

Linking population-level risk assessment with landscape and habitat models

H. Resit Akçakaya

Applied Biomathematics, 100 North Country Road, Setauket, NY 11733

Abstract

Ecological risk assessment at the population level often involves predicting the effects of a particular change in the land-use patterns on the viability of native species. A common method of addressing such questions is modeling the metapopulation dynamics of the species in the landscape. However, the landscape and, as a result, the spatial structure of the metapopulation usually do not remain unchanged, thus the assessment of viability must incorporate the dynamic nature of the landscape. A new link being developed between a metapopulation modeling program (RAMAS), and a landscape dynamics program (LANDIS) will allow the transitional dynamics of the landscape to be incorporated into assessment of viability and threat. This approach combines methods of landscape prediction with those of metapopulation simulation. The link between the landscape model and metapopulation model is provided by statistical models of habitat suitability for the species in focus.

Key words: metapopulation model; viability; landscape model; risk assessment; habitat fragmentation; patch dynamics; RAMAS; LANDIS

Introduction

Distribution and abundance of threatened and endangered species are adversely affected by changes in the land-use patterns that cause habitat loss, habitat fragmentation, pollution or other disturbances.

The natural heterogeneity of habitats, as well as habitat loss and fragmentation as a result of human impact, cause most species to exist in a number of relatively isolated populations that may occasionally exchange individuals (a *metapopulation*). The metapopulation concept is one of the most important paradigms in conservation biology because of the need to evaluate management options and human impacts that are relevant at the metapopulation level (Hanski 1989; Gilpin and Hanski 1991; Burgman et al.1993). Management options relevant at the metapopulation level include reserve design, translocations and reintroductions; human impacts relevant at the metapopulation level include increased fragmentation, isolation, and dispersal barriers. Because of the interdependence of the dynamics of populations, dynamic changes at the metapopulation

level can be modeled only by considering the dynamics of all population simultaneously in a metapopulation model, instead of extrapolating from multiple single population models.

Designing nature reserves, as well as assessing anthropogenic impact on native species, often involves predicting the effects of a particular change in land-use patterns. For example, to assess the viability of an amphibian population in a series of ponds and lakes, it is necessary to model the metapopulation dynamics of these species in this patchy habitat. Or, to assess the persistence of a bird species dependent on old-growth forests in a proposed set of habitat conservation areas, it is necessary to model the metapopulation dynamics in this fragmented habitat.

There are several types of models or assessment methods developed for these cases. Some of these methods (such as habitat suitability indices) are based only on the availability of suitable habitat, and do not consider demographic factors such as reproduction, survival and dispersal. Populations impacted by human activities such as pollution, hunting, harvest, and fragmentation, can decline sharply or even go extinct even if there is suitable habitat remaining. Thus, methods that ignore demographic factors are not likely to give realistic assessment of species threatened by human impact.

Other methods are based on the dynamics of metapopulations inhabiting patchy or fragmented landscapes (see reviews by Gilpin and Hanski 1991; Breininger et al. 2000; Akçakaya and Sjögren-Gulve 2000). These methods incorporate the spatial structure (location and size of habitat patches), as well as age and stage structured dynamics within each population inhabiting a habitat patch (see Akçakaya 2000 for a review). However, there are two interrelated issues in using metapopulation models to assess viability of species in fragmented habitats.

- In metapopulation models, some parts of the landscape are considered habitat patches and the remainder as unsuitable habitat only used for dispersal. In many cases, the habitat of species in question does not have sharp boundaries, making the identification of habitat patches arbitrary.
- In most impacted landscapes, the habitat patches do not remain static. Thus, the number, location and size of habitat patches, as well as the demographic parameters of the populations inhabiting them, change through time. However, metapopulation models are based on static landscapes, and do not incorporate patch dynamics.

In the following sections, I describe a model designed to address these two deficiencies of metapopulation models. The first issue has been addressed in a metapopulation model that incorporates habitat requirement and determines the spatial structure of the metapopulation based on distribution of suitable habitat. This model is summarized in the next section. The second issue is being addressed in an extension of this model that is currently being developed. Addressing this issue involves identifying and simulating dynamic changes in the spatial structure of patches and linking the metapopulation model to a landscape model that predicts such changes in the landscape. These aspects of the current development are discussed in later sections.

Incorporating habitat requirements

An important step in developing metapopulation models is the identification of populations. Some species have habitat requirement with sharp boundaries in the landscape, making patch identification quite straightforward. An amphibian inhabiting ponds in a forest, a reptile inhabiting islands in an archipelago, a warbler inhabiting woodlots in an agricultural landscape, and a mountain sheep inhabiting mountaintops in a desert are examples of such cases.

Habitats for other species do not have such clear-cut boundaries (at least for human observers). Many species respond to more than one habitat variable, and thus the borders of patches of suitable habitat may be determined by the interaction among factors such as elevation, slope, aspect, vegetation, distance from water, etc. When such species are modeled, the location of patches may be arbitrary.

One method of avoiding arbitrary definition of subpopulations is to divide the landscape into a regular grid, and to regard each cell as a separate subpopulation (e.g., see Price and Gilpin 1996). However, the regular pattern of the grid is itself arbitrary and often does not correspond to the distribution of the species or its habitat in the landscape. In addition, with this approach the size and number of populations become a function of the resolution of the grid (the size of each cell on the ground). Consequently, model results may be sensitive to the resolution of the underlying map.

To avoid the problem of arbitrary definition of populations, we developed a method that determines the spatial structure of a metapopulation (including size, location and number of its populations) based on the characteristics of the landscape (Akçakaya 1998, 2000). This method involves studying the habitat requirements of the species in question, because different species will perceive the same landscape differently. The method expands spatially explicit metapopulation models by incorporating information about habitat relationships of the species and the characteristics of the landscape in which the metapopulation exists.

The model operates in the steps described below.

1. Landscape data are analyzed to create a habitat suitability map. This analysis starts with maps of habitat variables important for the species. Statistical methods such as multiple logistic regression are used to calculate a relationship between these variables and the presence or abundance of the species. This relationship is then used to create a habitat suitability map. The value in each cell of this map is calculated with the regression equation, using the values of the habitat variables at that location.
2. The habitat suitability (HS) map is used to calculate the spatial structure of the metapopulation by identifying clusters of suitable cells. This calculation uses two parameters. *Threshold HS* is the minimum HS value below which the habitat is not suitable for reproduction and/or survival (although it may be suitable for dispersal). *Neighborhood distance* is used to identify nearby cells that belong to the same patch. Suitable cells (as defined by the threshold HS) that are separated by a distance less than or equal to the neighborhood distance are regarded to be in the same patch. A small neighborhood distance means that the species perceives the landscape as more patchy. Given the same HS map, a higher threshold HS and/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.
3. For each patch, parameters of a population inhabiting that patch are calculated. These parameters may include carrying capacity (which may, for example, depend on total value of habitat suitability). The distance among the patches may be used to calculate the rate of dispersal among patches.
4. Temporal dynamics of the landscape (e.g., trends due to expected future habitat loss) are incorporated as a time series of model parameters based on expected changes in the landscape (see below).
5. The metapopulation model is built by combining spatial and demographic information. The type of demographic data used to parameterize the model includes census, mark-recapture, and nest surveys. These data are used to develop stochastic, age- or stage-structured models for each population.
6. Simulations are run to estimate risks of extinction or decline, and to predict the abundance and distribution of individuals in the metapopulation.

This method has been applied to develop a habitat model and to analyze factors affecting the risk of decline of the threatened California Gnatcatcher (Akçakaya and Atwood 1997); to evaluate the effects of habitat quality and connectivity on the threatened Florida Scrub-Jay (Root 1998); to assess the effect of timber harvest on the viability of the threatened Northern Spotted

Owl (Akçakaya and Raphael 1998); and to evaluate management options for the endangered Helmeted Honeyeater (Akçakaya et al. 1995).

Identifying patch dynamics

The assessment of viability must incorporate the changes in habitat patches. Such changes may be due to drought (smaller ponds disappearing, larger ones possibly splitting into smaller ones), or above-average rainfall (new ponds appearing, small and close-by ponds merging into large ones). Habitat patches may also change as a result of various types of human actions (habitat alteration, pollution, etc.) that create or destroy habitat.

In landscapes with frequent disturbances, the habitat patches may disappear within a short period, comparable to the generation time of the species dependent on the habitat in these patches. The viability of these species depends on the balance between the rate of appearance and spatial arrangement of patches on the one hand, and the dispersal ability and reproductive capacity of the species on the other. Thus, neither habitat dynamics nor demographic properties alone can tell whether, for example, a certain forest management plan will result in a viable population. The only way such an assessment can be made is by considering both habitat dynamics and population dynamics simultaneously. The transitional dynamics of the landscape can be incorporated into assessment of viability and threat by combining methods of landscape prediction with those of metapopulation simulation.

In cases where the habitat is expected to change in the future, the analysis of landscape structure as described above can be extended to account for these changes. This 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.

However, demographic parameters of individual populations are not the only aspects of a metapopulation model that change as a result of the changes in the landscape. More fundamentally, the spatial structure of the metapopulation can change. When the spatial structure of a metapopulation is analyzed based on habitat variables, with the method outlined in the previous section, the following kinds of changes are possible for each patch in the landscape:

- (1) No change (remain as is)
- (2) Decrease in size (e.g., because of habitat degradation)
- (3) Increase in size (e.g., because of habitat growth)
- (4) Split into two or more distinct patches (fragmentation)
- (5) Merge with one or more other patches into a single patch (e.g., because of habitat growth in the “matrix”)
- (6) Disappear (habitat loss)
- (7) Appear (e.g., as a result of increase in habitat suitability)

The method we are developing is based on a comparison of two raster maps that represent the spatial structure of patches in 2 consecutive time steps. The value of each cell in this raster map is either zero (no patch) or the patch identification number. An example is given in Figure 1, which shows the same landscape in two consecutive time steps. In the first time step (left map), 8 habitat patches are identified. The changes to these habitat patches in the second time step (right map) are summarized in Table 1.

By comparing 2 consecutive raster maps cell-by-cell, the method we developed first fills an “overlap” matrix. The element (i, j) of this matrix gives the amount (in number of cells) of the overlap between patch j in the old map (previous time step) and patch i in the new map (current time step). The overlap matrix for the example in Figure 1 is given in Table 2. Columns refer to the old patch structure, and rows refer to the new patch structure.

The last row gives the area of patches in the first time step. The difference between the total

“overlap” in a column, and the last row stems from a decrease in the patch size (for example, column 3), including the disappearance of the patch (for example, column 2).

The last column gives the area of the patches in the second time step. The difference between the total “overlap” in a row and the last column stems from an increase in patch size (for example, row 7), or a patch that appears in the second time step (as in row 4).

An analysis of this matrix determines which of the 7 events listed above applies to each patch existing in any of the two maps. Multiple non-zero overlap values in a column represent a patch that splits, while multiple non-zero overlap values in a row represent merging patches. An all-zero overlap column (e.g., 2) represents a disappearing patch, while an all-zero overlap row (e.g., 4) represents an appearing patch.

The next step is re-ordering the patches to facilitate modeling their dynamics (Figure 2). This results in a unique ID for each patch that ever existed (Table 3). Thus, for example, the patch that appeared in the second time step, and that was labeled as 4 in Figure 1 is now labeled 11 in Figure 2. Similarly, the new patches that split from patch 1 are given new ID labels. This step is necessary for the algorithm to correctly identify the lineage of all the patches, and to keep a record of all patch changes such as splits and merges.

Simulating dynamic patches

Once the lineage of the patches is determined, the next step is the simulation of the dynamics of a species inhabiting these patches. It is reasonable to assume that in most cases, the changes in the landscape (vegetation succession, habitat fragmentation, etc.) will occur at time scales slower than the time scale of population dynamics (reproduction and mortality) of the species in question. While for most species a yearly time scale for population dynamics is appropriate, it may be sufficient to update the patch structure every 3 to 10 years. Even then, simulating dynamic changes in the spatial structure of habitat patches is a complicated problem because of the following reason.

For each simulation, the metapopulation model is typically run thousands of times (replications) in order to have a representative sample of random variables such as survivals and fecundities that change stochastically due to environmental fluctuations. Each replication simulates the dynamics of the metapopulation for tens to hundreds of time steps (usually years), with the same parameters, but a different sequence of random numbers used to simulate environmental fluctuations. Each run must use the same patch structure, or series of structures if the patches are dynamic. If the dynamic changes in the landscape involve a changing number of populations (e.g., through fragmentation or habitat growth), various model parameters and structures must also change within a single replication. For example, dispersal among populations is modeled with a dispersal matrix, and spatial correlation among the fluctuations of different populations is modeled with a correlation matrix. Each row and column of these matrices represent one population inhabiting one habitat patch. When patches split and merge in time (within a single replication), the structure of these matrices, as well as many other model parameters, must be changed as well. This process is time-consuming, very complicated to implement within the existing program and potentially error-prone.

Instead of updating the spatial structure of the metapopulation, we developed an alternative approach. The algorithm we developed starts with the most complex structure (largest number of patches) ever occurring during the simulation. It sets the carrying capacity (K) and the initial abundance (N) to zero for those patches not existing at time step 0 (because they later split from an existing patch). It sets $K=0$ and $N=0$ when patches disappear at later time steps (because of habitat loss or because they merge with another patch). For each time step where the spatial structure changes, it simulates these changes by changing the carrying capacity of patches. These

can be combined with increasing or decreasing habitat by changing the total K from “previous” to “current” time step.

Number of individuals in each stage is also divided or summed at the same time as the patches split or merge. Ignoring this would create spurious declines in abundance whenever a patch splits or several patches merge.

When non-existing patches are modeled with $K=0$, dispersal to these patches does not make sense. This is because in many cases these patches are just “placeholders” for patches that will split from others in the next time step. However, the metapopulation model has a dispersal matrix with a fixed dimension (the number of populations). Using the same dispersal matrix would model dispersers into non-existing patches (with $K=0$). This would make the model work (incorrectly) as if these patches exist as sinks, causing an overestimation of the extinction risk of the metapopulation.

This problem can be solved by changing the dispersal matrix at each time step, but this is cumbersome. Instead, we added a density-dependent dispersal feature that makes dispersal dependent on the carrying capacity of the target population. This dependence is specified with a population-specific function that governs the immigration into that population. The function has a single parameter (“Target K ”), which is the value of the carrying capacity of the target patch below which immigration into the patch is reduced as a linear function of the carrying capacity.

Integrating metapopulation and landscape models

There are a number of approaches to modeling metapopulation dynamics (Gilpin and Hanski 1991; Breininger et al. 2000). When these models incorporate natural variability, they are often used to assess the viability of populations and species. Population viability analysis (PVA) evaluates the threats faced by populations, their risks of extinction or decline, and their chances for recovery, based on species-specific data and models (Boyce 1992; Burgman et al. 1993). PVA based on single-species modeling provides a rigorous methodology that can be validated, can incorporate uncertainties and natural variabilities, and can make predictions that are relevant to conservation goals (Akçakaya and Sjögren-Gulve 2000; Brook et al. 2000; Akçakaya 2000).

There are also several approaches to studying and predicting changes in landscape and land-use. These approaches are based on modeling the dynamics of vegetation, based on natural processes such as disturbances (fire, floods, wind, etc.) and succession, and human impacts such as timber harvest and pollution.

In future developments of the methods described above, we aim to integrate the metapopulation and landscape modeling approaches, in order to make extinction risk assessments for species and populations based on expected habitat changes. This integration will overcome the deficiencies of the two approaches when taken in isolation: metapopulation models generally ignore specific predictions about future habitat patterns, and landscape models do not make predictions about species viability or assess extinction risks. To achieve this integration, we are developing software that will combine a model that predicts landscape patterns and changes in the structure of a species' habitat, with a metapopulation model that incorporates dynamic spatial structure and estimates the extinction risk. The resulting software will utilize information on both land-use patterns and the structure of a species' habitat, and data on the demography and ecology of the species.

In future versions of the program, we will integrate the landscape model LANDIS with the metapopulation model RAMAS. LANDIS (Mladenoff et al. 1996) predicts changes in forest stand structure, including species composition, dominant tree species, and age distribution. RAMAS (Akçakaya 1998) simulates the dynamics of species that inhabit distinct habitat patches. Both models are flexible, i.e., they can be (and have been) easily customized by the users to apply to different landscapes and species.

Discussion

Ecological risk assessment can be done at various levels. At or below the level of the individual organism, the methods of toxicology and physiology allow realistic and reliable assessment of the effects of environmental impacts. However, the relevance of these effects to the ecology of the impacted area can only be determined by considering interactions at higher levels. Thus, assessments at or below the level of the individual may be reliable, but they are rarely relevant.

At the other end of the spectrum are community and ecosystem levels. Assessments at these levels are highly relevant because of their comprehensiveness: the ultimate goal of most conservation and environmental protection efforts is the preservation of well-functioning, representative, natural ecosystems. However, the complexity of interactions among species and our lack of understanding of community and ecosystem dynamics make these assessments intractable. The contingencies and complexities involved may make it impossible to find general laws in ecosystem ecology (Lawton 1999). Currently, ecosystem-based approaches to practical problems in conservation suffer from vagueness and circularity (Goldstein 1999).

Population-level risk assessment provides a practical compromise between the individual and the ecosystem levels. Although it has many unresolved aspects, the theory of single-species dynamics is more complete than that of species interactions and community dynamics. The single-species approach is obviously not completely satisfactory, and conservation biologists recognize the need for preserving whole ecosystems. Nevertheless, until there are more rigorous definitions of concepts such as "biodiversity" and "ecosystem", well-defined endpoints for assessing "ecosystem viability", and models of trophic interactions that theoreticians can agree on, it seems that single-species dynamics will remain one of the major practical methods for conservation purposes. Despite its shortcomings, the single-species approach to conservation has important advantages when it focuses on endangered species, which, by the virtue of being under threat, are usually considered to be indicators of ecosystem stress. In addition, the endangered species that most conservation efforts are concentrated on require large areas of undisturbed habitat, which may make them "umbrella species" that secure many other species. Finally, the single-species approach is implicit in the Endangered Species Act, which is one of the most important legal tools for protecting species and their habitats in the United States.

One of the major limitations of the single-species approach is that species do not exist in isolation of other species. The most obvious dependence between species is the dependence of an animal species on plants that make up its habitat. The methods described in this paper expand population-level risk assessment by incorporating habitat requirements and dynamics of the landscapes in which the species live. Thus, these methods expand the single-species approach by linking a model that predicts changes in the forest landscape with a model that predicts the effect of such changes on the viability of a species that depend on this forest landscape. Such landscape changes often involve multiple species. Thus, although the viability predictions still focus on a single-species, the model is based on changes in multiple species. When completed, the integrated model will be used in predicting the viability of metapopulations inhabiting fragmented landscapes in which the patch structure may be changing due to human impacts or as a result of natural processes and disturbances.

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Table 1. Habitat patches changes represented in Figure 1.

Old ID	Fate	New ID
1	splits into 3 patches	1, 2, 3
2	disappears	none
3	remains (with decrease)	6
4	merges with 2 others	5
5	merges with 2 others	5
6	remains (with increase)	7
7	merges with 2 others	5
8	remains (same size)	8
none	appears	4

Table 2. The overlap matrix for the change in patch structures given in Figure 1.

	1	2	3	4	5	6	7	8	Area
1	1387	0	0	0	0	0	0	0	1387
2	1110	0	0	0	0	0	0	0	1110
3	1625	0	0	0	0	0	0	0	1625
4	0	0	0	0	0	0	0	0	371
5	0	0	0	575	1063	0	1319	0	7662
6	0	0	410	0	0	0	0	0	410
7	0	0	0	0	0	685	0	0	2434
8	0	0	0	0	0	0	0	1038	1038
Area	7194	4202	1073	575	1063	685	1319	1038	

Table 3. Habitat patches changes represented in Figure 2.

ID	Old area	Fate	New area
1	7194	split	1387
9	0		1110
10	0		1625
2	4202	disappears	0
3	1073	remains (smaller)	410
4	575	merge	0
5	1063		7662
7	1319		0
6	685	remains (larger)	2434
8	1038	remains (same size)	1038
11	0	appears	371

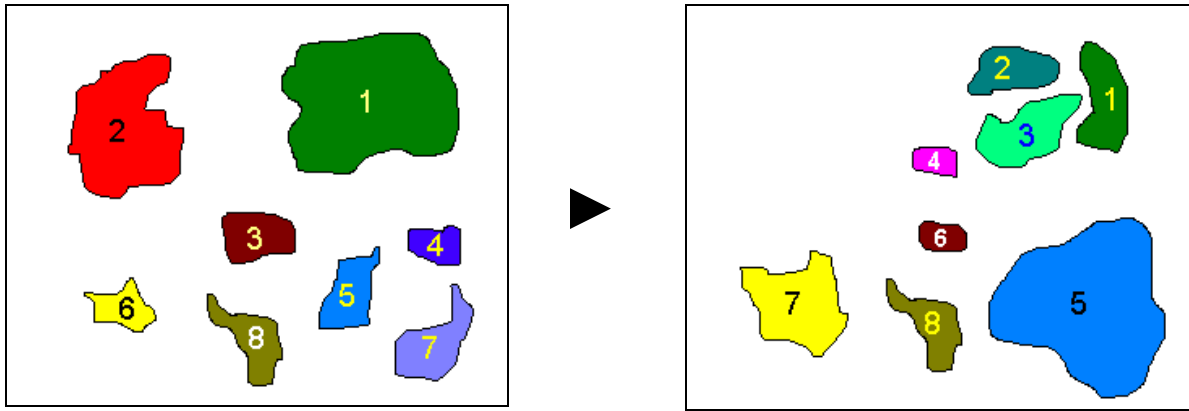


Figure 1. The structure of habitat patches in a hypothetical landscape in two consecutive time steps.

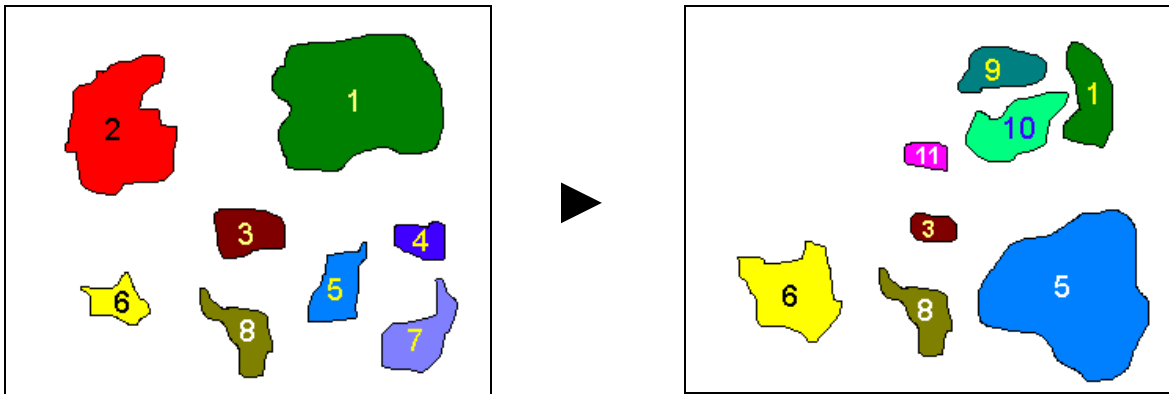


Figure 2. The patch structure in Figure 1 with re-numbered patch ID labels.