Conservation Biology

Research Note

Sensitivity Analyses of Spatial Population Viability Analysis Models for Species at Risk and Habitat Conservation Planning

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[Correction added after publication 16 September 2008: An error in the first author's name was corrected.]

Abstract: *Population viability analysis (PVA) is an effective framework for modeling species- and habitat-recovery efforts, but uncertainty in parameter estimates and model structure can lead to unreliable predictions. Integrating complex and often uncertain information into spatial PVA models requires that comprehensive sensitivity analyses be applied to explore the influence of spatial and nonspatial parameters on model predictions. We reviewed 87 analyses of spatial demographic PVA models of plants and animals to identify common approaches to sensitivity analysis in recent publications. In contrast to best practices recommended in the broader modeling community, sensitivity analyses of spatial PVAs were typically ad hoc, inconsistent, and difficult to compare. Most studies applied local approaches to sensitivity analyses, but few varied multiple parameters simultaneously. A lack of standards for sensitivity analysis and reporting in spatial PVAs has the potential to compromise the ability to learn collectively from PVA results, accurately interpret results in cases where model relationships include nonlinearities and interactions, prioritize monitoring and management actions, and ensure conservation-planning decisions are robust to uncertainties in spatial and nonspatial parameters. Our review underscores the need to develop tools for global sensitivity analysis and apply these to spatial PVA.*

Keywords: conservation planning, metapopulation, population viability analysis, sensitivity analysis, uncertainty

Análisis de Sensibilidad de Modelos de Análisis de Viabilidad Poblacional Espaciales para Especies en Riesgo y la Planificación de la Conservación de Hábitat

Resumen: *El análisis de viabilidad poblacional (AVP) es un marco de referencia efectivo para los esfuerzos de recuperación de especie y de hábitat, pero la incertidumbre en las estimaciones de parámetros y la estructura del modelo pueden llevar a predicciones no confiables. La integración de información compleja y a menudo incierta a los modelos de AVP espaciales requiere la aplicación de análisis de sensibilidad para explorar la influencia de parámetros espaciales y no espaciales sobre las predicciones de los modelos. Revisamos 87 análisis de modelos de AVP demográficos espaciales de plantas y animales para identificar métodos comunes de análisis de sensibilidad en publicaciones recientes. En contraste con las mejores prácticas recomendadas por la comunidad de modeladores, los análisis de los sensibilidad de AVP típicamente fueron ad hoc, inconsistentes y difíciles de comparar. La mayoría de los estudios aplicaron métodos locales a los análisis de sensibilidad, pero pocos variaron parámetros múltiples simultáneamente. La falta de estándares*

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Paper submitted December 20, 2007; revised manuscript accepted June 5, 2008.

Conservation Biology, Volume 23, No. 1, 225–229

DOI: 10.1111/j.1523-1739.2008.01066.x

para los análisis de sensibilidad y descripción en los AVP espaciales tiene el potencial de comprometer la habilidad de aprender colectivamente de los resultados de AVP, de interpretar con precisión los resultados en casos en que las relaciones de los modelos sean no lineales e incluyan interacciones, para priorizar las acciones de monitoreo y manejo y para asegurar que la planificación de las decisiones de conservación sean robustas ante la incertidumbre en los parámetros espaciales y no espaciales. Nuestra revisión subraya la necesidad de desarrollar herramientas para análisis de sensibilidad globales y aplicarlos a AVP espaciales.

Palabras Clave: análisis de sensibilidad, análisis de viabilidad poblacional, incertidumbre, metapoblación, planificación de la conservación

Introduction

Nearly all population viability analyses (PVA) require parameter estimates that are hard to obtain or highly uncertain, and this problem is compounded in spatial PVAs that aim to predict persistence of spatially structured populations (Reed et al. 2002; Beissinger et al. 2006). The complexity of spatial PVA increases demands for data, potential for error, and the magnitude of uncertainty in model structure and predictions (Conroy et al. 1995). Yet PVA models are used increasingly to guide species and habitat conservation planning (e.g., Reed et al. 2002; Akçakaya et al. 2004). Consequently, there is a real need to understand how spatial and nonspatial parameters influence the predictions of spatial PVAs and use this knowledge to reduce model uncertainty.

Four sources of uncertainty in ecological modeling are not knowing the current system state (parameter uncertainty); not knowing the rules for system change (uncertainty in model structure); not being able to predict natural stochasticity (environmental, genetic, and demographic); and having a limited ability to forecast future decisions and their implications (e.g., Regan et al. 2002; Fieberg & Jenkins 2005; Cariboni et al. 2007). Although uncertainty is a persistent feature of most models, sensitivity analysis is used to bound model predictions, identify influential parameters, allocate uncertainty to particular parameters or processes, evaluate competing model structures or management scenarios, and ultimately, to prioritize research and data collection (Drechsler et al. 1998; Akçakaya & Sjogren-Gulve 2000; Cross & Beissinger 2001; Mills & Lindberg 2002). We suggest the use of sensitivity analysis in PVA remains inconsistent despite wide recognition that it is an essential step in PVA application (McCarthy et al. 1995; Cross & Beissinger 2001; Reed et al. 2002; Curtis & Naujokaitis-Lewis 2008). We reviewed how sensitivity analysis was applied in recent spatial PVAs to identify common approaches, compare the frequency with which spatial and nonspatial parameters are included in sensitivity analyses, and provide recommendations for best practices in sensitivity analyses of PVAs.

Methods

We surveyed spatial PVAs in peer-reviewed papers published from January 2000 to February 2006. Plant and animal PVA studies were sourced from the ISI Web of Science database and a book of spatial PVA case studies (Akçakaya et al. 2004). Search terms included *PVA*, *metapopulation*, *population*, *viability*, *analysis*, *spatial*, and *extinction risk*. All PVAs reviewed used the ALEX (Possingham & Davies 1995), PATCH (Schumaker 1998), RAMAS Metapop (Akçakaya 1998), RAMAS GIS (Akçakaya 2002), RAMAS Landscape (Akçakaya et al. 2003), or VORTEX (Lacy 1993) software packages. We excluded models of single populations, hypothetical or extinct species, as well as incidence function or patch occupancy models because the latter are not explicitly demographic (our focus). User-defined PVAs with unusual structures and those not reporting parameter estimates were also excluded from this review.

For each spatial PVA, we recorded the type of sensitivity analysis applied and method used to quantify parameter influence. We recognized 3 types of sensitivity analysis (McCarthy et al. 1995; Saltelli et al.1999; Cariboni et al. 2007): local analyses, in which parameters were varied individually with others held at nominal values; multiple variable perturbations, in which more than 1 model parameter was varied simultaneously; and global analyses, in which all parameters were varied simultaneously over the plausible range of parameter space.

For PVA parameters commonly varied in sensitivity analyses (Table 1), we recorded the number of studies in which that parameter was evaluated and then expressed this number as a percentage of the studies reviewed that included that parameter in the model structure. Two broad groupings of parameters were recognized: those varied to assess data uncertainty (e.g., survival, fecundity, or dispersal rate) and those varied to assess the influence of dynamic landscapes. The former category was further delineated according to spatial and nonspatial attributes (Table 1).

Table 1. Percentage of 87 spatial demographic population viability analyses (PVAs) that included common spatial and nonspatial parameters as part of the model structure (included) and evaluated the influence of these parameters (evaluated).

Parameter	*Included*	*Evaluated*[a]
Spatial parameters		
carrying capacity[b]	100	34
number of populations (or patches)	100	14
population configuration	100	7
dispersal distance function parameters[c]	75	43
among-population correlations	45	13
GIS-based habitat quality	34	13
dispersal rate	25	59
dispersal survival	22	41
mean of spatial parameters	63	28
Nonspatial parameters		
survival	100	46
fecundity	100	38
initial abundances	100	23
variability in fecundity	69	28
variability in survival	69	27
catastrophes	40	49
within-population correlations	40	21
mean of nonspatial parameters	74	33

[a] *Calculated as a percentage of the studies that included these parameters in the PVA model structure.*
[b] *Population viability analyses that varied carrying capacity as a proxy for assessing the influence of changes in habitat quality and habitat quantity, or both, are combined with studies that varied carrying capacity per se.*
[c] *Included dispersal defined by a mathematical distance function in which dispersal varied with distance or in which a maximum dispersal distance was identified as a threshold.*

Results

We reviewed 87 spatial, demographic PVA models developed for birds (36%), mammals (33%), and a limited number of amphibians (9%), fishes (6%), reptiles (6%), plants (6%), and invertebrates (4%) (for references and a summary of study characteristics, see Supporting Information). Although some researchers reported results for multiple species (e.g., Schumaker et al. 2004), none modeled interspecific interactions. RAMAS Metapop and PATCH were used most frequently (32 and 30%, respectively), but some researchers used VORTEX (16%), RAMAS GIS (12%), ALEX (7%), and RAMAS Landscape (3%). The most common objectives of spatial PVAs were to evaluate the sensitivity of model predictions to parameter uncertainty (49%) and to compare and prioritize alternate management strategies (60%).

All but 3 of 87 studies reviewed (97%) included some form of sensitivity analysis, mainly to assess parameter influence on 1 or more of the following model response variables: population size (74%), patch occupancy (42%), risk of decline (35%), and extinction probability (21%). Almost half (40%) of sensitivity analyses applied a local approach, with each evaluated parameter varied one-at-a-time. About one-quarter of studies varied 2 or more parameters simultaneously (27%) or used a combination of single and multiparameter perturbations (32%), but none applied a global sensitivity analysis. Only one study tested for interactions among model parameters.

Three general methods were used to characterize the influence of parameters on model predictions: recording the magnitude and direction of change in response variables (85% of 84 studies); estimating coefficients of sensitivity (15%; Burgman et al. 1993; Drechsler et al. 1998); and applying significance tests or statistical models (10%). Although most studies included sensitivity analyses, certain parameters were included more often than others (Table 1). Relative to the subset of studies that included a parameter in their model structure, on average only 28% of studies varied spatial parameters, and 33% varied nonspatial parameters. Less than half the studies (40%) evaluated the influence of alternative scenarios of landscape dynamics, which included deterministic landscape change or succession dynamics.

Discussion

Sensitivity analysis is widely recommended as an essential step in the application of predictive models (e.g., Cross & Beissinger 2001; Reed et al. 2002; Saltelli et al. 2006), but the results of our review suggest that comprehensive analyses are rarely applied in spatial PVAs carried out with the more popular PVA software packages. To date, model sensitivity in spatial PVAs has been assessed most often in local analyses, which are most informative for linear models with parameters that do not interact (Saltelli et al. 1999). Nevertheless, the complexity of spatial PVAs suggests that global sensitivity analysis is more appropriate for real-world applications in which interactions of spatial and nonspatial parameters are likely (Katzner et al. 2006). Approaches to global sensitivity analysis are discussed by Sobol′ (1993; Sobol′ indices), McCarthy et al. (1995), and Cross and Beissinger (2001; standardized regression coefficients), and Cukier et al. (1973; Fourier amplitude sensitivity test [FAST]). According to Saltelli et al. (2006), global sensitivity analysis represents a best practice because it explores known sources of parameter uncertainty across a given model structure and evaluates those sources and their interactions simultaneously over the plausible range of parameter space. We suggest that the scarcity of global sensitivity analysis in spatial PVAs is due in part to the lack of options for such analyses in generic PVA software and to limits on PVA implementation and computational efficiency (McCarthy et al. 1995; Cariboni et al. 2007), which underscores the need for tools to facilitate its wider application.

A broader and more rigorous application of sensitivity analysis to spatial PVAs should improve species and habitat recovery planning because it would help identify parameters that consistently influence the dynamics of particular taxa in real-world landscapes. On the basis of conclusions of the authors of the 87 PVAs we reviewed, spatial parameters, including population configuration, number of patches, carrying capacity, dispersal survival, and dispersal rates, were usually more influential than nonspatial parameters. Spatial data and parameters were also less likely to have been derived for the species and locations modeled, which suggests spatial parameters may also be more uncertain than nonspatial parameters. Unfortunately, summarizing these results via meta-analysis was not possible due to a lack of standardization and transparency in methods and inconsistent reporting of parameter values and intervals. Local sensitivity analyses are unlikely to facilitate such comparison (see Supporting Information). Even local elasticity analyses, which permit comparison across studies (de Kroon et al. 2000), are subject to problems of interpretation when vital rates are varied by different amounts or when variability in vital rates exists due to spatial and temporal variation (e.g., see Mills et al. 1999; Wisdom et al. 2000). As with other methods that focus strictly on vital rates (e.g., life-stage simulation analysis, life-table response experiments), varying only these rates does not allow for interpretation of the relative influence of all parameters across a given model structure. In contrast, global approaches to sensitivity analyses are likely to be more informative than local analyses for scenarios in which demographic parameters interact over space and time and are also more likely to produce information that facilitates syntheses across taxa.

Failing to include parameters in sensitivity analyses may contribute to an inefficient use of resources, financial or otherwise, especially when sensitivity analysis is used to direct management actions. It seems likely that sensitivity analyses in spatial PVA have not evaluated the influence of spatial parameters because methods to do so are unavailable, difficult to implement (require additional programming skills), or time-consuming. Generic PVA software packages currently offer relatively simple tools to create and explore the dynamics of PVA models, carry out analyses of elasticity and sensitivity of vital rates, vary subsets of parameters, or generate batch files for time-consuming and often inefficient comparisons of alternative models. Although no package we are aware of currently offers a comprehensive approach to global sensitivity analysis for spatial PVA, accessory tools to facilitate such analyses are available (e.g., Curtis & Naujokaitis-Lewis 2008). The following are some best practices we suggest for sensitivity analyses in spatial PVAs that will enhance transparency in model predictions, promote model reliability, and help prioritize costly research for guiding the recovery of species at risk.

1. Broaden the application of sensitivity analyses to reflect the full complexity of PVAs, including all spatial and nonspatial parameters.
2. Standardize methods for sensitivity analyses of PVAs to include global sensitivity analyses, which evaluate the full range of plausible parameter space.
3. Increase transparency in the results of PVAs by clearly identifying model structure, sources of data used to estimate parameters, and the rationale for the scope and type of sensitivity analysis applied.
4. Identify data, research priorities, and influential parameters derived from the outcomes of the modeling and sensitivity analysis process to facilitate collective learning in species- and habitat-recovery planning.

Acknowledgments

We thank A. Stewart and P. Shepherd for valuable discussions and assistance and 2 anonymous reviewers for comments that improved this paper. Our work was supported by a Species at Risk Recovery Education and Action Fund grant from Parks Canada to J.R. and P.A., logistic support from the British Columbia Ministry of Environment and Centre for Applied Conservation Research, and a Natural Sciences and Engineering Research Council postdoctoral fellowship to J.M.R.C.

Supporting Information

The study characteristics of all reviewed spatial PVAs (Appendix S1) and a summary of sensitivity analysis methods used in spatial PVA models (Appendix S2) are available as part of the on-line article. The author is 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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