, 1020–1030.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer, Sunderland, MA.
- Caswell, H. (2007) Sensitivity analysis of transient population dynamics. *Ecology Letters*, **10**, 1–15.
- Childs, D.Z., Rees, M., Rose, K.E., Grubb, P.J. & Ellner, S.P. (2003) Evolution of complex flowering strategies: an age- and size-structured integral projection model. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 1829–1838.
- Childs, D.Z., Rees, M., Rose, K.E., Grubb, P.J. & Ellner, S.P. (2004) Evolution of size-dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 425–434.
- Childs, D.Z., Coulson, T.N., Pemberton, J.M., Clutton-Brock, T.H. & Rees, M. (2011) Predicting trait values and measuring selection in complex life histories: reproductive allocation decisions in Soay sheep. *Ecology Letters*, **14**, 985–992.
- Clark, J.S. (2003) Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology*, **84**, 1370–1381.
- Colchero, F., Jones, O.R. & Rebke, M. (2012) BaSTA: an R package for Bayesian estimation of age-specific survival from incomplete mark-recapture/recovery data with covariates. *Methods in Ecology and Evolution*, **3**, 466–470.
- Coulson, T. (2012) Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos*, **121**, 1337–1350.
- Coulson, T., Tuljapurkar, S. & Childs, D.Z. (2010) Using evolutionary demography to link life history theory, quantitative genetics and population ecology. *Journal of Animal Ecology*, **79**, 1226–1240.
- Coulson, T., MacNulty, D.R., Stahler, D.R., vonHoldt, B., Wayne, R.K. & Smith, D.W. (2011) Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science*, **334**, 1275–1278.
- Dahlgren, J.P. & Ehrlén, J. (2009) Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology*, **97**, 666–674.
- Dahlgren, J.P. & Ehrlén, J. (2011) Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos*, **120**, 1183–1190.
- Dahlgren, J., García, M.B. & Ehrlén, J. (2011) Nonlinear relationships between vital rates and state variables in demographic models. *Ecology*, **92**, 1–7.
- Dalgleish, H.J., Koons, D.N., Hooten, M.B., Moffet, C.A. & Adler, P.B. (2011) Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, **92**, 75–85.
- Eager, E.A., Haridas, C.V., Pilon, D., Rebarber, R. & Tenhumberg, B. (2013) Disturbance frequency and vertical distribution of seeds affect long-term population dynamics: a mechanistic seed bank model. *American Naturalist*, **182**, 180–190.
- Easterling, M., Ellner, S. & Dixon, P. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology*, **81**, 694–708.
- Ellner, S.P. (2012) Comments on: Inference for size demography from point pattern data using integral projection models. *Journal of Agricultural, Biological, and Environmental Statistics*, **17**, 682–689.
- Ellner, S. & Rees, M. (2006) Integral projection models for species with complex demography. *American Naturalist*, **167**, 410–428.
- Ellner, S. & Rees, M. (2007) Stochastic stable population growth in integral projection models: theory and application. *Journal of Mathematical Biology*, **54**, 227–256.
- Evans, M.E.K., Holsinger, K.E. & Menges, E.S. (2010) Fire, vital rates, and population viability: a hierarchical Bayesian analysis of the endangered Florida scrub mint. *Ecological Monographs*, **80**, 627–649.
- Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters*, **4**, 244–266.
- Ghosh, S., Gelfand, A.E. & Clark, J.S. (2012) Inference for size demography from point pattern data using integral projection models. *Journal of Agricultural, Biological, and Environmental Statistics*, **17**, 641–667.
- Haridas, C.V. & Tuljapurkar, S. (2007) Time, transients and elasticity. *Ecology Letters*, **10**, 1143–1153.
- Hegland, S.J., Jongejans, E. & Rydgren, K. (2010) Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models. *Oecologia*, **163**, 695–706.
- Hesse, E., Rees, M. & Müller-Schärer, H. (2008) Life-history variation in contrasting habitats: flowering decisions in a clonal perennial herb (*Veratrum album*). *American Naturalist*, **172**, E196–E213.
- Hunter, C.M. & Caswell, H. (2005) The use of the vec-permutation matrix in spatial matrix population models. *Ecological Modelling*, **188**, 15–21.
- Jacquemyn, H., Brys, R. & Jongejans, E. (2010) Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. *Journal of Ecology*, **98**, 1204–1215.
- Jongejans, E., Sheppard, A.W. & Shea, K. (2006) What controls the population dynamics of the invasive thistle *Carduus nutans* in its native range? *Journal of Applied Ecology*, **43**, 877–886.
- Jongejans, E., Skarpaas, O. & Shea, K. (2008) Dispersal, demography and spatial population models for conservation and control management. *Perspective in Plant Ecology, Evolution and Systematics*, **9**, 153–170.
- Jongejans, E., Shea, K., Skarpaas, O., Kelly, D. & Ellner, S. (2011) Importance of individual and environmental variation for invasive species spread: a spatial integral projection model. *Ecology*, **92**, 86–97.
- de Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology*, **81**, 607–618.
- Kuss, P., Rees, M., Aegisdóttir, H.H., Ellner, S.P. & Stöcklin, J. (2008) Evolutionary demography of long-lived monocarpic perennials: a time-lagged integral projection model. *Journal of Ecology*, **96**, 821–832.
- Metcalfe, C.J.E., McMahon, S.M. & Clark, J.S. (2009a) Overcoming data sparseness and parametric constraints in modeling of tree mortality: a new nonparametric Bayesian model. *Canadian Journal of Forestry Research*, **39**, 1677–1687.
- Metcalfe, C.J.E. & Pavard, S. (2007) Why evolutionary biologists should be demographers. *Trends in Ecology and Evolution*, **22**, 205–212.
- Metcalfe, J., Rose, K. & Rees, M. (2003) Evolutionary demography of monocarpic perennials. *Trends in Ecology and Evolution*, **18**, 471–480.
- Metcalfe, C., Rose, K., Childs, D., Sheppard, A., Grubb, P. & Rees, M. (2008) Evolution of flowering decisions in a stochastic, density-dependent environment. *Proceedings of the National Academy of Sciences*, **105**, 10466.
- Metcalfe, C., Horvitz, C., Tuljapurkar, S. & Clark, D. (2009b) A time to grow and a time to die: a new way to analyze the dynamics of size, light, age, and death of tropical trees. *Ecology*, **90**, 2766–2778.
- Metcalfe, C., McMahon, S.M., Salguero-Gómez, R. & Jongejans, E. (2013) IPMpack: an R package for integral projection models. *Methods in Ecology and Evolution*, **4**, 195–200.
- Miller, T.E.X., Williams, J.L., Jongejans, E., Brys, R. & Jacquemyn, H. (2012) Evolutionary demography of iteroparous plants: incorporating non-lethal costs of reproduction into integral projection models. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2831–2840.
- Morris, W. & Doak, D. (2002) *Quantitative Conservation Biology: the Theory and Practice of Population Viability Analysis*. Sinauer Associates, Sunderland, MA.
- Neubert, M.G. & Caswell, H. (2000) Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.
- Nicolé, F., Dahlgren, J.P., Vivat, A., Till-Bottraud, I. & Ehrlén, J. (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology*, **99**, 1211–1218.
- Nussey, D.H., Watt, K., Pilkington, J.G., Zamoyska, R. & McNeilly, T.N. (2011) Age-related variation in immunity in a wild mammal population. *Aging Cell*, **11**, 178–180.
- Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S. & Coulson, T. (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, **466**, 482–485.
- Ozgul, A., Coulson, T., Reynolds, A., Cameron, T.C. & Benton, T.G. (2012) Population responses to perturbations: the importance of trait-based analysis illustrated through a microcosm experiment. *American Naturalist*, **179**, 582–594.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ramula, S., Rees, M. & Buckley, Y.M. (2009) Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. *Journal of Applied Ecology*, **46**, 1048–1053.
- Record, S. (2010) *Conservation While Under Invasion: Insights from a Rare Hemiparasitic Plant, Swamp Lousewort (Pedicularis lanceolata Michx.)*. PhD thesis, University of Massachusetts, Amherst, Massachusetts.
- Rees, M. & Ellner, S. (2009) Integral projection models for populations in temporally varying environments. *Ecological Monographs*, **78**, 575–594.
- Rees, M. & Rose, K.E. (2002) Evolution of flowering strategies in *Oenothera glazioviana*: an integral projection model approach. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1509–1515.
- Rees, M., Childs, D.Z., Metcalfe, J.C., Rose, K.E., Sheppard, A.W. & Grubb, P.J. (2006) Seed dormancy and delayed flowering in monocarpic plants: selective interactions in a stochastic environment. *American Naturalist*, **168**, E53–E71.
- Salguero Gómez, R. & Plotkin, J.B. (2010) Matrix dimensions bias demographic inferences: implications for comparative plant demography. *American Naturalist*, **176**, 710–722.

- Salguero-Gómez, R., Siewert, W., Casper, B.B. & Tielborger, K. (2012) A demographic approach to study effects of climate change in desert plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3100–3114.
- Schindler, S., Neuhaus, P., Gaillard, J.-M. & Coulson, T. (2013) The influence of nonrandom mating on population growth. *American Naturalist*, **182**, 28–41.
- Smallegange, I.M. & Coulson, T. (2013) Towards a general, population-level understanding of eco-evolutionary change. *Trends in Ecology and Evolution*, **28**, 143–148.
- Tuljapurkar, S. (1990) *Population Dynamics in Variable Environments*. Lecture Notes in Biomathematics 85, Springer, New York.
- Wallace, K., Leslie, A. & Coulson, T. (2012) Re-evaluating the effect of harvesting regimes on Nile crocodiles using an integral projection model. *Journal of Animal Ecology*, **82**, 155–165.
- Williams, J.L., Miller, T.E. & Ellner, S.P. (2012) Avoiding unintentional eviction from integral projection models. *Ecology*, **93**, 2008–2014.
- Yang, S., Jongejans, E., Yang, S. & Bishop, J.G. (2011) The effect of consumers and mutualists of *Vaccinium membranaceum* at Mount St. Helens: dependence on successional context. *PLoS ONE*, **6**, e26094.
- Yule, K.M., Miller, T.E.X. & Rudgers, J.A. (2013) Costs, benefits, and loss of vertically transmitted symbionts affect host population dynamics. *Oikos*, **122**, 1512–1520.
- Zuidema, P.A., Jongejans, E., Chien, P.D., During, H.J. & Schieving, F. (2010) Integral Projection Models for trees: a new parameterization method and a validation of model output. *Journal of Ecology*, **98**, 345–355.

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Supporting Information

Additional Supporting Information may be found in the online version of this article. Data for examples in supplementary materials is available at DOI: 10.5061/dryad.6575f

Appendix S1. R code for various IPMs.