A Protocol for Better Design, Application, and Communication of Population Viability Analyses

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ABSTRACT

Population viability analyses (PVAs) contribute to conservation theory, policy, and management. Most PVAs focus on single species within a given landscape and address a specific problem. This specificity often is reflected in the organization of published PVA descriptions. Many lack structure, making them difficult to understand, assess, repeat, or use for drawing generalizations across PVA studies. In an assessment comparing published PVAs and existing guidelines, we found that model selection was rarely justified; important parameters remained neglected or their implementation was described vaguely; limited details were given on parameter ranges, sensitivity analysis, and scenarios; and results were often reported too inconsistently to enable repeatability and comparability. Although many guidelines exist on how to design and implement reliable PVAs and standards exist for documenting and communicating ecological models in general, there is a lack of organized guidelines for designing, applying, and communicating PVAs that account for their diversity of structures and contents. To fill this gap, we integrated published guidelines and recommendations for PVA design and application, protocols for documenting ecological models in general and individual-based models in particular, and our collective experience in developing, applying, and reviewing PVAs. We devised a comprehensive protocol for the Design, Application, and Communication of PVAs (DAC-PVA), which comprises 3 primary elements. The first defines what a useful PVA is; the second element provides a workflow for the design and application of a useful PVA and highlights important aspects that need to be considered during these processes; and the third element focuses on communication of PVAs to ensure clarity, comprehensiveness, repeatability, and comparability. Thereby, DAC-PVA

should enhance communication and repeatability of PVAs, strengthen the credibility and relevance of PVAs for policy and management, and improve the capacity to generalize PVA findings across studies.

INTRODUCTION

Population viability analysis (PVA) is a process of identifying and evaluating threats to a species and estimating the (relative) probability of a population persisting for a given time into the future (Akçakaya et al. 1998). Population viability analyses are used to address a broad range of conservation questions, including identifying the relative importance of factors affecting population dynamics and viability (Gilpin & Soulé 1986), assessing extinction risk and conservation status (Reed et al. 2002; IUCN 2010), identifying critical habitats, weighing ecological and socioeconomic trade-offs (e.g., Curtis & Vincent 2008; Johst et al. 2011), prioritizing management alternatives (Bekessy et al. 2009), communicating conservation problems to stakeholders (Shaffer et al. 2002), and identifying information gaps to direct further research (Akçakaya & Sjögren-Gulve 2000; Akçakaya et al. 2004). The application of PVAs to species conservation has been facilitated by growing computational capacity and the availability of software programs such as VORTEX (Lacy 1993), ALEX (Possingham & Davies 1995), the RAMAS family of models (Akçakaya 1994, 2002; Akçakaya & Root 2003), METAPHOR/METAPOP (Verboom et al. 2001), and SPOMSIM (Moilanen 2004).

Most PVA studies focus on the dynamics of a single species in a given landscape in relation to particular threats or management options and entail a case-specific set of performance criteria. Consequently, recent attempts to synthesize and generalize the results of multiple PVA studies have failed to overcome the methodological idiosyncrasies and find meaningful generality in meta-analysis (e.g., Naujokaitis-Lewis et al. 2009). This study highlights the problem of case specificity in PVA methods and reporting and identifies a need for standardization. We examined whether PVA implementation and reporting have changed or improved over time, assessed whether published guidelines for PVA design and implementation have been used or offer solutions, and devised a comprehensive protocol for design, application, and communication of PVAs. To achieve our objectives, we reviewed individual PVA studies and synthesized literature that provided specific advice on PVA design and implementation and more general guidance on documenting ecological models.

DATABASE CONSTRUCTION AND LITERATURE REVIEW

This study was instigated by challenges that arose while assembling and analyzing 2 databases of published PVAs. The first database was assembled to identify general properties across taxa on the relative influence of demographic and spatial parameters on population viability (Naujokaitis-Lewis et al. 2009). The second database was developed within the EU project SCALES (Henle et al. 2010), the goal of which was to generalize viability requirements across species and ecosystems. The SCALES database synthesized PVAs for terrestrial animals; it summarizes 260 parameters from 78 published PVA studies. The database includes metadata; information on model design and parameter values, including those related to life history, population growth, population structure, landscape attributes, dispersal patterns, and sources of stochasticity; and qualitative and quantitative results of simulations and sensitivity analyses (details available in Supporting Information).

Among the many published recommendations on aspects of design, application, and communication of PVAs, we synthesized 9 publications that offered relatively comprehensive guidelines: Boyce (1992), Beissinger and Westphal (1998), Akçakaya and Sjögren-Gulve (2000), Burgman and Possingham (2000), White (2000), Morris and Doak (2002), Ralls et al. (2002), Shaffer et al. (2002), and International Union for Conservation of Nature (IUCN) (2010). We identified 214 guidelines for PVA design, implementation, and communication. Because some guidelines addressed more than one topic, we distinguished 318 pieces of specific advice from these 9 sources (Supporting Information).

In addition to guidelines specific to PVAs, we sought protocols that could offer structural advice on reporting. Such advice was lacking from within the PVA literature. However, we identified 2 relevant protocols that provide advice on how to structure model reports. The ODD ("overview, design concept, details") protocol was designed to describe individual-based and agent-based models, but is also useful for directing model design and implementation (Grimm et al. 2006; Grimm et al. 2010). The TRACE (transparent and comprehensive ecological modeling [Schmolke et al. 2010]) protocol aims to improve the documentation of ecological models, especially applied models, throughout the process from model development to application. Using the general reporting recommendations of ODD and TRACE, we integrated these guidelines into our PVA-focused protocol (Supporting Information).

Methods

In a recent analysis of trends in plant ecology and conservation, Crone et al. (2011) identified a tendency of PVAs to increase in complexity, become more spatially explicit or spatially realistic, and increasingly oriented toward management issues over time. Based on a search of publications listed in the ISI web of knowledge we also found that a large number of recent PVA studies address land-use change (58 studies as of October 2012) and climate change (113 studies, of which 44 were published since January 2011). These values suggest a growing responsiveness to threats, policy, and management needs. But do they also indicate improvements in PVA design, application, and communication over time?

JUSTIFICATION OF PVA DESIGN Modeling approaches differ in applications, advantages, and limitations and explore different questions on the basis of different model structures and parameter sets (Ralls et al. 2002) (Fig. 1). Accordingly, PVA models differ along a continuum of complexity from, in order of increasing complexity, occupancy models, to spatially structured population and metapopulation models, to complex individual-based models (IBM) (Akçakaya & Sjögren-Gulve 2000). The addition of spatially explicit information introduces further complexity. Software packages for PVAs use different structures and models specifications, such that even when used for the same purpose different PVA software can yield different outcomes (e.g., Mills et al. 1996; Brook et al. 1999; Lindenmayer et al. 2003). As computational capacity improves and modeling techniques advance, increasingly complex models can be used to perform a PVA. However, parameterizing such complex models with sufficient field data remains a challenge and does not always yield substantially greater capacity to answer specific goals.

The need to carefully select and justify model structure, methodological approach, and software was repeatedly raised in the 9 publications we examined: 35 of 318 (11.7%) guidelines addressed this topic. Authors generally suggested building the simplest model that encompasses the most important parameters or the most complicated model that could be supported by available data of sufficient quality. Through the SCALES database we observed an increase in the application of IBMs compared with other model types (on the basis of logistic-regression model outcomes, effect of year = 0.09, $p = 0.04$) (see Supporting Information for analysis methods), but we did not observe a significant increase in model complexity (Fig. 2) as reported elsewhere (Crone et al. 2011). This was partly because authors often provided incomplete information regarding model structure. More generally, both Naujokaitis-Lewis et al. (2009) and the SCALES review indicated that authors rarely justified model selection or described how model structure related to species attributes, the system in question, data constraints, or the functionality of the software used. Lack of such justifications impedes the capacity of readers to assess the appropriateness of methodological approaches. Some exceptions within the SCALES database included Lindenmayer et al. (1995), Akçakaya and Raphael (1998), Forys and Humphrey (1999), and Grimm et al. (2003).

Processes and parameters included in PVA application

We found a marked discrepancy between parameters identified by previous authors as affecting PVA outcomes, and those that were incorporated and explored in practice. Specifically, underrepresented parameters in PVA sensitivity analyses related to density dependence, catastrophes, and landscape attributes such as connectivity and number of patches (Naujokaitis-Lewis et al. 2009) (Fig. 3).

Density-dependent processes often have strong effects on population dynamics and extinction risk, and numerous authors endorsed better inclusion of these processes in PVAs (e.g., Boyce 1992; White 2000; Sæther & Engen 2002; Henle et al. 2004; IUCN 2010). However, we could not find an increase over time in the inclusion of density dependence in PVA studies (logistic regression with the inclusion of density dependence as a binary response variable; effect of time (years) = 0.02, p = 0.69). Of the PVA models that included density dependence (28 studies in the SCALES database), only 2 studies incorporated Allee effects (7%) and 15 assumed a simple ceiling-type behavior (54%), which may lead to overestimating extinction risks (Regan et al. 2003; Henle et al. 2004; Münkemüller & Johst 2006). Often it was difficult to discern how density-dependent processes were modeled.

Sources of stochasticity and catastrophes received attention in many published guidelines, and there were repeated calls to distinguish among environmental, demographic, and genetic sources of stochasticity (e.g., Morris & Doak 2002) and to address all sources of stochasticity, including catastrophes, in sensitivity analyses (White 2000). Catastrophes and disturbances (e.g., fires or floods) may differ from regular environmental stochasticity (e.g., fluctuations in temperature or rainfall) in amplitude, in the processes involved, and the nature of their effects on different life stages, individuals, populations, and the recovery of the environment itself (White 2000; Morris & Doak 2002). Our analyses verified that catastrophes and environmental stochasticity exerted strong effects on PVA outcomes (Fig. 3a), but we did not observe an increase over time in the proportion of studies that examined their effects (Fig. 4a) or considered a larger number of sources of stochasticity in a given study (Fig. 4b).

Landscape attributes, such as structural connectivity, and spatial processes, such as dispersal, have strong effects on population viability as well (e.g., Taylor et al. 1993; Beissinger & Westphal 1998; Tischendorf & Fahrig 2000). More than one-third of the PVA models in the SCALES database (38%) were either without spatial structure or spatially implicit (i.e., landscape structure and configuration ignored). The use of spatially explicit PVA approaches did not increase significantly over time (logistic regression with spatial representation as a binary response variable, effect of year = 0.08, $p = 0.13$). Of the models that included landscape features, 7 studies (33%) included spatial heterogeneity, but there was no temporal trend in its inclusion. Sixty percent of the studies addressed dispersal, but the level of details, or explanation of the details, differed substantially among studies. In general, spatial structures and processes included in PVA models were poorly described and would not allow evaluation of the approaches taken.

Detail on parameter ranges and sensitivity analyses

When preparing and running PVA simulations, one should carefully consider assumptions as well as parameterization of baseline values, ranges, and distributions used to represent all processes and parameters. A well-designed sensitivity analysis is further required to identify parameters that are likely to have a strong effect on the system, characterize interactions between parameters, and quantify the effects of various sources of uncertainty (Cross & Beissinger 2001). Because these explorations strongly affect interpretation and recommendations that are based on PVA outcomes, it is important to distinguish between parameters that affect model behavior, those that affect population dynamics in nature, and those that relate to management actions (Cross & Beissinger 2001; Mills & Lindberg 2002). Yet both databases ([SCALES] Naujokaitis-Lewis et al. 2009) found the majority of PVA studies provided insufficient detail on model assumptions and parameter values and their ranges, and rarely reported complete information about initial conditions. These shortcomings hinder verification, validation, and especially replication of such studies.

Furthermore, authors rarely applied recommended methods for sensitivity analysis where multiple parameters are varied simultaneously in order to identify interactions and quantify relative effects (i.e., whole-model sensitivity analyses [Naujokaitis-Lewis et al. 2009]).

Communication of PVA results

Population Viability Analyses vary widely in the kinds of outputs produced and reported, time horizon over which population dynamics are projected, and viability measures used. Regardless of model structure and complexity, a systematic approach to reporting would facilitate interpretation of PVA model results and comparability among scenarios, models, and studies. However, in most studies we examined, PVA results were not reported systematically across scenarios and populations. Rather, examples were usually provided from 1 or 2 populations or from a selection of scenarios. Moreover, the presentation of a baseline scenario was often lacking.

A particular challenge was identified with respect to the selection of time horizon and viability measures. Factors that may affect the choice of time horizon include study goals, species’ characteristics, relevant time horizon for informing or assessing conservation actions, need to differentiate between the outcomes of alternative scenarios, and propagation of uncertainty over time. Reported time horizons varied considerably among studies; half the papers reported the probability of extinction $P_{(t)}$ for a time horizon (t) of 100 years – a value established by listing authorities (e.g., IUCN 2010) primarily for the sake of standardization. The choice of viability measures often relates to the time horizon, but it also reflects different aspects of population behavior over time. Guidelines on both are found in many publications, but as we discuss later, there is no consensus and some of the guidelines are contradictory. Accordingly, within the SCALES review we encountered various measures of viability. Probability of extinction ($P_{(t)}$), time to extinction (T_0), and population size at a given time were most commonly reported (Table 1). Although differences in viability measures among studies increased over time, there was no clear shift in the viability measures reported (Fig. 5a). There was also no apparent increase in the number of viability measures reported for a given PVA, as recommended by Ralls et al. (2002) and possibly in response to the on-going debate regarding appropriate metric selection (Fig. 5b).

Based on our literature review, the lack of consistent communication of PVAs and their outcomes is an impediment to meta-analysis and collective learning. The logical progression from analysis of field data to model development and presentation of results was incomplete and disorganized, and our analyses revealed little progress in the presentation of standardized PVA results. In practice, inconsistent reporting and a variety of time horizons and viability measures reported in the 2 databases of PVA studies (Naujokaitis-Lewis et al., 2009; SCALES database) rendered any quantitative analyses on the basis of model results impossible.

WHAT IS OFFERED BY EXISTING GUIDELINES AND PROTOCOLS

PVA guidelines in the literature emphasize issues related to model selection; parameter estimation based on empirical data; model parameterization; validation; presentation of results; management-relevant interpretation; and a recurrent request to analyze and discuss model assumptions and limitations. By contrast, far less attention is given to details relating to model description (Supporting Information). None of the published sets of guidelines are structured according to a natural sequence of tasks, and none tackled the question of how to ensure that descriptions are reported in an orderly and consistent fashion. For instance, general suggestions such as describe the model “clearly and in enough detail that someone else could replicate it” (Ralls et al. 2002) or list all assumptions and formulas (Burgman & Possingham 2000; Ralls et al. 2002; IUCN 2010) are not detailed enough to delineate exactly which elements should be documented and in which order or how.

In terms of adherence to existing standard protocols for reporting, the ODD has not been adopted by PVA developers. For instance, of 705 PVAs listed by ISI web of science 2008-2011 (search words *population viability analysis model* and *ecology or conservation* [February 2012]), only 9 cited the ODD. Thus, although the ODD offers a useful template for describing ecological models (Supporting Information), it has seen limited application in PVA, perhaps because most PVAs are not individual or agent based. The ODD does not explicitly address issues specific to many PVAs, such as the projection matrix for stage-based models or the effects of density dependence. Users of existing PVA software may also see little reason to apply the ODD to describe the structure of a model that is described elsewhere, although this may be a misconception because the ODD can nevertheless be used to organize documentation and to consider and justify assumptions. The most important deficiency of the ODD, however, is that it focuses on model description, whereas standardized documentation of PVAs requires a protocol that encompasses the entire modeling process, from problem formulation to application to interpretation and recommendations. This is partially addressed by the TRACE protocol, but due to its generality, TRACE does not offer recommendations that are precise enough to facilitate its application for PVAs (Supporting Information). Furthermore, for a protocol to be relevant for PVAs, we found a need to extend beyond the ranges of TRACE – which primarily ends with communication of model results – and define more explicitly how a PVA can direct monitoring, management, model validation, and collective learning (see below).

PROTOCOL FOR PVA **D**ESIGN, **A**PPLICATION, AND **C**OMMUNICATION

Our results demonstrate that despite the existence of guidelines for the design of PVAs and protocols for model description and documentation, a systematic and comprehensive protocol is lacking that could standardize the design, application, and communication of PVAs without limiting the flexibility and variety of PVA structures and contents. To overcome this gap, we propose the use of DAC-PVA as a comprehensive protocol for PVA **d**esign, **a**pplication, and **c**ommunication. The protocol draws on and integrates solutions from 5 sources: the TRACE protocol as a canvas for structuring overall documentation; the ODD protocol for describing the model itself; factors, processes, and parameters that are routinely included in PVAs (as identified through building the abovementioned databases); the 9 published collections of PVA guidelines; and our collective experience with PVAs.

The DAC-PVA protocol has 3 primary elements. The first defines a useful PVA: This element can be considered an introduction for a newcomer to the world of PVA or a quality checklist for those already working with PVAs. This element may further help one evaluate PVA studies. The second element addresses the design and application of a useful PVA. This element provides a workflow and highlights important aspects that need to be considered during the analytical process. The third element focuses on communication of PVAs to ensure clarity, comprehensiveness, repeatability, and comparability.

Elements of a useful PVA model

Schmolke et al. (2010) defined a set of "elements of [any] good model" (Table 2) that can be aligned with the design, application, and communication of a model. Furthermore, a PVA should build on past experience and knowledge and direct future monitoring, research, management, and learning. Shaffer et al. (2002) propose 5 ways to improve PVAs: develop standards for PVA application, perform long-term field studies of population dynamics, experiment and validate PVA models, create easily accessible databases, and formulate rules of thumb. A useful PVA model can therefore be defined as one that addresses these issues and supports such improvements. Table 2 contains an outline of critical elements of good PVA practice. A checklist and guidelines appear in Supporting Information and can be used for ensuring that a PVA comprehensively covers important processes, parameters, and knowledge gaps.

DESIGN AND APPLICATION OF A USEFUL PVA MODEL

An informative PVA is not only a rigorous process of development and analysis, but it is also amenable to supporting management decisions, guiding research, and contributing to collective learning. In the following sections we discuss important decisions that need to be made in order to ensure reliable model design and application (see Supporting Information for further guidelines).

Decisions on **model complexity and approach**: A first stage in model design is to ensure that model complexity corresponds appropriately to data availability and that relevant processes and parameters are included (Ralls et al. 2002). Processes and parameters that are not data supported may be carefully investigated through sensitivity and uncertainty analyses. We recommend scanning the checklist in Supporting Information to determine whether a given model component is relevant or important and whether the means to parameterize the component are available.

Uncertainty, stochasticity, and parameter estimation: Uncertainty is an inherent feature of PVAs that affects the reliability of PVA predictions (Beissinger & Westphal 1998; Shaffer et al. 2002). Beissinger and Westphal (1998) listed 4 sources of uncertainty: poor quality or low quantity of data, difficulties in parameter estimation, weak ability to validate models, and effects of alternate model structures. The first 2 issues are strongly related to sampling methods and temporal and spatial extents of the studies from which data are obtained and should be considered during model design as well as during the selection of methods for parameter estimation and parameterization. One must obtain estimates of demographic parameters in a manner that addresses and captures the limitations of the field data and translate uncertainty into parameter ranges, variances, or statistical distributions. During parameter estimation, one needs to distinguish and quantify different sources of variability and potential biases, especially between sampling versus process variability. Sampling variability and errors may lead to poor estimates of population parameters, which should be accounted for, whereas process variability, as manifested for instance as variance in vital rates, may reflect true attributes of population dynamics that should be carried forward into a PVA. Similarly, the existence and form of density dependence and the degree of spatial autocorrelation among local population dynamics, incorporate spatiotemporal sources of variance that are difficult to discern without detailed, often long-term data.

Another important distinction to make is between uncertainty and stochasticity or between lack of knowledge (epistemic uncertainty) and natural variation (Regan et al. 2002). Uncertainty emerges from various sources, stochasticity being only one of them, and not all sources of uncertainty can be handled by having more or better data (Boyce 1992; Ruggiero et al. 1994). In Supporting Information we provide various guidelines relating to uncertainty during all stages of model design, application, and communication. We also provide separate guidelines for the different types of stochasticity.

Decisions concerning **calibration, verification, and validation**: Beissinger and Westphal (1998) and Burgman and Possingham (2000) note that model validation, especially field validation of PVA predictions, is rarely undertaken. They consider this a violation of a basic principle in the use of model outcomes in decision making (Bart 1995). Verification should involve consideration of omissions and errors in both model design and parameter estimation (White 2000). Even when using existing software, PVA users should ensure that the model performs qualitatively and quantitatively as expected . Schmolke et al. (2010) differentiate among calibration, verification, and validation, and we emphasize that the latter may be an iterative process, for example, through the use of newly accumulated data or monitoring of management outcomes.

Sensitivity analyses are of utmost importance in PVAs because they facilitate identification of parameters that have a strong effect on viability assessment. However, cautious interpretation of the results of sensitivity analyses is encouraged because dependencies between model parameters may be artifacts of model structure rather than a reflection of important ecological processes. Moreover, synergistic effects may prevent sensible interpretation of model sensitivity if parameter sensitivities are analyzed individually (Saltelli et al. 2006; Saltelli & Annoni 2010). It is therefore advisable to assess the importance of interactions among model parameters and of nonlinearities in model response to parameter variation (see also Cross & Beissinger 2001).

Decisions concerning **simulation duration and time horizon**: To avoid mismatches between the temporal scales of ecological processes, management decisions, and ecological studies (Henle et al. 2010; Crone et al. 2011), we believe careful consideration of simulation duration and reported time horizon is needed. The latter relates to the choice of viability measures (discussed below). The former, however, requires consideration of various trade-offs during model application. Identification of long-term population trends, avoiding transient dynamics due to initial conditions and distinguishing among outcomes of alternative management scenarios all tend to favor long simulation duration. Short simulation duration, however, is favored by the propagation of uncertainty over time, as well as relevance to specific, often pressing conservation decisions.

PVA to support decision making: The utility of a PVA in decision making depends on how well the range of decision options and their effects on species persistence can be captured within the structure of a PVA. Ensuring that management scenarios represented within a PVA are realistic and relevant, that the most salient uncertainties are characterized, and that criteria for evaluating differences among management outcomes can be identified is a challenging process that has been achieved in few real management situations (Burgman & Possingham 2000). A notable exception is the case of the Northern Spotted Owl (*Strix occidentalis caurina*), where multiple PVAs of different types and approaches, addressing various factors, were conducted in a management context, evaluated, and used to rank alternative scenarios to support conservation decisions over a large area (Noon & McKelvey 1996). There is ample advice on performance criteria for ranking management options (Possingham et al. 1993; Lindenmayer & Possingham 1996; Beissinger & Westphal 1998; McCarthy et al. 2003; Bakker & Doak 2009) but few examples where trade-offs between management options have been quantified (e.g., Curtis & Vincent 2008; Johst et al. 2011; Wintle et al. 2011). In general, for PVA to be accepted as a useful tool by managers, model results should correspond to multiple management options (Pielke 2007) and its application would be greatly strengthened by considering the costs and benefits of those actions (e.g., Sebastian-Gonzalez et al. 2011). A PVA report should also be transparent about model limitations (see below where elements of an informative discussion are described).

COMMUNICATION OF PVAS

To enhance standard and comprehensive communication of PVAs, the DAC-PVA protocol recommends that researchers design their report according to 5 sections (Supporting Information): Background, model description, model application, outcomes, and discussion. The background section delineates the context, motivation, and aims for PVA development. This section establishes links between the real world and model. Model description follows the general structure of the ODD protocol (model overview, design concepts, and model details).Model application includes details on parameterization, selection of time horizons and viability measures, analytical methods, and means for interpretation. Outcomes include baseline and systematic coverage of model results, sensitivity and uncertainty analyses, and management ranking. Discussion covers key recommendations, limitations, practical outcomes, and outlook.

We identified a standard, comprehensive PVA report as one that follows the checklist and considers the elements and guidelines in Supporting Information. We do not anticipate one to report on every component within the checklist; some may be irrelevant (e.g., when users employ a published model). However, one should demonstrate that all elements and components of the DAC-PVA were at least considered and that decisions made were well justified. Among the issues to address in a comprehensive report, we selected a number that are particularly important for clear and comprehensive communication of PVAs: delineation of assumptions, communication of important processes and emergent properties, communication of initial conditions, systematic reporting of results, selection of viability measures, and coverage of the main elements of an informative discussion.

Some authors emphasize the importance of carefully communicating all underlying **assumptions** in terms of model structure, parameterization, and analyses. Although the IUCN (2010) recommends summarizing model assumptions in a separate file, assumptions are made throughout the process of model conception, development, and implementation and therefore communication may be most effective if associated with relevant components of the model description. Examples and guidelines on important assumptions are listed in Supporting Information.

Our **communication checklist** and guidelines favor a detailed structure that ensures the complexity of PVA elements does not cause ambiguity or omission of important descriptions. Examples of key attributes specific to PVAs but not addressed in more general protocols such as TRACE and ODD include population dynamics, movement and dispersal, and environmental processes (see Supporting Information). Another example is the communication of density dependence, which can be described in the section population processes if it is applied through a formula or as a subcomponent in the section emergence if density dependence emerges from the behavior of individuals in an IBM.

Grimm and Wissel (2004) stressed the importance of distinguishing an initial transient phase, where the simulated population dynamics depend on **initial conditions** from an established phase (quasi-stationary state) in which population dynamics are driven primarily by the inherent attributes of the simulated population, such as vital rates and stochasticity. It is important to separate these 2 phases. We further recommend that the relation between initial conditions and carrying capacity (*K*) be reported.

To ensure repeatability of PVA studies, it is important to **depict results fully and systematically**. Results for a baseline scenario should be reported first, , followed by the outcomes of sensitivity and uncertainty analyses and finally by management-relevant results such as ranking of scenarios. Results should be reported in consistent units and for a consistent selection of populations if it is not possible to report on all populations. Authors should strive to describe all input and output parameters and provide means, ranges, and distributions. Although publication space is typically limited, online materials allow such systematic reporting of parameters and scenarios as explored in sensitivity analyses, as well as systematic reporting of their effects on model outcomes.

The **selection of viability measures** should be made in accordance with the time frame analyzed, the purpose of the study, comparability with other studies, and the audience. Different viability measures reveal different aspects of the behavior of populations and thus affecting communication of PVA results to relevant stakeholders. There is no consensus on which viability measures are most suitable. For example, Akçakaya and Sjögren-Gulve (2000) suggest focusing on risk of decline instead of extinction risk, McCarthy and Thompson (2001) suggest the expected minimum population size (EMP) serves as an effective indicator for the propensity of decline, and Grimm and Wissel (2004) propose the intrinsic mean time to extinction (T_m) as a measure independent of initial conditions or time horizon. None of these measures has been broadly adopted (Table 1). It is beyond the scope of our study to review and evaluate them. Instead, we outlined important or commonly used measures that may be favored when communicating PVA results, the means for calculation, and their potential applications (Table 3). We recommend authors report on several viability measures for every scenario examined (Ralls et al. 2002), including the extinction probability by year 100 where possible to promote comparability and consistency with international listing thresholds (e.g. IUCN 2010).

To strengthen the use of PVAs to direct management and further research, we suggest **elements of an informative discussion** include a summary of important results, including assessment of alternative management scenarios; recommendations for management, monitoring, and (iterative) validation; discussion of limitations, including potential sources of uncertainty (e.g., model errors, assumptions or parameters that were not addressed); report on on-the-ground actions which may have emerged from the study; and outlook for advancing collective learning, for instance by setting the PVA in the context of other studies and discussing potential applications of the model or its outcomes to other circumstances or species.

DISCUSSION

The complexity of PVA studies and their tendency toward specificity, combined with poor communication and lack of comprehensiveness, may have contributed to the lack of generalizable results of PVAs (Burgman & Possingham 2000; Naujokaitis-Lewis et al. 2009). Common use of a standardized protocol may assist in identifying general solutions to this and other challenges outlined here (Pullin & Stewart 2006; Grimm et al. 2010; Schmolke et al. 2010). Despite efforts to improve the documentation and communication of ecological models, the development of a protocol specific to PVA models is important to address the specific needs and wide range of applications of PVA studies.

Our protocol makes several contributions, not only for modelers but also for those using existing, well-documented software. First, any protocol that follows a logical sequence and allows users to encounter a familiar structure, will facilitate understanding by readers (Gopen & Swan 1990). Second, transparent and comprehensive communication is particularly important when the concepts are diverse and complex, as clearly is the case in the PVA context. Clear communication bolsters understanding of models by the scientific community, decision makers, and stakeholders and allows them to assess their suitability to answer questions at hand. Third, following a common protocol allows authors and readers to perform a quality check to verify that all components were considered when designing, applying, and communicating a model (Akçakaya et al. 2004; Grimm et al. 2010). Lastly, systematic reviews and meta-analyses that are based on published material are facilitated by standardized structures and units (Pullin & Stewart 2006). Given the rarity of generalizations and rules of thumb originating from PVAs (e.g. Shaffer et al. 2002), use of a standardized protocol may enhance reviews of PVAs and their applicability in ecological systems and thus strengthen the value of single PVA studies for inclusion in such reviews. Here, our discussion of time horizons and viability measures, issues that clearly remain unresolved, may offer additional guidance to improve comparability en route to obtaining generalizations and rules of thumb.

The DAC-PVA protocol further offers the means to enhance the relevance of PVA studies to policy and management and to ensure their use to evaluate relative efficacy of different conservation options in light of uncertainty (Possingham et al. 1993). We anticipate our protocol will aid in identifying challenges and next steps to further facilitate collective learning. As with any other standard protocol, it is open to the scientific community to choose whether or not to use it, and critiques and improvements are to be expected. We welcome such critiques; they will contribute to the many efforts to generate synergies from cumulative conservation evidence (Pullin & Stewart 2006; Pullin & Knight 2009).

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Supporting Information

A full checklist of elements to consider during PVA design and application (Appendix S1), specific guidelines for each of the elements appearing in Appendix S1 (Appendix S2), and information on the compilation and analysis of the PVA database within SCALES project (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

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TABLE 1:

Viability measures provided by authors of PVAs covered by the SCALES database, based on 78 studies covering 82 species.

Code	Viability measure	Number of cases
a	Probability of extinction	39
b	Population size at a given time	19
c	Time to extinction*	18
d	Probability of quasi-extinction	7
e	Occupancy	7
f	Probability of decline	6
g	Growth rate	6
h	Time to quasi-extinction	5
i	Minimum Viable Population (MVP)	5
j	Minimum Area Requirement (MAR)	2
k	Relative population size	2
l	Expected minimum total abundance	1
m	Minimum patch number	1
n	Mean density	1
o	Mean number of breeding individuals per year per flock	1
	Other measures	7

* including 4 cases reporting the intrinsic mean time to extinction

TABLE 2:

Elements of a good model in general (Schmolke et al. 2010), and elements of a useful PVA, delineated along the steps of model design, application and communication.

	Elements of a good model	Elements of a good PVA
During design	• includes stakeholders • formulates objectives; justifies choice of model approach & complexity	• includes stakeholders in model design, validation and interpretation • builds on (long-term) high quality data • performs and justifies a careful model selection
During application	• careful parameterization • calibration, verification, validation • quantification of uncertainties • applies multiple models	• includes relevant parameters based on knowledge of the system and the literature and in consideration of gaps • applies careful parameter estimation and parameterization • performs calibration, verification and validation or directs further monitoring and validation efforts • performs sensitivity analyses and addresses uncertainty in a systematic and transparent way • compares the outcomes of alternative models where possible • differentiates among parameters affecting i) the model, ii) the real world and iii) those that are management relevant • ranks management scenarios to support decision-making
During communication	• formulates assumptions • effective documentation and transparency • peer reviewed	• communicates the entire modeling cycle and justifies decisions and assumptions along the way • reports all inputs and outputs systematically to allow repeatability • uses carefully selected time horizon and viability measures and reports using consistent units to allow comparability • demonstrates that the PVA serves its purpose by, e.g., leading to on-the-ground actions • enhances collective learning and potential generalization • both the model (design, code, application) and the report are peer reviewed

TABLE 3:

(Next page):

Important viability measures, their meaning, potential application, and recommendations for usage.

Viability measure	Meaning	Calculation	Recommendations for PVA
$\boldsymbol{P_0(t)}$	Probability of extinction by time horizon t	Count extinction events over multiple simulations versus the time at which they occur and plot their cumulative distribution over time.	Report $P_0(t)$ for several time horizons; for consistency with international listing thresholds and to facilitate comparison across studies, report $P_0(100)$ as one of these time horizons.
$\boldsymbol{P_N}$	Quasi-extinction risk	Plot the minimum population size N observed during the course of each simulation iteration, against their cumulative distribution.	Can be used when global extinction is not possible (Burgman et al. 1993); to advance comparability report outputs for multiple values of N, including $N = 0$ if possible, for comparison with $P_0(t)$.
$\boldsymbol{T_m}$	Intrinsic mean time to extinction	Plot $ln(1 - P_0(t))$ versus time t. The plot yields a straight line with slope $1/T_m$ (Grimm & Wissel 2004).	Use T_m to enable approximating $P_0(t)$ for any time horizon based on $P_0(t) \approx t/T_m$; it is insensitive to initial simulation conditions, and may reveal generic information about extinction risk and viability.
EMP	Expected minimum population size	Record the smallest population size obtained in each simulation iteration.	Rarely reported in PVA studies; a simple and effective measure which should be more frequently used especially for sensitivity analyses and when the risk of extinction is small (McCarthy & Thompson 2001).
$\boldsymbol{N_e}$	Expected population size	Plot N_e over time to provide a simple and intuitive visualization of	An important “currency” for decision makers, but the tails of distribution must be depicted to account for the range of potential

		population behavior and comparison between scenarios.	outcomes; should be considered in conjunction with other measures of risk. 0
λ	Mean intrinsic growth rate of a population	Provides a simple measure of the potential for population growth.	Useful for differentiating alternative population trends (Caswell 2002); should be reported in conjunction with viability measures that provide a measure of risk.
MVP	Minimum Viable Population	Run simulations with a range of initial population sizes to define the lowest threshold that maintains a viable population (i.e., predefined probability of survival over a given time horizon).	Strictly speaking, not a viability measure but a measure of what would be required to achieve viability. Often relevant for policy decisions; provides intuitive information for communication; however oversimplifications may yield misinterpretation, therefore interpret and communicate carefully.
MAR	Minimum Area Requirement	Run simulations with a range of initial area (or other spatial attributes) to identify the area necessary to support a viable population.	See MVP.

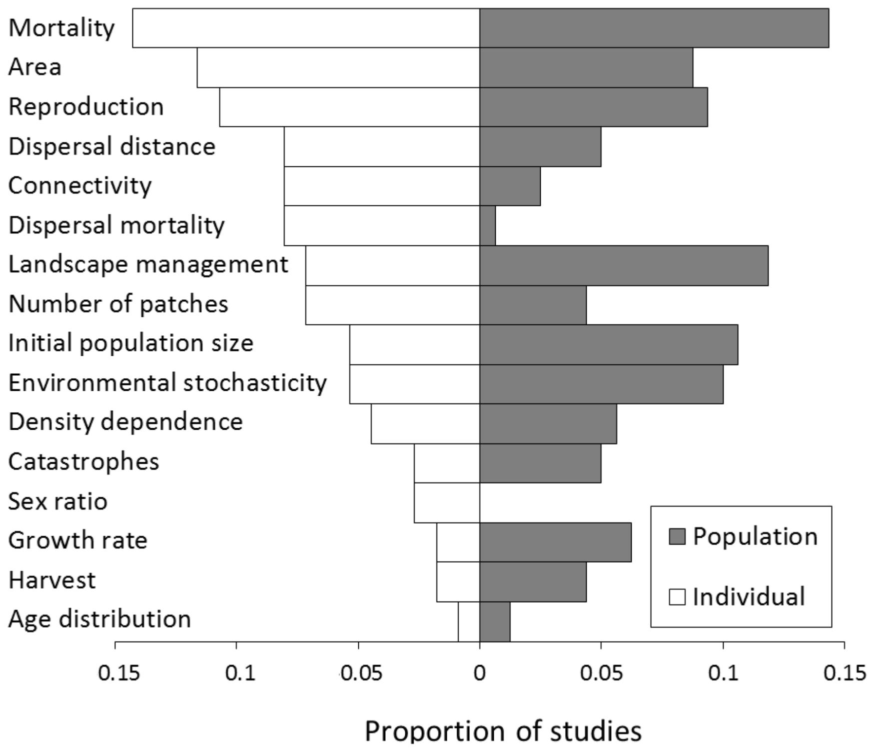
Figure 1: The frequency of papers reviewed in the SCALES project that explored the effect of key parameters on viability on the basis of individual-based (white) or population-based (shaded) models.

Figure 2: Results of an analysis of model complexity versus time on the basis of 3 approaches: (a) number of parameters considered among a predetermined list, (b) number of variables used to parameterize important processes, and (c) number of stages used in the models.

Figure 3: Of the papers in the SCALES database that quantified the relative effect of a given parameter (a) the proportion in which the parameter had a strong effect, weak effect, and no effect on viability and (b) the proportion in which the effect of each parameter was tested (correlation between [a] and [b], 0.434, $p = 0.09$).

Figure 4: (a) The proportion of studies in the SCALES database that included environmental stochasticity and catastrophes over time and (b) the proportion of studies that included 2 or >2 types of stochasticity.

Figure 5: (a) Viability measures reported by authors of PVA studies in the SCALES database plotted against time. Letter codes on the y-axis are defined in Table 1. Shading represents different proportions of studies reporting a given viability measure. (b) Number of viability measures reported per study plotted against time.


Mortality
Area
Reproduction
Dispersal distance
Connectivity
Dispersal mortality
Landscape management
Number of patches
Initial population size
Environmental stochasticity
Density dependence
Catastrophes
Sex ratio
Growth rate
Harvest
Age distribution
Population
Individual
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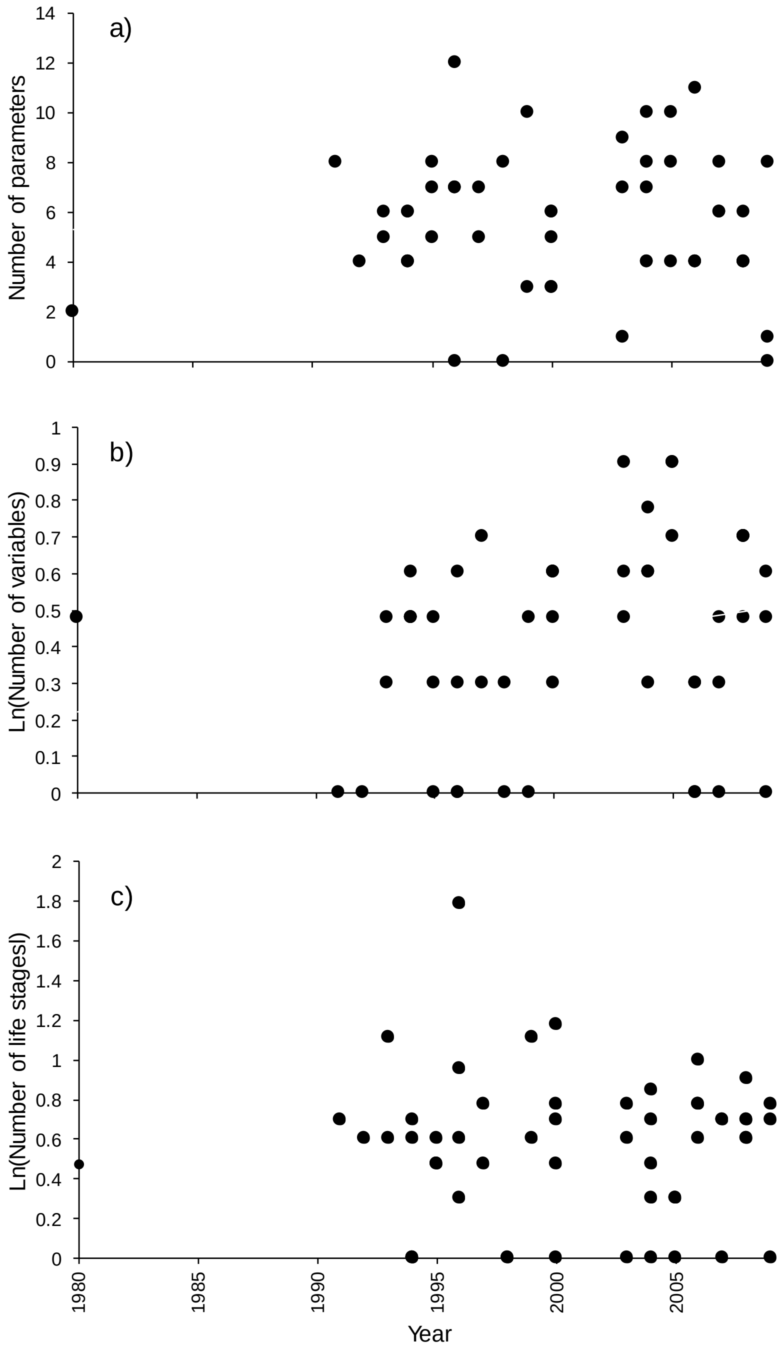
0.15
Proportion of studies


a)
Number of parameters
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12
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8
6
4
2
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b)
Ln(Number of variables)
1
0.9
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0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
c)
Ln(Number of life stagesl)
2
1.8
1.6
1.4
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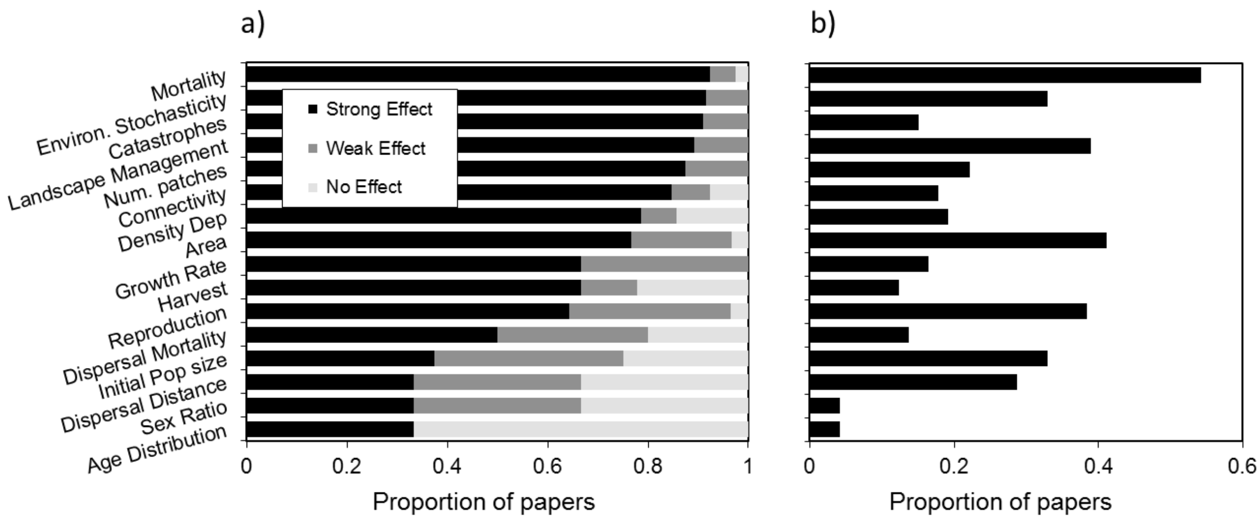
Year



a)
b)
Strong Effect
Weak Effect
No Effect
Mortality
Environ. Stochasticity
Catastrophes
Landscape Management
Num. patches
Connectivity
Density Dep
Area
Growth Rate
Harvest
Reproduction
Dispersal Mortality
Initial Pop size
Dispersal Distance
Sex Ratio
Age Distribution
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Proportion of papers
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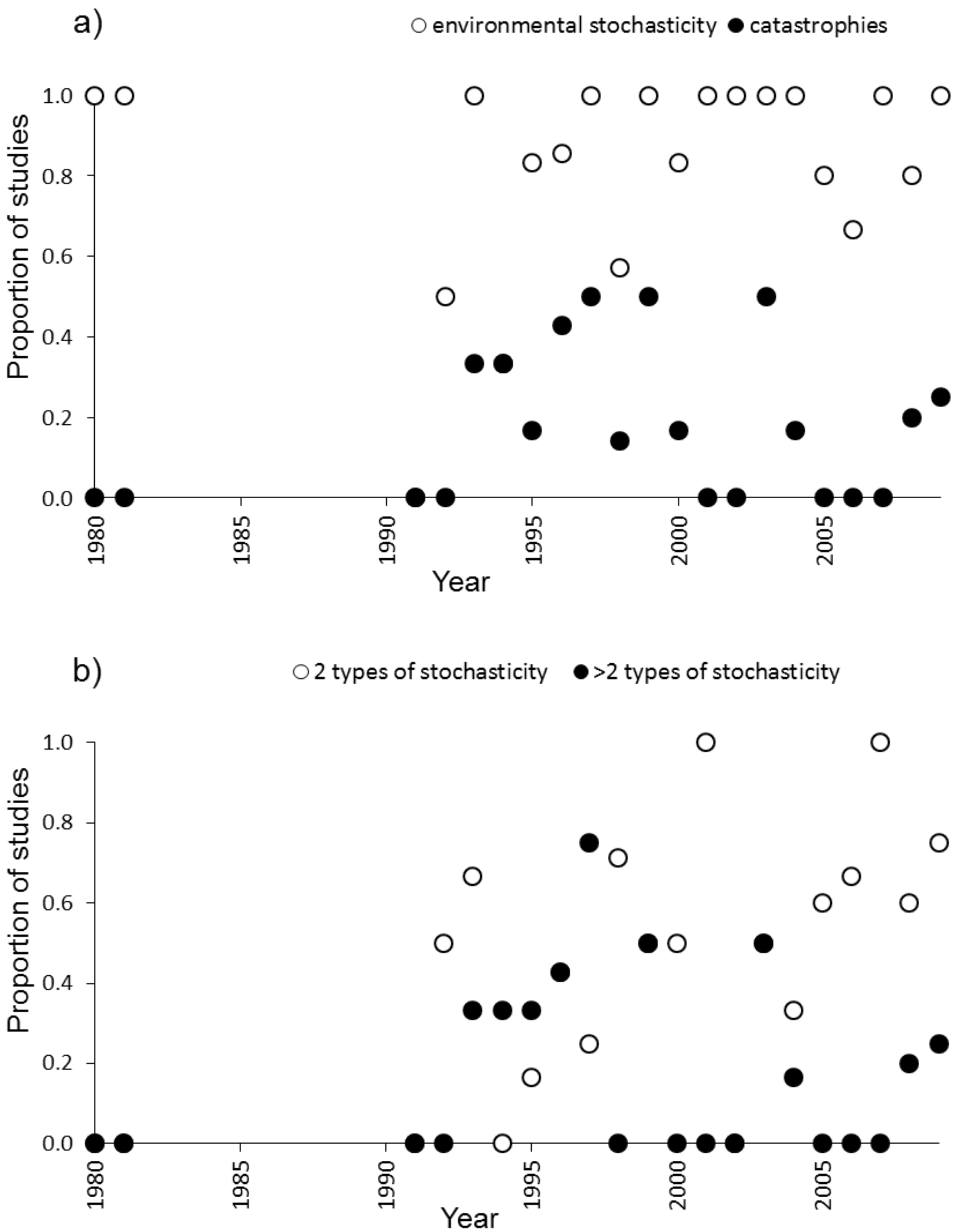
Proportion of papers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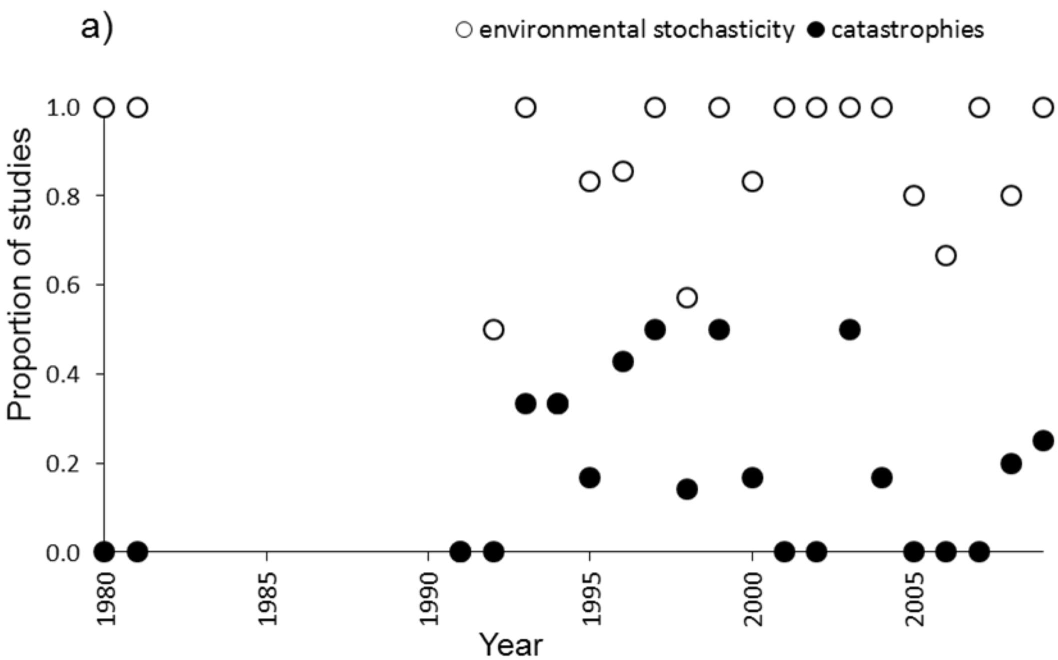
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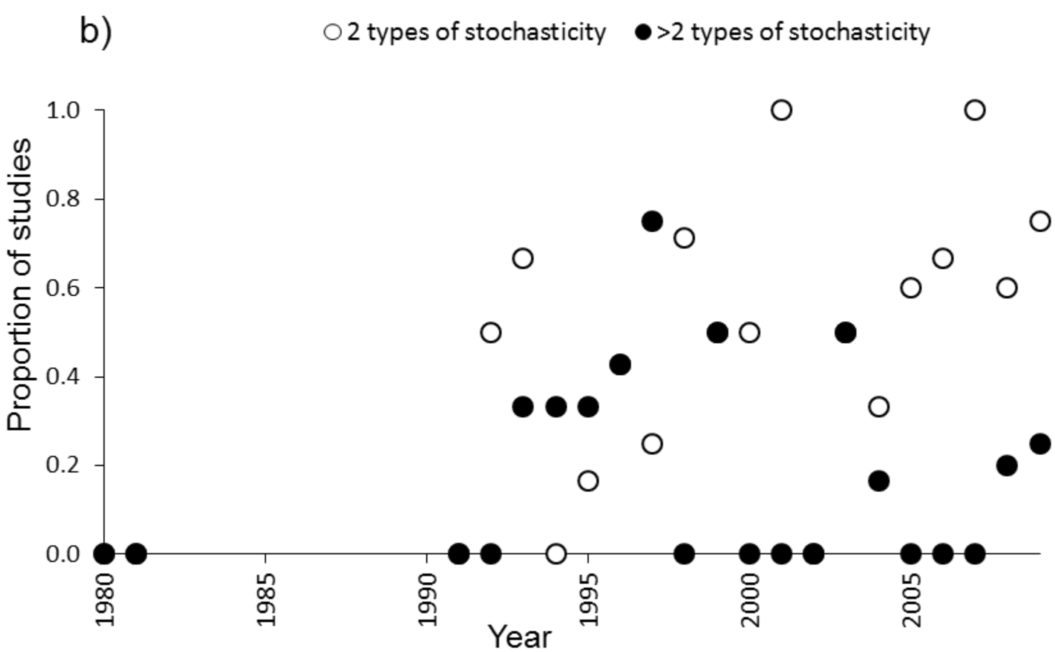
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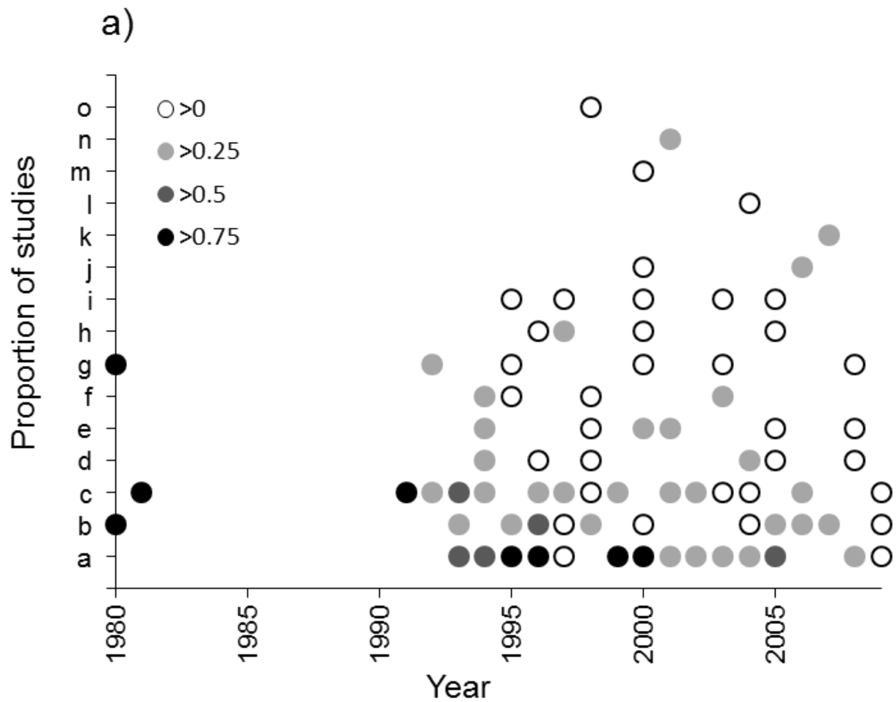
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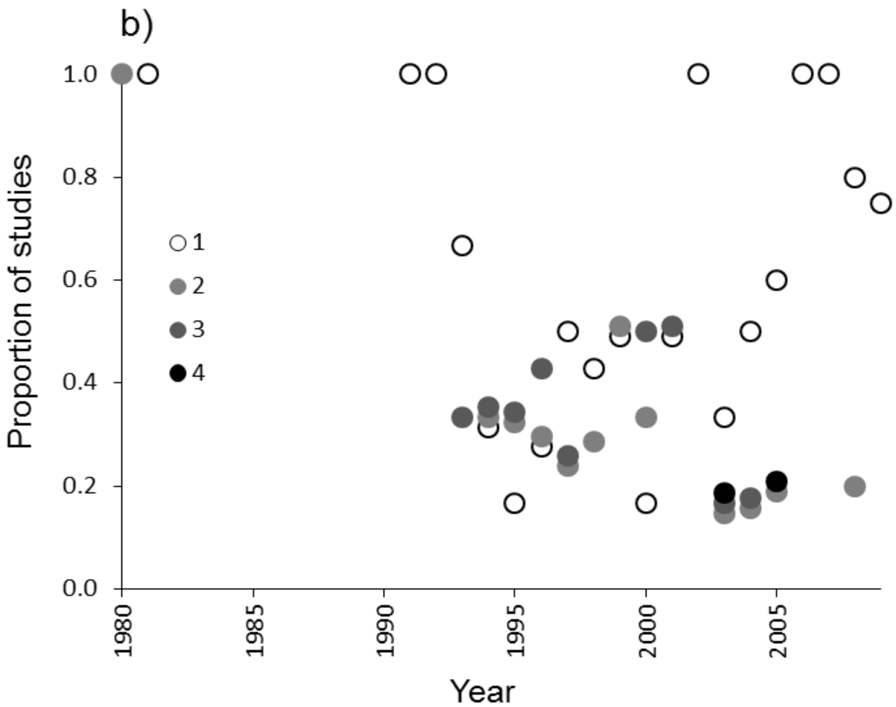
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