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Review

Actual and Potential Use of Population Viability Analyses in Recovery of Plant Species Listed under the U.S. Endangered Species Act

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Abstract: *Use of population viability analyses (PVAs) in endangered species recovery planning has been met with both support and criticism. Previous reviews promote use of PVA for setting scientifically based, measurable, and objective recovery criteria and recommend improvements to increase the framework's utility. However, others have questioned the value of PVA models for setting recovery criteria and assert that PVAs are more appropriate for understanding relative trade-offs between alternative management actions. We reviewed 258 final recovery plans for 642 plants listed under the U.S. Endangered Species Act to determine the number of plans that used or recommended PVA in recovery planning. We also reviewed 223 publications that describe plant PVAs to assess how these models were designed and whether those designs reflected previous recommendations for improvement of PVAs. Twenty-four percent of listed species had recovery plans that used or recommended PVA. In publications, the typical model was a matrix population model parameterized with ≤5 years of demographic data that did not consider stochasticity, genetics, density dependence, seed banks, vegetative reproduction, dormancy, threats, or management strategies. Population growth rates for different populations of the same species or for the same population at different points in time were often statistically different or varied by >10%. Therefore, PVAs parameterized with underlying vital rates that vary to this degree may not accurately predict recovery objectives across a species' entire distribution or over longer time scales. We assert that PVA, although an important tool as part of an adaptive-management program, can help to determine quantitative recovery criteria only if more long-term data sets that capture spatiotemporal variability in vital rates become available. Lacking this, there is a strong need for viable and comprehensive methods for determining quantitative, science-based recovery criteria for endangered species with minimal data availability.*

Keywords: matrix model, minimum viable population, population growth rate, population model, recovery planning

Uso Actual y Potencial del Análisis de Viabilidad Poblacional para la Recuperación de Especies de Plantas Enlistadas en el Acta de Especies En Peligro de E.U.A

Resumen: *El uso de análisis de viabilidad poblacional (AVP) en la planificación de la recuperación de especies en peligro ha enfrentado tanto apoyo como críticas. Revisiones previas promueven el uso de AVP para fijar criterios de recuperación objetivos y con bases científicas y recomiendan mejoras para incrementar la utilidad de la herramienta. Sin embargo, otras han cuestionado el valor de los modelos de AVP para definir criterios de recuperación y afirman que los AVP son más apropiados para comprender los pros y contras de acciones de manejo alternativas. Revisamos 258 planes de recuperación finales para 642 especies de plantas enlistadas en el Acta de Especies En Peligro de E.U.A. para determinar el número de planes que usaban o recomendaban AVP en la planificación de la recuperación. También revisamos 223 publicaciones que describen AVP de plantas para evaluar el diseño de estos modelos y si esos diseños reflejaban recomendaciones*

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previas para el mejoramiento de los AVP. Veinticuatro porciento de las especies enlistadas tenían planes de recuperación que usaron o recomendaron AVP. En las publicaciones, el modelo típico fue el modelo matricial con parámetros de ≤5 años de datos demográficos que no consideraron estocasticidad, genética, denso dependencia, bancos de semillas, reproducción vegetativa, latencia, amenazas o estrategias de manejo. Las tasas de crecimiento poblacional para poblaciones diferentes de la misma especie o para la misma población en diferentes puntos en el tiempo a menudo fueron estadísticamente diferentes o variaron en >10%. Por lo tanto, puede que los AVP con parámetros de tasas vitales con este grado de variación no predigan con precisión los objetivos de recuperación en toda el área de distribución de una especie o en escalas de tiempo mayores. Afirmamos que los AVP, aunque una herramienta importante de un programa de manejo adaptativo, pueden ayudar a determinar criterios de recuperación cuantitativos solo si se dispone de conjuntos de datos de largo plazo que captan la variabilidad espaciotemporal de tasas vitales. Si se carece de ello, hay una fuerte necesidad de métodos viables e integrales para definir criterios de recuperación cuantitativos, basados científicamente, para especies en peligro con mínima disponibilidad de datos.

Palabras Clave: modelo matricial, modelo poblacional, planificación de recuperación, población mínima viable, tasa de crecimiento poblacional

Introduction

The Endangered Species Act of 1973 (ESA) established a visionary commitment to protecting biological diversity in the United States based on the best available science. The primary goals of the ESA are to prevent extinction and to recover species such that they cease to require protection under ESA provisions. Recovery is achieved through development and implementation of recovery plans that specify scientifically based, measurable, and objective recovery criteria (e.g., numbers of populations or population sizes) and management actions that ameliorate threats. However, recovery plans for many species do not establish such criteria (Gerber & Hatch 2002; Neel et al. 2012), and, when they do, criteria have been criticized for being unrelated to inherent biological characteristics (Elphick et al. 2001; Clark et al. 2002; Gerber & Hatch 2002) or insufficient for maintaining populations into the future (Tear et al. 1993; Tear et al. 1995; Neel et al. 2012).

Population viability analyses (PVAs) and other quantitative demographic models have been advocated as tools for establishing recovery criteria, assessing threat effects, and developing recovery strategies (Schemske et al. 1994; Carroll et al. 1996; Menges 2000). We define PVA as any quantitative demographic model used to evaluate current or future trends in population size or growth rate (which may be used as a measure of viability or extinction risk) for a given species. In PVA models, quantitative methods are applied to forecast the future status of a population (Morris & Doak 2002), and PVA models require biologists to be more explicit in their reasoning, integrate knowledge from multiple sources, identify important model structures and parameters, and guide future data collection (Walsh et al. 1995; Akcakaya & Sjögren-Gulve 2000; Burgman & Possingham 2000).

PVAs have been criticized because uncertainty inherent to the modeling process may make the tool inappropriate for assessing absolute outcomes or for prescribing absolute population sizes (Beissinger & Westphal 1998; Reed et al. 2002; Shaffer et al. 2002; Crone et al. 2011). Uncertainty in PVA is particularly problematic when demographic data are limited (Ruckelshaus et al. 1997; Beissinger 2002), which is typical for endangered species (Neel et al. 2012). Although Menges (2000) promoted use of PVA in plant conservation in a review of 95 plant PVAs, he found that most were not parameterized with data from enough individuals or years to capture demographic or environmental variability and did not include important components, such as metapopulation dynamics.

Multiple studies describe the ideal PVA characteristics (Table 1), and we discuss them here as potentially important components, especially for PVAs used to determine population thresholds for setting quantitative recovery criteria. According to these studies, PVA structure should include enough complexity to capture important components of the species' life history (Lindenmayer et al. 2000; Stephens et al. 2002) and be as simple as possible to reflect limitations in data and knowledge (Beissinger & Westphal 1998). When possible and relevant to a focal system, PVAs should incorporate stochasticity, genetics, species-specific demography, and other relevant factors (e.g., density dependence, Allee effects, etc.) (Boyce 1992; Menges 2000; Ralls et al. 2002). Stochasticity is an especially important driver of population dynamics in small populations typical of endangered species and those in variable environments (Boyce 1992; Ralls et al. 2002; Melbourne & Hastings 2008). Environmental stochasticity can decrease long-term population growth rates, demographic stochasticity can create Allee effects and unstable equilibria, and stochastic fluctuations in population size can lead to chance extinctions (Lande 2002). Viability is likely to be substantially overestimated when all factors contributing to stochasticity are not incorporated into models (Melbourne & Hastings 2008).

Genetic factors are also critical to include in PVAs, especially those that focus on small or isolated populations,

Table 1. Characteristics of a reliable, robust population viability analysis according to reviews in the published literature.

Characteristic	*Example*	*Reason*	*Selected citations*
Model structure			
balanced between complexity and simplicity	———	Model must be simple enough to match data availability and allow for scientifically based parameterization but complex enough to capture important life-history and ecological processes.	Beissinger & Westphal 1998; Courchamp et al. 1999; Lindenmayer et al. 2000; Ralls et al. 2002; Grimm et al. 2005
Incorporate in model			
adequate data to parameterize model and capture variability	>15 years of data; large number of individuals or multiple populations observed	Populations and the individual demographic rates that govern their dynamics are naturally variable, and data sets must be large enough to capture temporal and spatial variability in those rates.	Boyce 1992; Beissinger & Westphal 1998; Doak et al. 2005; Fiske et al. 2008
species-specific demography	recruitment; seed banks; plant dormancy	Life-history attributes specific to a species or taxon, in addition to basic processes such as fecundity and survival, are the fundamental drivers of population dynamics.	Boyce 1992; Doak et al. 2002; Reed et al. 2002
stochasticity	demographic; environmental	Stochasticity can cause chance extinctions while increasing the probability of extinction of small populations.	Boyce 1992; Ralls et al. 2002; Lande 2002; Melbourne & Hastings 2008
genetics	inbreeding depression; drift	Genetic factors such as inbreeding depression and genetic drift can increase the probability of extinction for small, isolated populations.	Ellstrand & Elam 1993; Allendorf & Ryman 2002; Brook et al. 2002; Reed et al. 2002
other intrinsic and extrinsic processes	density dependence; dispersal; predator-prey relations; threats; management actions	Other processes (such as those listed to the left), especially extrinsic threats, can be the largest drivers of species extinctions.	Boyce 1992
Model evaluation			
perturbation analyses	elasticity analyses; sensitivity analyses; life-table response experiment	Identifies important stages for management and allows user to explore the effect of uncertainty in a model.	Akcakaya & Sjögren-Gulve 2000; Ralls et al. 2002; Beissinger 2002
multiple PVA models	compare results of matrix model and individually based model	Results can be affected by model structure.	Werner & Caswell 1977
validation	comparison of predicted population size with observed size	Necessary to test the robustness of predictions.	Beissinger & Westphal 1998; Akcakaya & Sjögren-Gulve 2000; Beissinger 2002; Ralls et al. 2002

because inbreeding and genetic drift in these populations can increase the probability of extinction. Unconsidered genetic variables can lead to overly optimistic predictions and incorrect management recommendations (Ellstrand & Elam 1993; Allendorf & Ryman 2002; Brook et al. 2002). Other important additions to PVA models, when relevant, include density dependence, Allee effects, movement or metapopulation structure, extrinsic threats, and management interventions because these factors can be the largest drivers of population dynamics (Boyce 1992).

Furthermore, the ideal PVA for setting recovery criteria should be parameterized with sufficient data to describe spatiotemporal variability in vital rates and to accurately represent population dynamics throughout the species' geographic range (Beissinger & Westphal 1998; Doak et al. 2005; Fiske et al. 2008; Crone et al. 2011). Models should also be tested with perturbation analyses to assess the implications of uncertainty in parameter estimation (Beissinger & Westphal 1998; Beissinger 2002; Holmes et al. 2007). Consideration of both natural stochasticity and uncertainty is especially important when determining quantitative recovery criteria because these criteria must be sufficient to ensure species persistence despite variation. Finally, PVA models should be validated with observed population dynamics when possible to provide confidence in model outputs (Akcakaya & Sjögren-Gulve 2000; Ralls et al. 2002).

We reassessed actual and potential use of PVA in determining scientifically based, measurable recovery criteria for endangered plant species. We examined 258 final recovery plans for 642 plant species listed under the ESA as of 2010. We also reviewed 223 peer-reviewed studies containing 280 plant PVAs to assess whether the state of the art in PVA is sufficient for determining quantitative recovery criteria and whether PVA design has improved since Menges' 2000 publication.

Methods

PVA in ESA Recovery Planning

To assess use of PVA in endangered species recovery planning, we reviewed 258 final recovery plans for 642 plant species that were approved by the U.S. Fish and Wildlife Service prior to 30 June 2010. For each recovery plan, we searched for the keywords *population viability analysis*, *minimum viable population*, *matrix*, *model*, and *viability*. We noted how PVA was discussed in applicable plans, including whether the plan discussed a PVA study conducted previously or as part of the plan; an existing PVA informed recovery criteria; recovery criteria were written in the language of PVA (e.g., the population should have a specific probability of persistence to be considered recovered); PVA was recommended as part of the recovery strategy; and PVA was recommended to determine, evaluate, or refine recovery criteria. In addition, for the 251 listed plant species for which delisting was considered possible, we recorded qualitative statements in recovery criteria that were related to viability.

Characterizing Plant PVAs

To assess whether the state of the art in published PVAs met the characteristics of an ideal PVA for setting quantitative recovery criteria (Table 1), we used ISI's Web of Science database and the search engine Google Scholar to search for PVA-related peer-reviewed literature for plants irrespective of the focal species' listing status. We used the search terms *population viability analysis*, *viability*, and *matrix population model* to find all studies published through December 2008. Publications that provided demographic information but no model of current or future population trends, extinction risk, or minimum viable population (MVP) estimates were excluded. We found 223 studies describing 280 PVAs for 246 plant species (Supporting Information).

We noted the type of model used (e.g., age- or stage-based matrix model, individual-based model, or other model type such as a periodic projection matrix, equation-based model, or reaction-diffusion model). We also noted whether authors applied multiple PVA methods in the same study to determine the sensitivity of PVA results to model structure. We determined whether PVAs considered complex attributes of plant life history (e.g., seed bank, clonal reproduction, and plant dormancy) and whether they incorporated stochasticity, genetics, ecological processes, and interactions (e.g., density dependence, natural disturbances), or external population drivers (e.g., threats or management actions). We also recorded the number of populations and years of observation used to parameterize PVAs. Finally, we noted whether perturbation analysis or model validation was used to explore the effect of parameter uncertainty on predictions. To determine whether PVA design has changed since Menges (2000), we used chi-square tests to compare the number of PVAs parameterized with ≥ 5 years of data that were published before ($n = 116$) and after ($n = 164$) 2001. Similarly, we used chi-square tests to compare the number of PVAs that incorporated stochasticity, genetics, density dependence, disturbances or catastrophes, and metapopulation dynamics or dispersal before and after 2001.

For each focal species, we noted its listing status as determined under the ESA and by the International Union for Conservation of Nature (IUCN), life-form, and whether the species was annual, biennial, or perennial. We also recorded finite rate of population growth (λ), probability of and mean time to extinction, MVP size, and sustainable harvest levels as predicted by PVA models when given. When perturbation analyses were conducted, we noted whether sensitivity analyses, elasticity analyses, or a life-table response experiment was used and the stage class or life-history process that was ranked as most important for population growth. Stage classes included adults (also termed "reproductive" or "large" individuals), juveniles (also termed "nonreproductive," "vegetative," or "medium-sized" individuals), seedlings (also termed "saplings" or "small" individuals), seeds, or dormant plants. Life-history processes included stasis (or survival), progression (or growth), reproduction, germination (or establishment), recruitment, retrogression, and clonal growth.

Finally, we evaluated within-species variability in PVA results to determine the consistency of results for a single species across methods, space, and time. For studies reporting population growth rates as predicted from different PVA methods or across different sites or years, we noted whether rates were statistically different as determined by the study's author(s). We also calculated the arithmetic average, standard deviation,

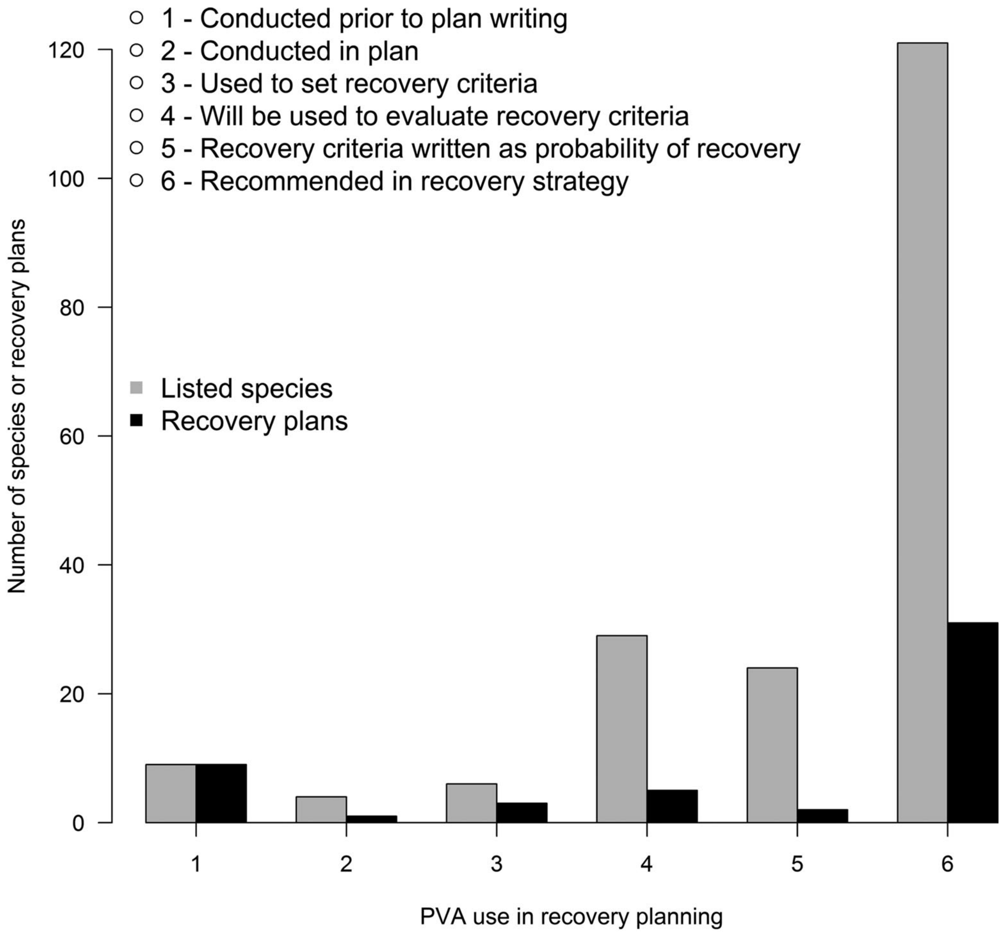

Figure 1. Contexts under which population viability analysis (PVA) is used or recommended in the final recovery plans for 642 plant species listed under the U.S. Endangered Species Act.

and percent difference between minimum and maximum population growth rates to describe the magnitude of within-species variability for all studies, irrespective of whether authors statistically compared growth rates.

Results

PVA in ESA Recovery Planning

Use of PVA in ESA recovery planning was limited; 15% of the 258 final recovery plans for 24% of the 642 listed plant species mentioned or recommended PVA. However, the concept of viability was nearly ubiquitous in recovery criteria. Recovery plans for 233 of the 251 species for which delisting was considered possible included qualitative statements requiring viability in a broad sense (Supporting Information).

PVA was used or recommended in 5 different contexts in recovery plans (Fig. 1). Of the 38 plans that mentioned or recommended PVA, 9 (for 9 species) referenced results of published PVA studies conducted for the species prior to approval of the recovery plan (Supporting Information). In these recovery plans, models were typically discussed in the "Life History/Ecology" section to describe life-history attributes and threat considerations. For example, the final recovery plan for the sentry milkvetch (*Astragalus cremnophylax*) (U.S. Fish and Wildlife Service 2006) referenced Maschinski et al. (1997) to describe how the removal of trampling led to population stabilization in models. Similarly, the results of population modeling for Furbish's lousewort (*Pedicularis furbishiae*) (Menges 1990) were cited in the species' recovery plan (U.S. Fish and Wildlife Service 1991) to support that populations naturally persist through local extinction and recolonization events in a metapopulation structure.

Authors of 3 recovery plans for 5 species conducted PVAs to determine recovery criteria for downlisting and delisting (Supporting Information). Completion of a PVA was suggested in 31 plans (for 145 species) to determine or to evaluate existing recovery criteria as part of those species' recovery strategies. Future PVA use was implied in an additional 5 plans (for 29 species) in that the

Table 2. Characteristics of plant population viability analyses (PVAs) in the published literature.

Characteristic	*Number of PVAs (%)*	*Characteristic*	*Number of PVAs (%)*
	total 280 PVAs	Model validation	total 280 PVAs
Focal species listed under Endangered Species Act	23 (8)	compared predicted stage or age distribution with actual	87 (31)
Focal species listed by International Union for Conservation of Nature	28 (10)	compared model predictions with observed dynamics	13 (5)
Model types	total 280 PVAs	Special model components	total 280 PVAs
stage- or age-based matrix	250 (89)	seed banks	84 (30)
other matrix model (e.g., periodic projection matrix)	11 (4)	vegetative reproduction	7 (3)
generic PVA program	24 (9)	dormancy	15 (5)
individual-based model	3 (1)	movement and dispersal	15 (5)
other simulation model	2 (<1)	density dependence	24 (9)
integral projection model	3 (1)	habitat	35 (13)
reaction diffusion model	2 (<1)	natural disturbance	32 (11)
life table or path analysis	2 (<1)	stochasticity	73 (26)
other equation-based model	12 (4)	genetics	5 (5)
Use of multiple PVA model structures in study	8 (3)	Threats included in models	total 35 PVAs (13%)
Data set length	total 231 species	fire	1
5 years or less	160 (69)	flooding	1
6–10 years	52 (23)	hurricanes	1
11–15 years	10 (4)	drought	4
16–20 years	2 (<1)	disease	3
>20 years	7 (3)	general catastrophe	1
Data set size	total 275 species	harvest	11
1 population	146 (53)	pollinator limitation	2
2 populations	43 (16)	herbivory, predation, or grazing	10
3 populations	16 (6)	trampling	1
4 populations	16 (6)	Management included in models	total 28 PVAs (10%)
5 populations	12 (4)	controlled burns	4
>5 populations	42(15)	grazing	3
Perturbation analysis	total 164 PVAs (5%)	herbivore, predator, or trampling exclusion	5
sensitivity analysis	45	clipping/mowing	5
elasticity analysis	128	reintroduction	1
life-table response experiment	35	seedling control	4
		removal of reproductive limitation	2
		biocontrol or weed agents	4

downlisting or delisting criteria were written in the language of PVA. For example, paper nailwort (*Paronychia chartacea*) can be delisted when "enough demographic data are available to determine the appropriate numbers of self-sustaining populations and sites needed to assure 95% probability of persistence for 100 years" (U.S. Fish and Wildlife Service 1999).

Recommendations for demographic monitoring and research in recovery plans suggested that more PVAs could be conducted in the future; 97% of the 642 listed plant species have recovery plans that recommended monitoring or research related to demography, specific life-history stages, and genetic viability as part of the recovery strategy (Supporting Information). Furthermore, demographic monitoring was specifically required in downlisting and delisting criteria for 98 and 97 species, respectively.

Plant PVA Characteristics

In 280 published plant PVAs, the typical model was an age- or stage-based matrix model (89% of PVAs) that focused on a species that was not listed under the ESA (92%). It was parameterized with ≤ 5 years of demographic data (69%) from a single population (53%) and did not include parameters for stochasticity (74%), genetics (95%), or density dependence (91%). The typical model did not include special components relevant to plant species, such as seed banks (70%), vegetative reproduction (97%), or dormancy (95%), nor did it include threats (87%) or management strategies (90%). It did include perturbation analyses (59%) but did not evaluate multiple PVA methods (97%) or validate model results by comparing model predictions with actual population trends (95%) (Table 2). The number of PVAs published subsequent to Menges' (2000) publication that

Table 3. Components considered in population viability analyses (PVAs) before versus after 2001, following Menges (2000) in which specific features were recommended for future plant PVAs.

PVA component	*Number of PVAs containing component before 2001 (%) ($n = 116$ PVAs)*	*Number of PVAs containing component after 2001 (%) ($n = 164$ PVAs)*	*Chi-square (p)*	*Percentage of PVAs containing component in Menges 2000*
Parameterized with data from study >5 years duration[a]	20 (21)	47 (34)	4.3 (<0.05)	30
Stochasticity (environmental or demographic)	20 (17)	53 (32)	8.0 (<0.05)	27[b]
Disturbance or catastrophe[c]	19 (16)	39 (24)	2.2 (0.13)	16
Density dependence	9 (8)	15 (9)	0.2 (0.68)	12
Spatial factors[d]	17 (15)	26 (16)	0.1 (0.78)	8
Genetics	1 (<1)	4 (2)	0.96 (0.32)	3

[a] *Not all PVAs in our study gave the study duration, and the sample size for this component is 94 for 2001 and earlier and 139 after 2001.*

[b] *We did not separate PVAs that considered environmental versus demographic stochasticity as Menges (2000) did. To compare our results with the results of Menges, we added the percentage of PVAs that contained environmental stochasticity with the percentage that contained demographic stochasticity from Menges' results. This total may be an overestimate if the PVAs that included environmental stochasticity also included demographic stochasticity.*

[c] *To compare our study results with Menges' (2000) results, we determined the percentage of PVAs that considered natural disturbances or threats and compared that to the percentage that considered disturbances or catastrophes in Menges. However, because we did not separate catastrophes from other threats, our percentage of PVAs considering disturbance or catastrophe may be high compared with Menges'.*

[d] *To determine the percentage of PVAs that included spatial factors, we determined the percentage of PVAs that included parameters for movement, habitat, or environment in our study. This total corresponded to the percentage of PVAs that were spatially explicit or included metapopulation modeling according to Menges (2000).*

considered density dependence, spatial factors, or genetics was not significantly different from the number published prior to that publication (Table 3). However, significantly more PVAs considered stochasticity (32%; $\chi^2 = 8.0$, $p < 0.05$) and were parameterized with >5 years of data (34%; $\chi^2 = 4.3, p < 0.05$) following Menges' (2000) publication (Table 3).

Finite rates of population growth were reported in 173 PVAs for 1754 populations. Values ranged from 0.0004 for wild teasel (*Dipsacus sylvestris*) (Werner & Caswell 1977) to 15.54 for sweet alyssum (*Lobularia maritima*) (Pico et al. 2002). The mean was 1.08 (SD 0.64; median 1.00). Forty-four percent of populations had growth rates <1 (values that indicate a declining population). Despite an overall mean population growth rate of 1.05 (SD 0.71; median 0.97) for populations of species listed under the ESA ($n = 157$), 61% of these populations had declining growth rates with a mean rate of 0.81 (SD 0.21; median 0.87).

Eleven plant PVAs reported MVP sizes, and these ranged from 12 individuals for the Albany cycad (*Encephalartos latifrons*) (Daly et al. 2006) to 70,000 for viper's grass (*Scorzonera humilis*) in nutrient-rich sites (Colling & Matthies 2006). Mean MVP size was 4199 individuals (SD 16,426; median 202).

Perturbation analyses conducted in 164 PVAs for 150 species indicated that population growth rates were most sensitive to changes in the dynamics of adult individuals (70% of species) followed closely by changes in the dynamics of juvenile individuals (67%). The most important demographic process for these species was stasis (95%) followed by progression (53%) and reproduction (32%). Percentages listed here do not sum to 100% because some studies indicated multiple stages or processes as being equally important for population stability and growth. However, these results may not broadly reflect important life-history stages or demographic processes for all plants because the majority of plant species with PVAs included in our data set were perennials (86%), and adult survival is generally most important for longer lived, late-maturing species (Heppell et al. 2000; Garcia et al. 2008).

Variability within Species

Sixty-nine percent of the 32 species for which authors statistically compared growth rates from different sites yielded significantly different growth rates among populations. The percent difference between highest and lowest growth rates across populations for these 32 species plus an additional 29 species for which population growth rates were reported for multiple populations but were not compared statistically ranged from 0.33% for purple avens (*Geum rivale*) (range: $\lambda = 0.997$–1 across 2 populations) (Kiviniemi 2002) to 185% for St. Anthony's turnip (*Ranunculus bulbosus*) (range: $\lambda = 0.2$–6.1 across 10 populations) (Sarukhan & Gadgil 1974). Only 19% of these species had populations in which the difference was $\leq 10\%$ (Fig. 2).

Population viability analyses for 98 species provided statistical comparisons of population growth rates across

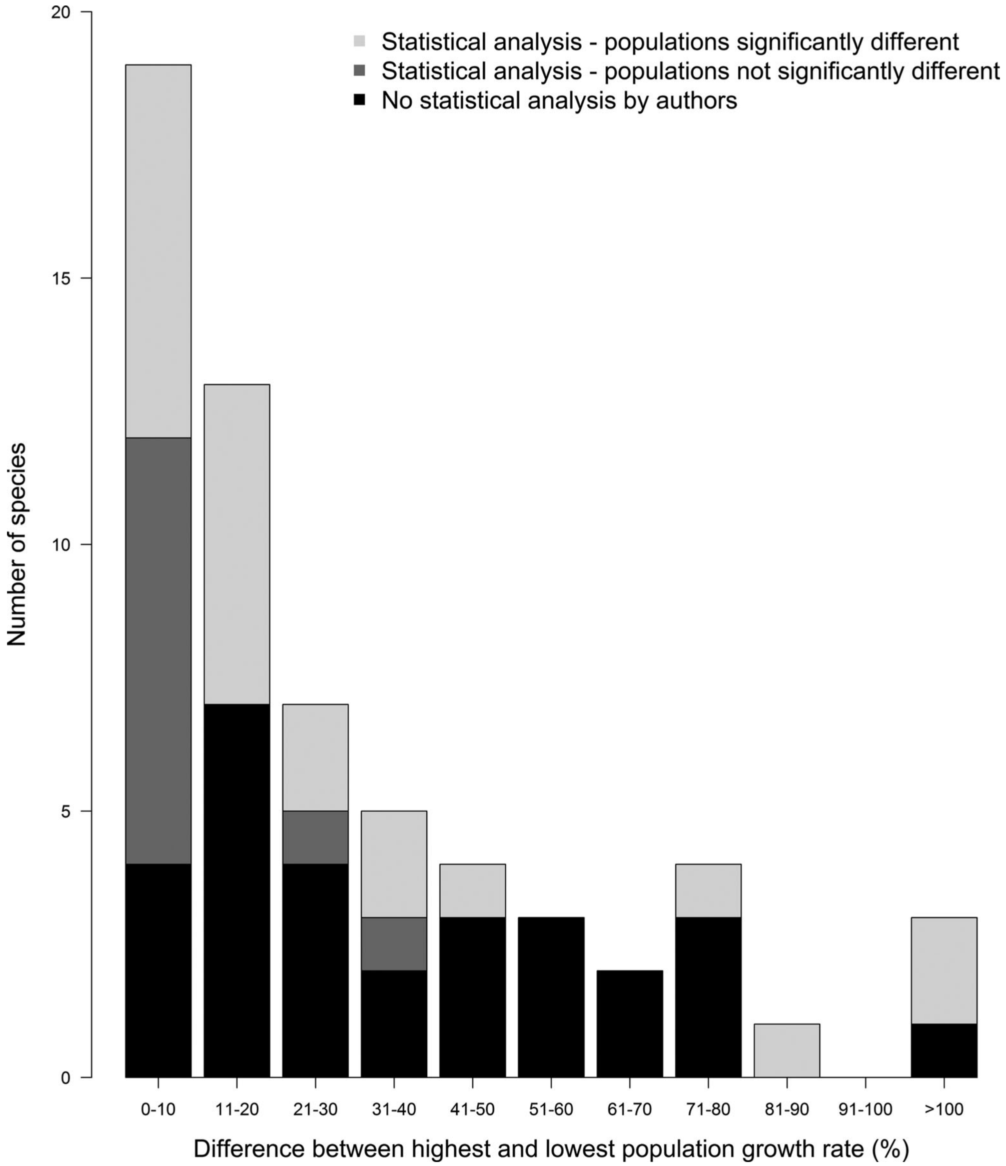

Figure 2. Percent difference between the highest and lowest population growth rates for different populations of the same species compared within the same year in published population viability studies.

≥2 years; 48% of these species had significantly different growth rates among years. For these species plus the 65 species for which growth rates across years were given but were not compared statistically, the lowest percent difference was 0.5% across 2 consecutive years for *Heliconia acuminata* (Bruna 2003). The largest difference was for a population of viper's bugloss (*Echium vulgare*), for which growth rates ranged from 0 to 2.4 (Klemow & Raynal 1985). This range represented instances of both drastic decline and substantial growth in consecutive years. Fifty-nine species (57%) had a percent difference in population growth rate ≤10% across years, and 19 species (18%) had percent differences ≥100% (Fig. 3).

In 8 studies (11 species), authors assessed the effect of model structure on PVA results by applying the same input parameters to at least 2 different types of models. For example, Werner and Caswell (1977) explored differences in population growth rates for wild teasel through both age- and stage-based matrix models. Seven of those studies (for 17 populations and 5 species) reported population growth rates for each structure, and most models were generally in agreement irrespective of model structure (Fig. 4). Seven of the 17 populations had growth rates that differed by ≤10% across models, 8 populations had growth rates that differed by 10–50%, and 2 populations had growth rates that differed by >50% between models. Thus, population growth rates were generally robust to differences in model structure, a result that contrasts with the high within-species spatiotemporal variability in growth rates.

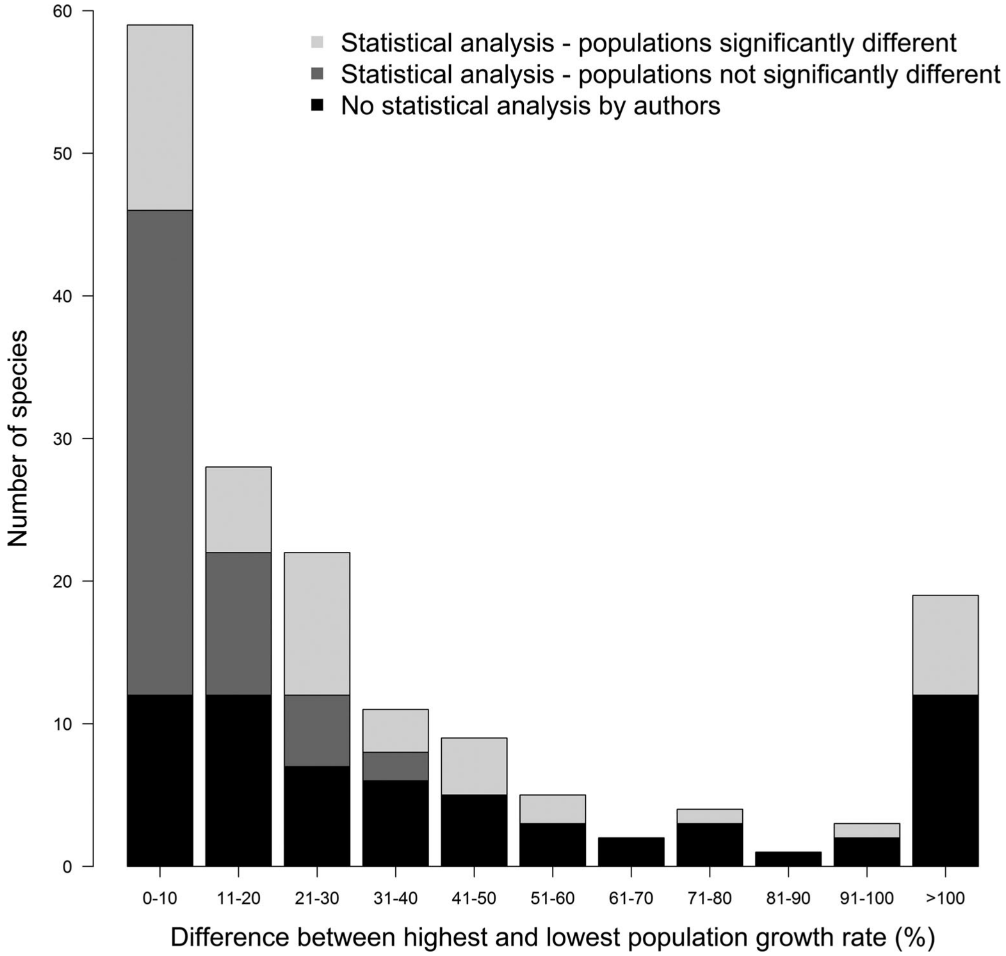

Figure 3. Percent difference between the highest and lowest population growth rates for the same population of a species compared across multiple years in published population viability studies.

Discussion

PVA in Recovery Planning

A species can be delisted under the ESA when it is neither "in danger of extinction throughout all or a significant portion of its range" (ESA sec. 3[6]) nor likely to become so "within the foreseeable future" (ESA sec. 3[20]). Accordingly, delisting requires that a species be biologically secure (i.e., sufficiently abundant with stable or increasing population trends) and that threats be manageable or nonexistent such that the species can persist without the ESA's provisions. Determining measurable, objective recovery criteria that reflect these definitions is one of the most difficult challenges in conservation practice. It is intuitive that PVA could inform these criteria by forecasting extinction or quasi-extinction probabilities over a specified period, determining population status or trends, or establishing MVP sizes. However, our results suggest, in agreement with findings of previous studies (e.g., Beissinger & Westphal 1998; Crone et al. 2011), that PVAs as currently implemented may be unsuitable for determining absolute, species-level quantitative recovery criteria due to data limitations and substantial shortcomings in PVA use that lead to unacceptable levels of bias and lack of precision.

Data limitations include lack of demographic data from a sufficient number of individuals, populations, or years and lack of information on life-history traits that can affect model outcomes. Effects of the length of a data set (i.e., numbers of years of data on which vital rates or population estimates are based) on predicted population growth rates and extinction risk are well known (Crone et al. 2011) and can account for far more variation in certain PVA results than biological variables (Reed et al. 2003). Typically, 15–20 years of data are needed to reliably estimate population growth trends or extinction risk (Fagan et al. 1999; Doak et al. 2005; Holmes et al. 2007; Che-Castaldo & Inouye 2011), and reliably forecasting future extinction risk can require as much as a 5:1 ratio of observation to forecast years (Fieberg & Ellner 2000). Extended periods of observation are especially important for plants species that naturally exhibit a high degree of spatial and temporal variation among populations (Silvertown et al. 1996), particularly shorter-lived species,

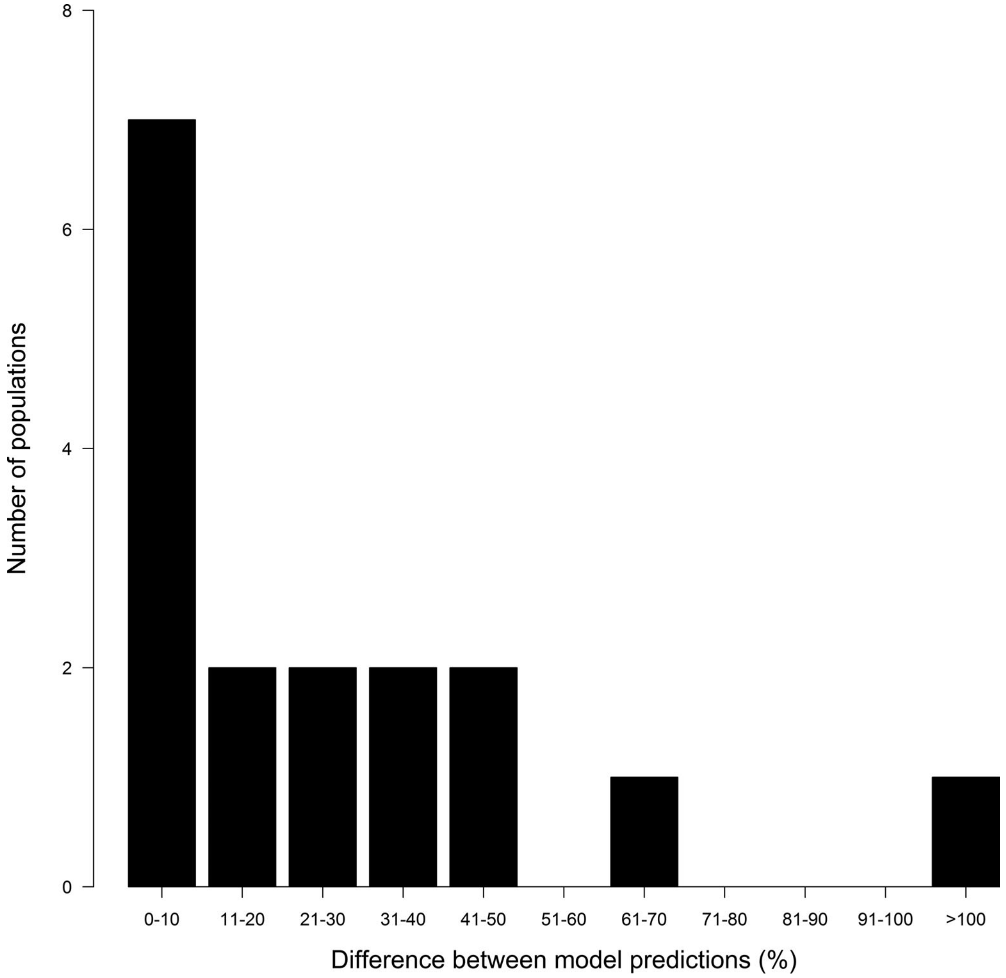

Figure 4. Percent difference between the highest and lowest population growth rates for the same population of a species compared with multiple model structures in published population viability studies.

which tend to show far greater temporal variability than their longer-lived counterparts (Garcia et al. 2008). Of the 231 PVAs we reviewed, only 4% were based on $\geq$15 years of data, and 69% were based on $\leq$5 years (Table 2). Although significantly more PVAs published after Menges (2000) were based on >5 years of data (Table 3), the median data set length after 2001 was still 4 years, indicating a need for continued increases in data set length.

Limited spatial extent of data sets (i.e., the number of populations observed) is also problematic because population growth rates, viability, and underlying vital rates are highly context specific. For example, MVP sizes, which are predominantly determined through PVA, are known to vary substantially within species depending on interactions between life history, environmental context, and extrinsic threats (Flather et al. 2011). Forty-three percent of PVAs predicted growth rates that differed by >10% for multiple populations of the same species. Thus, observations of multiple populations from throughout a species' range over multiple years are needed to adequately capture species-level dynamics. However, 53% of PVAs in our review were parameterized with observations of a single population. Recovery plans typically specify that all populations conserved must be viable in a broad sense because spatiotemporal variation is the norm. Accordingly, evaluating the probability of persistence in one or a few populations over short time frames contributes little to understanding whether this requirement is met and whether extinction is likely throughout all or a substantial portion of the species' range.

The need for 15–20 years of data from multiple populations to account for spatiotemporal variation in vital rates makes parameterizing even simple stage- or age-based models for all listed species a daunting task. Chronic lack of funding for endangered plants (Campbell 1991) has resulted in little existing demographic data (Schemske et al. 1994). Even population sizes at the time recovery plans were written and historical abundances are lacking for 67% and 98% of species with recovery plans, respectively (Neel et al. 2012). Although the U.S. Fish and Wildlife Service recognizes the need for such data (97% of recovery plans for plant species recommend demographic monitoring and research), implementing these recommendations will require a commitment of funding and personnel that far exceeds historical levels (Male & Bean 2005).

Beyond lack of demographic data sets, lack of knowledge about key life-history traits can also limit PVA applications. Models that exclude important population processes can overestimate population viability (Lindenmayer et al. 2000; Melbourne & Hastings 2008) and yield inaccurate projections of population dynamics (Letcher et al. 1998; Courchamp et al. 1999; Grimm et al. 2005). Features that are known drivers of population dynamics for plants (e.g., seed banks and plant dormancy; Boyce 1992; Doak et al. 2002; Reed et al. 2002) are often difficult to quantify (Crone et al. 2011). In our study, most models did not consider stochasticity (74% of PVAs), genetics (95%), density dependence (91%), seed banks (70%), vegetative reproduction (97%), or dormancy (95%). Although we do not imply that these factors are relevant for every species, models for many species are lacking critical factors, given the extremely low percentage of PVAs that included these components. As with lack of demographic data mentioned previously, a greater commitment to research on endangered plant species could reduce the severity of this issue.

Even if data availability and model complexity are improved, we believe there is a fundamental mismatch between how PVA is most often used and recovery planning. For example, models tend to focus on effects of intrinsic demographic processes, such as pollen limitation, interannual variation in seed germination, or seedling survival, whereas extinction risk is often more affected by large-scale and chronic, extrinsic, human-mediated threats, such as resource extraction, nonnative species introductions, and land-use change (Lawler et al. 2002). These extrinsic processes can cause regional or species-wide declines with effects that are orders of magnitude larger than demographic processes but may not alter demographic rates (Brook et al. 2008). In the few cases in which PVAs we reviewed considered extrinsic threats (13% of species), authors experimentally monitored changes in vital rates following pressure from a single threat or considered threats as catastrophes that could occur with some probability each year in stochastic models. As such, these models do not reflect the multiple external, systematic processes that typically cause species-level declines.

In addition, threatening processes can cause declines in population abundance, numbers of whole populations, and extent of occurrence (i.e., area of habitat or range). Loss of entire populations is more common in plants than in animals (Leidner & Neel 2011) and, in these cases, the amount and distribution of high-quality habitat may be more indicative of potential for species' persistence than the demographic details at one or a few sites (Neel et al. 2012). Although multiple-site PVAs are possible, they require even more extensive data and are rarely implemented (Morris & Doak 2002). Users of PVAs tend to focus on numbers of individuals, which may at worst be a fundamentally inappropriate measure of recovery and at best addresses only one aspect of endangerment (Neel et al. 2012; Neel & Che-Castaldo 2013). Effective recovery planning requires a means of determining the most pertinent measures of decline, such as individuals, populations, habitat area, or range, and threshold values for each of those measures above which a species is no longer at risk of extinction throughout all or a substantial portion of its range. It also requires techniques that efficiently assess trends in each of these measures with sufficient precision to determine whether thresholds have been met. Because of the limited focus of PVAs, these models do not provide guidance regarding which combination of habitat area, number of populations, and number of individuals is an adequate measure of recovery for a particular species.

Although we believe conservationists should not rely on PVA for setting absolute quantitative recovery criteria given the observations described previously, we stress that PVA is still potentially useful as part of the recovery-planning process. It can be critical for integrating knowledge from multiple sources, identifying key model structures and parameters through perturbation analyses, and guiding future data collection (Walsh et al. 1995; Akcakaya & Sjögren-Gulve 2000; Burgman & Possingham 2000). It is also a useful tool for ranking relative risk between different species or the importance of varying threats or management actions for a single species (Beissinger & Westphal 1998; Crone et al. 2011). However, even these PVA applications require a clearer understanding of the ecology and distribution of variation for a given species, and a need continues to exist for carefully designed studies of a sample of populations that can identify demographic drivers and characterize spatiotemporal variation.

Alternative Techniques and Approaches

Several alternatives to PVA have been proposed and could have applications for recovery planning. Genetic monitoring has been recommended as a potential means of quantifying population characteristics (Schwartz et al. 2007) and can be used in the same manner as mark-recapture data to estimate abundance and trends, individual identities, historical population size, and ecological processes, such as dispersal, that are not available from other sources (Luikart et al. 2010). Although costs of genotyping with high throughput sequencing technologies are rapidly declining (Truong et al. 2012), it can still be cost prohibitive to collect data from the number of individuals and loci over sampling time frames and populations needed to obtain sufficiently unbiased and precise estimates of current status and trends (Luikart et al. 2010;

Tallmon et al. 2010). The amount and type of genetic data required under different population structures to detect change in population size or connectivity in management-relevant time frames also remains unknown (Tallmon et al. 2010).

Alternative population models that may be more robust to data limitations have also been suggested. Integral projection models produce less biased and more precise estimates of population growth rate than matrix models for small data sets (e.g., $\leq$300 individuals; Ramula et al. 2009), but they do not overcome issues related to short time series or poorly designed ecological studies. Models based on species occurrence rather than abundance offer a potential solution because presence and count data are more widely available than stage- or age-based data (Skarpaas & Stabbetorp 2011), but testing is needed to explore utility of these models with limited spatiotemporal data extents. Noon et al. (2012) suggest occupancy models as an efficient means of determining population trends in vertebrates; however, certain life-history attributes for many plants make this application of occupancy data challenging. For example, many species exhibit plant dormancy or seed banks, and it is often difficult to determine whether the species is truly absent from a given habitat patch or merely absent above ground (Harrison & Ray 2002). In addition, unless multiple surveys are conducted over short periods, occupancy models demonstrate only snapshots of occupancy and fail to describe possibly important periods of turnover.

Two alternative measures of viability have been proposed but remain untested. Minimum expected population size over a given time horizon does not depend on an arbitrary quasi-extinction threshold and may be compared across species (Crone et al. 2011). Change in extent of occupancy, which is more typically available than counts of individuals, may also be used to assess extinction risk on the basis of theoretical relations between area of occupancy and abundance (He 2012). However, the limitations of occupancy models described previously also apply to this measure of viability.

Surrogate approaches that use biological similarities among species to leverage data from relatively well-studied to poorly studied species have been widely suggested in conservation. In this context, detailed demographic data for one species could be used to guide the formulation of recovery criteria for biologically similar species. Unfortunately, there is no evidence that listed plant species are sufficiently similar to form surrogate groups (Che-Castaldo & Neel 2012), and even closely related or biologically similar species do not have similar population growth rates (Buckley et al. 2010; Flather et al. 2011). This lack of similarity and predictability is not surprising given demographic variations among populations within species, as we found here. Again, the highly contextual nature of measures of population dynamics within and among species (Flather et al. 2011) may limit application of these values for setting recovery criteria for individual species.

Of any approach, the IUCN framework (Mace et al. 2008) for assessing extinction risk is the most comprehensive and most closely meets the requirements for setting recovery criteria. This framework integrates risks arising from low abundance and distribution with those due to extrinsic threats. Although this is more holistic than PVA alone, the system assigns species to broad risk categories only on the basis of specified thresholds (e.g., 80% and 50% loss of individuals for critically endangered and endangered classifications, respectively) rather than generating a precise extinction risk. Furthermore, limited abundance and decline data mean that, in practice, species assessments are made primarily through expert opinion rather than via objective, abundance-based methods. Despite widespread use of IUCN methods, evaluation of its reliability has only begun (but see Keith et al. 2004; Porszt et al. 2012). In addition, this framework is designed for placing species on the IUCN Red List, and criteria for determining when conservation provisions are no longer necessary cannot be determined as the reverse of those for listing.

We stress that PVAs, especially as currently implemented, are not sufficiently robust for setting quantitative endangered species recovery criteria. Given the overwhelming amount of data needed to produce robust results with PVA, it is unlikely that PVA models would be widely applicable beyond comparative evaluation of risk in an adaptive-management framework. The IUCN framework provides a more comprehensive evaluation of species-level endangerment, but drawbacks described previously limit its use. Although specific alternative techniques described in this section may offer appropriate analytical approaches for determining objective recovery criteria for specific species on a case-by-case basis, few species listed under the ESA have the volume of data needed to overcome the limitations inherent with the majority of these techniques. Either a large increase in data collection efforts and funding needs to occur (unlikely) or viable and comprehensive methods for determining quantitative, science-based recovery criteria for endangered species with minimal data availability must be developed. In particular, there is a need for methods that link general principles of extinction risk to provide more precise risk estimates that can be compared across species and allow for monitoring of key aspects of abundance that can be used to reliably determine status and trends.

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Supporting Information

A description of all studies found in the literature review (Appendix S1), a list of the number of species with qualitative viability criteria (Appendix S2), a list of how PVA is used in recovery plans for listed plant species (Appendix S3), and the number of species for which demographic research or monitoring is recommended in recovery plans (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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