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1 **Population viability analysis of plant and animal populations with**
2 **stochastic integral projection models**

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19 **Author Contributions:** MJ and JFLG conceived and designed the study. MJ and JFLG

20 designed the models and JFLG provided data. MJ performed all analyses. MJ and JFLG wrote

21 the manuscript.

22

23

24 **Abstract**

25 Integral projection models (IPM) make it possible to study populations structured by
26 continuous traits. Recently, Vindenes *et al.* (2011) proposed an extended IPM to analyse the
27 dynamics of small populations in stochastic environments, but this model has not yet been
28 used to conduct population viability analyses. Here, we used the extended IPM to analyse the
29 stochastic dynamics of IPM of small size-structured populations in one plant and one animal
30 species (evening primrose and common lizard) including demographic stochasticity in both
31 cases and environmental stochasticity in the lizard model. We also tested the accuracy of a
32 diffusion approximation of the IPM for the two empirical systems. In both species, the
33 elasticity for λ was higher with respect to parameters linked to body growth and
34 size-dependent reproduction rather than survival. An analytical approach made it possible to
35 quantify demographic and environmental variance in order to calculate the average stochastic
36 growth rate. Demographic variance was further decomposed to gain insights into the most
37 important size classes and demographic components. A diffusion approximation provided a
38 remarkable fit to the stochastic dynamics and cumulative extinction risk, except for very small
39 populations where stochastic growth rate was biased upward or downward depending on the
40 model. These results confirm that the extended IPM provides a powerful tool to assess the
41 conservation status and compare the stochastic demography of size-structured species, but
42 should be complemented with individual based models to obtain unbiased estimates for very
43 small populations of conservation concern.

44

45 **Keywords:** extinction, life cycle, population viability analysis, trait-based approach.

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47

48 **Introduction**

49 Ecological impacts of human activities have altogether caused a massive loss of species
50 (Hughes et al. 1997), and the abundance of many species has crossed a critical threshold for
51 the population viability (Gilpin and Soulé 1986). Therefore, a better understanding of small
52 population dynamics should give crucial insights to predict, and where possible remedy,
53 extinction. Population dynamics results from an interplay between deterministic components,
54 stochastic components, and the life history (Benton et al. 2006; Lande et al. 2003). For
55 example, populations of common lizards are regulated by density dependent feedbacks (i.e.,
56 deterministic component) and also fluctuate due to yearly changes in weather conditions (i.e.,
57 random component, Le Galliard et al. 2010). Given that importance of stochastic factors in
58 small populations, one major topic in conservation biology is to evaluate how random,
59 demographic variation affects population viability across diverse life histories (Beissinger and
60 McCullough 2002; Morris and Doak 2002). Demographic variation can be explained by
61 random fluctuations in climate, resource availability, and other extrinsic factors that generate
62 simultaneous changes among individuals at a given time (i.e., environmental stochasticity).
63 Demographic variation can also be explained by random inter-individual differences (i.e.,
64 demographic stochasticity), non-random differences among individuals (e.g., differences in
65 quality at birth) and sampling effects (Kendall and Fox 2002).

66 Models to describe stochastic dynamics and calculate extinction risk for small
67 populations often hypothesise a discrete time process and a discrete stage structure
68 (Beissinger and McCullough 2002; Caswell 2001; Morris and Doak 2002). They rely on a
69 projection matrix whose entries are transition rates within and between stages (e.g., survival
70 and reproduction in an age structured population, Caswell 2001). Such matrix projection
71 models (MPM) make it possible to include, for example, effects of environmental (Lande and
72 Orzack 1988; Tuljapurkar 1990) and demographic stochasticity (Engen et al. 2005). Thus,

73 most population viability analyses (PVA) are based on MPM for which robust protocols have
74 been defined to assess conservation status, make demographic projections and test alternative
75 management scenarios (Morris and Doak 2002). However, the life history of many species is
76 often characterised by a life history structure that depends on continuous traits, sometimes in
77 conjunction with a discrete stage structure (Benton et al. 2006; Ellner and Rees 2006). For
78 example, size (or height in plants) are key determinants of demographic variation in natural
79 populations of snakes and lizards (Baron et al. 2013; Le Galliard et al. 2010), and many
80 species of mammals, birds and plants (Merow et al. 2014).

81 Continuously structured life histories can be modelled with a large transition matrix
82 made out of numerous classes and the demographic parameters in a MPM can be estimated
83 from regression on continuous traits (Gross et al. 2006). In such cases, however, the use of
84 MPM may come at the cost of precision of model parameters, generate difficulties of
85 numerical implementation in small data sets, and induce potential changes in the ranking of
86 sensitivities (Easterling et al. 2000; Enright et al. 1995; Pfister and Stevens 2003). Instead,
87 Easterling *et al.* (2000) and Ellner and Rees (2006) recommended to use regression
88 techniques to estimate demographic traits in an integral projection model (IPM). Ramula *et al.*
89 (2009) further demonstrated that the IPM can outperform the MPM for small data sets
90 because the IPM estimates the asymptotic growth rate λ with less bias and variance. In a
91 recent study, Vindenes *et al.* (2011) proposed an extended IPM to model continuously
92 structured life histories for small populations in fluctuating environments. This extension of
93 IPM theory assumes small demographic fluctuations (i.e., small noise approximation) and
94 allows to approximate population dynamics by a diffusion process. The new mathematical
95 framework of Vindenes *et al.* (2011) should provide a useful addition to the PVA toolbox in
96 conservation biology because it allows to model size-structured stochastic population
97 dynamics. However, to our knowledge, this new framework has never been applied in real life

98 situations and the accuracy of the small noise approximation have not been thoroughly
99 investigated.

100 In this study, we used the newly developed, extended IPM and tested the accuracy of
101 the diffusion approximation for two particular empirical systems. First, we applied the
102 extended IPM to the case of two natural populations, including (i) a widespread monocarpic
103 perennial plant species (redsepal evening primrose, *Oenothera glazioviana*) previously
104 studied with a deterministic IPM (Rees and Rose 2002), and (ii) a widespread lizard species
105 (common lizard, *Zootoca vivipara*) characterised by a strong size structure and temporal
106 fluctuations in survival (Le Galliard et al. 2010). We chose these two study systems because
107 they represent an increasing complexity from a system influenced solely by demographic
108 stochasticity to a system influenced by the combined action of demographic and
109 environmental stochasticity. In addition, the primrose represents a natural situation with a
110 positive deterministic growth, which is encountered in some reintroduction programs in
111 conservation biology (Beissinger and McCullough 2002; Morris and Doak 2002). On the
112 contrary, the lizard represents a natural situation with a negative growth typical of the study of
113 endangered, declining species. Thus, these two examples are useful testbeds to demonstrate
114 the flexibility of the extended IPM for conservation biology. In each case study, we used the
115 extended IPM to conduct a standard PVA including the calculation and decomposition of the
116 stochastic population growth rate, the analysis of demographic stochasticity, and the
117 simulation of extinction dynamics. We compared outcomes of this PVA with those of an
118 individual based, simulation version of the IPM. Second, we also quantified the accuracy of
119 the diffusion approximation in numerous, alternative parameterisations of the primrose model
120 ranging from positive to negative growth and from low to very high values of demographic
121 variance. We did so to investigate more thoroughly the accuracy of the diffusion
122 approximation without confounding effects of differences in life history structure between the

123 two species.

124 **Materials and methods**

125 **Integral projection model**

126 Let's assume that the life history is structured by one continuous variable called y such that
 127 individuals differ by y only and y is a major determinant of vital rates; for example y could
 128 correspond to body size in animal or height in a plant. The population can then be described
 129 by the probability density of individual size y at time t , defined by the continuous function
 130 $n(y,t)$, such that $n(y,t)dy$ is the number of individuals between trait values y and $y+dy$
 131 at time t (Easterling et al. 2000). Total population size at time t is called $n(t) = \int_{\Omega} n(y,t)dy$,
 132 where Ω is the domain of possible values for trait y . The general structure of the
 133 time-invariant IPM of a large population writes like:

134
$$n(y,t+1) = \int_{\Omega} k(y,x)n(x,t)dx = \int_{\Omega} [s(x)f_s(y,x) + b(x)f_b(y,x)]n(x,t)dx \quad (1)$$

135 where $k(y,x)$ is the kernel describing transition rates from state x at time t to state y at time
 136 $t+1$. According to equation (1), the kernel can be further decomposed into (1) the
 137 survival-growth kernel where $s(x)$ is the survival probability of an individual with trait value
 138 x , and $f_s(y,x)dy$ is the probability of reaching trait value between y and $y+dy$ at time
 139 $t+1$ for an individual of trait value x , and (2) the fecundity kernel where $b(x)$ is the fecundity
 140 of an individual with trait value x , and $f_b(y,x)$ is the probability density function of the trait
 141 value of offspring. This deterministic IPM can be considered as a matrix projection model
 142 (MPM) with an infinite number of discrete classes. Thus, according to the seminal paper by
 143 Easterling *et al.* (2000), most of the properties of MPM can be generalised to IPM, including
 144 the calculation of the deterministic population growth rate λ , the determination of
 145 equilibrium population structure $u(y)$ and reproductive values $v(y)$ and the calculation of

146 deterministic elasticities of λ . Here, we used a numerical method to simulate IPM by
 147 discretising the state-space Ω into C classes of the same width and computing integrals
 148 using Simpson's 3/8 method, a more accurate numerical integration method than the standard
 149 mid-point rule (Merow et al. 2014). A spectral analysis of this discretised IPM allows to
 150 determine the dominant eigenvalue (called λ), the right eigenvector $u(x)$ scaled so that
 151 $\int_{\Omega} u(x)dx = 1$, and the left eigenvector $v(x)$ scaled so that $\int_{\Omega} v(x)u(x)dx = 1$. The right
 152 eigenvector corresponds to the stable trait distribution, while the left eigenvector corresponds
 153 to the reproductive value distribution, which measures the contribution of an individual to
 154 future population growth relative to other individuals in the population.

155 **Finite population in a stochastic environment**

156 To describe the dynamics of a small population in a fluctuating environment, we introduce the
 157 stochastic IPM:

$$158 \quad N(y, t+1) = \int_{\Omega} K(y, x, Z_t) N(x, t) dx, \quad (2)$$

$$159 \quad K(y, x, Z_t) = s(x, Z_t) f_s(y, x, Z_t) + b(x, Z_t) f_b(y, x, Z_t)$$

160 where N is the discrete population size, K is a stochastic kernel, and Z_t is a random
 161 vector describing parameter values at time t and thus the environmental state. The model
 162 described by equation (2) is similar to the deterministic model of equation (1) conditional on
 163 Z_t . Here, we consider that Z_t is a vector of year-specific parameters and assumed that
 164 parameter values vary randomly over time according to the random effects model of Rees and
 165 Ellner (2009). This implies that elements of the stochastic kernel of the IPM are drawn
 166 randomly each year from some parametric statistical distributions. However, the exact
 167 distribution from which the elements are taken is not defined *a priori* and will be
 168 representative of the model species. The most common assumption is that time-varying kernel
 169 elements are drawn independently from symmetric, Gaussian distributions, but it is possible

170 to use any other type of multivariate parametric statistical distribution (Rees and Ellner 2009).

171 The dynamics of the expected population size at time $t+1$ given population size at time
 172 t can be written as:

$$173 \quad E[N(t+1)|N(t)] = \int_{\Omega} \int_{\Omega} \bar{k}(y, x) N(x, t) dx dy \quad (3)$$

174 where $\bar{k}(y, x)$ is the mean kernel defined by averaging the stochastic kernel over all possible
 175 environmental state values. Similar to equation (1), this dynamics is characterised by an
 176 expected growth rate $\bar{\lambda}$, the stable state structure $\bar{u}(x)$ and the reproductive value $\bar{v}(x)$. The
 177 total reproductive value of the population can then be defined as $V = \int \bar{v}(x) N(x)$, which
 178 equals total population size only when the population has the exact stable state structure. The
 179 instantaneous rate of increase of the total reproductive value is then given by

$$180 \quad \Lambda_t = \frac{V_{t+1}}{V_t} = \bar{\lambda} + E_t + D \quad (4)$$

181 where E_t and D are random variables describing environmental stochasticity (i.e.,
 182 between-year deviation from the mean kernel of the average individual contribution to total
 183 reproductive value) and demographic stochasticity (i.e., within-year deviation from the mean
 184 of the year of the individual contribution to total reproductive value), respectively (Engen et
 185 al. 2007; Vindenes et al. 2011). Assuming no covariance between demographic and
 186 environmental stochasticity, the variance in the instantaneous growth rate can be written as

$$187 \quad \text{Var}(\Lambda_t | V_t) = \text{Var}(E_t | V_t) + \text{Var}(D | V_t) = \sigma_e^2 + \sigma_d^2/V_t \quad (5)$$

188 for the case of a structured population model, including the IPM (Engen et al. 2007; Lande et
 189 al. 2003; Vindenes et al. 2011). In equation (5), σ_e^2 and σ_d^2 are the environmental and
 190 demographic variances, respectively. According to equation (5), the contribution of
 191 demographic stochasticity depends on the demographic variance σ_d^2 and is inversely
 192 proportional to the total reproductive value.

193 An important property of a stochastic IPM is the long-run logarithmic growth rate,
 194 denoted $\ln \lambda_s$, which describes the asymptotic exponential growth rate of the population size
 195 after a sufficiently long time (Lande et al. 2003; Rees and Ellner 2009; Tuljapurkar 1990). For
 196 a structured population, this long-run growth rate is best described by the dynamics of the
 197 total reproductive value, which is Markovian, obeys a first-order autoregressive process, and
 198 grows exponentially according to the same long-run growth rate as population size (Engen et
 199 al. 2007; Engen et al. 2005). The long-run logarithmic growth rate can be approximated
 200 assuming a small environmental noise, which implies that the population stays close to its
 201 stable distribution (e.g., for IPM Rees and Ellner 2009). Following earlier work on
 202 age-structured populations (Engen et al. 2007), Vindenes et al. (2011) showed that the
 203 first-order approximation of the long-run growth rate of the stochastic IPM writes like

$$204 \quad \ln \lambda_s \approx \ln \bar{\lambda} - \frac{\sigma_e^2}{2\bar{\lambda}^2} - \frac{\sigma_d^2}{2\bar{\lambda}^2 V}, \quad (6)$$

205 where $\bar{\lambda}$ is the deterministic population growth rate of the mean kernel.

206 Calculation of environmental and demographic variances

207 The demographic variance σ_d^2 from equation (5) is given by the first-order approximation:

$$208 \quad \sigma_d^2 \approx \int_{\Omega} \bar{u}(y) \sigma_d^2(y) dy, \quad (7)$$

209 where the demographic variance due to an individual with trait value y , called $\sigma_d^2(y)$, is
 210 weighted by the stable state structure $\bar{u}(y)$ calculated for the mean kernel. Based on the work
 211 by Vindenes et al. (2011), the term $\sigma_d^2(y)$ can be further computed by using the expectation
 212 of the demographic variance over all environmental states and a decomposition of the
 213 individual contribution to total reproductive value, such that

$$214 \quad \sigma_d^2(y) = \underbrace{\bar{s}(y) \bar{\sigma}_{vs}^2(y)}_{\text{Growth variance}} + \underbrace{\bar{b}(y) \bar{\sigma}_{vb}^2(y)}_{\text{Offspringsize variance}} + \underbrace{\bar{\mu}_{vs}^2(y) \bar{\sigma}_s^2(y)}_{\text{Survival variance}}$$

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$$215 \quad + \frac{\overline{\mu_{vb}^2}(y) \overline{\sigma_B^2}(y)}{\text{Fecundity variance}} + \frac{2 \overline{\sigma_{BS}^2}(y) \overline{\mu_{vs}}(y) \overline{\mu_{vb}}(y)}{\text{Survival-Fecundity covariance}} \quad (8)$$

216 All terms in equation (8) involve mean values over environments. They are precisely defined
 217 in Appendix A, where we describe methods to estimate them. The three first variances can be
 218 computed numerically from the model parameters and the reproductive value. The fecundity
 219 variance depends on properties of the fecundity probability distribution, while the
 220 survival-fecundity covariance is influenced by structural details of the model. For example, if
 221 demographic census occurs after reproduction, reproduction is conditional on the survival of
 222 parents, which implies a positive covariance between survival and fecundity.

223 In addition, the environmental variance is given by the first-order approximation:

$$224 \quad \sigma_e^2 \approx \int_{\Omega} \int_{\Omega} \overline{u}(x) \overline{u}(y) c(x, y) dx dy, \quad (9)$$

225 where $c(x, y) = \text{cov}(E[W_x|Z], E[W_y|Z])$ is the covariance of expected contribution of
 226 individual of trait value x (W_x) and trait value y (W_y) to the total reproductive value
 227 (Vindenes et al. 2011). A first order approximation of the environmental variance can be
 228 computed by calculating the variance in the population growth rate $\lambda(z)$ with respect to the
 229 environment state value z using stochastic simulations of large populations. Here, we
 230 computed the asymptotic population growth rate $\lambda(z)$ for 10,000 environments taken
 231 randomly from the empirical probability distribution.

232 **Simulation of the IPM for finite populations**

233 We used an individual based, numerical version of the IPM (IBM) to simulate the stochastic
 234 IPM for finite populations. The IBM included random, sampling variation for growth,
 235 survival and reproduction according to the empirical distribution laws. We also parameterised
 236 a diffusion approximation of the IBM following Vindenes *et al.* (2011), where the stochastic
 237 discrete time dynamics is approximated by a continuous time Wiener process with drift,
 238 which is entirely described by a drift term and an infinitesimal variance term (Lande and

239 Orzack 1988). We used the diffusion approximation to model the natural logarithm of the
240 total reproductive value (Engen et al. 2005). The drift term is equivalent to the average
241 logarithm of the stochastic growth rate from equation (6), while the variance term depends on
242 the deterministic growth rate and the environmental and demographic variances (see
243 Appendix B for detailed justification).

244 We simulated 50,000 runs of the IBM all starting from a reproductive value of 100
245 and from the same state structure calculated from the stable state structure of the mean kernel.
246 We calculated the instantaneous growth rate at each time step (Λ_t in equation (4)) and used
247 all simulated trajectories to quantify the sample mean and sample variance of the growth rate
248 from time t to time $t+1$ given the reproductive value at time t . The diffusion approximation
249 was simulated with the Matlab's econometry toolbox starting from a reproductive value of
250 100. Similar qualitative results were obtained starting from a smaller or a larger population
251 size. We calculated cumulative quasi-extinction risk during the first 50 years of the
252 simulation, a reasonable time horizon for a PVA, with three quasi-extinction thresholds ($N=1$
253 equivalent to true extinction, $N=10$, and $N=50$). We also calculated the cumulative extinction
254 risk according to a previously published analytical expression that uses a diffusion
255 approximation without demographic variance (Lande and Orzack 1988). We called this
256 approximation the "large population analytical approximation" below (see equation (B10) in
257 Appendix B for details). By comparing this analytical expression with results from the IBM
258 and diffusion approximation of the IPM, it is thus possible to quantify the effects of
259 demographic stochasticity on extinction risks.

260 **Prospective perturbation analyses**

261 Tools for the prospective analysis of IPM in response to small perturbations of the kernel
262 include the deterministic elasticity (relative change of the deterministic growth rate λ) and
263 the stochastic elasticity (relative change of the long-run stochastic growth rate defined by

264 equation 3) to the mean and variance for kernel elements, parameters and functions
 265 (Easterling et al. 2000; Rees and Ellner 2009). Here, we calculated only the deterministic
 266 elasticity and the elasticity of the demographic variance constant σ_d^2 , which are crucial to
 267 PVA (Mills and Lindberg 2002). For the former, we calculated both (1) the elasticity surface
 268 of λ to changes in the kernel, given by the relative sensitivity of λ to changes in the
 269 function $k(y, x)$ in a small area around y and x , and (2) the elasticity of λ to functions
 270 of the kernel and model parameters (Easterling et al. 2000). We also evaluated the relative
 271 impact of small changes in each parameter value on the demographic variance constant
 272 defined in equation (5). This was done numerically through a slight (1%) perturbation of the
 273 initial model. Because some parameter values were negative, we scaled sensitivities relative
 274 to the absolute value of each parameter to obtain meaningful estimates.

275 **Case studies**

276 We gathered life history data for one plant species characterised by a life cycle structured by
 277 height (redsepal evening primrose, *Oenothera glazioviana*) and one animal species
 278 characterised by a life cycle structured by body size (common lizard, *Zootoca vivipara*). The
 279 primrose population did not include estimates of environmental variance and was already
 280 studied with a deterministic IPM by Rees and Rose (Rees and Rose 2002). Both IPM included
 281 an annual census of the female portion of the population and were parameterised with life
 282 history data collected inside one reference population for each species. Detailed information
 283 on life cycles and model parameters is provided in Appendix C.

284 We first characterised all components of the stochastic growth rate in each study
 285 species, and conducted the elasticity analyses and numerical simulations of finite populations.
 286 In the case of the primrose model, further simulations were done where we tested different
 287 parameter values for the seed mortality rate and the residual variation (standard deviation of
 288 the random noise) of the growth function, which allowed us to test situations of decreasing,

289 almost stable and increasing populations with distinct patterns of deterministic growth and
290 demographic variation (see Appendix C). The primrose model was chosen to do this analysis
291 because it is simpler. In all models, we checked that our definition of the trait space did not
292 bias the model outcomes through eviction of individuals near size limits (Merow et al. 2014).
293 To do so, we calculated the size-dependent fraction eviction from the IPM conditional on
294 survival and the unconditional fraction using equation (2) in Williams et al. (2012). The
295 magnitude of eviction was negligible, even in the case of the primrose where size growth was
296 linear with a high variance (e.g., less than 1% and 0.001% for unconditional and conditional
297 fractions, respectively), and the fraction of evicted individuals was not influenced by changes
298 in model parameters.

299 **Results**

300 **General characteristics of IPM**

301 Deterministic predictions for the growth rate (Table 1) and for the stable size structure (not
302 shown) were similar to previously published observations. The primrose had an increasing
303 population (+5% annual increase) in accordance with Rees and Rose (2002). The common
304 lizard population displayed a local annual decrease of 10% in line with previous estimations
305 from MPM (Le Galliard et al. 2010) and direct estimates of local recruitment and immigration
306 (Lepetz et al. 2009). An analytical expression of each term in equation (8) made it possible to
307 compute $\sigma_d^2(y)$ using equation (7) and demographic variance using equation (6). The
308 primrose population was characterised by the strongest demographic variance (see Table 1).
309 In the common lizard, environmental variance was significant, since according to equation
310 (6), the population size where demographic variance equals environmental variance is around
311 20 individuals. A decomposition of the demographic variance according to size and the five
312 variance terms in equation (8) showed that most demographic stochasticity was due to body
313 growth and survival of adults while fecundity had little effects in the primrose (Figure 1a). A

314 strong negative correlation between fecundity and survival was observed. In the common
315 lizard (Figure 1b), body growth had little influence on the demographic variance, which was
316 almost entirely due to survival and fecundity.

317 **Elasticity analysis**

318 Elasticity surfaces represent the relative sensitivities of the deterministic growth rate to
319 changes in the kernel. For the primrose (Figure 2a), the elasticity surface indicates the
320 dominance of one size-specific transition, corresponding to transition of individuals into the
321 reproductive stage, relative to two size-specific transitions of equal importance corresponding
322 to growth of immature plants and offspring production. For the common lizard (Figure 2b),
323 three size-specific transitions of equal relative importance were identified: survival and
324 growth of juveniles, survival and growth of older individuals, and offspring production. We
325 further calculated the elasticity of the growth rate (λ) and demographic variance (σ_d^2) for
326 parameters in the primrose and lizard models (see Appendix E). In the primrose, elasticity of
327 λ was strongest for fecundity slope (measuring the increase of fecundity with rosette size),
328 growth intercept (measuring mean rosette size early in life) and growth slope (measuring size
329 increment per unit size at time t), followed by survival intercept (measuring mean survival
330 early in life). In the common lizard, fecundity and growth parameters had the strongest
331 influence followed by juvenile survival, and adult survival had a weak influence. The
332 elasticity of λ to change in one model parameter was positively correlated with the
333 elasticity of σ_d^2 to change in the same model parameter (Figure 2c).

334 **Population dynamics and extinction trajectories**

335 In the case of the common lizard, population dynamics predicted by the diffusion model fitted
336 extremely well those observed in the IBM. This very good fit was observed throughout 50
337 years of simulation in this case (see Figure 3a), but held over longer times with different
338 initial conditions (results not shown). The relationship between the stochastic growth rate Λ_t

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339 and population reproductive value predicted by the diffusion model was coherent with the one
340 observed in the IBM or the one predicted by equation (6), except in very small populations
341 where the diffusion approximation under-estimated the median and range of variation of the
342 stochastic growth rate distribution of the IBM (Figure 3b). In this species, the diffusion
343 approximation thus under-estimated slightly the variance of stochastic growth rate in very
344 small populations (Figure 3c), where the probability distribution of the stochastic growth rate
345 from the IBM did not fit the log-normal distribution assumed by the diffusion model (Figure
346 3d).

347 Despite these small biases at very small population sizes, the cumulative
348 quasi-extinction risk curves in the common lizard were very well predicted by the diffusion
349 model even at low quasi-extinction thresholds (relative difference less than 5%, Figure 4a).
350 Starting from ca. 100 individuals, this population had declining trends and characteristics
351 quasi-extinction times of less than 50 years very well matched by the diffusion
352 approximation. In the primrose population with positive growth, the risk of extinction was on
353 average very small (ultimate quasi-extinction risk of less than 10%) and we identified a
354 difference between predictions from the diffusion approximation and simulations of the IBM
355 (relative difference more than 5%, Figure 4b). In this species, rare extinctions were caused by
356 random events of rapid initial decline and demographic variance was very high due to
357 stochastic variation in plant size. In this situation, the stochastic trajectories are likely to be
358 more poorly captured by the diffusion approximation. In addition, as expected, differences
359 between the diffusion approximation and the large population analytical approximation were
360 higher at lower quasi-extinction thresholds in the lizard, i.e., when effects of demographic
361 stochasticity on extinction times were stronger (Figure 4a).

362 In the primrose, increased parameter values for seed establishment probabilities and
363 growth rate residual variance were associated with higher deterministic growth rate but also

364 higher demographic variance (see Table C1b in Appendix C), with a net negative effect on
365 extinction risk. An analysis of the relative difference between quasi-extinction curves
366 predicted by the diffusion approximation and those observed in the IBM revealed stronger
367 biases during transient dynamics (intermediate simulation times) and when populations were
368 less at risk of extinction (Fig. 5a, b). In all cases, the diffusion approximation under-estimated
369 time to extinction and it also under-estimated the total cumulative risk of extinction for
370 populations with positive intrinsic growth. To unravel if these biases were associated with
371 differences in the characteristic dynamics of the populations or systematic failure to capture
372 the properties of very small populations like in the common lizard, we plotted the bias for
373 stochastic growth rate against population reproductive value. The results strongly suggested
374 that this bias depended on population size irrespective of the model parameter values (Fig. 5c,
375 d). The diffusion approximation systematically over-estimated the mean stochastic growth
376 rate of the IBM in very small populations (less than 10-20 individuals).

377 **Discussion**

378 Until recently, the analysis of stochastic, size-structured populations rested essentially on
379 individual based or matrix population models (Easterling et al. 2000; Enright et al. 1995;
380 Pfister and Stevens 2003; Ramula et al. 2009). Here, we applied a new mathematical
381 framework (Vindenes et al. 2011) designed specifically for small, size-structured populations
382 and including both environmental and demographic variation. We performed basic population
383 viability analyses, evaluated the model's accuracy in two species characterised by contrasted
384 life cycles, and tested robustness of the model's predictions to changes in some model
385 parameters in one model species. We found three results: (1) the extended IPM allows to
386 decompose demographic variance to gain insights into most important size classes and
387 demographic components, (2) the diffusion model with three parameters provided in general a
388 very good approximation of the transient stochastic dynamics and ultimate extinction risks,

389 but (3) the diffusion approximation produced model-dependent biased estimates of the
390 stochastic growth in very small populations.

391 **Model construction**

392 Given the number of tools available to conduct a PVA (Beissinger and McCullough 2002),
393 one must be fully aware of the opportunities and constraints of the stochastic IPM. The kernel
394 construction and parameter estimation are the most critical steps of the construction of an
395 IPM. The kernel includes functions for growth, survival and reproduction. For our case
396 studies, growth and reproduction functions and their yearly variation could be estimated
397 relatively easily with regression techniques (Easterling et al. 2000; Rees and Ellner 2009).
398 However, an accurate estimation of the survival function was more difficult to obtain for the
399 lizard population since not all animals could be sampled. Thus, we used
400 capture-mark-recapture models for closed populations, a procedure that can under-estimate
401 true survival (animals can be lost due to movement outside the study site) and that makes it
402 more difficult to assess size-dependent survival than standard logistic regressions (but see
403 Frederiksen et al. 2013). In rare or declining species of conservation concern, accurate
404 repeated censuses of the same population through time and a reasonable sample of individual
405 records of one or two traits (e.g., body size) are therefore critical to parameterize the IPM and
406 conduct a PVA (Ramula et al. 2009). For example, we have found it possible to parameterize
407 an IPM for the critically endangered meadow viper with individual records of body size and
408 reproduction in a very small population (less than 50 individuals, unpub. data).

409 Anyone willing to develop a stochastic IPM will also face three other difficulties.
410 First, even if IPM provide more accurate estimates of λ than MPM for small data sets
411 (Ramula et al. 2009), uncertainty in parameter values may lead to uncertainty in model
412 predictions. Confidence intervals for model predictions could be obtained using Monte Carlo
413 simulations or bootstrap re-sampling (McGowan et al. 2011). Second, the regression models

414 used to parameterize the IPM assumed small and normally distributed inter-annual variation.
415 This assumption was backed up by long term data from the field, but other species may be
416 characterised by catastrophic variation in survival (Baron et al. 2010). Individual-based
417 simulations could be used to test the demographic consequences of such catastrophic
418 variation. Third, a good knowledge of the probability distribution of kernel functions is
419 required to model demographic stochasticity. We used binomial distribution for survival and
420 Gaussian distribution for growth, but had no a priori expectation for the probability
421 distribution of fecundity. In the common lizard, the generalized Poisson distribution was the
422 best fit for the data because sample values were truncated at zero and had a clear upper bound
423 (Kendall and Wittmann 2010).

424 **Stochastic growth rate calculation**

425 The diffusion approximation and variance decomposition made it possible to describe
426 stochastic dynamic with only three parameters (Vindenes et al. 2011): deterministic growth
427 rate (λ), demographic variance (σ_d^2) and environmental variance (σ_e^2). This decomposition
428 provides a very powerful tool to assess the conservation status and compare the demography
429 of size-structured species. The primrose population was characterised by a strong
430 size-dependent demography and very high demographic stochasticity. The small demographic
431 stochasticity in the common lizard dominated environmental variance only in populations of
432 less than 20 individuals; thus, stochastic population dynamics were mainly driven by
433 inter-annual effects similar to previous studies (Le Galliard et al. 2010). We anticipate that
434 quantitative estimates of demographic and stochastic variance could be obtained in other
435 size-structured species of plants and animals. Their comparison would be extremely useful to
436 understand the relationship between stochastic population dynamics and life history similar to
437 what was done with stage-structured animal populations (Saether et al. 2013).

438 A good understanding of demographic stochasticity is particularly relevant in

439 conservation biology. Here, we proposed a graphical approach to decompose the demographic
440 variance which requires an analytical expression. This decomposition indicated that
441 demographic variance was mostly due to growth variation for the primrose but survival
442 variation in yearlings and adults for the common lizard. That plant growth contributed
443 strongly to demographic variation in the primrose population may be due to the prolonged and
444 weakly canalized compensatory growth trajectories. Plant growth lasted up to 10 years until
445 maturation, and there was also a very high variability in growth rate (Kachi and Hirose 1983).
446 In general, patterns of increasing size variability with age are common in plants because
447 growth rates of individuals are often dependant and/or positively correlated through time
448 (e.g., Pfister and Stevens 2002). The stochastic IPM would allow a better understanding of the
449 effects of these complex growth strategies on demographic variance.

450 One important assumption made in the two case studies is that the life cycles are
451 structured by one continuous covariate only. The framework of IPM also allows to include
452 more than one continuous variable or a mixture of continuous and discrete state variables
453 (Childs et al. 2003). To test the feasibility of this, we parameterised an additional IPM for the
454 meadow viper (*Vipera ursinii ursinii*), an endangered species characterised by a complex life
455 cycle structured by body size, age and breeding status (Baron et al. 2013; Ferrière et al. 1996).
456 The combined size and stage structure was justified by the fact that maturation is conditional
457 on the age (7 classes) and body size of immature females and because adult females alternate
458 breeding and non-breeding years independent of their size (Baron et al. 2013). Unfortunately,
459 the analytical expressions of the extended IPM were too cumbersome to allow a direct
460 calculation and decomposition of the demographic stochasticity, and we had to rely on
461 numerical simulations (results not shown). This difficulty could be encountered in many other
462 species where demography is shaped by both continuous traits and discrete attributes such as
463 stage, age, or habitat type (Ellner and Rees 2006). In such cases, we recommend to use the

464 IBM approach when the life cycle cannot be simplified without substantial loss of
465 information, or to simplify the life cycle to a stage or age structured matrix population model.

466 **Elasticity analysis**

467 Prospective perturbation analysis of stochastic population dynamics include the calculation of
468 many elasticities (this study, Easterling et al. 2000; Rees and Ellner 2009). In a real-life PVA,
469 the conclusions of the elasticity analysis should be weighted by the feasibility and costs of all
470 options available to improve the conservation status of the population. Here, we did not
471 attempt to compute and compare all elasticities, but instead focused on the elasticity analysis
472 of λ and σ_d^2 . We found a positive correlation between elasticity for λ and for σ_d^2 . Such
473 correlations are expected whenever a management action to improve the mean of a trait also
474 changes its variance, as is the case for the probability distributions of survival or fecundity.
475 This correlation means that traits contributing more to deterministic growth may have lower
476 effects on stochastic population growth than expected, especially at low population sizes.

477 The IPM is a useful tool for elasticity analysis of λ in a size-structured population
478 because elasticities are not influenced by stage duration (Easterling et al. 2000). Elasticity
479 surfaces indicate the most important size classes during a reintroduction or reinforcement
480 program. In addition, the IPM allows to evaluate the elasticity to body growth and
481 size-dependent demography, which is critical to the management of many important size
482 structured populations such as hunted game species or marine fishes for example (Merow et
483 al. 2014). Traditional PVA focuses on transition between stages (i.e., survival or migration)
484 and fecundity, but tends to ignore body growth (Beissinger and McCullough 2002; Morris and
485 Doak 2002). In life history theory, growth strategies are important because differences in
486 body growth have implications for age and size at maturation, future fecundity and future
487 survival. In addition, many species are characterised by plastic growth rates (French et al.
488 2011; Gurnell et al. 2004). In the primrose and common lizard, the two parameters with the

489 highest elasticity for λ were the slope between fecundity and size and the basal size
490 increment. Thus, conservation programs increasing body growth by improvement of habitat
491 quality, removal of competitors, and food or nutrient supplementation should provide the
492 most efficient management strategies in these species.

493 **Extinction dynamics**

494 Under the small noise approximation, Vindenes *et al.* (2011) constructed a diffusion model
495 and demonstrated that this model fitted well the stochastic dynamics of one hypothetical
496 stable size-structured population subject to demographic and environmental stochasticity. Our
497 results obtained in two model species with contrasted life cycles, including one model species
498 analysed with 25 different combinations of parameters, confirm these conclusions except in
499 situations where the assumption of the small noise approximation is not met. We found that
500 the diffusion approximation fitted very well the results of the stochastic IBM in intermediate
501 and large populations (as a rule of thumb, when $N > 20$), but tended to under-estimate or
502 over-estimate the stochastic growth rate in very small populations. The direction of the bias
503 was different in the two model species, and the impact of the bias was greater when
504 populations had positive growth and thus extinction was not certain. According to our
505 descriptive analyses, the differences were explained by a failure of the diffusion
506 approximation to capture the probability distribution of the stochastic growth rate in very
507 small populations.

508 Relatively few ecological studies have tested for sources of deviations between the
509 diffusion approximation and the full stochastic model. It is expected that the diffusion
510 approximation should fail when populations sizes are very small and growth variance
511 becomes very large, especially in populations with large demographic variance such as the
512 primrose. Engen *et al.* (2005) analysed a large number of age structured population models
513 and found a reasonable fit in most cases, except for populations structured according to a

514 large number of age classes where the diffusion approximation could over-estimate the
515 extinction risks. The case of density-dependent dynamics was investigated more
516 systematically, and significant but relatively unpredictable model-dependent deviations were
517 found (Kendall 2009; Wilcox and Possingham 2002). Wilcox and Possingham (2002) stated
518 that such deviations could come from (1) inaccuracy in the estimation of the parameters of the
519 diffusion approximation, (2) difficulties to capture unstable dynamics or rare events of
520 population decline, and (3) unrealistic assumptions of the diffusion approximation. In our
521 case, we included both demographic and environmental stochasticity in the diffusion
522 approximation, and population dynamics were relatively smooth. Thus, the failure of the
523 diffusion approximation at small population sizes was probably a consequence of the
524 structural assumption of unbounded and normally distributed population growth rates (Lande
525 et al. 2003; Ovaskainen and Meerson 2010). The magnitude of this bias will be difficult to
526 predict because it seems to depend on the life cycle. Thus, we recommend to complement the
527 extended IPM approach with individual based models to obtain unbiased estimates for very
528 small populations of conservation concern.

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635 **Figure legends**

636 **Figure 1.** Decomposition of demographic variance according to size and demographic
 637 components in the primrose (a) and common lizard (b) after equation (9). The primrose model
 638 was structured by rosette size (mm, log scale) and the common lizard model was structured by
 639 body size (snout-vent length, mm). The areas of different colour indicate the relative
 640 contribution of each component to total demographic variance at a given size, including
 641 negative contributions.

642 **Figure 2.** Elasticity analysis of the deterministic growth rate and of the demographic variance.
 643 a-b. Elasticity surfaces of the deterministic growth rate λ with respect to the projection kernel
 644 of the primrose (a) and the common lizard (b). c. Elasticity of the demographic variance
 645 against elasticity of the deterministic growth rate λ with respect to the same model parameter
 646 for the common lizard (squares) and primrose (circles) models. Elasticity was calculated with
 647 respect to a small change in the value of each parameter describing size-dependent survival,
 648 growth and reproduction functions of the projection kernel (see Appendix D for raw data).

649 **Figure 3.** Comparison of the simulations of the diffusion approximation of the IPM
 650 (diffusion) with the simulations of the individual based model (IBM) and the predictions from
 651 the small-noise first order approximation (LPA) for the common lizard. a. Population
 652 trajectories (75% , 50% and 25% quantiles of the total reproductive value) predicted by the
 653 diffusion approximation and the IBM. b. Stochastic growth rate (mean and quantiles) against
 654 population reproductive value from the diffusion approximation, the IBM and the small-noise
 655 approximation of equation (6). c. Variance of the stochastic growth rate variance against
 656 inverse of population reproductive value from the diffusion, the IBM and the small-noise
 657 approximation of equation (6). For the diffusion approximation and the IBM, reproductive
 658 values and stochastic growth rate statistics were calculated from the simulations displayed in
 659 panel a. The inverse of the population reproductive value was used to ease visualization. d.

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660 Probability distributions of the stochastic population growth rate in small (20 individuals) and
661 very small (5 individuals) populations from the diffusion approximation and the IBM. Similar
662 qualitative results were obtained with the other models.

663 **Figure 4.** Cumulative extinction risks predicted by the diffusion approximation of the IPM
664 (diffusion), the individual based model (IBM) and the large population analytical
665 approximation (LPA) of Lande and Orzack (1988). The latter was not plotted in the primrose
666 model because this model does not include environmental variation. Extinction probability
667 was computed for a quasi-extinction threshold of 50 (black), 10 (grey) and 1 (light grey)
668 individuals for the common lizard (a) and the primrose population (b). All simulations started
669 from a reproductive value of 100. Note the difference in the y-axis range in panel (b) where
670 population growth was positive and ultimate extinction risk is less than 1.

671 **Figure 5.** Sensitivity analysis of the quality of the IPM diffusion approximation in the
672 primrose model. Relative difference between the cumulative quasi-extinction curves of the
673 diffusion approximation of the IPM and those of the IBM with increasing values (from dark
674 to light curves) of the seed establishment probability (a) and the residual variation (standard
675 deviation) of the size growth (b). A negative relative difference indicates that the diffusion
676 approximation tends to under-estimate the extinction probability. To understand the observed
677 patterns, we calculated the relative difference between the mean stochastic growth rate of the
678 diffusion approximation and of the IBM (c, d). Mean stochastic growth rate was calculated at
679 each reproductive value reached by the simulations and curves were then smoothed with a
680 moving average method to ease interpretation. Fluctuations come from small sample size of
681 data to calculate extinction risk and biases between the diffusion approximation and IBM.
682 Deterministic growth is higher than 1 when seed establishment probability < 0.008 (panels
683 a-c) and when growth residual variation < 0.3364 (panels b-d).

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685 **Table 1**

686 Estimates of the asymptotic growth rate (λ), demographic variance (σ_d^2) and environmental
 687 variance (σ_e^2) from equation (3). In the primrose, no estimate of environmental variance was
 688 available implying that estimate of demographic variance was probably inflated.

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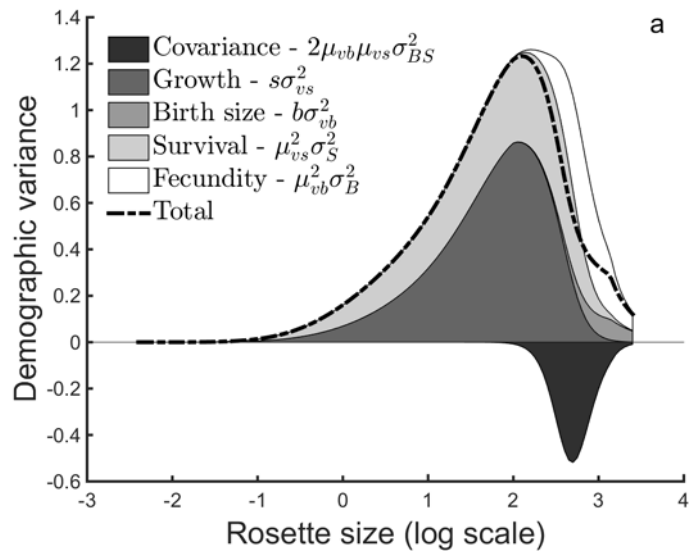
<i>Model</i>	λ	σ_d^2	σ_e^2
<i>Oenothera glazioviana</i> (primrose)	1.0526	2.2487	0
<i>Zootoca vivipara</i> (common lizard)	0.9077	0.4566	0.0204

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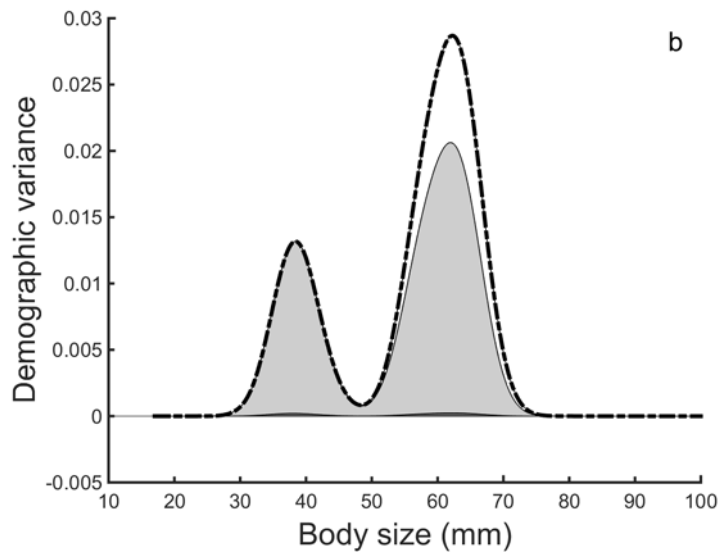
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692 **Figure 1**

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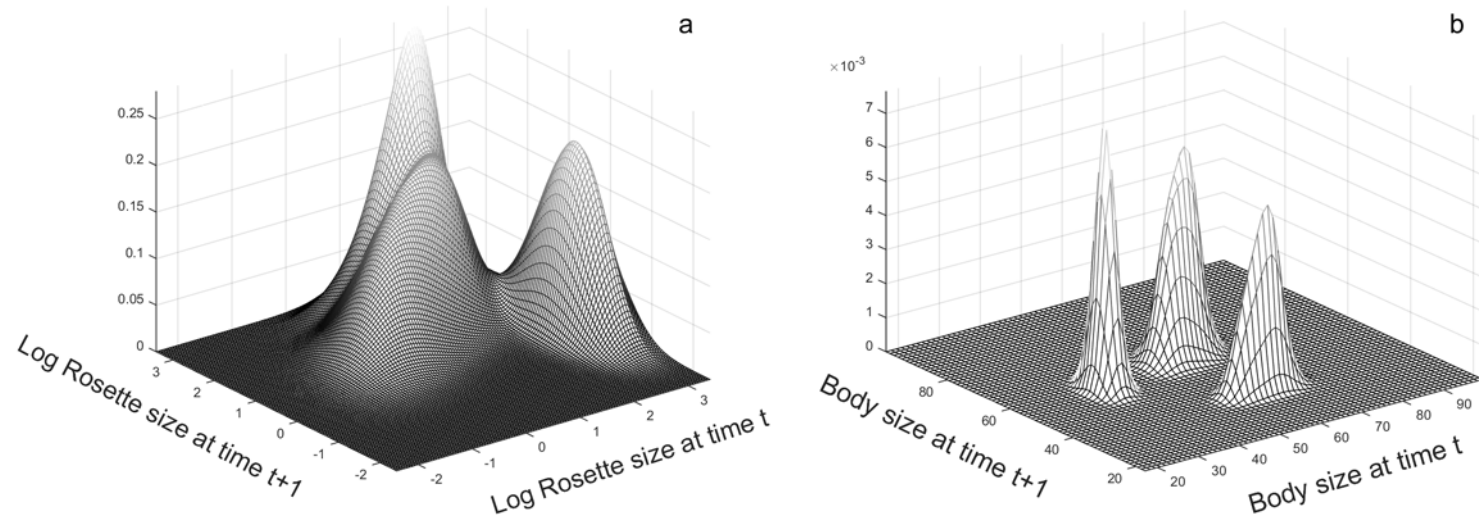


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697 **Figure 2**

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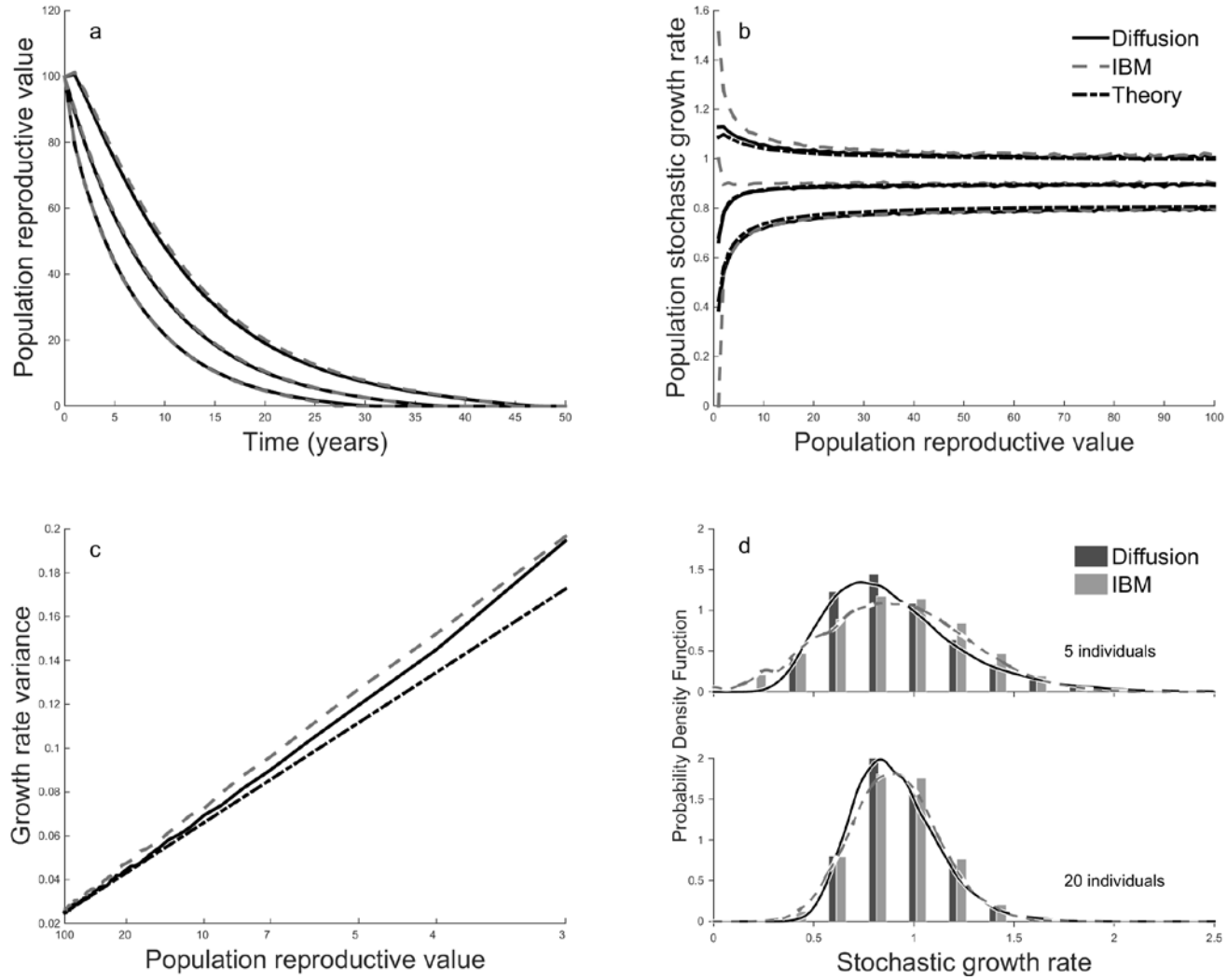


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702 **Figure 3**

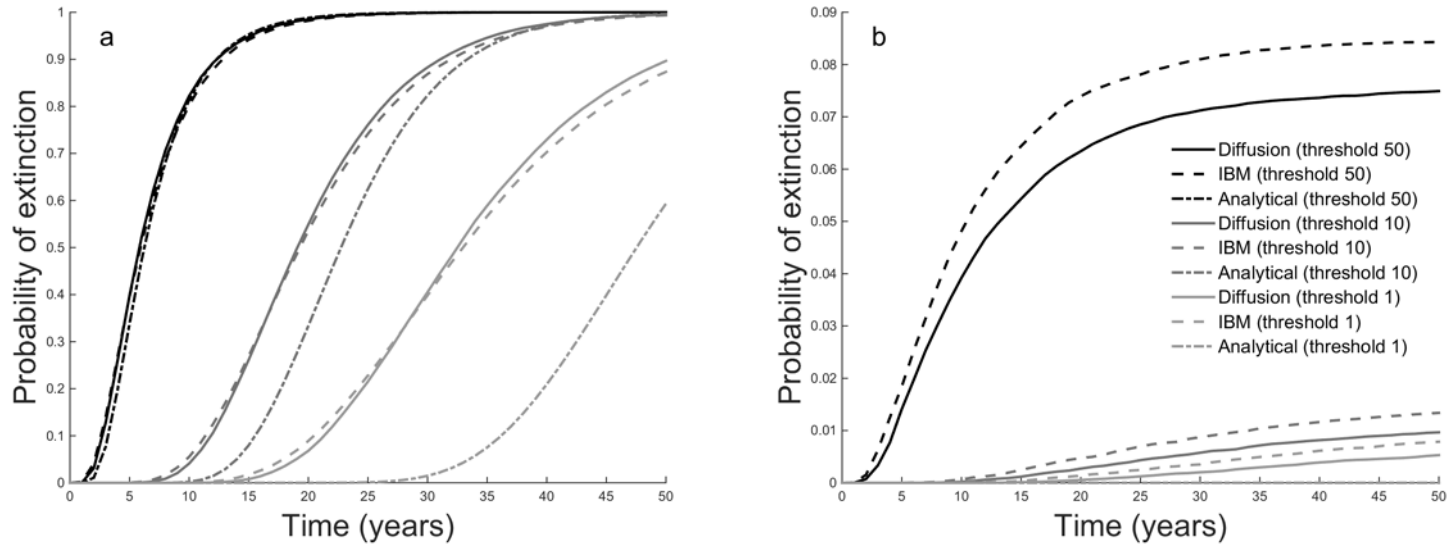


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706 **Figure 4**



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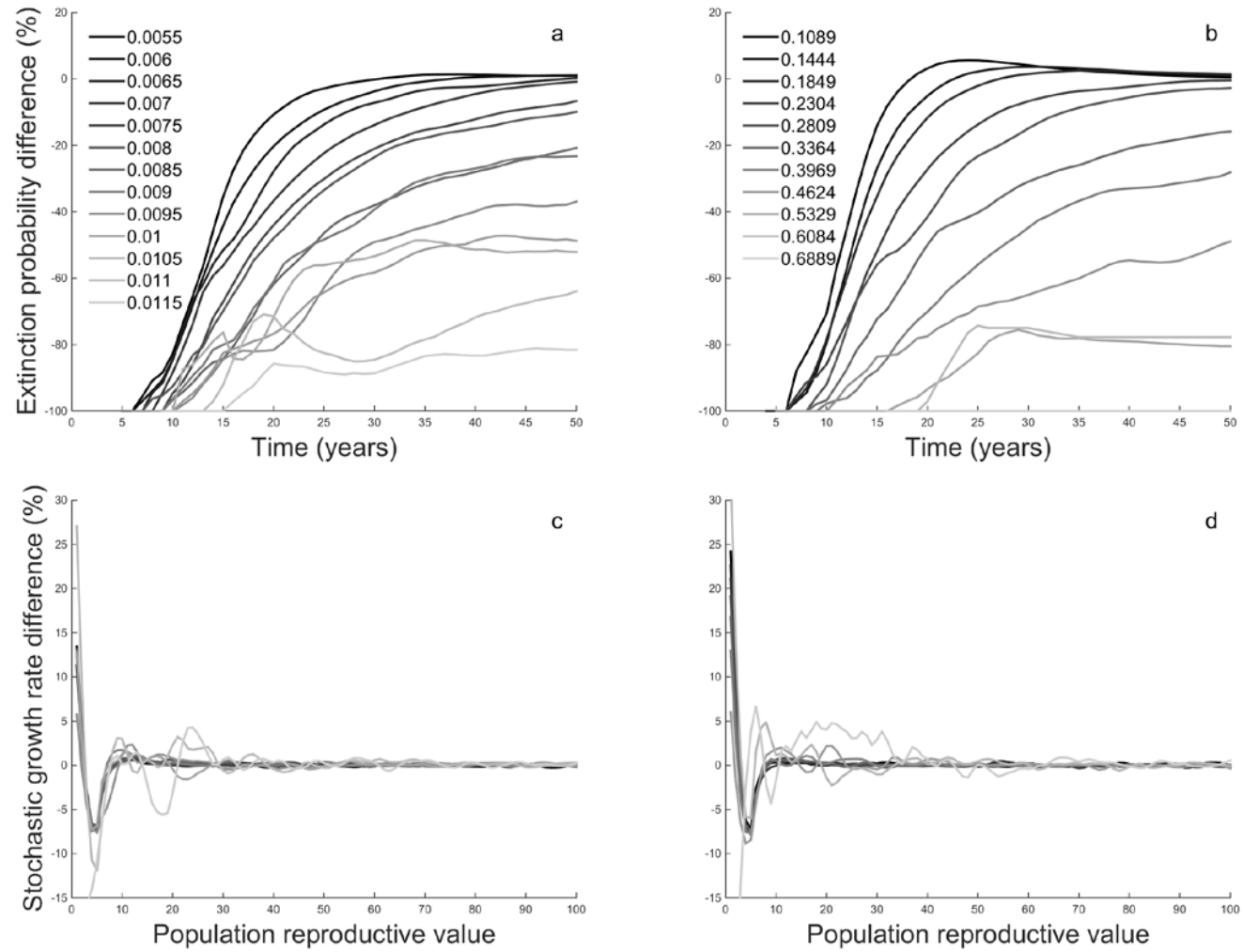
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710 **Figure 5**



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