Metapopulation dynamics

Ilkka Hanski

Metapopulation biology is concerned with the dynamic consequences of migration among local populations and the conditions of regional persistence of species with unstable local populations. Well established effects of habitat patch area and isolation on migration, colonization and population extinction have now become integrated with classic metapopulation dynamics. This has led to models that can be used to predict the movement patterns of individuals, the dynamics of species, and the distributional patterns in multispecies communities in real fragmented landscapes.

Figure 1 Three approaches to spatial ecology: Theoretical ecologists typically assume homogeneous continuous or discrete (lattice) space. Landscape ecologists tend to analyse the structure of complex real landscapes, with less emphasis on modelling population dynamics. Metapopulation ecology, in the middle, makes the simplifying assumption that suitable habitat for the focal species occurs as a network of idealized habitat patches, varying in area, degree of isolation and quality (the latter is not shown or discussed here, but see ref. 77), and submerged in the midst of uniformly unsuitable habitat.
A mathematical model of plants as ecosystem engineers

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Abstract

Understanding the structure and dynamics of plant communities in water-limited systems often calls for the identification of ecosystem engineers—key species that modify the landscape, redistribute resources and facilitate the growth of other species. Shrub species are excellent examples: they self-organize to form patterns of mosaics which provide habitats for herbaceous species. In this paper we present a mathematical model for studying ecosystem engineering by woody plant species in drylands. The model captures various feedbacks between biomass and water including water uptake by plants' roots and increased water infiltration at vegetation patches. Both the uptake and the infiltration feedbacks act as mechanisms for vegetation pattern formation, but have opposite effects on the water resource: the former depletes the soil-water content under a vegetation patch, whereas the latter acts to increase it. Varying the relative strengths of the two feedbacks we find a trade-off between the engineering capacity of a plant species and its resilience to drought stress. We further identify two basic soil-water distributions associated with engineering at the single patch level, hump-shaped and ring-shaped, and discuss the niche they form for herbaceous species. Finally, we study how pattern transitions at the landscape level feedback to the single patch level by affecting engineering strength.

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Table 2: Relations between non-dimensional variables and parameters and the dimensional ones appearing in the dimensional form of the model equations (2)-(9)

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Scaling</th>
</tr>
</thead>
<tbody>
<tr>
<td>s \textsuperscript{1}</td>
<td>\textsuperscript{1}\textsuperscript{R}E, s \textsuperscript{1}\textsuperscript{M}</td>
</tr>
<tr>
<td>w \textsuperscript{1}</td>
<td>\textsuperscript{1}\textsuperscript{M}N/d</td>
</tr>
<tr>
<td>h \textsuperscript{1}</td>
<td>\textsuperscript{1}\textsuperscript{M}</td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{E}K</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{E}X</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{F}M</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{M}N</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{N}M</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{E}M</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{E}X</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{F}M</td>
<td></td>
</tr>
<tr>
<td>\textsuperscript{1}\textsuperscript{N}M</td>
<td></td>
</tr>
</tbody>
</table>

The infiltration term is given by
\[ f = \text{exp} \left( \frac{1}{\text{E}M} \right) \]

the growth rate term \( G \) is written as
\[ G(A, E, x) = \int g(x, x', x, x', v) \text{d}v \]
and similarly, the soil water consumption rate can be written as
\[ G(y, x, x') = \int d(x, x', x, x', v) \text{d}v \]

In obtaining Eqs. (3) (9) we eliminated four dependent parameters (E, M, A, x). The non-dimensional form of the precipitation parameter
\[ p = \frac{A}{E} \]

proves the equivalence of increasing the precipitation rate, \( P \), to increasing the mortality ignition rate, \( M \), or the evaporation rate, \( N \), in traversing the basic instabilities of the system. The non-dimensional precipitation \( p \) can be

Fig. 2. Relaxation diagrams for homogeneous and stationary solutions of the model equations (Figs. 7-8) showing the increase in p with precipitation \( p \) (panel 1) and soil water \( g \) (panel 2) for plane topography. The solution branch at small \( p \) is denoted, respectively, the hump-shaped and ring-shaped vegetation solutions. Solid lines represent stable steady state solutions, dotted lines represent solutions which are unstable to homogeneous perturbations, and dotted line represents solutions which are stable to homogeneous perturbations. Also shown are the basic vegetation patterns using the precipitation gradient, solid (panel A), single (panel B) and gaps (panel C), obtained by numerical integration of the model equations. The shade of grey represents high biomass density. The same sequence of patterns has a characteristic time of 10-100 days, for a precipitation less than 3 mm/month. The relaxation times in panels A and B are \( \eta = 0.5 \) (for A) and \( \eta = 1 \) (for B). The relaxation times in panel C are \( \omega = 1.5 \) (for A), \( \omega = 2 \) (for B). The parameters used are given in Table 1.
Microhabitat cover

- Costra
- Mantillo
- Arbustos
- H. squamatum

Cover %

- 100
- 80
- 60
- 40
- 20
- 0
Levin’s vision

An ordinary population persists in a balance between “deaths” (local extinction) and births (colonization of unoccupied sites).

Extinction-colonization and regional stochasticities
### Table 1 Processes influencing extinction in metapopulations

<table>
<thead>
<tr>
<th>Scale of extinction</th>
<th>Scale of process</th>
<th>Extinction due to stochasticity</th>
<th>Extinction due to extrinsic causes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Demographic*</td>
<td>Habitat loss</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Environmental</td>
<td>Generalist enemies and competitors</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Genetic*</td>
<td>Persecution by humans etc.</td>
</tr>
<tr>
<td>Local extinction</td>
<td>Local processes</td>
<td>Migration in small populations</td>
<td>Specialist enemies and competitors</td>
</tr>
<tr>
<td></td>
<td>Metapopulation processes</td>
<td>Extinction-colonization Regional</td>
<td>Habitat loss and fragmentation, extinction typically delayed</td>
</tr>
</tbody>
</table>

The processes that operate in the well studied Glenville fritillary butterfly metapopulation are printed in bold.

* Demographic and genetic stochasticity assume an increased significance in metapopulations with many small local populations.
Patch level: Archbold Biological Station

110 Rosemary scrub patches

*H. cumulicola* occupancy = 58 %
**Hypericum cumulicola**

occupancy related to patch size and patch isolation ($p<0.001$)

Quintana-Ascencio & Menges. (1996)
Transplants to occupied and un-occupied patches

- 607 seedlings
- > 1.5 m from shrubs
- 9 unoccupied patches
- 19 occupied patches
- 3 to >30 years since fire
- monitored for 18 months
- evaluated survival, growth, fecundity and recruitment

Quintana-Ascencio, Dolan & Menges (1996)
86% survival after 550 days

No significant effect of time since fire (p=0.44) or prior patch occupancy (p=0.183)

Similar demography in un-occupied & occupied patches
Number of fruits & flowers: 161 ± 163; 2-1033

significant effect of time since fire (p=0.04), but not of prior patch occupancy (p=0.09)

Similar demography in un-occupied & occupied patches

Quintana-Ascencio, Dolan & Menges (1996)
Figure 2 The probability of extinction in the Glenville fritillary butterfly is influenced both by ecological factors and by heterozygosity, which is here used as a measure of the level of inbreeding\textsuperscript{99}. The vertical axis gives the probability of extinction for 42 populations as predicted by a model including several ecological factors\textsuperscript{99}. The horizontal axis gives the average number of heterozygous loci per individual in a sample of eight polymorphic enzyme and microsatellite loci. The size of the symbol is proportional to the probability of extinction predicted by a model including both the ecological factors and heterozygosity (the isodlines of equal extinction risk were drawn by eye). Of the 42 populations studied, seven populations (black) went extinct in one year\textsuperscript{99}.\textsuperscript{99}
Incidence Function model

\[ J_i = \frac{C_i}{C_i + E_i}, \]

\[ C_i = \frac{M_i^2}{M_i^2 + y^2}. \]

\[ E_i = \frac{e}{A_i^x}. \]

\[ M_i = \beta S_i, \]

where

\[ S_i = \sum p_j \exp(-\alpha d_{ij}) A_j. \]
Response to habitat destruction predictions

The response is not linear

Occurs with a time lag

The equilibrium amount of empty habitat before destruction equals the extinction threshold (the minimum amount of habitat required for long-term persistence “Levins Rule”
Occupied

Unoccupied
Figure 3. Patch presence (filled circles) or absence (open circles) of plant species almost or completely restricted to open areas, and with rosemary scrub occupancy related to patch size (ha) and patch isolation index or their interaction.
No regional stochasticity
\( \sigma = 0.4 \)
\( \sigma = 0.8 \)

Removal from each patch

Random removal

Continuous area

Expected

Realized (100 year)
Removal from each patch

Random removal

Continuous area

Expected ●

Realized (100 year) ○
**Colonization potential**

**Figure 4** Bifurcation diagrams for the fraction of occupied habitat in metapopulations. **a,** Theoretical result in which the fraction of occupied habitat is plotted against colonization rate parameter in a deterministic structured model\(^2\). The continuous line represents stable equilibria, the broken line is unstable equilibria. **b,** Empirical result for 66 semi-independent patch networks of the Glanville fritillary butterfly with at least 5 patches\(^7\) and with the fraction of occupied habitat plotted against the colonization potential described in Box 1. Stars indicate patch networks for which the IFM had two alternative equilibria (Box 1). **c,** Expected fraction of occupied habitat as predicted by the IFM parameterized for the butterfly (Fig. 3b). **d,** One snapshot from stochastic simulations of the IFM. In this case, a small probability of colonization (0.01) from outside the patch network was assumed for each patch to prevent permanent metapopulation extinction.
Table 17.1 Predictions about the correlation between species frequency and abundance and the shape of the frequency distribution from four different versions of the metapopulation model

<table>
<thead>
<tr>
<th>Model</th>
<th>Predictions</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immigration</td>
<td>Extinction</td>
<td>Correlation</td>
</tr>
<tr>
<td>Dependent</td>
<td>Dependent</td>
<td>Positive</td>
</tr>
<tr>
<td>Dependent</td>
<td>Independent</td>
<td>Zero</td>
</tr>
<tr>
<td>Independent</td>
<td>Dependent</td>
<td>Positive</td>
</tr>
<tr>
<td>Independent</td>
<td>Independent</td>
<td>Zero</td>
</tr>
</tbody>
</table>

Note: The models are classified by the dependence of immigration and extinction rates on the fraction of sites that are occupied (see text for details).
Species may be absent where environmental conditions are favourable

Species may be present where conditions are not favorable

Currently unoccupied habitat fragments may be critical for long term persistence

Reduce the impact of regional stochasticity

The living dead