REPORT

How accurate are population models? Lessons from landscape-scale tests in a fragmented system

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Abstract

There is a growing debate about the ability of Population Viability Analysis (PVA) to predict the risk of extinction. Previously, the debate has focused largely on models where spatial variation and species movement are ignored. We present a synthesis of the key results for an array of different species for which detailed tests of the accuracy of PVA models were completed. These models included spatial variation in habitat quality and the movement of individuals across a landscape. The models were good approximations for some species, but poor for others. Predictive ability was limited by complex processes typically overlooked in spatial population models, these being interactions between landscape structure and life history attributes. Accuracy of models could not be determined a priori, although model tests indicated how they might be improved. Importantly, model predictions were poor for some species that are among the best-studied vertebrates in Australia. This indicated that although the availability of good life history data is a key part of PVA other factors also influence model accuracy. We were also able to draw broad conclusions about the sorts of populations and life history characteristics where model predictions are likely to be less accurate. Predictions of extinction risk are often essential for real-world population management. Therefore, we believe that although PVA has been shown to be less than perfect, it remains a useful tool particularly in the absence of alternative approaches. Hence, tests of PVA models should be motivated by the cycle of testing and improvement.

Keywords

INTRODUCTION

Assessment of species extinction risk lies at the heart of conservation biology (Burgman *et al.* 1993; Fagan *et al.* 2001; Fieberg & Ellner 2001; Beissenger & McCullough 2002). Consequently, recent strong criticism of the ability of Population Viability Analysis (PVA) to predict extinction probabilities (Ludwig 1999) requires rebuttal and/or the development of alternative methods for assessing viability. In contrast to these strong criticisms is work that lends support to PVA models (Brook *et al.* 2000) [but see (Coulson *et al.* 2001; Ellner *et al.* 2002)]. To date, the focus of most of that work has been time series analysis of population abundance. The key question has been – given a model and data on a single population – how accurately can we predict future trajectories? We took an alternative approach to testing PVA models by accepting that models

are imperfect representations of reality, and we aimed to identify and improve model deficiencies. This approach avoided the confusing debate about whether PVA is accurate and/or useful. As with all attempts to model complex systems, it is inevitable that PVAs will not be accurate in all respects. That is, we do not know all we would like about population dynamics. Nevertheless, PVA models are still useful if they provide the best currently available tools for making much needed predictions about extinction risks.

Most previous PVA modelling efforts have focused on a single species or group (e.g. butterflies) using a single spatially explicit population model (Hanski 1998), or on single populations of different species in which landscape scale effects are ignored [for example (Brook *et al.* 2000; McCarthy & Broome 2000)]. In contrast, our study represents the first landscape-scale test of the predictive

ability of a set of differently structured models for an array of species with quite different life history characteristics.

MATERIALS AND METHODS

Study area

Our work occurred at Tumut, 100 km west of Canberra in south-eastern Australia. In 1932, extensive areas of native eucalypt forest first began being cleared at Tumut and were replaced with stands of exotic softwood plantation Radiata Pine (*Pinus radiata*). Clearing continued until 1985 and it created what is now a 70 000 ha pine plantation. One hundred and ninety-two patches of original eucalypt forest cover were left uncleared amidst the plantation (Fig. 1). This created an important opportunity for natural landscape 'experiments' for the following reasons.

1 The eucalypt patches vary in size, shape, forest type, and other attributes enabling a powerful randomised and replicated experimental design (Lindenmayer *et al.* 2002a).
2 'Control areas' exist in large continuous areas of unfragmented native forest thereby avoiding confounding environmental conditions with habitat modification.

3 The long-term (65+ year) history of fragmentation is precisely known (to the week). Hence, 'extinction debts' (*sensu* Tilman *et al.* 1994) should be apparent (if they occur).
4 Patterns of disturbance in the Radiata Pine surrounding the eucalypt patches are well documented and are included in the experimental design – a factor that is often overlooked in many fragmentation studies (Simberloff *et al.* 1992).

PVA modelling

The natural advantages of the Tumut region stimulated a major set of integrated studies encompassing the distribution and demography of fragmented vertebrate populations (Lindenmayer *et al.* 2002a), patterns of genetic variability within and among patchy populations (Lindenmayer & Peakall 2000) and computer modelling of population dynamics. Modelling involved using a set of PVA models to predict the presence and abundance of species in the patch system at Tumut and then comparing such forecasts with data from detailed field sampling of the same patches. Taxa from different vertebrate groups (two species of small terrestrial mammals, five species of arboreal marsupials, and
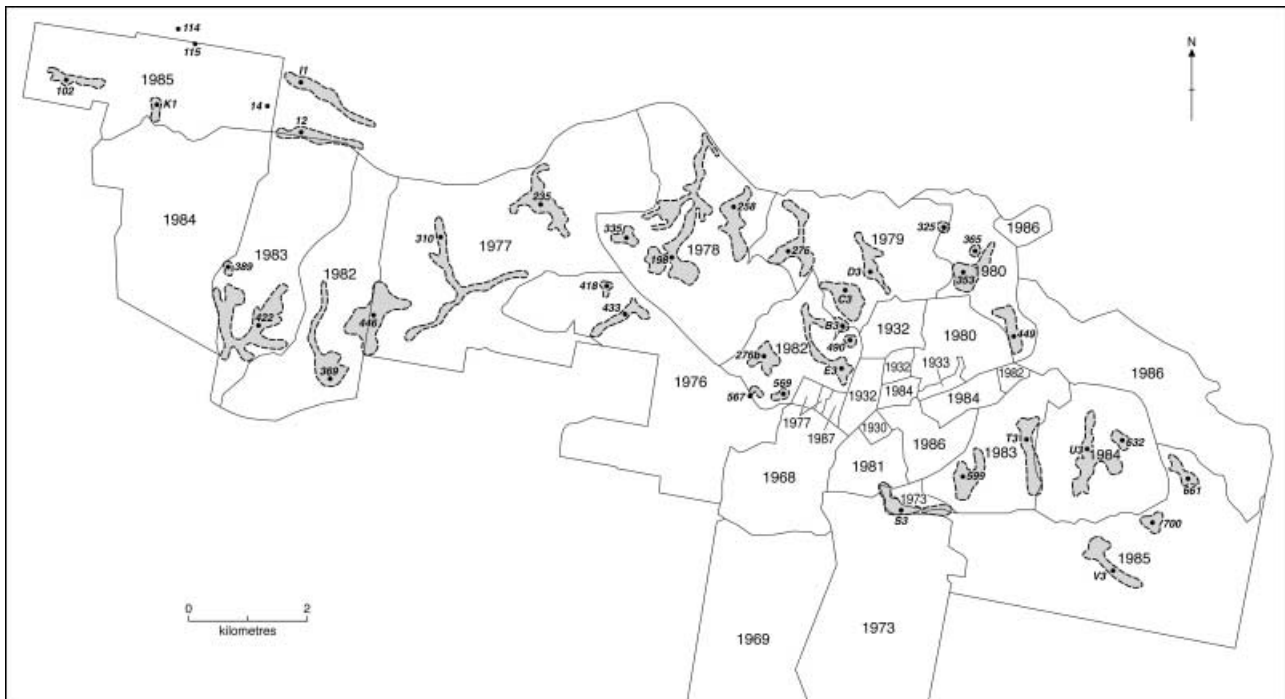

Figure 1 Pattern of clearing and patch isolation in a subsection of the Tumut region in south-eastern Australia where detailed PVA model testing was undertaken. The shaded areas show remnant patches of native eucalypt forest and the clear areas correspond to compartments of plantation Radiata Pine. The boundaries of each compartment are highlighted by the solid lines. The dates signify the year in which a given compartment of pine was established.

four species of birds) with quite different life history attributes and movement capabilities were analysed using three widely available models – VORTEX (Lacy 2000), ALEX (Possingham & Davies 1995) and Hanski's incidence model for metapopulation dynamics (Hanski 1994a) (Table 1). The three models are structured quite differently and they simulate population processes in markedly different ways. A detailed description of the models is beyond the scope of this paper, and a comprehensive discussion of each one is presented in papers by the respective architects of each model (Hanski 1994a; Possingham & Davies 1995; Lacy 2000). In addition, Lindenmayer et al. (1995) outlined the key differences and similarities in several widely available generic PVA models including two used in the work at Tumut.

All model testing used a network of 39 patches (see Fig. 1) where exhaustive field sampling of vertebrates had been completed. Information on the life histories of species used to parameterize the models was based on literature values (e.g. fecundity, fledging period) or it came from our own extensive field studies in unfragmented areas of native forest adjacent to the pine plantation at Tumut (e.g. home range/territory size, population density). The models were *not* parameterized using data from the actual study site. We can think of the modellers' predictions being like asking someone, in 1932, to assess the consequences of the formation of the pine plantation on the distribution and abundance of several species if they had modern computers, population models, and local life history information for each species. This is precisely what the users of PVA models do now to assess the possible consequences of development.

Different modelling studies were conducted independently of one another by five different modellers and therefore not all species were tested with all models. This study synthesizes new findings that have emerged from both the integration of results *across* the different modelling studies, and recent insights from ongoing field-based studies. The synthesis provides an understanding that would not have been possible from any single study and it allows a unique assessment of spatially explicit PVA models for natural systems with the inherent complexity typical of fragmented landscapes that support many species. Indeed, from our collective experience of modelling an array of different species in the landscape system at Tumut it was possible to determine circumstances where predictions from PVA models were likely to be more accurate and less accurate.

RESULTS AND DISCUSSION

Lessons from the fragmented ecosystem at Tumut

The predictive ability of the modelling was highly variable and outcomes differed markedly between species (Table 1). For example, predictions for the Greater Glider (*Petauroides*

volans) were remarkably accurate with all models, whereas for others, like the two species of small terrestrial mammals [the Bush Rat (*Rattus fuscipes*) and Agile Antechinus (*Antechinus agilis*)], the predictions of all the models were poor. These small mammals are some of the most well studied in Australia (e.g. Taylor & Calaby 1988), and the poor predictive ability was *not* due to a paucity of high quality life history data. Our results indicate that despite the quality of existing life history data, model predictive ability can still be low. Other factors appear to be important (see Table 2) including several that could not have been anticipated prior to the commencement of our work, and are not part of generic spatial PVA models.

First, some aspects of the life history of species in an unfragmented setting were very different from those in habitat fragments. In our study area, home range sizes and patterns of den tree use in arboreal marsupials varied significantly between small and large patches. Population densities also varied significantly between patches of different size (Pope, Lindenmayer & Cunningham, unpublished data) – a result that has been reported in some other species of mammals (e.g. Krohne & Hoch 1999; Singer et al. 2001) but not previously in arboreal marsupials, even though they are some of the best studied mammals in Australia (Lindenmayer 2002). Trophic interactions are likely to be different between habitat patches and continuous forest. In particular, the susceptibility of arboreal marsupials to owl predation appeared to be greater in fragments than in continuous areas of native forest. Conversely, for birds such as the Laughing Kookaburra (*Dacelo novaeguineae*), territory sizes appeared to have increased with increasing inter-patch distance to enable animals to harvest resources from several more widely spaced fragments (Lindenmayer et al. 2001a).

The second suite of unanticipated results was related to spatial complexity in the patch system at Tumut. Many studies have shown strong relationships between patch size, patch isolation and levels of patch occupancy and within-patch animal abundance (Hanski 1994b). Patch size and patch isolation are fundamental planks in many spatial population models, for example Hanski (1994a); Lindenmayer et al. (2001a). However, species responses to the patch system were more complex at Tumut than could be captured by simple measures of patch size and patch isolation. In the case of small mammals such as the Bush Rat, the direct linear distance between patches was a poor measure of patch isolation. Most dispersal took place along streamlines. Inter-patch dispersal was low among patches not connected by gullies (even those close together) (Peakall, Ruibal & Lindenmayer, unpublished data). For other species, the hostility of the surrounding matrix to dispersal appeared to lead to fence effects (*sensu* Wolff et al. 1997) in which animal densities *increased* within patches and reached the highest levels in the more *isolated* patches

Table 1 Population modelling outcomes at Tumut. The third column overviews modelling outcomes from the many scenarios and several millions of simulations completed for each species. Further details of the array of model forecasts tested are given in the accompanying references

Group/species	Model*	Short summary of outcomes	Reference
Arboreal marsupials			
Greater Glider (*Petauroides volans*)	A	Good congruence with actual patch occupancy and population size	McCarthy *et al.* (2001b)
			Lindenmayer *et al.* (2001b)
Greater Glider	V	Good congruence with actual patch occupancy and population size after adding extra model complexity	Lindenmayer *et al.* (2000)
Greater Glider	H‡	Good congruence with actual patch occupancy	Lindenmayer *et al.* (1999)
Common Ringtail Possum (*Pseudocheirus peregrinus*)	A	Poor predictive ability for patch occupancy and population size, with under-prediction even when additional information added to increase model complexity	McCarthy *et al.* (2001b)
Common Ringtail Possum	V	Good congruence with actual patch occupancy and population size after adding extra model complexity	Lindenmayer *et al.* (2000)
Common Ringtail Possum	H‡	No congruence with actual patch occupancy, impossible to derive parameter estimates required by model	Lindenmayer *et al.* (1999)
Mountain Brushtail Possum (*Trichosurus caninus*)	A	Poor predictive ability for patch occupancy and population size, with under-prediction even when additional information added to increase model complexity	McCarthy *et al.* (2001b)
			Lindenmayer *et al.* (2000)
Mountain Brushtail Possum	V	Good congruence with actual patch occupancy and population size after adding extra model complexity	Lindenmayer *et al.* (2000)
Mountain Brushtail Possum	H‡	No congruence with actual patch occupancy	Lindenmayer *et al.* (1999)
Common Brushtail Possum (*Trichosurus vulpecula*)	H‡	Good congruence for patchy occupancy	Lindenmayer *et al.* (1999)
Yellow-bellied Glider (*Petaurus australis*)	A	Accurately forecast species extinction in patch system	McCarthy *et al.* (2001b)
Terrestrial mammals			
Bush Rat (*Rattus fuscipes*)	A	Poor predictive ability for actual patch occupancy and population size	Ball, Lindenmayer & Possingham, unpublished data
Bush Rat	V	Poor predictive ability for actual patch occupancy and population size, even when additional complexity added to the model	Lindenmayer & Lacy (2002)
Agile Antechinus (*Antechinus agilis*)	A	Poor predictive ability for actual patch occupancy and population size	Ball, Lindenmayer & Possingham, unpublished data
Agile Antechinus	V	Poor predictive ability for actual patch occupancy and population size, even when additional complexity added to the model	Lindenmayer & Lacy (2002)
Birds			
White-throated Treecreeper (*Cormobates leucophaea*)	A	Predicted patch occupancy reasonable but underestimated; improved with additional model complexity (e.g. foraging in the matrix)	McCarthy *et al.* (2000)
Red-browed Treecreeper (*Climacteris erythrops*)	A	Predicted patch occupancy reasonable but underestimated; improved with modifications to the model (increased population growth rate)	McCarthy *et al.* (2000)
			McCarthy *et al.* (2000)
Laughing Kookaburra (*Dacelo novaeguineae*)	A	Poor congruence for actual patch occupancy with over-prediction even after model adjustments (e.g. accounting for habitat suitability)	Lindenmayer *et al.* (2001a)
Sacred Kingfisher (*Halcyon sancta*)	A	Good congruence with patch occupancy	Lindenmayer *et al.* (2001a)

*Codes for models: A, ALEX; V, VORTEX; H, Hanski's Incidence Model.
‡Model forecasts patch occupancy and not population size.

Table 2 Contrasts between characteristics of populations whose fates are likely to be more accurately predicted by PVA and those likely to be less accurately predicted

More accurate population prediction	Less accurate population prediction
Single population	Metapopulation
Closed population	Open population
Discrete habitat boundaries	Diffuse habitat boundaries
Uniform habitat conditions	Heterogeneous habitat conditions
Constancy of life history attributes across habitat types and landscape conditions	Variation in life history attributes between habitat types and landscape conditions (e.g. fragmented vs. unfragmented landscapes)
Constancy of species interactions across habitat types and landscape conditions	Variation in species interactions between habitat types and landscape conditions
Distance-related dispersal patterns	Habitat-related dispersal patterns
Simple social systems	Complex social systems

(Lindenmayer *et al.* 2002b) – contrary to expectations at the start of work at Tumut and contrary to predictions from any standard spatially explicit population model.

The third set of unanticipated results was that field studies of birds and arboreal marsupials demonstrated that relationships between patch size and animal abundance were often far from simple. Sometimes relationships were strongly influenced in complex ways by patch quality – which varied on a species-specific basis (Lindenmayer *et al.* 2002a). In other cases, patch size and behavioural interrelationships were important. For example, recent analyses integrating bird abundance and bird vocalization data showed that vocal activity rates were significantly higher in remnant patches than in large areas of continuous forest (even when values were statistically adjusted for differences in abundance) (Cunningham & Lindenmayer unpublished data). The most likely explanation is conspecific attraction which leads to dispersing birds being more likely to settle in habitat patches where there are already conspecifics vocalizing (Smith & Peacock 1990; Eens 1994). Increased activity in eucalypt remnants (compared with large continuous areas of unfragmented forest) during the spring could be related to birds attempting to attract mates to colonize these areas (Smith & Peacock 1990).

All models invariably simplify the systems they attempt to portray (Burgman *et al.* 1993; Fieberg & Ellner 2001), as their purpose is to create simple representations that still capture the important aspects of the dynamics of the real systems. Spatially explicit models are no different in this regard (Hanski 1994a) and many practitioners consistently favour simplicity above model complexity (Ludwig 1999). Simplicity can often be justified on theoretical and practical grounds (Doak & Mills 1994). However, in the case of some of our models for arboreal marsupials and birds (such as the two species of treecreepers and the Laughing Kookaburra), reasonable congruence between model predictions and actual field data was obtained only when model complexity was added (such as matrix effects on dispersal mortality, the

ability to forage in the matrix and/or the influence of habitat quality on within-patch population size) (Lacy 2000; Lindenmayer *et al.* 2000). The standard models for simulating the dynamics of species in fragmented systems were too simple for several species to capture even their qualitative response to fragmentation. Indeed, the three broad types of unanticipated complexities or 'ecological surprises' outlined above would have been impossible to model a priori because they are, by definition, unpredictable. Notably, any alternative modelling framework to PVA for predicting extinction risk will also be susceptible to such types of 'ecological surprises' and is likely to have similar difficulties in dealing with them. In the case of the work at Tumut, the three broad groups of unanticipated results that emerged from our set of studies highlighted the use of studying the species in a given system before applying PVA to those taxa – thereby reducing the potential for ecological surprises.

A striking finding from Tumut was that even if modelling outcomes for one species were reasonably accurate, they often were not for a closely related taxon in the same system. Three relatively closely related species-pairs were among the taxa examined – the Common Brushtail Possum (*Trichosurus vulpecula*) and the Mountain Brushtail Possum (*Trichosurus caninus*), the Greater Glider (*Petauroides volans*) and the Common Ringtail Possum (*Pseudocheirus peregrinus*), and the White-throated Treecreeper (*Cormobates leucophaea*) and Red-browed Treecreeper (*Climacteris erythrops*). In each case, the modelling outcome for one species was *not* informative about the outcome of the other species in the pair. Therefore, it may be inappropriate to extrapolate the results of modelling from one species to another, even if they are closely related. Moreover, it was often not possible to predict beforehand which species would be modelled successfully – as outlined above, the predictions for species for which good life history data were available were not always accurate.

Studies by some authors, e.g. Brook *et al.* (2000) have found good predictive ability for PVA models (but see

critiques by Coulson *et al.* 2001; McCarthy *et al.* 2001a; and Ellner *et al.* 2002). This contrasts with our integrated large-scale studies where the predictive ability for measures such as the occupancy of particular patches and within-patch abundance varied from very poor to remarkably good. The differences in results may be due, in part, to the fact that Brook *et al.* (2000) focused on the dynamics of single populations, whereas our work targeted a more complex system comprised of multiple patches of varying size, spatial location, isolation, and habitat quality – a situation typical of many modified landscapes world-wide. Accurate predictions of population dynamics using models like those used for PVA will be difficult in such systems because, as demonstrated in this study, there is a raft of complex (and often interacting) processes that influence multi-patch systems. However, our experience from extensive modelling and model testing at Tumut made it possible for us to draw some broad conclusions about the sorts of populations and life history characteristics where model predictions are likely to be less accurate. These are briefly summarized in Table 2.

Based on our findings from Tumut, we argue that three broad categories of complex spatial processes may be important to add to existing models:

1 interactions between landscape structure and life history attributes such as fence effects, conspecific attraction, and altered patterns of space use in habitat fragments (e.g. changed home range size);
2 altered patterns of interspecific interactions in fragmented landscapes such as elevated predation rates; and
3 well documented spatially based metapopulation phenomena like rescue effects (Brown & Kodric-Brown 1977), extinction–recolonization dynamics (Hanski 1998), spatial correlation in distribution patterns (Koenig 1998; McCarthy & Lindenmayer 2000), and environmental correlation between habitat patches (Stacey & Taper 1992).

CONCLUSIONS

Given that accurate forecasts of extinction probabilities from PVA models appear unlikely for most species, particularly in fragmented landscapes where many complex processes may operate, a better approach might be to use these widely applied tools to assess the *relative* efficacy of different conservation options (Possingham *et al.* 1993; McCarthy, Andelman and Possingham unpublished data). However, plausible estimates of the probability of extinction are sometimes required for planning, such as designation of levels of species threat and setting priorities for conservation action (for example, IUCN threat categories, Mace & Lande 1991). For those purposes, the use of general rules of thumb derived from theoretical considerations might be more

appropriate than estimating the probability of extinction from PVA models. However, any alternative to PVA needs to be able to make as good or better predictions, or to make predictions more efficiently, for it to be worthwhile. Such alternatives should be rigorously evaluated in the same way that PVA is currently being assessed. Although PVA has been shown to be imperfect, it can be improved and remains useful in the absence of a better alternative.

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