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Species survival in fragmented landscapes: where to from here?

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Abstract. We summarise the contributions of empiricists, modellers, and practitioners in this issue of *Biodiversity and Conservation*, and highlight the most important areas for future research on species survival in fragmented landscapes. Under the theme 'uncertainty in research and management', we highlight five areas for future research. First, we know little about the effects of density dependence on the viability of metapopulations, a requirement for fragmented landscapes. Second, successful early attempts suggest that it is worth developing more rigorous calibration methods for population viability analysis with spatially explicit, individual-based models. In particular, the balance between model complexity, ease of calibration, and precision, needs to be addressed. Third, we need to improve methods to discriminate between models, including alternatives to time-series approaches. Fourth, when our ability to reduce model uncertainty is weak, we need to incorporate this uncertainty in population viability analysis. Fifth, population viability analysis and decision analysis can be integrated to make uncertainty an explicit part of the decision process. An important future direction is extending the decision framework to adaptive management. Under the theme 'tools for quantifying risk and predicting species sensitivity to fragmentation', we highlight three areas for future research. First, we need to develop tools to support comparative approaches to population viability analysis. Second, population modelling can be used to find rules of thumb to support conservation decisions when very little is known about a species. Rules of thumb need to be extended to the problem of managing for multiple species. Third, species' traits might be useful for predicting sensitivity but predictions could be further refined by considering the relative importance of population processes at different scales. Under the theme 'tools for reassembling fragmented landscapes', we consider the 'focal species' approach, and highlight aspects of the approach that require more rigorous testing. Finally, we highlight two important areas for future research not presented in the previous themes or papers in this volume. First, we need to incorporate the deterministic effects of habitat modification into the modelling framework of population viability analysis. Second, an avenue of research that remains largely unexplored is the combination of landscape-scale experiments and population modelling, especially using data from existing fragmentation experiments and from experiments designed to test the effects of defragmenting landscapes.

Key words: Extinction, Focal species, Habitat fragmentation, Habitat modification, Metapopulation, Modelling, Population viability analysis, Rules of thumb, Traits

Introduction

This volume brings together contributions by empiricists, modellers, and practitioners with the common goal of assessing what we know about species survival in fragmented landscapes and determining the most promising avenues for future research. The nine papers in this volume address three themes: (1) uncertainty in research and management, (2) tools for quantifying risk and predicting species sensitivity to fragmentation, and (3) tools for reassembling fragmented landscapes. In this paper, we first summarise and discuss the conclusions of those papers, grouped under the above three headings. We highlight future directions specific to each theme and to each paper. In a final section we discuss two other important areas for future research not presented in the previous papers in this volume but that were highlighted in the workshop: (1) incorporating the deterministic effects of habitat modification into the modelling framework of population viability analysis, and (2) combining experiments and models.

Uncertainty in research and management

Models for population viability analysis routinely incorporate density dependence, yet we have little systematic understanding of the consequences of density dependence for population viability. Lack of knowledge about the forms and consequences of density dependence in a population is a source of uncertainty about model structure. Of the 247 models used in 219 case studies of population viability analysis examined by Henle et al. (pp. 9–52), sixty-eight percent incorporated some form of density dependence. Among these case studies, density-dependent models resulted in both increases or decreases in extinction probability compared to density-independent models. The outcome depended on the type of density dependence and its interaction with environmental variability, growth rate at low population density, and initial population size. This finding contrasts with a previous conclusion that density-independent models result in higher extinction probability than models with moderate density dependence (Ginzburg et al. 1990). The review highlights three areas where future study is necessary to predict viability in fragmented landscapes. First, populations in fragmented landscapes might often be structured as metapopulations, yet we know little about the effects of density dependence on the viability of metapopulations, as opposed to local, closed populations. Henle et al. found opposite effects of density dependence in case studies of metapopulations compared to local, closed populations. Such variable effects of density dependence are consistent with recent advances in theories of spatially structured populations, which emphasise the important role of density dependence in metapopulation dynamics (Bolker and Pacala 1997; Chesson 1998). Application of this new body of theory to population viability analysis would have much to contribute to understanding the effects of density dependence on viability in fragmented landscapes. Second, there are some density-dependent processes that we need to know much more about, including Allee effects, density-dependent dispersal, and interaction of density-dependent processes in different life-history stages. Third, we need to improve methods for model selection. Discrimination of density-dependent models is an active area of research in statistical ecology but most research is directed at time-series data (e.g., Kendall et al. 1999). It would be worthwhile to pursue experimental and observational approaches that are not based on long time-series, such as density perturbation experiments (Cappuccino and Harrison 1996). Finally, while our ability to reduce uncertainty about density dependence is weak, we need to incorporate this structural uncertainty in population viability analyses using sensitivity analyses (Pascual et al. 1997).

Spatially explicit models are natural candidates for modelling population viability in fragmented landscapes. However, the usefulness of spatially explicit models for population viability analysis has been questioned recently in several publications because of high parameter uncertainty (Ruckelshaus et al. 1997; Beissinger and Westphal 1998). These criticisms are based on the premise that model parameters, such as fecundity and dispersal, are obtained from direct observations of these rates. In contrast to direct estimates, Wiegand et al. (pp. 53–78) showed that parameter uncertainty in spatial models can be reduced by calibrating models against independent data. Using data collected for brown bears (*Ursus arctos*) they calibrated a population model that is spatially explicit and individual based. Out of several sources of data, the most useful data sets were a 10-year time series of females with cubs in one sub-area and the spatial pattern of bear densities across a large part of the study area. Calibration of the model with these data increased the precision of model predictions by as much as fourfold, compared to the uncalibrated model that used parameter estimates obtained directly. In a second contribution (pp. 79–114) Wiegand et al. compared the use of different data for model calibration and global versus more restricted searches of parameter space. It was reassuring for their approach that different data yielded similar model predictions. This is one of the first attempts to calibrate a spatially explicit, individual-based model using independent data (see also Lindenmayer et al. 2000) and this early success suggests that it is worth developing a more rigorous approach to calibration. An important related issue is the balance between model complexity, ease of calibration, and precision. The two contributions by Wiegand et al. are a first step towards understanding how the search in parameter space can be restricted for complex models. However, while it can be argued that spatially explicit, individual-based models ensure the structural integrity of a model, it is far from clear that spatially explicit, individual-based models outperform simpler models in predictive ability. Certainly, complex models are more difficult to calibrate than simpler models because more parameter space must be searched. This issue of model complexity needs to be explored rigorously by confronting complex and simple models against the same data.

Insufficient data, uncertainty about the effects of management actions, and conflicting interests or goals are also pervasive problems for management decisions. Drechsler and Burgman (pp. 115–139) reviewed ways to combine population viability analysis and decision analysis, covering both probabilistic and non-probabilistic approaches. Whereas population viability analysis is providing increasingly more sophisticated tools to quantify uncertainties, decision analysis provides a formal framework for deciding on an action in the presence of these uncertainties. Drechsler (pp. 141–164) extended the combination of population viability analysis and decision analysis to the more realistic scenario, where there is not simply uncertainty in model predictions but also disagreement about the goals of management. Integration of population viability analysis with decision analysis is an important first step for making uncertainty an explicit part of the decision process. An important future direction in this area is extending the decision framework to adaptive management.

Tools for quantifying risk and predicting sensitivity to fragmentation

The first two papers in this section (Grimm et al. (pp. 165–188) and Frank (pp. 189–206)) recognised the need for quantitative risk assessment tools, like population viability analysis, because verbal classifications of populations as being ‘too small’ are too vague to be useful in decision-making. They also recognised that producing and analysing models requires experience and time, making the development of a model for every threatened species impossible. In addition, population viability analysis focuses on single species problems when we are in need of tools that allow us to consider multiple species. Grimm et al. and Frank presented two alternatives to population viability analysis of single species: (1) generic models for population viability analysis, which can be applied to many populations (Grimm et al.), and (2) rules of thumb drawn from extinction theory and specific population viability analyses (Frank). The final paper in this section (Henle et al., pp. 207–251) explored the use of demographic and ecological traits to predict the sensitivity of species to fragmentation.

Grimm et al. presented a generic software package, META-X, for metapopulation viability analysis. The philosophy underlying META-X is that population viability analysis is a tool to deal with uncertainty, rather than to overcome uncertainty. Under this paradigm, population viability analysis is a tool for decision support rather than decision-making, and should be used to make relative contrasts rather than absolute ones (Possingham et al. 1993; Burgman and Possingham 2000). The most important use of META-X is the design and evaluation of comparative simulations. As a result, META-X helps to focus on comparative rather than absolute risk assessment. A feature of META-X is that it is not completely 'canned' since external submodels are required to fully parameterise the metapopulation model, thus engaging the modeller in decisions about model structure. Finally, META-X uses a unifying currency, 'intrinsic mean time to extinction', to quantify viability, which further facilitates a comparative approach to population viability analysis.

Frank showed how the results of population modelling could be used to support decision-making by developing rules of thumb for the re-establishment and conservation of metapopulations. Rules of thumb are necessary when very little is known about a species. Frank derived rules of thumb using an analytical solution to a metapopulation model. Compared to simulation models, in which we can only examine viability by simulation experiments, the analytical solution provides a strong mechanistic understanding of population viability. Using the analytical solution, Frank looked at the importance of four ecological attributes of a species: sensitivity to environmental fluctuations, emigration rate, dispersal ability, and local extinction rate. Of these, only sensitivity to environmental fluctuations mattered. Two rules of thumb result. (1) If a species is weakly sensitive to environmental fluctuations then metapopulation viability is greatest if all patches in the habitat network are nearly of the same size. (2) If the species is highly sensitive to environmental fluctuations then metapopulation viability is greatest if the relative size of the patches corresponds to their degree of connectedness. The striking outcome of these two rules of thumb is that different kinds of species suggest different optimum designs for reserve networks. However, Frank examined alternative reserve designs for single species only. Projecting rules of thumb to reserve design for multiple species will mean looking at a full range of trade-offs between different traits of species and alternative designs for reserve networks.

Henle et al. examined the use of demographic and ecological traits to predict the sensitivity of species to fragmentation. Their review of the literature explored theoretical and empirical evidence for traits as predictors of sensitivity to fragmentation. They found that the species most sensitive to fragmentation will have combinations of five traits: low natural abundance/high area requirement, high population fluctuations, low reproductive potential, low dispersal power, and specialised habitat requirements. These predictions could be further refined by considering the relative importance of habitat fragmentation for local, within-fragment, processes like habitat modification versus between-fragment processes like altered colonisation and extinction rates, on a range of species with a wide spectrum of traits (Davies et al. 2001b). This may be an avenue for understanding why one process is important in determining one species' response to fragmentation, while for another species, different processes matter. We recognise that it is not always that easy to forecast which species will be most sensitive. For example, Mac Nally et al. (2000) showed that even for birds, a well-studied group, predictions about likely sensitivity were not good. Nonetheless, the ability to categorise species by their sensitivity to fragmentation may be a powerful tool for conservation because it provides a basis for preventative management (Davies et al. 2000).

Tools for reassembling fragmented landscapes

The final paper by Freudenberger and Brooker (pp. 253–274) presents experience gained using the 'focal species' approach (Lambeck 1997) in conservation programs aiming to reassemble fragmented landscapes. The focal species approach uses threat-based indicators, based on the habitat requirements of the most sensitive species, to provide management guidelines for the reconstruction of fragmented landscapes (Lambeck 1997). The focal species approach has received much attention both in the scientific literature and in management arenas (e.g., Brooker 2002; Gaston et al. 2002; Kintsch and Urban 2002; Lambeck 2002; Lindenmayer et al. 2002; Noss et al. 2002). The approach has wide appeal because it is easy to understand and simple to apply. Using a series of case studies, Freudenberger and Brooker illustrated that the focal species approach is a useful starting point for reconstructing landscapes and that the approach is flexible enough to be extended and modified. For example, Brooker (2002) showed that it is possible to extend the approach so that multiple threatening processes are considered simultaneously and a larger spatial extent is included. Both are significant improvements to the original approach that illustrate the potential of the focal species framework to help make decisions about reconstructing landscapes, based on the requirements of species in those landscapes.

Nevertheless, it is clear that the focal species approach is in need of more rigorous testing (Lindenmayer et al. 2002), especially given initial enthusiasm and adoption by managers. Further case studies are needed to fully explore the implicit assumptions of the approach, including the ability for one taxonomic group to provide guidelines for all others and the relative importance of managing for ecosystem processes in the landscape versus managing for the persistence of species in the landscape. However, it is not possible to fully test the focal species method using case studies, since we can never have full knowledge of a system. An alternative is to test the method using simulation models. Using models, we can systematically vary assumptions about how communities are structured, and the distributions of all species in relation to all threats are known. We can then test the ability of the focal species approach to detect species' responses to threats and the ability of the approach to provide guidelines for reconstructing the landscape. By testing the method in this way we can explore a range of conditions and determine if and when the approach is likely to hold or fail.

Other important areas for future research

In addition to these research priorities, we see two areas not covered in the published papers but highlighted as an outcome of the working groups that would contribute greatly to our understanding of species survival in fragmented landscapes.

Incorporating the deterministic effects of habitat modification into the modelling framework of population viability analysis

The focus on metapopulation theory in fragmentation studies has centred attention on the importance of dispersal and between-patch dynamics for persistence. However, although models have demonstrated the importance of dispersal, empirical evidence from real landscapes suggests that local dynamics are at least as important over the short term (Harrison and Bruna 1999). For example, local processes, such as edge effects and other physical changes to habitat, are important drivers of change in the distribution and abundance of organisms in fragmented landscapes (e.g., Malcolm 1994; Didham et al. 1998; Laurance et al. 1998a,b; Davies et al. 2000, 2001b). But current models largely ignore the deterministic effects of habitat modification. Metapopulation models that focus on isolation and dispersal allow general guidelines to be developed but if habitat modification is important, such guidelines may be inappropriate. It is important that deterministic effects like habitat modification be incorporated into the modelling framework of population viability analysis (Davies et al. 2001a).

Combining experiments and models

An avenue of research that remains largely unexplored is the combination of landscape-scale experiments and population modelling. Although not strictly experimental, recent examples of this approach include McCarthy et al. (2000), and Lindenmayer et al. (2000, 2003). The advantage of combining landscape-scale experiments and population modelling is that the two approaches are highly complementary. For example, approaches to population viability analysis could be improved by testing with experimental data, experiments could be set up specifically to calibrate models used for population viability analysis, or population models could be used to directly test hypotheses of fragmentation experiments. There are two important opportunities in this area. The first is using data from existing fragmentation experiments, some of which now include time series of spatial data that exceed a decade (Margules 1993). The second opportunity is in what we will call 'reconstruction experiments', designed to test the effects of defragmenting landscapes. In landscapes where reconstruction is planned, we should not overlook the importance of learning in the process. We envisage a research program where explicit predictions are made about the effects of reconstruction on species (e.g., based on species traits), reconstruction is designed under an experimental paradigm so that decisive tests can be made of predictions, and that this effort is backed up by population modelling and detailed studies. Such efforts should incorporate key elements of experimental design, such as controls and pre-treatment data, and be underpinned by adequate models, which should consider effects of the matrix, population structure within and between fragments, and habitat modification.

References

Beissinger S.R. and Westphal M.I. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62: 821–841.

Bolker B. and Pacala S.W. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. Theoretical Population Biology 52: 179–197.

Brooker L. 2002. The application of focal species knowledge to landscape design in agricultural lands using the ecological neighbourhood as a template. Landscape and Urban Planning 60: 185–210.

Burgman M.A. and Possingham H.P. 2000. Population viability analysis for conservation: the good, the bad and the undescribed. In: Young A.G. and Clarke G.M. (eds), Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge, UK, pp. 97–112.

Cappuccino N. and Harrison S. 1996. Density-perturbation experiments for understanding population regulation. In: Floyd R.B., Sheppard A.W. and De Barro P.J. (eds), Frontiers of Population Ecology. CSIRO Publishing, Melbourne, Australia, pp. 53–64.

Chesson P. 1998. Making sense of spatial models in ecology. In: Bascompte J. and Solé R.V. (eds), Modeling Spatiotemporal Dynamics in Ecology. Landes Bioscience, Austin, Texas, pp. 151–166.

Davies K.F., Margules C.R. and Lawrence K.F. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81: 1450–1461.

Davies K.F., Gascon C. and Margules C.R. 2001a. Habitat fragmentation: consequences, management, and future research priorities. In: Soulé M.E. and Orians G.H. (eds), Conservation Biology: Research Priorities for the Next Decade. Island Press, Washington, DC, pp. 81–97.

Davies K.F., Melbourne B.A. and Margules C.R. 2001b. Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. Ecology 82: 1830–1846.

Didham R.K., Hammond P.M., Lawton J.H., Eggleton P. and Stork N.E. 1998. Beetle species responses to tropical forest fragmentation. Ecological Monographs 68: 295–323.

Gaston K.J., Pressey R.L. and Margules C.R. 2002. Persistence and vulnerability: retaining biodiversity in the landscape and in protected areas. Journal of Biosciences 27: 361–384.

Ginzburg L.R., Ferson S. and Akçakaya H.R. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. Conservation Biology 4: 63–70.

Harrison S. and Bruna E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22: 225–232.

Kendall B.E., Briggs C.J., Murdoch W.W., Turchin P., Ellner S.P., McCauley E. et al. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. Ecology 80: 1789–1805.

Kintsch J.A. and Urban D.L. 2002. Focal species, community representation, and physical proxies as conservation strategies: a case study in the Amphibolite Mountains, North Carolina, USA. Conservation Biology 16: 936–947.

Lambeck R.J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 11: 849–856.

Lambeck R.J. 2002. Focal species and restoration ecology: response to Lindenmayer et al. Conservation Biology 16: 549–551.

Laurance W.F., Ferreira L.V., Rankin-De Merona J.M. and Laurance S.G. 1998a. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79: 2032–2040.

Laurance W.F., Ferreira L.V., Rankin-De Merona J.M., Laurance S.G., Hutchings R.W. and Lovejoy T.E. 1998b. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conservation Biology 12: 460–464.

Lindenmayer D.B., Lacy R.C. and Pope M.L. 2000. Testing a simulation model for population viability analysis. Ecological Applications 10: 580–597.

Lindenmayer D.B., Manning A.D., Smith P.L., Possingham H.P., Fischer J., Oliver I. et al. 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology 16: 338–345.

Lindenmayer D.B., Possingham H.P., Lacy R.C., McCarthy M.A. and Pope M.L. 2003. Lessons from landscape-scale population modeling in a fragmented system. Ecology Letters 6: 41–47.

Malcolm J.R. 1994. Edge effects in Central Amazonian forest fragments. Ecology 75: 2438–2445.

Mac Nally R., Bennett A.F. and Horrocks G. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. Biological Conservation 95: 7–29.

Margules C.R. 1993. The Wog Wog habitat fragmentation experiment. Environmental Conservation 19: 316–325.

McCarthy M.A., Lindenmayer D.B. and Possingham H.P. 2000. Testing spatial PVA models of Australian treecreepers (Aves: Climacteridae) in fragmented forest. Ecological Applications 10: 1722–1731.

Noss R.F., Carroll C., Vance-Borland K. and Wuerthner G. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology 16: 895–908.

Pascual M.A., Kareiva P. and Hilborn R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology 11: 966–976.

Possingham H.P., Lindenmayer D.B. and Norton T.W. 1993. A framework for improved threatened species management using population viability analysis. Pacific Conservation Biology 1: 39–45.

Ruckelshaus M., Hartway C. and Kareiva P. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology 11: 1298–1306.