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Viability analyses with habitat-based metapopulation models

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Abstract Population viability analysis (PVA) models incorporate spatial dynamics in different ways. At one extreme are the occupancy models that are based on the number of occupied populations. The simplest occupancy models ignore the location of populations. At the other extreme are individual-based models, which describe the spatial structure with the location of each individual in the population, or the location of territories or home ranges. In between these are spatially structured metapopulation models that describe the dynamics of each population with structured demographic models and incorporate spatial dynamics by modeling dispersal and temporal correlation among populations. Both dispersal and correlation between each pair of populations depend on the location of the populations, making these models spatially structured. In this article, I describe a method that expands spatially structured metapopulation models by incorporating information about habitat relationships of the species and the characteristics of the landscape in which the metapopulation exists. This method uses a habitat suitability map to determine the spatial structure of the metapopulation, including the number, size, and location of habitat patches in which subpopulations of the metapopulation live. The habitat suitability map can be calculated in a number of different ways, including statistical analyses (such as logistic regression) that find the relationship between the occurrence (or, density) of the species and independent variables which describe its habitat requirements. The habitat suitability map is then used to calculate the spatial structure of the metapopulation, based on species-specific characteristics such as the home range size, dispersal distance, and minimum habitat suitability for reproduction.

Key words Spatial structure · Landscape PVA · Demography · Dispersal

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Introduction

Population viability analysis (PVA) is a collection of methods for evaluating the threats faced by species, their risks of extinction or decline, and their chances for recovery, based on species-specific data and models (Boyce 1992; Burgman et al. 1993; Akçakaya et al. 1999). There is a wide range of models used in PVAs, differing in the amount of data they require, the factors they incorporate, and their assumptions. The range of models, from simple to complicated, demonstrate the trade-off between flexibility (realism) and practicality (data requirements) (Akçakaya and Sjögren-Gulve, in press). The simplest are occupancy models that describe each population as full (occupied) or empty (extinct). The most complicated are individual-based models that follow the fate of each individual. In between these are scalar models that describe each population in terms of its total abundance, and structured models which describe each population in terms of the abundances of age classes or stages.

Importance of spatial structure

A set of populations of the same species in the same general geographic area is called a metapopulation. Many species live in metapopulations because of the natural heterogeneity of their habitats or because of human-induced habitat fragmentation. Analyzing the dynamics of species that live in multiple populations, or evaluating management options, requires a metapopulation modeling approach because in most cases the dynamics of a metapopulation cannot be deduced from the dynamics of its constituent populations. Single-population dynamics are determined by factors such as population size, life history parameters (fecundity, survivorship, and density dependence), and demographic and environmental stochasticity that cause variation in these parameters. The dynamics of a metapopulation or a species depends not only on these factors, but also on the spatial

variation in these factors and on other factors that characterize interactions among these populations. The additional factors that operate at the metapopulation or species level include the number and geographic configuration of habitat patches and dispersal and spatial correlation among these patches.

Spatial correlation refers to the similarity (synchrony) of environmental fluctuations in different parts of the landscape and, in the case of a metapopulation, in different populations. If the fluctuations in the environment are at least partially independent, so would be fluctuations in population dynamics. Thus, it would be less likely that all populations go extinct at the same time, compared to a case where the fluctuations were dependent, i.e., synchronous (Akçakaya and Ginzburg 1991; Burgman et al. 1993; LaHaye et al. 1994). In most metapopulations, fluctuations in demographic rates are caused by large-scale climatic factors such as rainfall, temperature, and flow rate. These factors are often correlated even at relatively large distances. For such metapopulations, models based on an assumption of independent fluctuations among patches will underestimate the temporal variability of population dynamics and therefore the extinction risk of the metapopulation.

Correlation among the fluctuations of populations is often a function of the distance among them. If two populations are close to each other geographically, they will experience relatively similar environmental patterns, such as the same sequence of years with good and bad weather. This similarity may result in a high correlation between the vital rates of the two populations. For example, Thomas (1991) found that silver-studded butterfly (*Plebejus argus*) populations that were geographically close tended to fluctuate in synchrony, whereas populations further apart (>600m between midpoints) fluctuated independently of one another. Similarly, Baars and van Dijk (1984) found that in two carabid beetles, *Pterostichus versicolor* and *Calathus melanocephalus*, the significance of rank correlation between fluctuations declined with increasing distance between sites.

When modeling metapopulations, the correlation among population fluctuations may be modeled as a function of the distance among habitat patches. This simulation can be done by sampling the growth rates of each population from random distributions that are correlated, and the degree of correlation may be based on the distance among populations. This approach was used by LaHaye et al. (1994) to model correlated metapopulation dynamics of the California spotted owl, *Strix occidentalis occidentalis*. LaHaye et al. (1994) modeled this spotted owl metapopulation by making the growth rates of each population correlate with the growth rates of other populations. They calculated the degree of correlation based on the similarity of rainfall patterns among the habitat patches.

Dispersal among populations may lead to recolonization of empty patches (i.e., extinct populations) by immigration from extant populations. Such recolonization would have a positive effect on overall metapopulation persistence. Dispersal rates depend on many factors, for example, species-specific characteristics such as the mode of seed dispersal,

motility of individuals, and ability and propensity to disperse. These factors determine the speed and ease with which individuals search for and colonize empty habitat patches. However, the dispersal rate between any two populations of the same species may also differ, depending on a number of population-specific characteristics. These characteristics include the distance between the populations, the type of habitat used during dispersal, and the density of the source population (Ebenhard 1991; Hansson 1991; Foppen and Reijnen 1994; Lidicker and Koenig 1996). Depending on these factors, dispersal from each local population to all others may not be possible. Consequently, the exact effect of dispersal on species extinction will depend on the topology (the network) of the migratory pathways or connections among populations.

The effectiveness of dispersal in reducing extinction risks depends to a large extent on the degree of similarity of environmental fluctuations experienced by different populations (i.e., their correlation or interdependence); this is because when all populations decline simultaneously, there will be less chance of recolonization of empty patches. However, if the fluctuations are at least partially independent (uncorrelated), then when some populations decline or become extinct others may remain extant or even increase, thus providing recolonization opportunities. The dynamics of metapopulations are very sensitive to the spatial factors that operate at the metapopulation level. Thus, ignoring spatial correlations, geographic location of habitat patches, or dispersal patterns may bias the predictions.

Spatial structure in PVA models

The models used in PVAs incorporate spatial dynamics in various ways. As in the case of the demographic structure of populations (e.g., age or stage structure), there is a wide spectrum of approaches to describing their spatial structure (Gilpin 1996). This spectrum of spatial structures is summarized below as three general types of models.

Occupancy models

At one extreme of the spectrum of models is the occupancy model of Levins (1970), which is based on the number of occupied populations, ignoring their location. More recent occupancy models incorporate some aspects of spatial structure. For example, incidence function models (Hanski 1994) take into account the sizes of and the distance between, habitat patches. However, occupancy models often make assumptions that are too unrealistic to apply these models to specific cases of risk assessment and management of threatened species. For example, they assume that local population growth is fast compared to the time scale of dispersal and recolonization, and they ignore local population dynamics. In addition, incidence function models and other occupancy models assume the metapopulation is in equilibrium, i.e., it is not increasing or decreasing.

One advantage of occupancy models is that they do not require detailed demographic data. For example, incidence function models require data on the occupied and unoccupied habitat patches, together with information on the size and isolation of the patches. Another type of occupancy model (state transition models; e.g., see Verboom et al. 1991; Sjögren-Gulve and Ray 1996) requires data on extinctions and recolonizations. This type of model does not make the assumption of equilibrium, but requires data for a long enough time period to allow a substantial number of local extinctions and recolonizations to be observed.

Individual-based models

At the other extreme are individual-based models, which describe the spatial structure with the location of each individual in the population, or the location of territories or home ranges (DeAngelis and Gross 1992; Pulliam et al. 1992; Lamberson et al. 1994; Dunning et al. 1995).

Individual-based models often require more data than are available for most species. In addition to demographic data such as survival rates and fecundities, individual-based models require data on behavior of individuals. These types of models are especially sensitive to the dispersal behavior of individuals. Small errors in dispersal mortality, mobility, and habitat suitability resulted in large errors in predicting dispersal success (Ruckelhaus et al. 1997).

Another source of error is the spatial structure of individual-based models, which is usually defined in terms of individual territories and home ranges. Often, there are not enough data to estimate the exact location and size of each territory or home range, and assumptions are made on the basis of median or average home range sizes. In addition, the grid structure of spatially explicit individual-based models is often based on this average size, assuming that all home ranges are identical in size and do not overlap substantially. Both these assumptions are likely to be invalid for many species.

Structured metapopulation models

Between the extremes of individual-based and occupancy models are spatially structured metapopulation models, which describe the dynamics of each population with structured demographic models and incorporate spatial dynamics by modeling dispersal and temporal correlation among populations. Both dispersal and correlation between each pair of populations depend on the location of the populations, making these models spatially structured. However, dispersal is modeled in terms of the proportion of individuals moving from one population to another, instead of the movement of each individual. The advantage of this approach is that it requires many fewer data than the individual-based modeling approach. Dispersal rates among populations can be estimated with mark-recapture methods, or they can be based on dispersal-distance functions fitted to data on the observed total dispersal distance of marked or radiocollared individuals.

The parameter of interest in modeling dispersal with metapopulation models is the rate of successful dispersal from one population to another between two successive time steps. Thus, these models do not make a distinction among dispersers that die during dispersal, those which die before they leave the source patch, and those that die after they reach the target patch (but before the next census). In other words, they assume that dispersal mortality is incorporated into the vital rates (e.g., specified in a stage matrix). This assumption does not mean that the dispersers necessarily have the same mortality as residents; it means that mortality during dispersal is accounted for by both the vital rates and the dispersal rates.

This point is a pragmatic assumption because, in most field studies, one cannot really measure the proportion of individuals leaving a patch (unless all individuals are radiotagged and continuously monitored) but can only count those that arrive in another patch. For example, marked individuals that are later found in another patch give an estimate for dispersal rate, and these, combined with those that are found in the same population in which they were marked, give an estimate of survivorship. The rest are assumed to have died between the two censuses. Presumably, some died within the same population and some of them died during dispersal. The distinction (as to where exactly dispersers die) is usually not only difficult to quantify but is also mostly irrelevant to the estimation of extinction risk. In most field studies, the estimates of survival rates would incorporate both types of mortality. The following simple example (from Akçakaya 1998) illustrates this point.

For this example, assume that 100 newborns in population A of a metapopulation are marked. In the next census, 1 year later, 50 marked 1-year olds are counted in population A and 10 marked 1-year olds are counted in population B. The other 40 individuals presumably died. The estimated survival rate of 0-year olds would be 0.6 [(50 + 10)/100], assuming that survival occurs before dispersal. The dispersal rate from population A to population B would be 0.167 (10 of the 60 survivors disperse to population B).

To check if these inputs are correct, one can go through what a simple metapopulation model will do with these numbers. When the model simulates the population dynamics with these inputs, it will start with 100 newborns. Of these, 60 will survive (0.6×100), and 16.7% of the survivors (10 of them) will disperse to population B, leaving 50 one-year-olds in population A, and adding 10 to the one-year-old class of population B, by the next census.

The parameterization (and the model prediction) will be the same, regardless of where the 40 individuals (that are not counted in the second census) have died. Suppose it is actually known that all 40 of them have died during dispersal (i.e., 50 individuals stayed in population A, 50 attempted to migrate, 10 succeeded in reaching population B). In this case, although the survival rate within the population and survival rate during dispersal are very different, the foregoing parameterization will still correctly describe the dynamics as observed. This is true because, in discrete time models, all rates are parameterized from one census to

the next. Note that in most cases it is impossible to know how many individuals attempted to disperse. Whether this information is available or not, using an overall survival rate (of resident and dispersers, from one census to the next) correctly accounts for dispersal mortality. When the goal of the model is to assess the viability of the population, rather than the exact distribution of individuals at any given time (between the two census times), the details about the relative mortality of dispersers and residents and where the dispersers died are not important from a modeling point of view.

The disadvantage of metapopulation models in terms of modeling dispersal is that they cannot predict which individual home ranges or territories will be occupied. Also, they cannot incorporate, or test the effect of, different types of dispersal behavior when such information is available.

Determining the spatial structure of metapopulation models

When dispersal rates are defined as the proportion of individuals moving among populations, they depend on the spatial arrangement of patches. In both metapopulation models and occupancy models, one task that may be difficult in some cases is the identification of populations. In these models, some parts of the landscape are considered habitat patches (that are or at least can potentially be occupied by populations) and the remainder as unsuitable habitat. In some cases, the species in question has a specific habitat requirement that has sharp boundaries, making patch identification quite straightforward. Many examples of patchy habitats (such as ponds in a forest, islands in an archipelago, woods in an agricultural landscape, or mountaintops in a desert) fit this category.

In other cases, the boundaries are not as clear cut (at least for human observers), and decisions about the location or even the total number of patches may be made differently by different researchers. What seems to humans as a homogeneous landscape may be perceived as a patchy and fragmented habitat by a species living there. Although it is usually easier to identify the spatial limits of a population than to model individual territories, identification of populations may be difficult when habitat patches from the species point of view do not correspond to clear-cut boundaries perceived by humans.

One type of spatially explicit metapopulation model circumvents this problem by defining populations based on a regular grid, each cell of which is modeled as a subpopulation of a metapopulation (e.g., Price and Gilpin 1996). The major limitation of this approach is that the regular pattern of the grid is often arbitrary and does not correspond to the distribution of the species or its habitat in the landscape. In addition, the size and number of populations are directly related to the resolution of the grid (the area that each cell covers on the ground). Thus, model results may be very sensitive to the resolution of the map.

The problem of the arbitrary definition of populations based on a grid can be addressed by determining the spatial

structure of a metapopulation (including size, location, and number of its populations) based on the characteristics of the landscape. This step requires studying the habitat requirements of the species in question because different species perceive the same landscape differently. The same landscape may represent a single population for a large mammal but a highly fragmented metapopulation for, say, an amphibian. Recognizing habitat patchiness from a species point of view requires utilization of spatial information on habitat suitability in coordination with metapopulation modeling. In the next section, I describe a method that expands spatially explicit metapopulation models by incorporating information about habitat relationships of the species and the characteristics of the landscape in which the metapopulations exists.

Habitat-based metapopulation model

This model is designed to link GIS-generated landscape data with a spatially structured metapopulation model for extinction risk assessment, viability analysis, reserve design, and wildlife management. The model operates in four steps. First, landscape data are analyzed to find the spatial structure of the habitat patches. The spatial structure is then exported to a metapopulation model. Second, temporal dynamics of the landscape (e.g., trends due to expected future habitat loss) are incorporated as time series of model parameters based on expected changes in the landscape. Third, the metapopulation model is built by combining spatial and demographic information. Fourth, simulations are run to estimate risks of extinction or decline and to predict the abundance and distribution of individuals in the metapopulation. The essential aspects of these four model components are summarized next.

Spatial structure

This method uses a habitat suitability map to determine the spatial structure of the metapopulation, including the number, size, and location of habitat patches in which subpopulations of the metapopulation live. The habitat suitability map can be calculated in a number of different ways, including statistical analyses (such as logistic regression) that find the relationship between the occurrence (or, density) of the species and the independent variables which describe its habitat requirements.

The habitat suitability (HS) map is then used to calculate the spatial structure of the metapopulation, based on species-specific characteristics such as the home range size, dispersal distance, and minimum habitat suitability for reproduction. Two important parameters provide the link between the HS map and the spatial structure of the metapopulation model and determine how the species perceives (or reacts to) the patchiness of the habitat. These parameters, threshold HS and neighborhood distance, are used by a patch-recognition process that delineates patches

on the HS map. *Threshold HS* is the minimum HS value below which the habitat is not suitable for reproduction or survival (although individuals may disperse or migrate through habitat that has a lower HS than this threshold); *neighborhood distance* is used to identify nearby cells that belong to the same patch. For an animal species, the neighborhood distance parameter may represent the foraging distance.

The patch-recognition process identifies clusters of suitable cells in a map. Suitable cells (as defined by the threshold HS) that are separated by a distance less than or equal to the neighborhood distance are regarded as being in the same patch. Thus, neighborhood distance determines the spatial separation above which suitable cells (or, clusters of suitable cells) are considered to belong to separate patches. A small neighborhood distance means that the species perceives the landscape as more patchy. Given the same HS map, a higher threshold HS or a smaller neighborhood distance will result in a greater number of smaller patches, i.e., a more patchy landscape. The result of this patch-recognition process is that groups of cells are combined into patches (Fig. 1). The HS values are based on the habitat requirements of the species; the threshold HS parameter is related to the minimum suitability of the habitat for the reproduction of the species; and the neighborhood distance parameter is related to the motility (e.g., foraging distance) of the species. Thus, the spatial structure of the metapopulation is based on the species-specific parameters, rather than the arbitrary resolution of the underlying map. Using maps with different resolutions changes the resolution of patch edges, but unlike the grid-based metapopulation models, it does not affect the number and size of the populations.

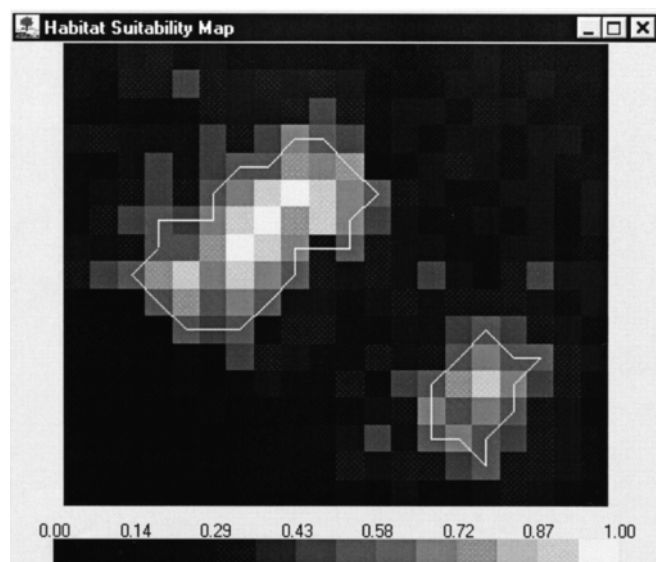


Fig. 1. Example of the result of patch-recognition. The habitat suitability (HS) map has values ranging from 0 (*dark*) to 1 (*light*). In this example, the patch-recognition algorithm has identified clusters of cells with $HS > 0.5$ that are within 1.5 cell lengths of each other (see text of details)

In addition to the location and number of habitat patches, the HS map (as well as other maps that contribute to the HS) can be used to calculate other parameters of the metapopulation model. For example, the carrying capacity of each patch can be based on the total HS in that patch. The total HS is calculated by adding the HS value of all cells in the patch. Thus, it incorporates both the size of the patch and the quality of the habitat within the patch. Other metapopulation model parameters, such as fecundities and survival rates, may be based on the average HS (total HS divided by the area of the patch).

Habitat dynamics

In cases where the habitat is expected to change in the future, the analysis of landscape structure as described here can be extended to account for these changes. This analysis can be done by calculating the spatial structure of the patches for each future time step and combining them in the form of a time series of demographic parameters.

One case in which the future changes in habitat dynamics are important is the assessment of the impact of planned logging of a forest or planned development that will gradually decrease the quality and size of habitat patches. In such a case, one or more of the habitat characteristics (such as amount of old-growth forest) that determine the suitability of habitat for the species in question may change through time in a deterministic way, whereas other characteristics (such as elevation) will remain the same. Using the approach outlined in the previous section for each time step creates a time series of metapopulation models. The changes in these models through time can be summarized as time series of deterministic changes in model parameters. For example, Akçakaya and Raphael (1998) analyzed the effect of timber harvest on the viability of the threatened northern spotted owl (*Strix occidentalis caurina*) metapopulation in the United States. In this model, the carrying capacity of each population was based on the total amount of old-growth forest in the habitat patch in which the population lived. The vital rates (survival rates and fecundity) of each population were based on the percentage of the old-growth forest in the habitat patch. Thus, the simulated timber harvest affected carrying capacities, survival rates, and fecundities of most populations in the metapopulation. The method of habitat analysis outlined earlier was used for each time step, and the results were summarized as time series of these population-specific parameters. This summary was then exported, together with the spatial structure, to a metapopulation model (see following).

Metapopulation model

In the third step, the spatial information for the metapopulation is combined with ecological (demographic) parameters of the species. The model may include any of the factors and parameters listed in Table 1. These are described next.

Table 1. Population-level and metapopulation-level factors incorporated into the model

Population dynamics	Metapopulation dynamics
Age/stage structure of each population	Metapopulation spatial structure
Vital rates (survival rates, fecundities)	Spatial variability in age structure
Density dependence in vital rates	Population-specific age/stage matrices
Logistic or Ricker (scramble competition)	Population-specific initial distributions
Beverton-Holt type (contest competition)	Dispersal rates among subpopulations
Ceiling (exponential growth to a ceiling)	Spatial variation
None (exponential growth or decline)	Age- or stage-specific
Allee effects	Density-dependent
Carrying capacities of populations	Distance-dependent or user-specified
Temporal trends in carrying capacities	Correlation of environmental fluctuations
Temporal trends in survival rates and fecundities	Distance-dependent spatial correlations
Variability	Regional catastrophes that affect:
Demographic stochasticity	Population abundances
Fluctuations in vital rates	Carrying capacities
Fluctuations in carrying capacities	Vital rates
Local catastrophes	Spatial variation in catastrophes

Age structure or *stage structure* within populations is modeled by a matrix model (Caswell 1989) that incorporates age- or stage-specific vital rates (survival rates and fecundities). Each population in the model can have a different matrix and different initial number of individuals in each age or stage.

Density dependence in population dynamics is modeled by modifying the mean values of survival rates and fecundities as a function of the population size (N). Density-dependent population growth may involve a simple ceiling model, logistic-like functions that describe contest- or scramble-type intraspecific competition (including Ricker and Beverton–Holt functions), Allee effects (i.e., density dependence at low population sizes), or Allee effects combined with density dependence at high population sizes (see Akçakaya et al. 1999). All density dependence functions are parameterized with the same set of parameters that include maximal growth rate (R_{\max}) and carrying capacity or ceiling (K), random variation in K , and temporal trend in K . Each population can have a different set of parameters.

Environmental stochasticity is modeled by random fluctuations in vital rates and in carrying capacities. The random fluctuations can be normal- or lognormal distributed, and can be correlated among populations. In addition to random variation, the average values of the vital rates can also change deterministically (e.g., a temporal trend). Such changes are specified as a time series of mean values. *Demographic stochasticity* is modeled by sampling the number of survivors from a binomial and the number of offspring from a Poisson distribution (Akçakaya 1991). *Catastrophes* (rare events with large impact such as fires and floods) can affect abundances (a proportion of all individuals die), vital rates (survival rates and fecundities are reduced after a catastrophe), or carrying capacities (which are reduced after a catastrophe). The spatial extent of catastrophes may be local or regional. The impact of catastrophes can be population specific (some populations may be more prone to, or more affected by catastrophes than other populations), or they may be stage specific (some stages, or even certain vital rates, may be more affected by catastrophes than others).

For example, seed mortality may be affected more than other vital rates from floods, whereas seed germination may be affected positively by fires.

Habitat loss and increase are modeled by specifying a rate of change for the carrying capacity through time, or a time series of carrying capacities for the affected populations. Habitat increase, in combination with catastrophes that affect carrying capacities, can be used to model, for instance, forest growth following disturbances such as fire or windfall.

Dispersal (migration) is modeled by specifying the proportion of individuals that move from each population to each other at every time step. These rates are input in the form of a dispersal matrix. In most cases, the rate of dispersal may be a function of the distance between source and target populations. This function can be used, together with the spatial structure of the metapopulation, to automatically specify the dispersal matrix. The matrix thus filled can be later edited to account for habitat corridors (by increasing the rate between specific pairs of populations) and for obstacles or geographic barriers to dispersal (by decreasing the rate). The dispersal rates may also be specified to be dependent on population size, to allow for density-dependent dispersal, or on the age or stage of the individuals, to allow for age- or stage-specific dispersal tendencies.

Correlations among populations describe the similarity of environmental patterns experienced by each population. This factor is important in the “rescue effect” in metapopulations: when fluctuations are spread over a number of separate populations, the overall risk faced by the metapopulation is reduced (see earlier). Correlated dynamics are modeled by sampling the vital rates of each population from a normal or lognormal distribution that is correlated with the vital rates of other populations according to a correlation matrix. Like dispersal rates, correlation may also depend on the distance between populations, because closer populations are more likely to experience similar environmental patterns. The two spatial factors, dispersal and correlation, have values that differ among each pair of patches according to their shapes and relative

geographic positions, thus making the model spatially structured.

Risk assessment

Because of the stochastic nature of the metapopulation model, most of the model results are related to risk assessment and report risk analytical measures. These results include the following:

- Risk of extinction (or decline) at the end of, or any time during, the simulated time period (for example, see Fig. 2)
- Risk of explosion (i.e., probability of exceeding a range of threshold population sizes) at the end of, or any time during, the simulated time period
- Cumulative time to extinction (or decline); i.e., cumulative probability that the metapopulation will fall below a specified threshold (or go extinct) at or before each time step
- Cumulative time to explosion; i.e., cumulative probability that the metapopulation will exceed a specified threshold at or before each time step

The three dimensions that define the viability of a metapopulation are (i) the probability that a decline will occur (or the metapopulation will become extinct), (ii) the amount of decline, if it does occur, and (iii) the time it will take the metapopulation to decline to this level (Akçakaya 1992). By giving the risk of decline to various levels (as well as risk of total extinction), and the whole distribution of time to extinction or decline (in addition to the median time

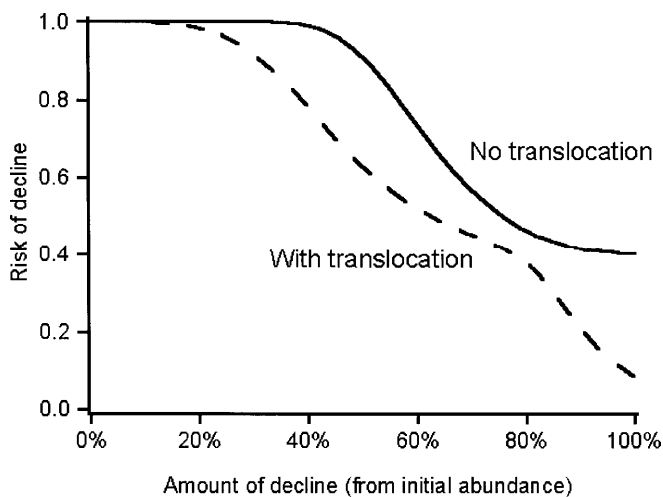


Fig. 2. Example of risk assessment with the habitat-based metapopulation model. The curves show the probability of a decline in the metapopulation of the helmeted honeyeater within 50 years, as a function of the amount of decline, with and without translocation of 10 adults to a new population (based on Akçakaya et al. 1995). Amount of decline is expressed as percent of initial abundance. Thus, 0% corresponds to no decline and 100% corresponds to extinction. In this particular model, translocation decreased the risk of extinction from about 0.4 to less than 0.1, and decreased the risk of an 80% decline from about 0.45 to about 0.35

to extinction), these results allow a complete characterization of the metapopulation viability.

The model can be run several times, to analyze the sensitivity of results to input parameters by varying them for each run; this allows evaluation of management options, or assessment of anthropogenic impact by comparing outputs from simulations with parameters for impacted and nonimpacted situations.

Assumptions and limitations

This model, as any model, makes a number of assumptions, and has certain technical limitations. These are summarized next.

The method of linking landscape data to the metapopulation model allows only one-way interaction between the landscape data and the metapopulation model. Thus, habitat affects population dynamics, but populations do not affect the quality of their habitat explicitly. The impact of population dynamics on habitat quality is one of the mechanisms of density dependence, which can be modeled by using the “scramble”-type density dependence function. Thus, the effect of metapopulation dynamics on habitat can be implicitly modeled.

The model is expressed in discrete time; it does not model continuous-time processes.

It can only address single species; it cannot explicitly represent competition, predation, mutualism, or other interspecific interactions. These interactions can be modeled as constant, fluctuating, or cyclic influences on demographic parameters.

Genetic effects are not explicitly modeled, but they can be incorporated through their effects on population dynamics, for instance, by modeling density dependence with Allee effects.

Population dynamics within each population is modeled with a stage- or age-structured matrix model. The model may also contain nonlinearities describing density dependence relations between matrix elements and the population abundance, providing flexibility. However, complex structures (for example, those requiring complicated rules representing social structure) cannot be incorporated unless they can be simplified to a matrix model.

In addition to these limitations, any particular application of this method will have a set of assumptions characterized by the values of the parameters. As with any other program or model, how realistic the model is largely depends on the amount and type of data.

Applications

The methodology described here has been implemented as the PVA software RAMAS GIS (Akçakaya 1998). It has been used in assessing the effectiveness of translocating individuals as a management option for the endangered helmeted honeyeater, *Lichenostomus melanops cassidix*, in

Australia (Akçakaya et al. 1995). Analyses with this model indicated that translocating helmeted honeyeaters to a new population may reduce the overall risk of extinction of the metapopulation (Fig. 2; see Akçakaya et al. 1995 for details).

Recently, the model was applied to the metapopulation of the threatened northern spotted owl in the United States (Akçakaya and Raphael 1998; see *Habitat dynamics*). This application focused on the effect of uncertainty in model parameters on the ability of the model to assess human impact. Despite the uncertainties, using relative risks and evaluating the impact under each assumption allowed the model to reliably detect human impact.

The model has also been applied to the threatened California gnatcatcher, *Poliophtila californica californica* (Akçakaya and Atwood 1997). The habitat data in this study included raster maps of coastal sage scrub vegetation, elevation, slope, aspect, distance from grasslands, distance from trees, and distance from wetlands. These data were used in a stepwise logistic regression in which the gnatcatcher observations were the dependent variable and values from habitat maps were independent variables. The resulting habitat suitability map was then validated by estimating the regression function from half the landscape and using this function to predict the habitat suitability for known locations in the other half. The validated habitat suitability map was analyzed to calculate the spatial structure of the species metapopulation (i.e., the number, size, carrying capacity, and location of its subpopulations), based on the distribution and quality of the habitat.

At the population level, the model for the California gnatcatcher incorporated demographic data on survival, reproduction, and environmental variability for each population inhabiting a habitat patch. At the regional (metapopulation) level, it incorporated data on spatial factors including dispersal among patches, catastrophes (Akçakaya and Baur 1996), and spatial correlation of environmental fluctuations among the patches (LaHaye et al. 1994). The gnatcatcher metapopulation model was used to perform a risk assessment that incorporated the effects of natural variability, as well as the uncertainties in model structure and parameters resulting from lack of knowledge and measurement errors.

Discussion

Both spatially explicit, individual-based models and grid-based metapopulation models have the disadvantage of being sensitive to the arbitrary grid structure of the underlying maps, which determine spatial structure of territories for the former and of the populations for the latter. Although it is possible to develop individual-based spatially explicit models without this drawback, this requires a lot more information than is available for most species.

The method described in this article for determining the spatial structure of metapopulation models, based on the structure of the landscape and the habitat requirements of

the species in question, provides an alternative to the individual-based and grid-based approaches to modeling spatial structure. The method allows the estimation of the spatial structure as well as population-specific demographic parameters (such as carrying capacity, survival, and fecundity) based on habitat maps. It also allows incorporation of variability in the form of deterministically changing mean values, stochastic environmental fluctuations, and chance events at the individual level (demographic stochasticity), as well as rare catastrophic events.

One of the most important considerations in developing models for PVA is uncertainty. Parameters and structure of models used in PVAs are often estimated on the basis of insufficient data, resulting in large uncertainties. Stochastic demographic models can be used to systematically incorporate uncertainties resulting from lack of information or measurement error, in addition to variabilities from environmental fluctuations and demographic stochasticity. When PVAs are used for impact assessment or making management decisions, accounting for these two fundamentally different types of variability allows the models to be more sensitive to the impact or the management action. Results of recent habitat-based PVAs were sensitive to the effects of alternative management actions or human impact, despite considerable model uncertainty (e.g., Akçakaya and Raphael 1998). These results suggest that in most cases it is possible to make robust assessments and management decisions despite the inevitable uncertainties.

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