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Avoiding unintentional eviction from integral projection models

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Abstract. Integral projection models (IPMs) are increasingly being applied to study size-structured populations. Here we call attention to a potential problem in their construction that can have important consequences for model results. IPMs are implemented using an approximating matrix and bounded size range. Individuals near the size limits can be unknowingly "evicted" from the model because their predicted future size is outside the range. We provide simple measures for the magnitude of eviction and the sensitivity of the population growth rate (λ) to eviction, allowing modelers to assess the severity of the problem in their IPM. For IPMs of three plant species, we found that eviction occurred in all cases and caused underestimation of the population growth rate (λ) relative to eviction-free models; it is likely that other models are similarly affected. Models with frequent eviction should be modified because eviction is only possible when size transitions are badly mis-specified. We offer several solutions to eviction problems, but we emphasize that the modeler must choose the most appropriate solution based on an understanding of why eviction occurs in the first place. We recommend testing IPMs for eviction problems and resolving them, so that population dynamics are modeled more accurately.

Key words: approximating matrix; integral projection model; matrix projection model; population growth rate.

INTRODUCTION

Structured population models are extremely useful for investigating population dynamics when vital rates such as growth, survival, and fecundity, depend on demographic state (size, stage, or age), and they have been applied to a variety of basic and applied questions in plant and animal ecology (Beissinger and Westphal 1998, Crone et al. 2011). In contrast to a matrix projection model, which requires discretization of the state distribution, an integral projection model (IPM) allows for the state variable (typically, and hereafter, size) to be treated continuously (Easterling et al. 2000, Ellner and Rees 2006). IPMs often have many fewer parameters to estimate than a conventional matrix model, making it possible to build a model with sparser data (Ellner and Rees 2006); they are more accurate for questions about traits that vary continuously such as size at reproduction (Williams 2009), and they avoid the problem of choosing class boundaries, which could influence model results (Ramula et al. 2009).

Given their potential advantages, use of IPMs in demographic studies is increasing, with 39 studies published to date (as of February 2012); more than half of those since 2009. These studies address a range of questions from examining the effects of herbivores on plants (Rose et al. 2005, Miller et al. 2009, Hegland et al. 2010, Williams et al. 2010), linking environmental variables to population growth through their effects on vital rates (Dahlgren and Ehrlén 2009, Ozgul et al. 2010, Dalgleish et al. 2011), and investigating life history evolution, particularly the optimal flowering size in plants (Rees and Rose 2002, Metcalf et al. 2003, Hesse et al. 2008, Williams 2009, Miller et al. 2012). Here we turn attention to a potential problem that can arise in constructing an IPM and can have important consequences for model results. Briefly, very small and/or large individuals can be unintentionally and unknowingly lost from the model, which artificially inflates mortality for these sizes and thus influences estimates of population growth rate (λ). We refer to lost individuals as being "evicted" from the model.

The objectives of this paper are to: (1) describe eviction in more detail, (2) use examples for three plant species to illustrate the effects of eviction on model results, and (3) offer guidelines for detecting and then correcting the problem. Although other studies have noticed the problem of eviction (e.g., Kolb et al. 2010, Dalgleish et al. 2011), the consequences and possible solutions have not yet been evaluated. Based on our results, we argue that users of IPMs should be aware of the problem and correct it when it occurs.

Brief introduction to size-structured IPMs

An integral projection model for a size-structured population takes the size-classified number of individu-

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als at time t ($n(x,t)$) and predicts the population at time $t + 1$ by the following:

$$n(y, t+1) = \int_{\Omega} [p(y,x) + f(y,x)] n(x,t) dx$$
$$= \int_{\Omega} k(y,x) n(x,t) dx. \quad (1)$$

The projection from t to $t + 1$ is based on k, a kernel composed of two continuous functions that describes all possible transitions from size x to size y within the interval of possible sizes, $\Omega = [L, U]$, where L and U are the lower and upper size limits, respectively. The fates of individuals present at time t are usually based on the product of size-dependent survival and growth, $p(y, x) = s(x)g(y, x)$, where $s(x)$ is the survival probability of an x-sized individual, and $g(y, x)$ is the probability density of size y in the subsequent time step for a currently x-sized individual. New individuals produced between t and $t + 1$ are introduced via the fecundity function $f(y, x)$, which represents the production of y-sized offspring from x-sized parents. The functions involved in modeling fecundity typically include the probability of reproducing, reproductive output as a function of size, the probability of offspring establishment, and the size distribution of new recruits. IPMs can be based on alternative or additional continuous state variables, but size-structured models are the most common applications of IPMs and are the clearest setting for explaining eviction.

In practice, an IPM is usually implemented by discretizing the continuous demographic functions into approximating matrices **P** (survival/growth) and **F** (fecundity). The size limits of the approximating matrices are set by the user, typically as a function of the minimum and maximum size observed. For example, some studies use $L = 0.9 \times$ (minimum size) and $U = 1.1 \times$ (maximum size) (e.g., Miller et al. 2009); others set bounds based on the standard deviation of the growth function (e.g., Easterling et al. 2000). In a basic IPM (i.e., without additional discrete stages such as a seed bank), eigenanalysis of $\mathbf{K} = \mathbf{P} + \mathbf{F}$ yields the asymptotic population growth rate, the stable size distribution, and other demographic quantities familiar to users of matrix models. For more details, see Ellner and Rees (2006) and Rees and Ellner (2009).

The problem of eviction

The potential for eviction resides mainly in the growth function $g(y, x)$ and the discretization process by which the **P** matrix is populated. Growth is modeled as a probabilistic process. Every x-sized individual is assigned a distribution of sizes y to which it may grow (or shrink). Usually, this is specified by fitting a parametric distribution to size-transition data, such as a Gaussian (normal) distribution giving the mean $m(x)$ and variance $V(x)$ of size at time t+1 given the size at time t. For any size x that an individual might realistically attain, the distribution of future sizes should integrate to one so that all surviving individuals are accounted for. Eviction occurs when future sizes having nonzero probability density are excluded from the **P** matrix because they are outside the size limits (Ω; illustrated in Fig. 1). Eviction is a problem in principle because it specifies unrealistic demographic fates, and in practice because it inflates mortality and biases model output.

Eviction is most likely near the corners of the approximating matrix, corresponding to the smallest and largest individuals. In these regions, current size (x), and hence, expected future size ($m(x)$) are close to the size boundaries (Fig. 1). Eviction is unavoidable when the largest individuals are predicted to grow larger still ($m(U) > U$) or if the smallest individuals are predicted to shrink ($m(L) < L$). In these cases, much of the future size distribution will be evicted for U- or L-sized individuals. However, even for well-behaved growth functions with $m(U) < U$ and $m(L) > L$, the tails of the future size distribution may be lost if the estimated variance in growth is sufficiently large (Fig. 1). For long-lived species, larger or older individuals tend to have greater eigenvalue elasticities (Franco and Silvertown 1996). Eviction, particularly at the upper limit of the size distribution, will therefore reduce the predicted population growth rate (λ), as we show below in *Consequences of eviction in published experimental studies*.

Although we focus on eviction due to the growth function, eviction may occur to some extent during the discretization process in any demographic model that uses non-bounded probability distributions. In IPMs, eviction may also occur in the matrix **F** that approximates the fecundity function $f(y, x)$. If part of the offspring size distribution falls below L, these individuals will be evicted. Because eviction from **F** typically affects only the smallest sizes (which typically have low elasticities), it should be less consequential than eviction of large individuals from **P**. Eviction from **F** is easy to avoid by choosing size boundaries that include any possible offspring size, or by choosing an offspring size distribution that constrains possible sizes to those observed. We therefore focus on eviction from **P**.

Detecting eviction

Here we describe two approaches for detecting eviction that are easy to calculate and interpret. First, the size-dependent fraction evicted from the **P** matrix, $\varepsilon(x)$, can be calculated by integrating the growth function over the bounds of the following model:

$$\varepsilon(x) = 1 - \int_{L}^{U} g(y,x) dy \, . \quad (2)$$

The size-dependent probability of eviction conditional on survival to the next time step is shown by $\varepsilon(x)$. The unconditional eviction probability for a currently size-x individual, $\rho(x) = s(x)\varepsilon(x)$, accounts for size-dependent survival. For a given size x, these two measures diverge as survival decreases, since even frequent eviction may be inconsequential if it occurs at a size with a low probability of survival.

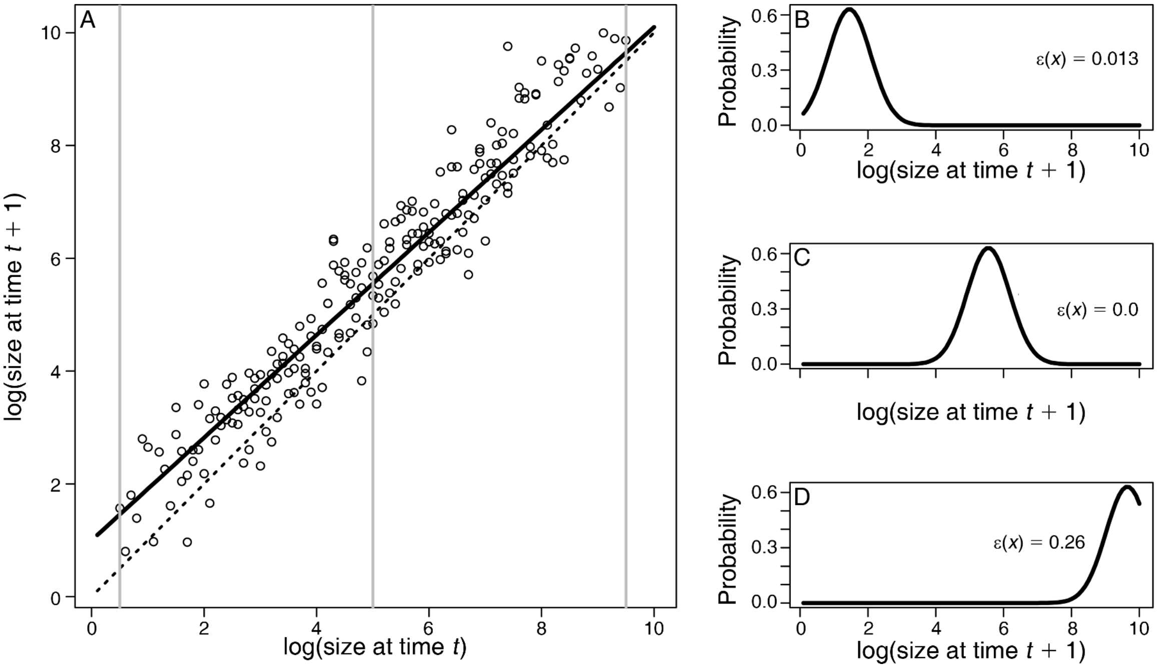

FIG. 1. (A) Hypothetical example of growth data (points) and fitted Gaussian growth function defined by mean $m(x)$ (black line), with constant variance. Vertical gray lines indicate the initial sizes corresponding to panels (B)–(D), which show the probability distributions of future size and the size-dependent probability of eviction [$\varepsilon(x)$; see *Detecting eviction* section] when the size limits used in the integral projection models (IPM) are $L = 0.1$ and $U = 10$, where L and U are the user-defined lower and upper size limits of the model, respectively. (The dotted line is the 1:1 line, indicating stasis.)

In a size-structured population, not all individuals contribute equally to population growth, so it is important to know the potential influence of the evictees on population metrics. One measure for the effect of eviction is the change in population growth rate ($d\lambda$) that results when the probability density lost through eviction is recovered by modifying the kernel so that previously evicted individuals instead grow or shrink to the size limit (L or U) that they grew or shrank beyond. The Appendix provides a derivation for $d\lambda$, and the Supplement includes an R function (R Core Development Team 2012) to calculate its value numerically, and an R script to apply the functions to example data. In the Appendix we also illustrate a less accurate, but more general approach using eigenvalue sensitivities to approximate the effect on λ when eviction is eliminated by other modifications of the kernel.

When $d\lambda$ is small, the effect of eviction on the predicted population growth rate is small even if a large proportion of individuals is evicted. For larger values of $d\lambda$, the problem may be more consequential. It is up to the modeler to decide what value of $d\lambda$ is large enough to warrant modifications to the IPM.

Solutions

The appropriate solution for minimizing eviction, if it is detected, will depend on the reason why eviction is happening. By determining this, it should be straightforward to choose a biologically sensible solution. The goal is to create growth and recruitment distributions that do not predict individuals much smaller or larger than actually observed. We caution that no single solution is appropriate for all situations.

Fig. 2A–C uses hypothetical growth functions to illustrate ways in which eviction can occur and possible solutions. In Fig. 2A, the function giving the mean size next year, $m(x)$, crosses the 1:1 line such that very small individuals tend to reach a much larger size by the next time step ($m(0) >> 0$) and large individuals tend to shrink ($m(10) << 10$). As a result, the eviction rate decreases as U increases. With $U = 8$ (the maximum size likely to be observed in this hypothetical population at stable size structure), the maximum eviction rate is $\varepsilon(U) \approx 0.17$ (illustrated in Fig. 2A with dashed blue line). For $U = 9$, this drops to $\varepsilon(U) < 0.014$ with $d\lambda < 10^{-5}$, so that further increases in the size range have minuscule effects on λ (illustrated in Fig. 2A with dashed orange line for $U = 10$). With this type of growth function, expanding the size limits will always solve an eviction problem. However, this solution may create size transitions that are not biologically realistic and requires the assumption that demographic performance can be linearly extrapolated to unobserved sizes.

In Fig. 2B, no expansion of the size range will eliminate eviction because the variance of the fitted growth function allows individuals of any size to continue growing (we present a real example of this kind below in *Consequences of eviction in published experimental studies*). There are then several possible

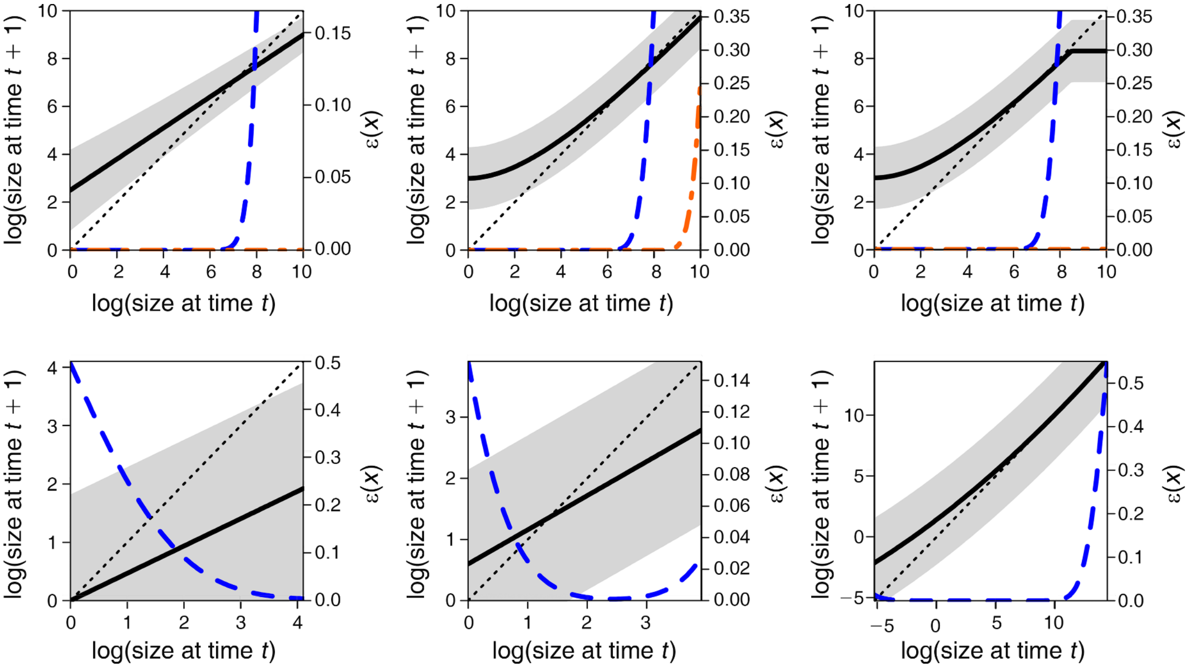

FIG. 2. (A–C) Hypothetical and (D–F) observed growth models illustrating eviction. The solid curve is the mean growth function $m(x)$, the dotted line is the 1:1 line, the blue and orange dashed curves are the size-dependent eviction fraction $\varepsilon(x)$, and the gray-shaded region represents 99% of the growth variation (±2.6 SD). (A–C) In hypothetical growth models, size at time $t+1$ was modeled as Gaussian. (A) A linear growth model with nonconstant variance. Eviction occurs if the size range is [0, 8], illustrated here (dashed blue line), corresponding to the limits of the stable size distribution, but is eliminated for size range [0, 9], illustrated here with size range extended to [0, 10] (dashed orange line). (B) A nonlinear growth model allowing indeterminate growth, so eviction persists for any size range (the dashed blue line again indicates size range of [0, 8] and the dashed orange line a size range of [0, 10]). (C) The same nonlinear model as in panel (B) with a "ceiling" imposed at size $x = 8.5$, slightly beyond the range of the stable size distribution (the dashed blue line is size range [0, 8], and eviction still occurs, but it is eliminated by the ceiling when size range is extended to [0, 10], the dashed orange line). (D–F) Fitted growth functions for (D) *Agrostis hyemalis* (endophyte positive), (E) *Anemone patens* (in native grassland), and (F) *Opuntia imbricata* (herbivores present). Line types and shading are as in panels (A–C). In panels (A–C), numbers are theoretical; in panels (D–F), the numbers represent actual measurements (with size on the axis for comparison) of: (D) log(tiller number); (E) log(leaf number); and (F) log(plant volume). Note the different scales on the left and right axes of each panel.

approaches to minimize eviction. First, consider if size-dependent variance improves the fit of the growth model, which should always be done when building an IPM. Eviction may be reduced or eliminated if large individuals have less variable growth because growth above U will be less likely. Second, a bounded probability distribution for growth (e.g., truncated normal or stretched beta) would guarantee that individuals cannot grow beyond an upper bound. (Note that fitting a truncated normal cannot be done by fitting a normal distribution and cutting off the tails; truncation redistributes the probability density between the size limits which modifies size transition probabilities.) Third, consider if a nonlinear model for mean size, such as a spline (Dahlgren and Ehrlén 2009), may provide a better fit to declining growth rate at larger sizes. Akaike information criterion (AIC)-based model selection procedures can aid in identifying whether size-dependent variance, a bounded distribution, or a nonlinear mean function provide a better fit to growth data.

Finally, eviction can be solved by setting a ceiling on changes in demographic rates for large individuals. In Fig. 2A and B, a parametric growth curve has been extrapolated beyond the range of sizes likely to be observed in a stable population. Alternatively (Fig. 2C), at some size x_b beyond the range of the data, the kernel can be modified so that $k(y, x) = k(y, x_b)$ for all $x \geq x_b$, as in Easterling et al. (2000). This treats extreme sizes the way matrix models do, by having a class of "very big" individuals that are demographically equivalent. The same can be done for "very small" individuals, that is, setting a floor. Once this change is made, increasing the size range eliminates eviction without allowing fates very different from those observed (Fig. 2C). We have provided a flowchart in Fig. 3 that summarizes the solutions.

Consequences of eviction in published experimental studies

We calculated eviction metrics for IPMs of three plant species that come from our previous studies (Table 1). These studies used IPMs to compare the effects of experimental treatments or habitat variation on λ, which allowed us to assess not only how eviction influenced the absolute values of λ, but also the relative differences between treatments and hence the qualitative conclusions of the experiments. For the native grass *Agrostis hyemalis* (Poaceae), the effects of symbiotic fungal endophytes on population growth were investigated by comparing IPMs for endophyte-positive and experimentally disinfected endophyte-negative plants (K. M. Yule, T. E. X. Miller, and J. A. Rudgers, *unpublished manuscript*). For the perennial forb *Anemone patens* (Ranunculaceae), we examined the effects of two invasive grasses on this native plant by comparing IPMs of *Anemone* growing in patches dominated by native grasses or by one of two invasive grasses (*Poa pratensis* and *Bromus inermis*; Williams and Crone 2006). For the Chihuahuan desert cactus *Opuntia imbricata* (Cactaceae), we assessed the effects of insect herbivores on population growth using treatments that excluded insects and incorporating the effects of herbivory into IPMs (Miller et al. 2009).

We found that the maximum eviction fraction (max $\varepsilon(x)$) from the approximating **P** matrices ranged from 0.15 to 0.63 (Table 1). Individuals were lost from both the largest and smallest sizes, and the patterns of size-dependent eviction were species specific (Fig. 2D–F, dashed blue line). The variation among species can be attributed to differences in the growth functions and the magnitudes of the growth variance, relative to the bounds of the observed size range. Although values of $d\lambda$ were generally low, even a 5% change in lambda upon model correction indicates the potential for eviction to bias model predictions. Based on these case studies (which we chose because we had the data), we expect that eviction will be a common problem in IPMs, though it may be more important for some species than others due to differences in life history and choices of model construction. For example, when size is a discrete measure (e.g., number of leaves or tillers), the minimum size is constrained by the lowest value that is biologically meaningful (e.g., 1 leaf) and eviction occurs when individuals are distributed below this size, as in *Agrostis* (Fig. 2D) and *Anemone* (Fig. 2E).

For all three species, we compared the population growth rates predicted by the original IPMs in which eviction occurred vs. IPMs in which the eviction problem was corrected using the ceiling/floor approach described above in *Solutions* (see full details of ceiling/floor and size range extensions in Table 1 notes). We chose this solution because either $g(x)$ did not cross the 1:1 line (and so expanding the size limits would not eliminate eviction), or because only expanding the size bounds of the model, without limiting demographic performance, led to unrealistic transitions (below the smallest or above the largest sizes that seemed biologically reasonable). Solving the eviction problems led to higher values of λ compared to models where eviction occurred (Table 1). The small change in λ in the corrected *Agrostis* model illustrates how eviction of mainly small (low reproductive value) individuals (Fig. 2D) will have a smaller effect than when larger individuals are evicted, as in the *Opuntia* model (Fig. 2F).

Because the amount of eviction varied among treatments within species, even the relatively modest effects we detected would have influenced the conclusions drawn from each study. For example, in the *Anemone* models, eliminating eviction raised λ above 1.0 for all types of grass patches. Even though *Anemone* populations are still predicted to do better when growing among native grasses, these new results suggest that all populations should persist if vital rates stay constant, contrary to the conclusions of the original study (Williams and Crone 2006). For the *Agrostis* and *Opuntia* models, correcting for eviction did not change qualitative conclusions, but led to slightly weaker effects of endophytes and herbivores, respectively, on plant population growth than expected based on the original models.

SUMMARY AND CONCLUSIONS

Given the increasing use of integral projection models to answer a wide variety of questions about plant and animal populations, it is critical that users be aware of technical issues with model construction that can affect results and interpretation. When the approximating matrix of an IPM is populated, individuals can be unintentionally evicted beyond the upper and/or lower size limits set by the user. We recommend that users calculate $\varepsilon(x)$ and $d\lambda$ to evaluate the potential magnitude of the problem and judge whether it is severe enough to affect their conclusions (R code in the Supplement). If so, the solutions are easily implemented and will improve the ability of the IPM to reflect population dynamics.

High eviction rates will usually reflect a problem with how growth is modeled, especially at the lower and/or upper limits of the size distribution, where data are inevitably sparse. However, it is still necessary to model the fate of individuals larger than observed, but small enough that they might well turn up in a larger sample. Biological knowledge or patterns in the observed data (such as size-dependent variance in growth) should guide how a growth model is extrapolated past the range of observations. Additional directed sampling effort to characterize extreme sizes, which may be missed in randomly sampled plots, would help to better define the rules of growth near the size boundaries. Otherwise, we suggest that a floor or ceiling (Fig. 2C), which in effect creates discrete categories of "very small" or "very big" individuals, is a sensible default. But these should not be used before asking whether the data provide more support for another alternative. We emphasize that users should consider which of the solutions we present (or others) is most appropriate for their population based on their understanding of why eviction is happening in the first place. Other causes of eviction may arise as IPMs are applied to a greater diversity of species or when additional continuous variables are included, which may then require new solutions.

Although our analyses focused on eviction due to some aspect of the growth function or the probabilities distributed around it, individuals can also be lost from

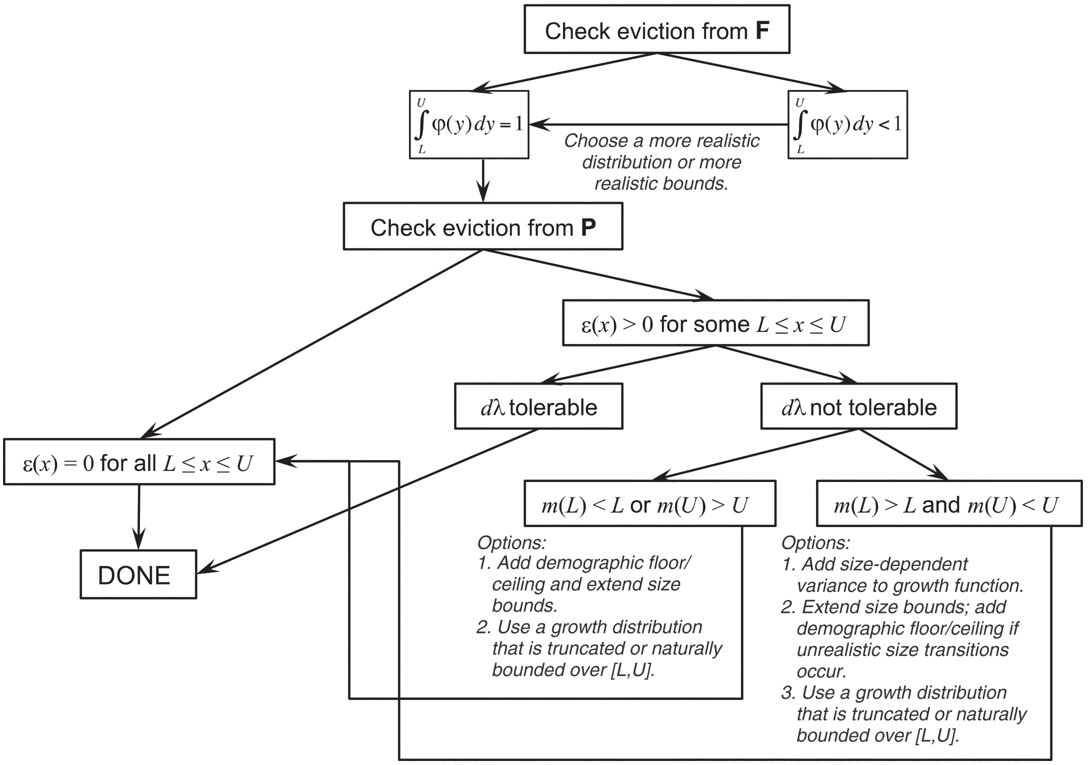

FIG. 3. Flowchart describing where eviction may occur in an integral projection model and which solutions (shown in italics) are appropriate for each cause. In **F**, $\varphi(y)$ is the size distribution of new recruits; if there are multiple recruitment stages (e.g., return of dormant individuals), check all distributions. In **P**, $m(x)$ is the mean future size of a currently x-sized individual, $\varepsilon(x)$ is the size-dependent eviction fraction, and L and U are the user-defined lower and upper size limits of the model. If the growth distribution is Gaussian (or another unbounded distribution) then $\varepsilon(x)$ cannot be exactly 0; "$\varepsilon(x) = 0$" then means that the maximum value of $\varepsilon(x)$ is small enough that eviction cannot possibly affect any conclusions from the model (e.g., less than one in a thousand).

the fecundity matrix if the smallest recruits are smaller than the lower size boundary (L). One way to interpret this phenomenon is that those recruits are too small to survive (Kolb et al. 2010), but losing tiny individuals may mean that the model incorporates lower recruitment rates than were observed. As described earlier in *The problem of eviction*, a straightforward solution is to use a probability distribution for offspring size that fits within the bounds of the model; this could include non-Gaussian distributions such as the stretched beta (as was used for *Agrostis*) or truncated normal as in several published IPMs (e.g., Dalgleish et al. 2011).

For studies that compare populations or treatments with different vital rates, the conclusions drawn from models

TABLE 1. Metrics describing the consequences of eviction from integral projection models (IPMs).

Species	Treatment	$\varepsilon(x)$	$d\lambda$	λ_{Evict}	λ_{Corr}
Agrostis hyemalis	endophyte negative	0.499	0.00264	0.1668	0.1694
Agrostis hyemalis	endophyte positive	0.499	0.00111	0.2329	0.2340
Anemone patens	native grasses	0.156	0.0210	1.0190	1.0427
Anemone patens	*Poa*	0.167	0.0324	0.9849	1.0186
Anemone patens	*Bromus*	0.188	0.0651	0.9532	1.0190
Opuntia imbricata	control	0.630	0.0340	1.0396	1.0751
Opuntia imbricata	insect exclusion	0.484	0.0325	1.1360	1.1696

Notes: Abbreviations are: $\varepsilon(x)$, the maximum size-dependent probability of eviction conditioned on survival to the next time step; $d\lambda$, an approximation of the potential effect on λ of correcting eviction (see *Detecting eviction* section); λ_{Evict}, the population growth rate when eviction occurs in the **P** matrix; and λ_{Corr}, the population growth rate when eviction is resolved by setting a ceiling and floor. In the calculations of λ_{Corr}, the ceiling and floor and the lower and upper size limits [L, U] were set as follows: *Agrostis*, floor = minsize, ceiling = 1.1 × maxsize, L = minsize − 4, U = maxsize + 2 [size is log(tiller number)]; *Anemone*, floor = minsize, ceiling = maxsize × 1.05, L = minsize − 1, U = maxsize + 1 [size is log(leaf number)]; and *Opuntia*, floor = minsize, ceiling = maxsize × 1.1, L = minsize − 1, U = maxsize + 4 [size is log(volume)]. Treatments are as follows: for *Agrostis*, plants contained symbiotic fungal endophytes (endophyte-pos) or had them experimentally removed (endophyte-neg); for *Anemone*, plants grew in habitats of native grass patches (native grasses) or in one of two types of exotic grasses (*Bromus* or *Poa*); for *Opuntia*, plants were exposed to insect herbivory (control) or insecticide was applied to exclude them (insect exclusion).

with eviction problems may not accurately reflect differences among populations or treatments if the corresponding IPMs suffer from different amounts of eviction. For example, we found that correcting for eviction changed qualitative conclusions regarding the effects of invasive grasses on *Anemone patens*. Based on the observed effects on λ, we expect that eviction will also influence perturbation analyses such as sensitivities and elasticities.

IPMs are powerful tools for addressing a wide variety of questions in ecology and evolution. Yet, as is true for all models, the results of an IPM are only as good as the underlying data and the estimation of model parameters. Modeling requires model selection. The functions underlying the IPM are estimated from the data, and eviction problems can arise if the "instructions" given to the model are incorrect in some sense. Solving the eviction problem gives the IPM better instructions. The improvements to model construction that we offer should better equip modelers (novices and old hands alike) to more accurately capture the dynamics of real populations.

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Supplemental Material

Appendix

Derivation of $d\lambda$ (*Ecological Archives* E093-191-A1).

Supplement

R scripts for calculating eviction measures and applying them to example data (*Ecological Archives* E093-191-S1).