A simple model of species viability in stochastic landscapes

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Abstract

Theoretical models predict that stochasticity is an important agent for extinction in populations and metapopulations. Such models usually assume the habitat itself to be static. Yet in nature, habitat patches are not static; they turn over because of disturbance and succession. Here, I examine species viability in model landscapes where habitat patches are dynamic. To simplify the problem, I assume a perfect species with no demographic or dispersal constraints other than carrying capacity. The stochastic patch model that I developed has the following assumptions: 1) Each landscape has three stationary traits: a rate of patch births, a mean patch size (or carrying capacity per patch) and a mean patch lifetime; 2) Patch dynamics have two kinds of stochasticity: Patch stochasticity is due to the discrete nature of patches and organisms. Landscape stochasticity is due to variability in the traits mentioned above; 3) Patch lifetimes are either fixed (in the succession version of the model), or geometrically distributed (in the disturbance version). Numerical simulation showed that extinction risk had a threshold when either patch formation or patch size were reduced in steps. The position of the threshold (in terms of mean capacity of the landscape) varied over at least three orders of magnitude, as an effect of: 1) whether patch birth rate or patch size was changed; 2) landscape stochasticity in each variable; and 3) whether succession or disturbance was assumed. The analysis suggests some conceptual links between viability concepts and hierarchy theory. The results predict a variety of ways in which disturbance regimes might be designed so as to incorporate species into managed landscapes. In particular, if disturbances are more evenly distributed in time and space, extinction risk may be reduced. However, realistic models are needed to examine the situation more precisely.

Keywords: biodiversity, landscape, patch dynamics, viability, disturbance regimes, succession

Introduction

Ecologists have long recognized that stochasticity in birth-death processes is a cause of species extinctions. Recently, Lande (1993) examined stochasticity in population-level events (the births and deaths of individual organisms). He described scaling relationships between extinction risk and three distinct forms of randomness: demographic, environmental, and catastrophic. Hanski (1991) sketched a comparable scheme for metapopulation-level events (the establishment and extinction of entire populations). The sketch implied that the forms described by Lande (1993) may generalize to other levels of biological organization.

Habitat patches may be one such level, because patches typically have "births" and "deaths" arising from the interplay of disturbance and succession. Assume simply that a species' abundance is bounded by the abundance of its habitat. If the number of patches goes to zero temporarily, extinction occurs. In this paper, I develop a simple theoretical model to explore the relationship between patch dynamics, stochasticity, and species viability. Better understanding should aid in making a conceptual link between species viability concepts, on the one hand, and ecosystem dynamics, on the other. Viability is closely related to population regulation, often defined as fluctuations within limits, where the lower limit is greater than zero. The hierarchy theory of ecosystems has a parallel concept of incorporation, that describes regulation of ecosystem attributes (O'Neill et al 1986). Since amount of habitat is such an attribute, incorporation may be relevant to species whose fluctuations are driven by patch dynamics.

References

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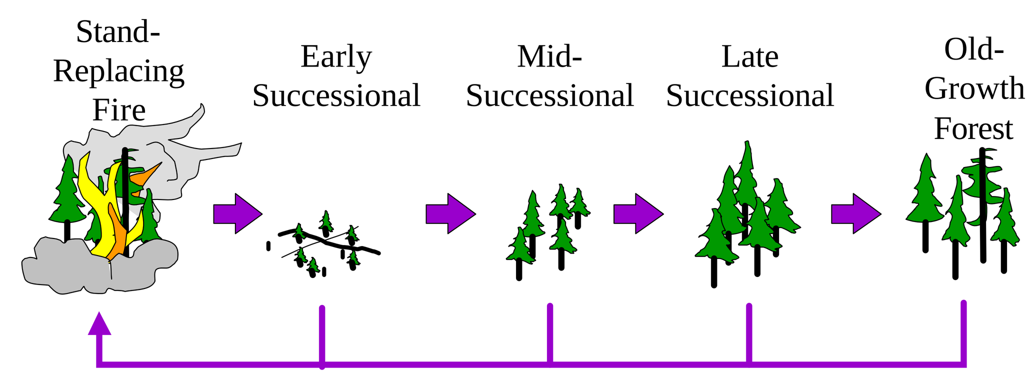
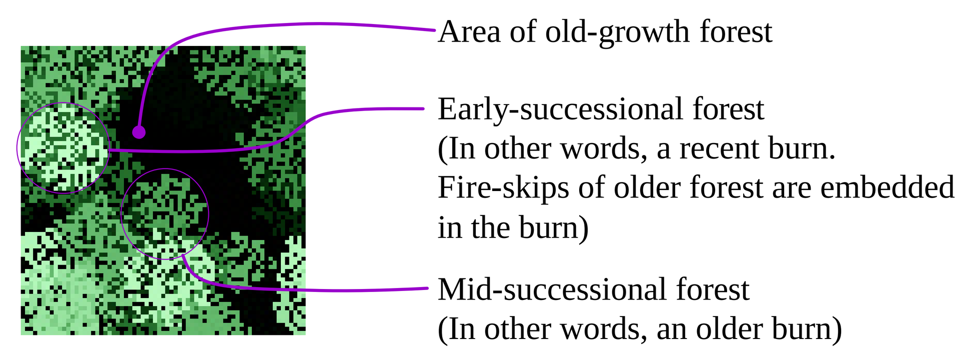
The Question

Patch Dynamics

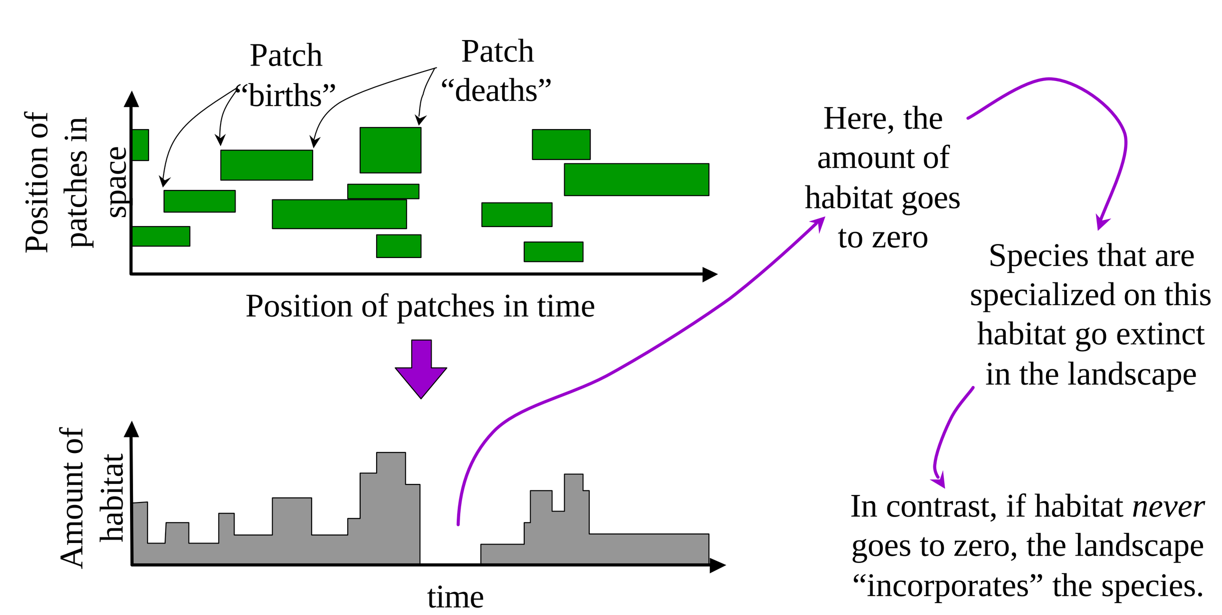
Imagine a landscape patch with disturbance and succession:



Now imagine an entire landscape composed of such patches. The landscape is under a natural disturbance regime:



The quantity of each habitat type (early, mid, late, old-growth) fluctuates stochastically due to the disturbance regime. Consider a "population" of patches of a particular habitat type. How does it vary with time, and what aspects of the disturbance regime determine whether the number of patches ever goes to zero?



Deterministic model

I use a deterministic model as a reference case. The model is adapted from Levin and Paine (1974):

$$\frac{dH}{dt} = ab - \frac{H}{s}$$

where
H = amount of habitat
a = mean area per patch
b = patch "birth" rate
s = mean patch "lifetime"

Assuming a, b, and s to be constant, the amount of habitat approaches an equilibrium value, the **mean capacity** of the landscape:

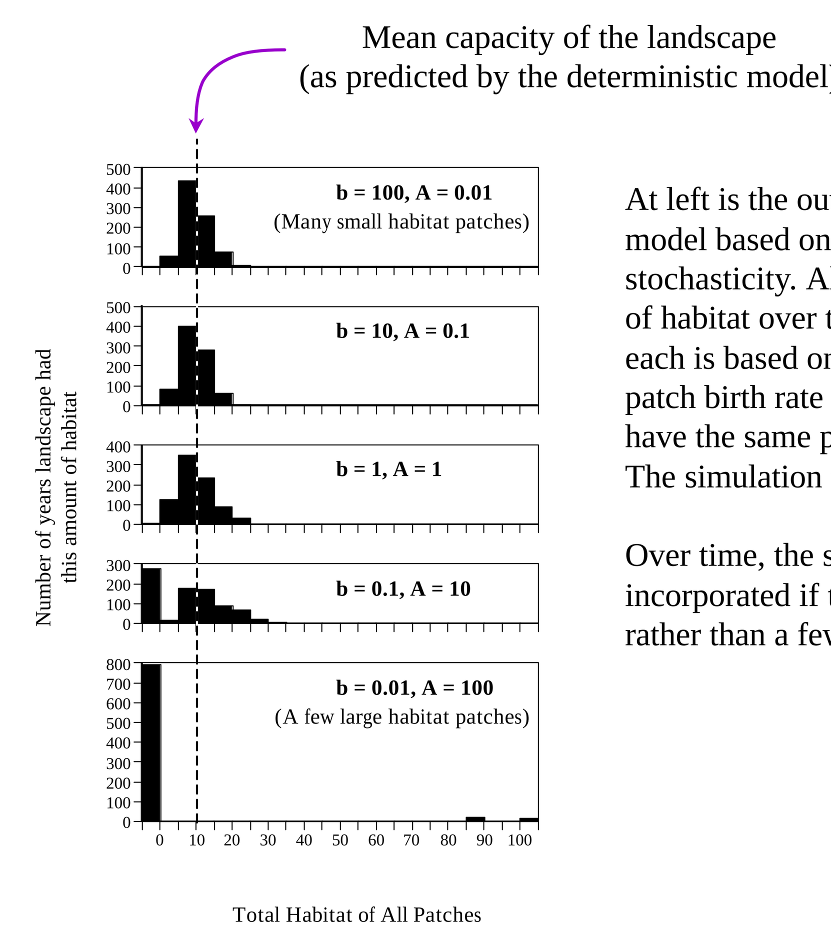
$$H_{\text{equil}} = bsa$$

In the deterministic model, the the landscape always incorporates the species, unless b, s, or a is zero.

Patch Stochasticity

Patch stochasticity is random events in the creation of individual patches. To add it to the model, assume:

Patch-births per year:	Drawn from a Poisson distribution with mean *b*.
Size of each patch:	Drawn from a Poisson distribution with mean *a*.
Lifetime of each patch:	Fixed at *s*.



At left is the output of a simple simulation model based on the above assumptions of stochasticity. All have the same mean amount of habitat over time (10 home ranges), but each is based on a different balance between patch birth rate (*b*) and patch size (*A*). All have the same patch lifetime (*s* = 10 years). The simulation was run for 1000 years.

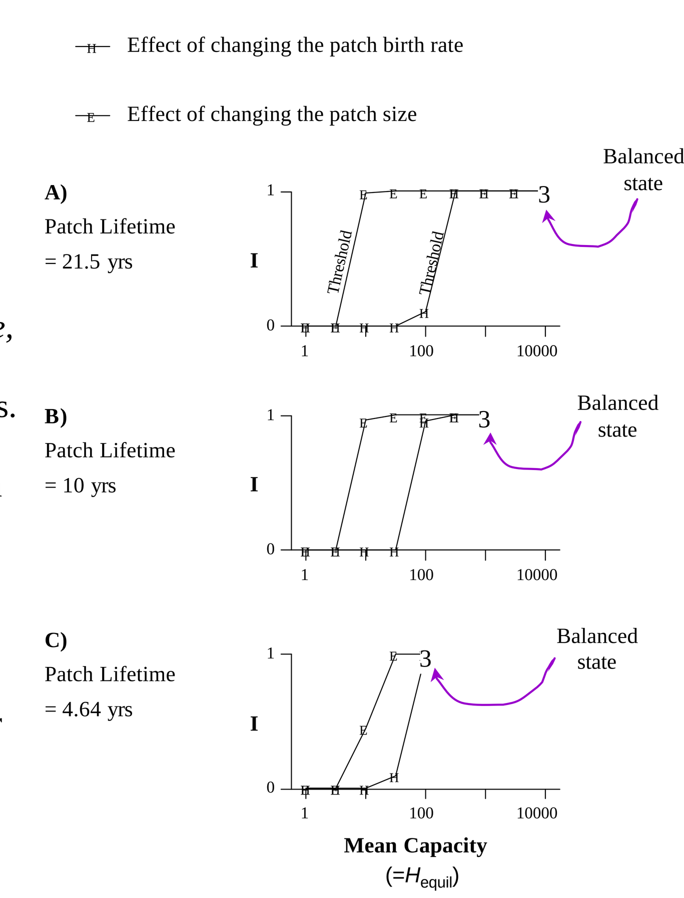
Over time, the species is more likely to be incorporated if there are many small patches rather than a few large ones.

At right are results for 3 model landscapes. In each case, I initiated the landscape in a balanced state (b = s= a). Then, the landscape's total capacity was decreased by decreasing either the patch birth rate (b) or the patch size (a).

The *y*-axis shows the *incorporation score*, the probability that habitat never goes to zero during 1000 years of patch dynamics.

In all cases, the incorporation score had a distinct **threshold**, where it rapidly went from 1 to zero.

The position of the incorporation threshold depended upon whether patch birth-rate or patch size was the parameter being changed.



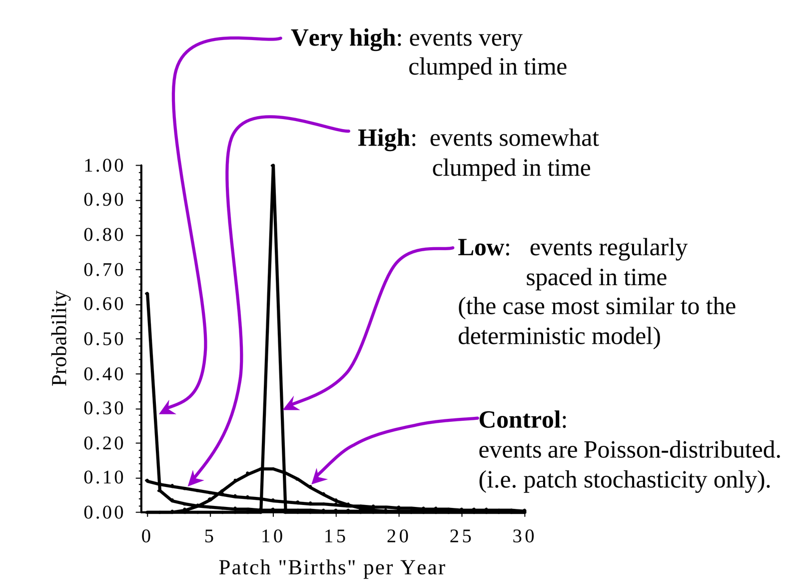
Conclusion:

For the cases examined, patch stochasticity was generally only important for small landscapes. If the mean amount of habitat had to be reduced, it was better to do it by reducing mean patch size rather than patch birth-rate (however, please note that the model assumes no edge effects or area effects).

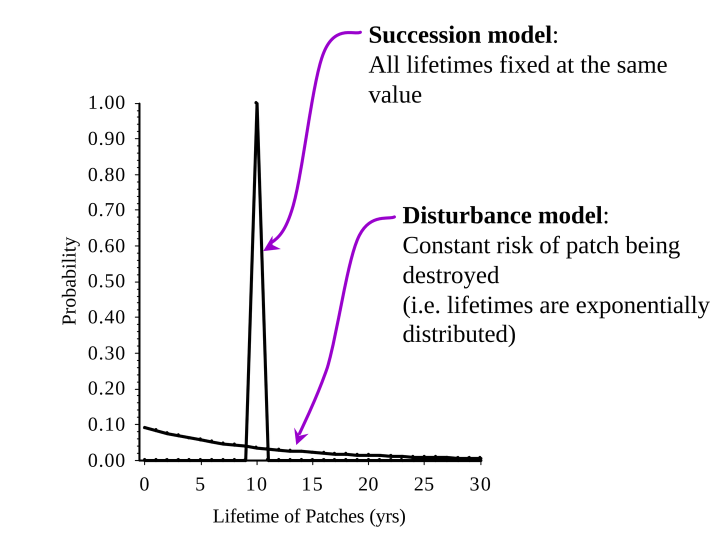
Landscape Stochasticity

Landscape stochasticity is year-to-year fluctuations in the mean size, birth-rate, and disappearance-rate of patches, caused by unpredictable weather, disturbances, and so forth. These are modelled using the following probability distributions:

Landscape stochasticity in patch birth-rate (and patch sizes):



Landscape stochasticity in patch lifetimes:



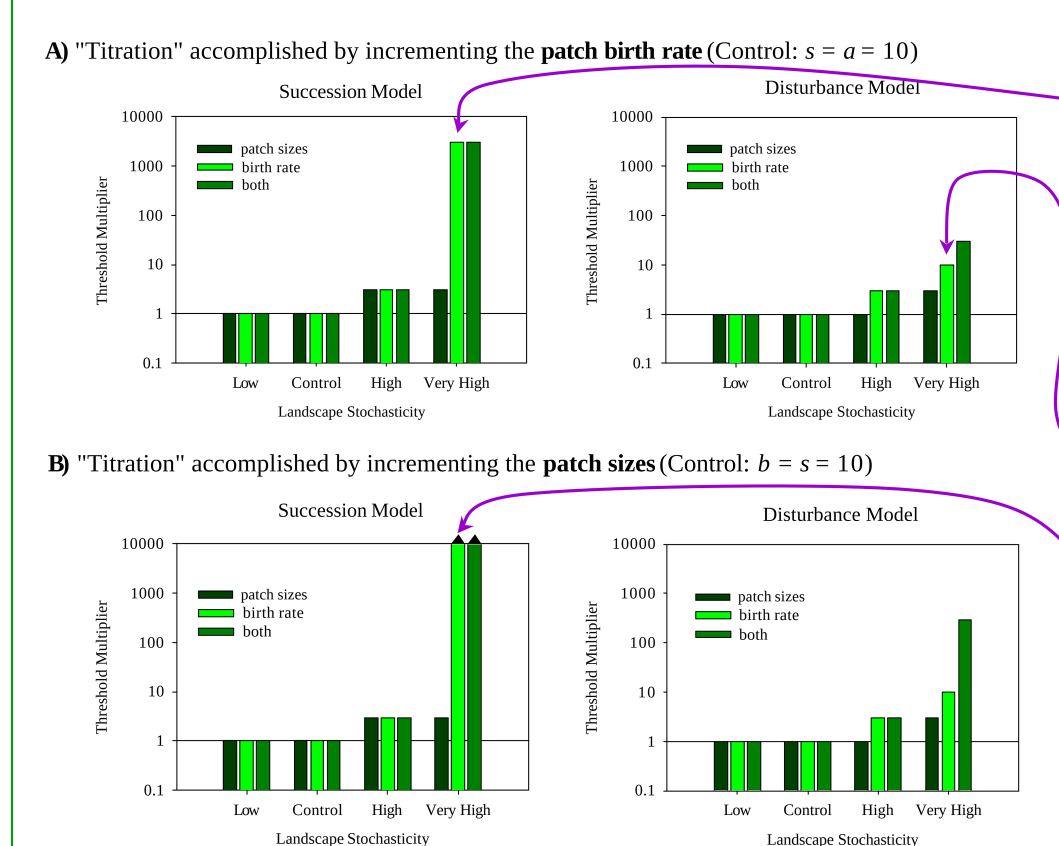
Landscape "Titration":

In general, higher landscape stochasticity moves the incorporation threshold into larger-capacity landscapes. I quantify this effect by "titrating" the landscape.

1) I set up a control landscape that is at the upper edge of the threshold.

2) Then, I adjust the *variability* in patch birth rate and/or patch size (the levels are: low, control, high, very high). This may push the landscape over the threshold.

3) Finally, I adjust the *mean* patch birth rate or patch size, to bring the landscape back to the upper edge of the threshold. The amount that the mean rate or area must be increased is the *Threshold Multiplier*, and measures the tradeoff between landscape stochasticity and average amount of habitat.



For example:

Consider the patch birth-rate. If its variability was increased from "Control" to "Very High," then its mean had to be multiplied by 3000 in order to compensate (i.e. in order to ensure that the amount of habitat never went to zero)

In contrast, in the disturbance model a much smaller increase (10 times) was needed to compensate for "Very High" variability.

Here, no amount of increase in patch size could compensate for "Very High" variability in patch birth-rate.

Conclusions:

1) Landscape stochasticity can cause a dynamic landscape to lose species. The model suggests the effect may be compensated by increasing the patch birth rate or the patch size. However, the amount of increase necessary can sometimes be orders of magnitude.

2) Alternatively, the model suggests a landscape can be managed to incorporate more species if patch-births are caused to be more regularly-distributed in time.

3) Effects of landscape stochasticity tended to be higher in the succession model than in the disturbance model.