

IDEA AND PERSPECTIVE

How do plant ecologists use matrix population models?

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Abstract

Matrix projection models are among the most widely used tools in plant ecology. However, the way in which plant ecologists use and interpret these models differs from the way in which they are presented in the broader academic literature. In contrast to calls from earlier reviews, most studies of plant populations are based on < 5 matrices and present simple metrics such as deterministic population growth rates. However, plant ecologists also cautioned against literal interpretation of model predictions. Although academic studies have emphasized testing quantitative model predictions, such forecasts are not the way in which plant ecologists find matrix models to be most useful. Improving forecasting ability would necessitate increased model complexity and longer studies. Therefore, in addition to longer term studies with better links to environmental drivers, priorities for research include critically evaluating relative/comparative uses of matrix models and asking how we can use many short-term studies to understand long-term population dynamics.

Keywords

Conservation, ecological forecasting, extinction risk, harvest, matrix projection models, plant population dynamics, population growth rate, population viability analysis, risk assessment, sensitivity analysis.

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INTRODUCTION

For more than 40 years, ecologists have used matrix projection models to understand and guide management of plant populations. By now, hundreds of demographic studies have been published for plants (see, e.g., Menges 2000a,b; Burns *et al.* 2010) and dozens more are published annually. These models combine multiple vital rates – and the possible effects of changes in these rates – into integrative measures of population dynamics. Therefore, they are a potentially powerful tool for assessing population status and extinction risk, as well as effects of past or future changes in management or in the environment. During the past two decades, population ecologists have repeatedly argued for increased use of quantitative demographic analysis to guide management (Schemske *et al.* 1994; Morris *et al.* 2002; Bakker & Doak 2009). Because demographic studies have been conducted with relatively similar methods for hundreds of species worldwide, they are also a powerful resource for comparative analysis (see, e.g., Silvertown *et al.* 1993 through Salguero-Gómez & de Kroon 2010).

A robust body of literature has discussed the merits of demographic models, particularly in the context of their utility for management (Beissinger & Westphal 1998; Menges 2000a; Coulson *et al.* 2001; Ellner *et al.* 2002; Simberloff 2003; Ellner & Holmes 2008). These papers tend to focus on how models *should* be used and interpreted, based on the authors' perceptions about available data and typical study goals. However, best practices surely depend on how well these perceptions reflect typical model use. Therefore, to assess the ways in which models are useful, it is also important to know how models *are* constructed and interpreted in practice. In this article, we systematically review how matrix models have been applied to plant populations. Our review is motivated by a general sense of disconnect between recent academic assessments of matrix models and our experience as plant ecologists using these models. Academic assessments have tended to focus on evaluating the ability of increasingly sophisticated models to accurately forecast population dynamics or extinction risk, using relatively extensive data sets. In contrast, our impression was that plant ecologists apply much simpler models to much more limited data sets, with little expectation that the models would literally forecast the future, even when we refer to them using terms that imply prediction, such as 'sustainable yield' or 'population viability analysis'.

To evaluate these general impressions, we review three aspects of model use and construction, in relation to available data and trends through time. First, what have been the broad objectives of each study (such as basic research or management of endangered, harvested, or invasive species)? Second, what metrics have been calculated from models to reach these objectives? And, third, how have users of matrix models interpreted their own work? Our review updates Menges (2000a) by adding a decade of additional studies (Fig. 1), and by analysing trends in model use and interpretation through time, as a function of management goals. We do not repeat Menges' basic introduction to matrix models, but refer readers to his summary (Menges 2000a, his boxes 1 and 2). We also systematically surveyed our collective view of the strengths and weaknesses of matrix models, as a representative group of practicing plant demographers (Box 1). This self-survey updates previous reviews of population models for plants or animals (e.g., Beissinger & Westphal 1998; Fieberg & Ellner 2000; Menges 2000a) by explicitly identifying areas where a group of experts with similar backgrounds agree and disagree. Together, the literature review and self-survey allow us to detect general consistencies and inconsistencies, and strengths and weaknesses, in the use of matrix models in plant ecology. Only by identifying and understanding these weaknesses can we move forward and propose better ways to work with these data.

REVIEW OF MATRIX MODELS

We attempted to census all matrix models for plant populations, published in peer-reviewed English-language journals through April 2009. To create this list of papers, we started with citation lists from previous reviews and meta-analyses conducted by members of our group (e.g., Menges 2000a; Burns *et al.* 2010; J.L. Williams, M.M. Ellis, M.C. Bricker, J.F. Brodie and E.W. Parsons, unpublished data) and with a prior database (Menges 2000b), updating these resources through additional literature searches and personal knowledge. We also searched Web of Science (<http://www.isiknowledge.com>) for all papers that cited reviews of matrix models, scanned all issues of key journals that publish large numbers of matrix model papers and updated this merged list with the reference libraries of all 16 working group members. We screened more than 400 candidate papers and found 396 published modelling studies for plant populations (a full citation list for these papers is accessible at: [http://](http://www.isiknowledge.com)

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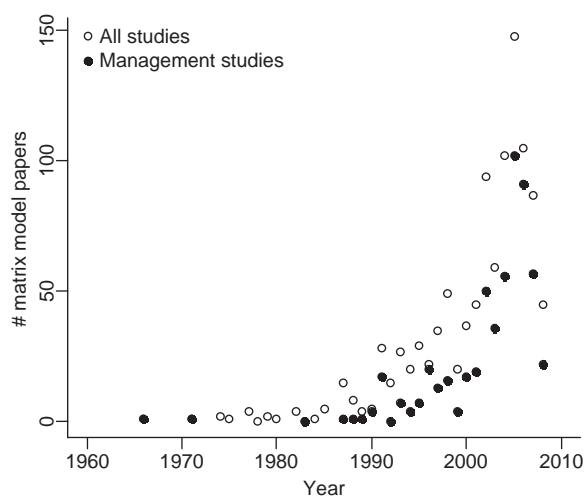


Figure 1 Number of published matrix models for plant populations through time. Data for 2009 are not shown, because we only included papers published through April 2009.

knb.ecoinformatics.org/knb/metacat/nceas.961/nceas). Of these, 355 papers included stage-, size- or age-based matrix models, highlighting the broad importance of matrix models as the dominant approach in plant population ecology. These studies include 20 papers on 25 species of annual plants, 194 papers on 189 species of herbaceous perennial plants and 139 papers on 154 species of woody plants. Of the 355 matrix model papers, 341 included enough information to be categorized systematically (see Table 1; our classifications of these papers are also available at: <http://knb.ecoinformatics.org/knb/metacat/nceas.961/nceas>). These papers, as well as our interpretation of models (Box 1), provide the basis for our systematic review.

Uses of matrix models

First, we categorized the overall goals and objectives of each published paper. Half (170) of the studies used matrix models for basic research and half (171) used matrix models to address management questions. Through time, however, the use of matrix models has shifted from basic to management questions (logistic regression of the proportion of studies directed at management questions: $\beta = 0.064$, $N = 341$ studies, d.f. = 1, $Z = -5.57$, $P = 0.0003$). Most applications to basic research (78%) used matrix models to study life history and population ecology. A substantial minority (11%) of basic research studies used matrix models for conservation biology or invasion biology, such as studies of effects of habitat fragmentation, studies of the rate of spread of non-native species or studies of how to best construct population viability models. This proportion has also increased through time (logistic regression: $\beta = 0.108$, $n = 170$ basic research studies, d.f. = 1, $Z = 2.02$, $P = 0.0165$).

Management studies most frequently modelled at-risk (38%), harvested (26%) and invasive (18%) plant populations; matrix models were also occasionally used to assess management of populations affected by fire (9%), grazing (6%) or restoration (3%) (Fig. 2). Goals of application to management have tended to shift through time, primarily due to increases in the proportions of studies investigating at-risk and invasive species (multinomial logistic regression, $\chi^2 = 23.9$, d.f. = 6, $P < 0.001$). For management-oriented papers, we also recorded the ways in which models were used to guide management ('additional management objectives' in Table 1). Forty-six per cent of papers measured some aspect of population status or population viability (defined broadly to include trends in population size over time as well as extinction risk *per se*; we discuss this issue further, below), 40% used matrix models to identify which life stages were most important to target for management and 27% used models to conduct simulation 'experiments' asking what-if questions about possible consequences of changes in vital rates, species interactions or the environment. Studies that made explicit relationships between vital rates and environmental factors were less common: 28% of studies used models to relate population dynamics to environmental drivers, such as fires, floods or climate factors, 19% of studies used demographic models to interpret consequences of short-term experiments and 8% of studies explicitly compared status of different sites or populations. Only 16% of studies used matrix models to explore consequences of species interactions; half of these looked at some aspect of biological control of invasive species.

Spatial and temporal extent of data in matrix models

Menges (2000a) and Morris & Doak (2002) have previously noted that matrix models for plants tend to be based on relatively few years of data, across relatively few

populations and over relatively small proportions of species' ranges. For our census of matrix models, we recorded the number of distinct matrices and the number of sites or populations in each study. For studies that included only one site and treatment, the number of matrices is a measure of study length. Thirty-four percent of matrix model papers for plant populations included only one projection matrix and 48% used data from only one site and/or treatment. The mean number of matrices per site or treatment was two; this is partly because one-third of the studies combined data from multiple sites to obtain one matrix, hence had < 1 matrix per site. Studies including data from only one site or treatment had a mean of 3.1 annual projection matrices (SD = 3.0, range 1–15). There has been some increase over time in the number of matrices per study, although this trend was only marginally statistically significant (Table 2A), and was largely driven by management-oriented studies (Fig. 3). There was no trend over time in the number of sites or treatments per study (Table 2B).

Management-oriented studies tended to draw on more matrices than basic research studies, even after accounting for trends through time (Table 2A; Fig. 3). However, the number of matrices used also differed among management studies with different goals. Relative to basic research, studies focused on population viability and, to a lesser extent, fire management, used more matrices, and studies focused on harvest used fewer matrices (Table 2A). The number of sites did not differ significantly between management-oriented and basic research studies, but did differ among management goals. Studies requiring an understanding of changing dynamics due to disturbance and/or recovery (fire, restoration and at-risk species) included more sites, whereas studies focused on harvest had fewer sites (Table 2B).

PREDICTIONS FROM MATRIX MODELS

After recording the objectives of each study, we recorded the metrics that were calculated from matrix models to address those objectives. Plant ecologists most often use matrix models to calculate three basic kinds of statistics (Fig. 4): (1) population growth rates (deterministic and/or stochastic λ), (2) relationships between changes in vital rates on population growth rates (such as sensitivity analysis) and (3) extinction risk. We encountered other uses of matrix models, but these were relatively rare. Transient analysis (an alternative to calculating long-term population growth rates and other asymptotic statistics) was first used by Caswell & Werner (1978) for life history analysis, and the technique was picked up by other plant demographers in the late 1980s. However, transient analyses remain infrequent (9% of all studies to date), and their use has not increased significantly over time (Fig. 4f; Table 3F). Only a handful of studies have used matrix models to analyse optimal disturbance frequencies or return intervals for floods, fires or hurricanes (16 studies, 5% of all matrix papers), and use of this metric has not changed significantly through time (though non-significance may be due to very small sample size, Table 3G). Below, we discuss how plant demographers use the three most commonly reported types of metrics.

Population growth rates

Most studies in our database (85%) used matrix models to calculate deterministic population growth rates (λ), the rate at which population size would change if vital rates remained constant over time. Only 22% of studies presented stochastic population growth rates (λ_S), the expected rate of change in variable environments. The proportion of studies using stochastic population models has increased over time, but even in the past decade, 46% of studies reported only deterministic population growth rates (Fig. 4a,b; Table 3B). For plant populations, stochastic population growth rates have most often been calculated using simple random matrix selection or element selection (*sensu* Kaye & Pyke 2003); fewer than half (45%) of studies that calculated λ_S included an environmental driver of stochasticity. Studies that report λ_S are based on significantly more matrices than other studies (Table 3B), but even these studies used a median of three matrices, and 75% of these studies used five or fewer matrices.

Reliance on simple density-independent population growth rates could be interpreted as evidence that plant ecologists are naïve about key population processes such as density dependence (cf. Bierzychudek 1999). However, an alternative interpretation may be that plant ecologists choose density-independent deterministic models because they are more appropriate for typical data sets. For example, many species (and probably most rare species) may be more influenced by environmental factors and interspecific competition than by their own densities. Typical demographic studies for plants parameterize 'density independent' models at realized levels of interspecific and intraspecific competition, not in the absence of competition. Therefore, these density-independent models may be reliable indicators of population dynamics in many contexts.

Similarly, stochastic population models are relatively uncommon in plant demography, in spite of the fact that vital rates of plants obviously vary among years. However, most published studies are based on few years of data, in spite of most increases over time in the number of matrices used to parameterize models. Relative to stochastic population growth rates, deterministic population growth rates are more precise under some conditions (e.g. high variance and < 5 years of data), with a directional and therefore correctable bias (Doak *et al.* 2005). Therefore, deterministic

Box 1 Self-survey

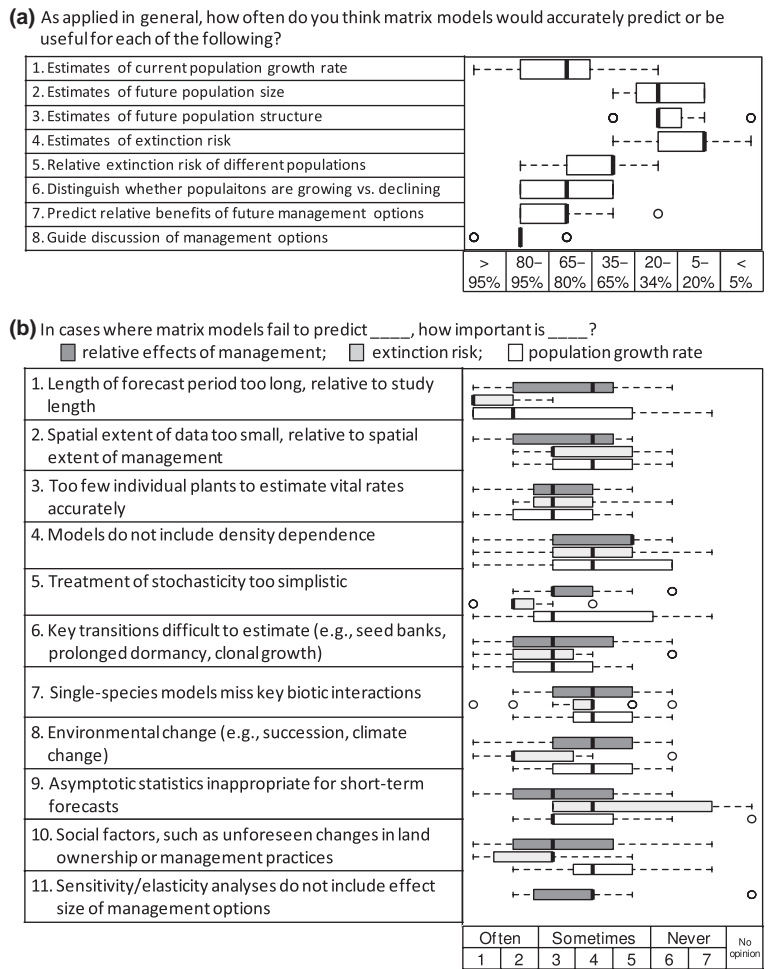
The peer-reviewed literature does not necessarily include all of the ways in which models are useful in practice. For example, not all models are published in peer-reviewed journals. Similarly, the review process is known to bias the results that get published, and could also bias the ways in which authors present their results. We evaluated our own opinions of how matrix models are most useful and reliable, and how much we agree on the strengths, limitations and most important improvements for matrix models.

Three of the authors (Crone, Menges and Ellis) assembled a working group of scientists (the authors of this paper) of varying backgrounds, but with these commonalities. All of us had: collected demographic data on plant populations, assembled projection matrices, analysed and/or modelled population dynamics based on these matrices and published their results and discussed the implications of this modelling with land managers and other conservation professionals. All literature reviews include some element of the authors' opinions; by presenting ours quantitatively, we identify (at least in part) where we agree and where there is little consensus, in spite of shared experiences and background.

We quantified our opinions using a combination of survey and discussion. This survey assayed each person's view of how well matrix models would predict population dynamic and management metrics such as growth rates and extinction probabilities (Fig. 5). Following standard risk assessment procedures for eliciting expert opinion (Burgman 2005), we began with an initial 'naive' survey, meant to help us articulate our own opinions. We then discussed areas where our answers differed, and the rationale behind our opinions. After group discussion, individuals retook the same survey. The results of this second survey are expected to identify true areas of agreement and disagreement, as opposed to individual differences in the interpretation of survey language.

The survey questions (Fig. 5) focused on subjective model interpretation in terms of how we think models are most useful (a) and how they might be best improved (b). Our responses show some areas of clear consensus [see Fig. 5a.8, b.1 (extinction risk) and b.5 (extinction risk)]. However, we were divided on many issues. Overall, we tended to agree more about how models are best interpreted as generally applied (a) than about why they fail (a measure of how they should be improved) (b).

Figure 5 Our opinions about when matrix models are useful. (a) Utility as typically applied and (b) reasons why they fail. Graphics are boxplots: thicker horizontal lines are medians, boxes enclose 25th and 75th percentiles, error bars span 10th and 90th percentiles, and circles are outliers.



models may be the most appropriate analysis for typical data sets. When we assessed our own opinions, we all felt that some aspects of matrix models could be improved, but there was little consensus about specifically how models should be improved (Fig. 5b.4, 5, 7, 8 and 9). Switching to more detailed or sophisticated models might require collecting much larger data sets, possibly at the expense of implementing management actions (cf. Simberloff 2003).

Sensitivity analyses

Matrix models can be used to evaluate the effects of possible changes in vital rates on λ , or to analyse the mechanisms behind observed changes in λ . The second most

common metric reported from matrix models was assessment of the relative contributions of different vital rates to the population growth rate, using sensitivities or elasticities (73% of papers). These were used with equal frequency in management and basic research studies, as they can be interpreted as the expected consequences of management that affects vital rates (Crouse *et al.* 1987) or the contributions of different vital rates to fitness (Lande 1982). Interestingly, only 40% of management-oriented studies had assessment of which life stages to target for management as a management objective (see above), much lower than the proportion that report some kind of sensitivity analysis. Life table response experiments (LTREs) retrospectively quantify mechanisms behind observed changes in λ , and were reported in 22% of studies. LTREs are typically used to quantify how the effects of experimental treatments or

Table 1 Information assessed in the literature survey. Depending on the survey item, each responder entered specific information or could select from among specified options*. All the data are available at: <http://knb.ecoinformatics.org/knb/metadata/nceas.961/nceas>

General information	Specific options or definitions
<i>Author and year</i> Maximum # annual transitions	Study wide, summed over populations (e.g., 5 populations × 2 matrices per population = 10)
Maximum # sites	Number of physical sites or populations, as defined by matrices. May be fewer than number of matrices if multiple matrices are constructed for a site (e.g., different treatments or years at one location)
<i>Species name(s)</i>	Woody, herbaceous perennial or annual
Life form	Management of rare/endangered/at-risk spp.†; management of invasive pest species, other management (e.g., harvest)‡
Overall objective if no management (one only)	Basic research in invasion/conservation biology, life history/population ecology, community ecology or other basic research
Overall objective if no management (one only)	Population status/viability for species of conservation concern, possible invasiveness of non-native species, prioritizing populations for protection or control, assessing impacts of species interactions (e.g., herbivory, competition, pollination) on population viability, assessing impacts of biological control, assessing impacts of interactions with invasive species on native (plant) species, assessing impacts of grazing on native plants, other species interactions, evaluate sustainable harvest, link population viability to specific abiotic environmental variables [climate change, fires, other extreme disturbances (hurricanes, floods, drought)]; evaluate life stages to target for management (e.g., LTRE, sensitivity/elasticity analysis); identify which of multiple threats is more important to viability; assess effects management options (numerical experiments; simulation study); assess effects management options (actual experiments/natural experiments/monitoring); monitor establishment of translocated plants/viability of restored populations
Additional management objectives (many possible)	Estimates of DETERMINISTIC population growth rate, estimates of STOCHASTIC population growth rate, estimates of extinction risk, sensitivity/elasticity, LTRE, transient behaviour of populations, optimal return intervals/inflection points for periodic disturbances
Metrics presented in the publication	1. Authors explicitly state that quantitative results SHOULD NOT be taken literally
Author's interpretation of results (choose one only)‡	2. Authors lean away from/tend to de-emphasize a literal interpretation of results
	3. Unclear whether interpretation is qualitative (not literal) or quantitative (literal)
	4. Authors lean towards/tend to emphasize a literal interpretation of results
	5. Authors explicitly state that quantitative results SHOULD be taken literally

LTRE, life table response experiment.

*Before reviewing papers, we all reviewed and independently categorized two papers that we had selected as training examples, and then discussed our answers as a group. After we were confident that our categorizations were consistent across reviewers, most papers were read and reviewed by a single reader. Each person reviewed 16–34 papers.

†We later subdivided studies classified as 'other management' into one of four primary management objectives: management of fire, grazing, harvest or restoration.

‡As subjectivity in assessing authors' interpretations was unavoidable, a subset of 24 papers was independently reviewed and scored by two randomly chosen readers, rather than one reader. We did not know in advance which of the papers we reviewed were in this subset. In 9 of the 24 cases (38%), the two reviewers' scores were identical; in 11 cases (46%) the scores differed by one rank out of five, and in 4 cases (17%) the scores differed by two ranks.

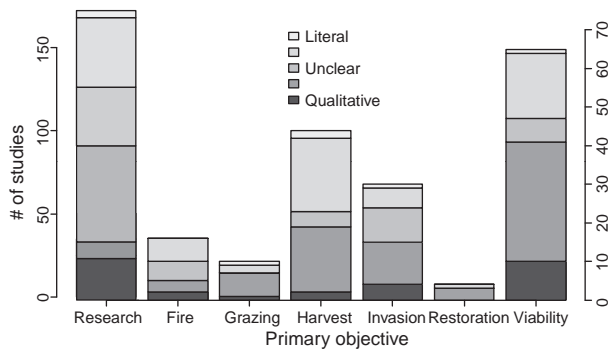


Figure 2 Number of matrix model papers, in relation to study objectives and model interpretation. Basic research studies are plotted on the left horizontal axis and management studies are plotted on the right axis.

Table 2 Analysis of data used in matrix models, in relation to study goals and year of publication

Metric	Factor	Estimate*	SE	Z†	P
A. Number of matrices	Management	0.145	0.096	1.68	0.093
	Fire	0.357	0.206	1.73	0.084
	Grazing	0.256	0.242	1.06	0.288
	Harvest	-0.279	0.139	-2.00	0.045
	Invasion	-0.045	0.166	-0.27	0.787
	Restoration	0.313	0.314	1.00	0.318
	Viability	0.353	0.105	3.35	0.001
	Year	0.009	0.006	1.44	0.151
B. Number of sites or treatments	Management	0.085	0.099	0.83	0.259
	Fire	0.477	0.229	2.18	0.029
	Grazing	0.190	0.272	0.70	0.484
	Harvest	-0.336	0.156	-2.14	0.032
	Invasion	-0.198	0.192	-1.03	0.302
	Restoration	0.703	0.349	2.02	0.044
	Viability	0.226	0.125	1.80	0.072
	Year	0.007	0.001	1.00	0.318

*In all analyses, the reference group is studies with no management goal, and coefficients are differences between each group and the reference group.
 †Z-statistics from generalized linear models (glm.nb function; R Development Core Team 2009), with negative binomial error structure to account for overdispersed count data. All statistical tests have model d.f. = 1. Sample sizes for different metrics are shown in Fig. 2. Statistically significant relationships are shown in bold font.

natural variation of individual vital rates contribute to differences in population growth rate. Therefore, the technique is potentially useful in guiding management. However, in practice, LTREs have been used more often for basic research than for management-oriented research (Table 3D).

During the past 15 years, ecologists have widely debated the merits of different forms of prospective and retrospective sensitivity analysis (Heppell *et al.* 2000). Use of both prospective sensitivity/elasticity and retrospective LTREs has increased over time (Table 3C,D), though the increase in LTREs has been faster. All of the various forms of sensitivity analyses (including deterministic and stochastic sensitivities, elasticities, LTREs and numerical methods that incorporate empirically estimated effect sizes) depend on the assumption that λ or λ_S is a meaningful way to integrate vital rates. If this assumption is reasonable, and if practitioners choose the appropriate sensitivity metric for their situation, then, by definition, sensitivity analyses should provide reasonable guidance. However, all of us thought that inappropriate use of sensitivity/elasticity at least ‘sometimes’ lead to misleading model outputs (Fig. 5b.11). For example, using effects of small changes in vital rates (analytical sensitivities or elasticities) to assess the consequences of management may be inappropriate, as the responses of vital rates to management may be large. Similarly, most sensitivity metrics are based on the assumption that vital rates can change independently, when, in fact, these may tend to change in variable ways in response to management.

Extinction risk

Use of matrix models to predict population fates has been considered broadly equivalent to population viability analysis (e.g., Menges 2000a; Kaye & Pyke 2003). However, only a small proportion (23%) of matrix models used in plant ecology are used for population viability analysis in the narrow sense of calculating extinction risk, including time to (quasi-) extinction and probability of (quasi-) extinction. Not surprisingly, extinction risk was calculated more often in management-oriented than basic research studies, and was most often presented in studies of at-risk species (Table 3E). Still, only about half (56%) of the studies of at-risk species calculated extinction risk. Extinction risk was also more likely to be presented in fire-management studies (38%), and, relative to basic research, was less likely to be presented in studies of invasive species (7%). There was a marginally significant trend towards presenting extinction risk more often over time, possibly reflecting increasing use of stochastic modelling as well as increased interest in population viability *per se*.

Limited emphasis on extinction risk could reflect realistic assessment of what can be done with available data. For example, Fieberg & Ellner (2000) calculated that extinction risk was only predictable with at least a 5 : 1 ratio of data years to forecast years. Holmes *et al.* (2007) suggested extinction risk could be predicted from as few as 1 : 1.5 (data years: forecast years). Even the more optimistic of these two guidelines would imply that we will rarely be capable of making meaningful forecasts of extinction risk for plants, given typical study lengths. In addition, predicting true extinction risk may be more problematic for plants than animals, because many plants have at least one unobservable life stage (*sensu* Kendall & Nichols 2002), such as dormant seeds and/or prolonged dormancy (*sensu* Lesica & Steele 1994) of mature plants (see Fig. 5b.6). These life stages are rarely surveyed, and are potentially quite long lived. Furthermore, we tended to believe that factors that cause extinctions are typically outside the scope of demographic studies: changes in the environment (Fig. 5b.8), social factors such as changes in land use (Fig. 5b.10) or stochastic processes that are

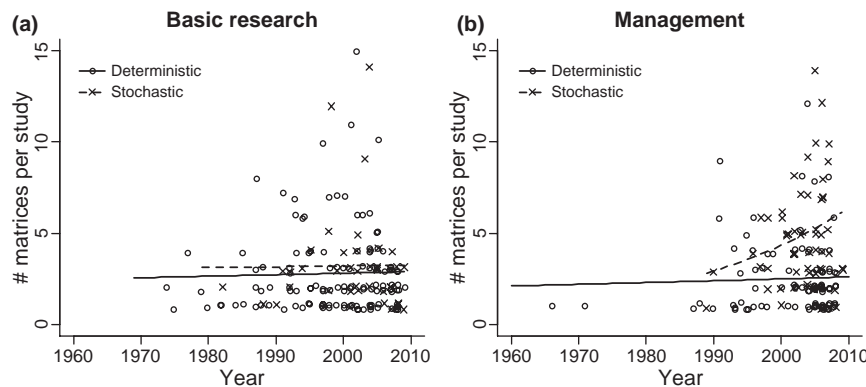


Figure 3 Temporal trends in the number of matrices used to construct matrix models in the peer-reviewed literature for (a) basic research studies and (b) management studies. For this figure, studies are separated into stochastic models, defined as studies that reported either λ_S or extinction risk, vs. deterministic models (all other studies). Lines are fitted regression curves for each subgroup (negative binomial generalized linear model). For visual clarity, points are slightly jittered, and one study is not shown on the graph, a stochastic, management-oriented study with 28 matrices, published in 2005.

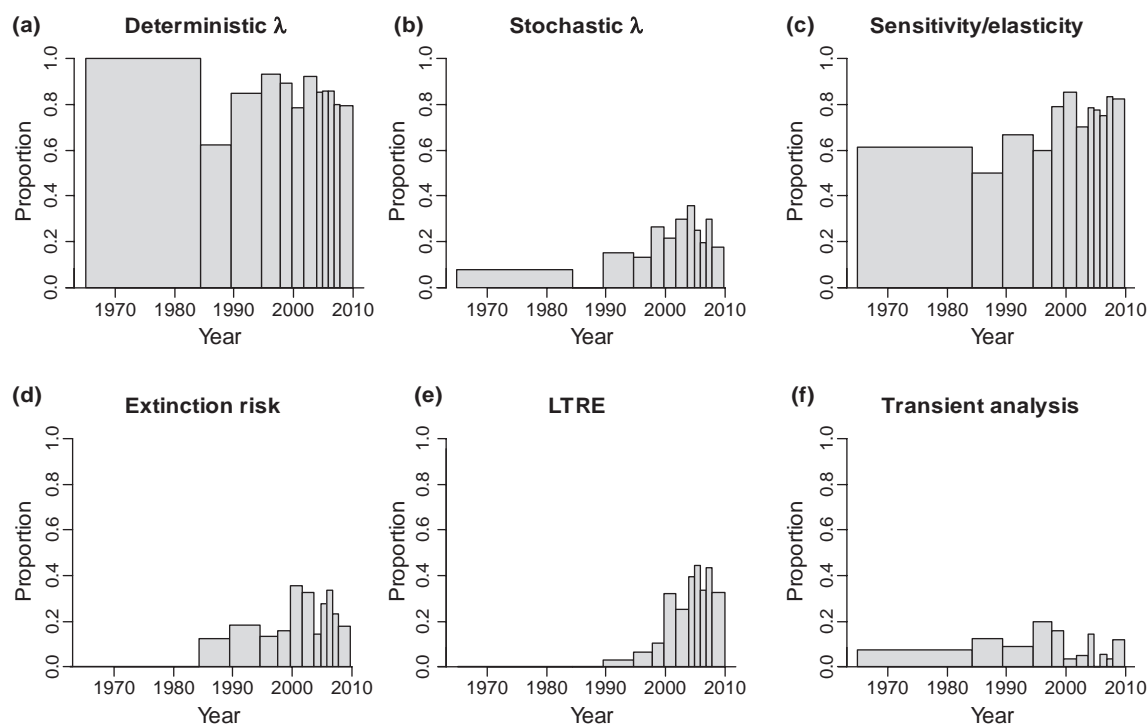


Figure 4 Temporal trends in the proportion of studies presenting the most common metrics in matrix model papers for plants. Data were binned into periods of years with at least 10 studies per period.

not captured by typical stochastic population models (Fig. 5b.5). Therefore, even if plant ecologists are interested in using models to predict extinction risk, we are sceptical that we have the necessary information to make these predictions.

In the past 10 years, some ecologists have noted a different possible use of quasi-extinction risk calculations: the minimum expected population size over some time horizon may be a robust measure of population status (McCarthy & Thompson 2001). Rather than calculating the probability that a population reaches some arbitrary size threshold during a specified time period, traditional extinction risk calculations can be rearranged to estimate the minimum size a population is likely to reach during that time period. Only one study in our database used extinction risk in this way (Keith *et al.* 2008), but this could be an intriguing use of extinction risk in future plant demography, or an interesting metric to calculate from existing demographic studies.

INTERPRETATION OF MODEL PREDICTIONS

Relatively early in the development and use of matrix models for population biology, Caswell (1989) cautioned that projections from matrix models should be interpreted as how a population *might* perform if the vital rates used to parameterize the model were to remain constant over time, a call that has been widely restated since then (Beissinger & Westphal 1998; Bierzychudek 1999; Akçakaya & Sjögren-Gulve 2000; Menges 2000a; Morris & Doak 2002; Reed *et al.* 2002). Nevertheless, as matrix models have become widely used to direct management actions, interest has grown in testing model predictions. Some researchers have concluded that these models make robust and reliable, 'accurate' predictions (Brook *et al.* 2000), whereas others have concluded that matrix models are unable to make forecasts with realistic amounts of data (Ludwig 1999; Fieberg & Ellner 2000; Coulson *et al.* 2001; Ellner *et al.* 2002).

We evaluated how users of matrix models interpreted their own work by scoring how each paper's author(s) interpreted their results. We scored papers using a five-point scale, from 'strict literal interpretation of model predictions' to 'containing numerous caveats that model results are not to be taken literally' (Table 1, final entry). In about half of the studies (52%), authors cautioned against interpreting quantitative model predictions literally (score of 1 or 2). In 32%, the language used by authors suggested that they were interpreting the quantitative metrics as literal predictions of population behaviour (score of 4 or 5), though this interpretation was rarely stated explicitly. We judged that the remainder (16%) was intermediate or else that they provided few clues about the authors' interpretation of these metrics (score of 3). There were no trends in model interpretation through time, or as a function of the number of matrices in each study (Table 4).

Management studies were more likely than basic research studies to caution against literal interpretation of model predictions, and were less likely to be unclear about

their interpretation (Table 4). However, this broad difference reflects considerable heterogeneity among studies with different management goals. Relative to basic research studies, studies focused on harvest were more likely to present results literally, whereas studies focused on population viability were more likely to explicitly caution against literal interpretation of model results (Table 4; Fig. 2). This difference may be partly justified based on differences in the objectives of the management studies. Harvest studies were less likely than endangered species studies to calculate extinction risk, a metric that can be highly sensitive to estimation error (Fieberg & Ellner 2000). Harvest studies may also be based on larger populations and therefore larger numbers of individual plants, which should increase predictive ability of models. At the same time, however, harvest studies tended to be based on fewer transition matrices (Table 2A).

Interpretation of models presented in the published literature may reflect biases in the review process, or in what users of matrix models expect reviewers to be looking for. Our self-survey (Box 1) was intended to remove some of these potential biases and provide more specific information about how we – as users of matrix models – usually interpret model outputs. This survey revealed broad consensus at the extremes of model interpretation, but also considerable heterogeneity of opinion. At the extremes, we agreed that matrix models are usually useful for guiding discussion of management options (Fig. 5a.8), and none of us expected models to forecast future population size, population structure or extinction risk with precision (Fig. 5a.2–4). We were more divided about whether matrix models would distinguish relative extinction risk, accurately weigh relative benefits of different management options within populations or discriminate growing from declining populations (Fig. 5a.5–7). We were most divided over whether population growth rates from matrix models would accurately reflect actual changes in population size at the sites and during the years the data were collected (Fig. 5a.1). This division of opinions is interesting because it is easily testable with existing data from demographic studies. To our knowledge, such a test has never been performed, perhaps because testing against the data used to construct the model superficially seems circular. In fact, factors such as poorly estimated vital rates, poor models for variation in vital rates and transient dynamics in populations far from a stable stage structure could cause typical population models to fail even this obvious test.

CONCLUDING REMARKS

To an outsider, it might seem puzzling that plant ecologists continue to rely on matrix models, more often than not with the explicit caveat that output from these models should not be taken literally. Why do we use this technique if we do not trust model predictions? Perhaps the most important message from this apparent contradiction is

Table 3 Analysis of metrics calculated from matrix models, in relation to study goals, year of publication and amount of data

Metric	Factor*	Estimate†	SE	Z‡	P
A. Deterministic growth rate (λ)	Management	0.369	0.334	1.10	0.269
	Year	-0.012	0.024	-0.49	0.623
	# Matrices	-0.021	0.054	-0.39	0.699
B. Stochastic growth rate (λ_s)	Management	0.148	0.284	0.52	0.601
	Year	0.060	0.026	2.35	0.019
	# Matrices	0.166	0.049	3.40	< 0.001
C. Sensitivity or elasticity	Management	0.147	0.264	0.56	0.577
	Year	0.054	0.017	3.11	0.002
	# Matrices	-0.038	0.043	-0.877	0.380
D. LTRE	Management	-0.547	0.279	-1.96	0.050
	Year	0.191	0.035	5.49	< 0.001
	# Matrices	0.037	0.044	0.85	0.394
E. Extinction risk	Management	0.803	0.289	2.78	0.005
	Fire	1.190	0.645	1.84	0.065
	Grazing	0.916	0.747	1.23	0.220
	Harvest	-0.515	0.577	-0.89	0.372
	Invasion	-1.703	1.053	-1.62	0.106
	Restoration	-0.044	1.151	-0.04	0.970
	Viability	1.745	0.343	5.08	< 0.001
	Year	0.047	0.026	1.78	0.074
F. Transient analysis	Management	0.064	0.423	0.15	0.880
	Year	-0.014	0.028	-0.48	0.633
	# Matrices	0.059	0.058	1.02	0.309
G. Disturbance return intervals	Management	1.170	0.788	-0.69	0.491
	Fire	3.551	0.952	3.73	< 0.001
	Grazing	-15.244	> 1000	0.00	0.997
	Harvest	1.376	1.024	1.34	0.179
	Invasion	-15.419	> 1000	0.00	0.994
	Restoration	-15.546	> 1000	0.00	0.997
	Viability	1.790	0.854	2.10	0.036
	Year	0.061	0.064	0.96	0.336
# Matrices	0.091	0.066	1.38	0.167	

LTRE, life table response experiment.

*Specific management goals are separated only when subdividing management objectives significantly improved model fit (likelihood ratio test of nested models, $P < 0.05$; for all others, $P > 0.15$).

†In all analyses, the reference group is studies with no management goal, and coefficients are differences between each group and the reference group.

‡Statistical tests based on logistic regressions (glm function; R Development Core Team 2009), after testing for overdispersion (for all statistics, scale factors were between 0.9 and 1.1, quite close to the expected value of 1.0). All statistical tests have model d.f. = 1. Sample sizes for different metrics are shown in Fig. 2. Statistically significant relationships are shown in bold font.

that the primary function of models is not to forecast the future. Because they are based strongly in basic biology, matrix models force us to outline how different aspects of the life cycle interact, and what aspects of natural history are known vs. unknown. It is tempting to speculate that the overwhelming popularity of matrix models in plant ecology stems from the fact that these models take biology that we can see and measure in the short term (stage-specific birth, growth and death rates), and calculate the logical long-term consequences of that biology. Setting up matrix models also emphasizes that management of one life stage, or of one vital rate, only affects population dynamics through its effect on the full life cycle. For example, a key and longstanding insight from matrix models is that not all vital rates are equally important for population dynamics or fitness (e.g., Crouse *et al.* 1987; Crone 2001). Therefore, users of matrix models can calculate the logical outcomes of observed environmental conditions and experimental manipulations, and use models to examine what-if scenarios that explore possibilities outside the range of observed conditions. These benefits do not require that matrix models make accurate predictions, simply that they integrate field data in a biologically meaningful way. Model predictions are also likely to be more robust and less biased than management assessments based on subjective judgment (McCarthy *et al.* 2004).

A second insight from the state-of-the-art of plant demography is that plant ecologists define 'population viability' broadly as the future fate of plant populations

Table 4 Interpretation of matrix models, in relation to study goals, year of publication and available data*

Factor	Unclear vs. literal		Qualitative vs. literal		Overall test of interpretation†	
	Coefficient	SE	Coefficient	SE	χ^2	P
Management	-0.74	0.36	0.14	0.26	19.18	0.038
1°: Fire	-0.25	0.04	-0.57	0.06	0.67	0.714
1°: Grazing	-216.47	NA	0.35	0.03	4.95	0.084
1°: Harvest	-1.61	0.07	-0.43	0.33	7.68	0.022
1°: Invasion	0.76	0.23	0.73	0.26	2.08	0.353
1°: Restoration	-182.5	NA	0.85	0.00	2.65	0.266
1°: Viability	-0.79	0.11	0.52	0.27	8.42	0.015
Year	-0.03	0.00	-0.03	0.00	0.81	0.668
# Matrices	0.04	0.06	0.02	0.05	0.81	0.667

*Multinomial logistic regression of data pooled into three categories (fit using multinom function in R, nnet package; Venables & Ripley 2002): literal (4 or 5), qualitative (1 or 2) or unclear (3). Coefficients represent contrasts between literal and unclear or qualitative groups. †Chi-square statistics from likelihood ratio tests, relative to reduced models with linear coefficients set to 0 (for tests of year and # matrices) or different management goals pooled with the reference group, basic research studies. All statistical tests have model d.f. = 2. Sample sizes for different metrics are shown in Fig. 2. Statistically significant relationships are shown in bold font.

(Menges 2000a). In contrast, most previous assessments of population viability analysis have focused narrowly on testing our ability to forecast extinction risk (Brook *et al.* 2000; Coulson *et al.* 2001; Ellner *et al.* 2002; Holmes *et al.* 2007; Ellner & Holmes 2008). These reviews include very few data for plant populations, so it may be that animal ecologists – for whom it is easier to define 'individual' organisms and who may also tend to draw on longer data sets for fewer species – take the concept of extinction risk much more literally than do plant ecologists. This does not mean that plant ecologists are not concerned about extinction. Rather, we tend to use population growth rates, rather than extinction risk *per se*, as a metric of relative viability: rapidly declining populations are likely to become extinct (even if they are large now), rapidly growing populations are likely to expand until resources and space limit growth, and populations near $\lambda = 1$ require more biological understanding to accurately predict their fates. Expected minimum population sizes (modified from quasi-extinction calculations) may be an equally robust or superior metric of relative population viability, at least over short time frames. However, we do not expect that plant ecologists will be able to calculate or precisely predict extinction risk for typical plant populations.

Our review revealed considerable variation in how much we trust the predictions of matrix models, both among published studies and within our working group. Most of us felt that models should be approached in a relative/comparative way, but a substantial minority of papers present results as literal predictions, and there has been no trend away from literal model interpretation through time. If we intend to use models to make predictions that are as accurate as possible, then it is also disturbing that recent studies also do not make use of the most sophisticated tools available. For example, methods for transient analysis have been around for decades, and they are likely to be relevant at the time scales over which we evaluate management, but these are rarely used in practice. However, it may be plant ecologists use matrix models specifically because these models lead to simple metrics that are consistent across studies, such as the asymptotic population growth rate, λ . These simple metrics are often omitted from or buried in more sophisticated analyses. Given limited data, it is also not clear that making quantitative predictions is realistic in most cases, even with the best models. Therefore, rather than recommending use of more sophisticated models, many (but not all) of us tend towards recommending more caution regarding literal interpretation of model outputs.

Finally, in spite of differences of opinion in some areas (Box 1), we agreed strongly that better understanding of environmental drivers of population dynamics would be likely to substantially improve models and model predictions. Correct understanding of drivers of stochasticity is also central to expectations for long-term population dynamics and evolution. Use of stochastic population models is growing in plant ecology, but these rely on very short data sets, and stochasticity is not often linked to environmental factors. For example, a number of recent studies have begun to use published matrix models for plant populations to explore patterns of stochasticity in natural populations (Morris *et al.* 2008; Jongejans *et al.* 2010; Buckley *et al.* 2010). Because most published matrix models are for very short time series, these comparative analyses use studies with as few as two or three estimates of each vital rate for stochastic modelling.

In this context, our review of plant demography implies two key needs for future research. First, we need better study designs and more long-term demographic data,

particularly in relation to drivers of variation in vital rates. This call cannot be repeated too often, but it is also important to remember that more detailed and long-term studies may come at a cost of breadth across populations and species. Our review shows, at best, modest increases study length through time (Table 2; Fig. 3). Although we have been conducting demographic studies for decades, plant ecologists have tended to accumulate short-term studies for more species, rather than longer term studies. Some constraints to study length are obvious, but others are probably much less so. In practice, we will always have more short-term studies than long-term studies. Therefore, the second need is to investigate critically how we can use these short-term studies. We need to focus on developing methods and tests for dealing with and quantifying the limitations of shorter term studies, as well as emphasizing the need for long-term data. It would also be interesting to know whether we can use short-term studies from hundreds of different species to understand long-term stochastic population dynamics.

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