

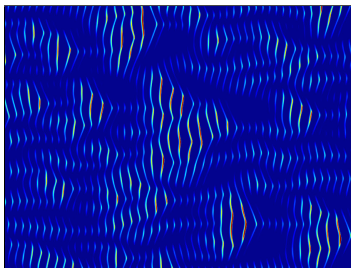
Ecological Dynamics

Spatial ecology (1 / 2)

Dr. Tarik C. Gouhier
<tarik.gouhier@gmail.com>

Northeastern University
<http://blackboard.neu.edu>

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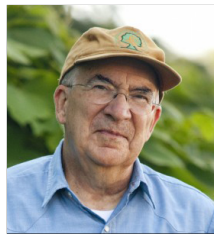
Ecology across scales

Contingency vs. regularity: a question of scale?

A debate erupted in the late 20th century about the appropriate scale for conducting ecological studies, with Lawton (1996) advocating for a shift to macroecology and Simberloff (2004) advocating for community ecology.

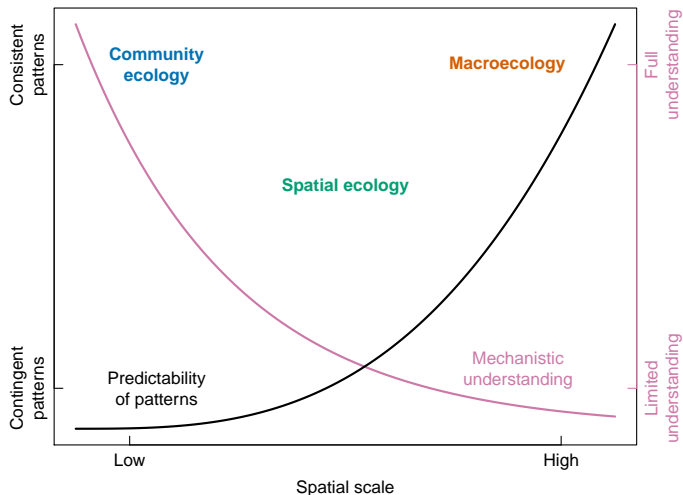


John Lawton



Daniel Simberloff

Ecology across scales

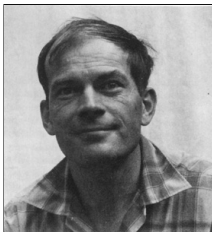


Tradeoff between regularity of ecological patterns and their mechanistic understanding.

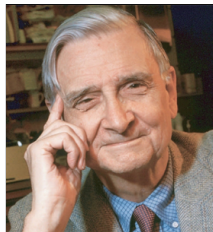
Early efforts to integrate space: island biogeography

Theory of island biogeography

MacArthur and Wilson (1967) developed the theory (and field) of biogeography to understand how the size and proximity of islands to the mainland could be used to predict community structure.

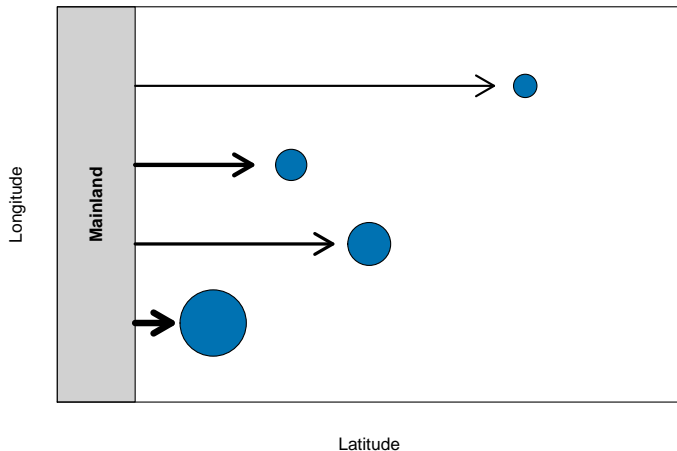


Robert H. MacArthur



E.O. Wilson

Island biogeography



Islands that are larger and closer to the mainland have from greater colonization rates than those that are smaller and farther.

Island biogeography

We can derive a simple mathematical model to depict the theory of island biogeography.

We begin by assuming that a fixed number of species S from the mainland makeup the species pool available to colonize an island.

Furthermore, we assume that the species colonize the available habitat on the island at rate c and go extinct from the island at rate e :

$$\frac{dp}{dt} = c(1 - p) - ep$$

Solving this equation at equilibrium will yield \hat{p} , the proportion of species from the species pool that can persist on the island.

Island biogeography

This can be converted to the number of species present $S_p = S\hat{p}$.

To obtain this value, we simply set $\frac{dp}{dt} = 0$ and solve for \hat{p} :

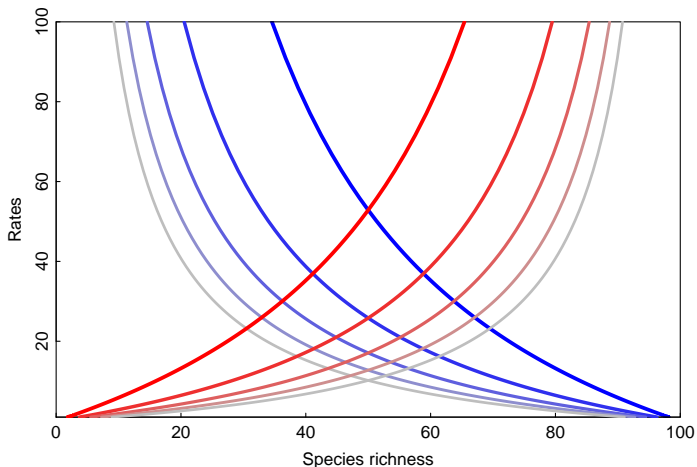
$$\hat{p} = \frac{c}{c + e}$$

As long as species have a non-zero probability of going extinct, there will always be some species found on the mainland but not on the island

Second, The number of species at equilibrium depends on the balance between colonization and extinction.

Third, islands that are larger (lower extinction) and closer (higher colonization) to the mainland will support more species than islands that are smaller (higher extinction) and farther (lower colonization) from the mainland.

Island biogeography



Equilibrium species richness corresponds to the intersection of the colonization (blue) and extinction (red) curves.

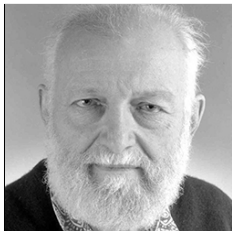
Assumptions

- **Constant rates:** c and e are constant in time and do not change due to environmental or demographic stochasticity
- **Species pool remains constant:** species pool remains constant on mainland and cannot be depleted
- **No spatial feedbacks:** No reciprocal feedbacks between island and mainland

From island biogeography to metapopulation theory

Metapopulation theory

Levins (1969); Levins and Culver (1971) and later (Hanski, 1991, 1998) used patch-dynamic models to understand the consequences of reciprocal spatial feedbacks between populations for conservation efforts.

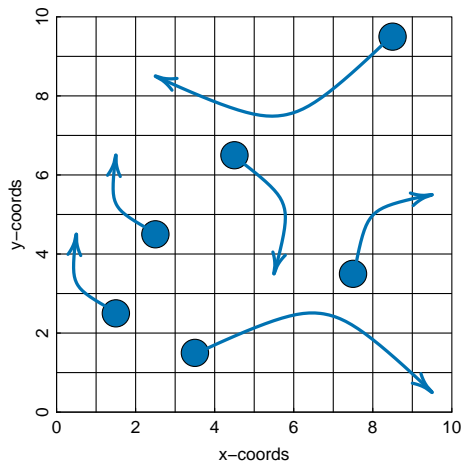


Richard Levins



Ilkka Hanski

Spatially-implicit patch-dynamic models



Dispersal is assumed to be global and local dynamics reach an equilibrium instantly relative to regional dynamics.

Metapopulation theory

Levins (1969) developed a simple metapopulation model to understand how reciprocal feedbacks between local populations could affect proportional abundance across an infinite landscape:

$$\frac{dp}{dt} = cp(1-p) - ep$$

Where c is the colonization rate and e is the extinction rate. Solving at equilibrium yields:

$$\hat{p} = 1 - \frac{e}{c}$$

This means that as long as a species has a non-zero extinction rate, it will not be able to occupy the entire landscape.

Assumptions

- **Constant rates:** c and e are constant in time and do not change due to environmental or demographic stochasticity
- **Implicit space:** spatial configuration of patches is undefined
- **Global dispersal:** species can disperse across the entire landscape
- **Separation of time-scales:** local processes operate at a much faster rate than regional processes

From metapopulation to metacommunity theory

Metacommunity theory

Levins and Culver (1971), Hastings (1980), and Tilman (1994) extended patch-dynamic models to understand the effects of reciprocal spatial feedbacks on community structure.



Alan Hastings



David Tilman

Patch-dynamic metacommunity models

We can start with a simple lottery competition version of the original patch-dynamic metacommunity model:

$$\begin{aligned}\frac{dp_1}{dt} &= c_1 p_1 (1 - p_1 - p_2) - e_1 p_1 \\ \frac{dp_2}{dt} &= c_2 p_2 (1 - p_1 - p_2) - e_2 p_2\end{aligned}$$

Solving at equilibrium yields:

$$\begin{aligned}1 - \hat{p}_1 - \hat{p}_2 &= \frac{e_1}{c_1} \\ 1 - \hat{p}_1 - \hat{p}_2 &= \frac{e_2}{c_2}\end{aligned}$$

Patch-dynamic metacommunity models

Coexistence requires that all species have the same e -to- c ratio. This applies for a metacommunity with an arbitrary number of species S :

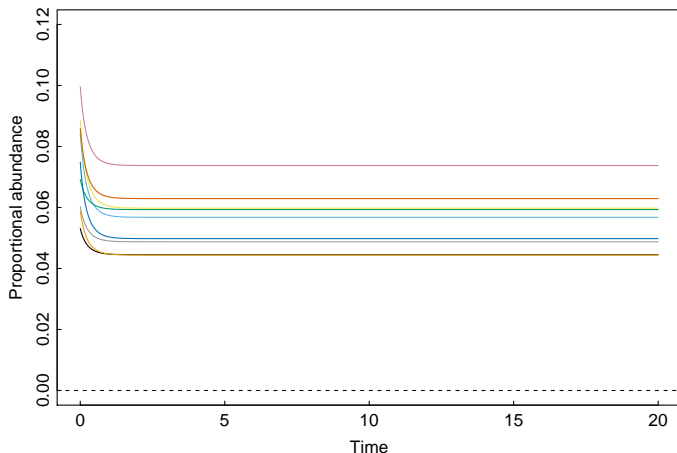
$$\begin{aligned}\frac{dp_i}{dt} &= c_i p_i \left(1 - \sum_{k=1}^S p_k\right) - e_i p_i \\ \frac{dp_j}{dt} &= c_j p_j \left(1 - \sum_{k=1}^S p_k\right) - e_j p_j\end{aligned}$$

Solving at equilibrium yields:

$$\begin{aligned}1 - \sum_{k=1}^S p_k &= \frac{e_i}{c_i} \\ 1 - \sum_{k=1}^S p_k &= \frac{e_j}{c_j}\end{aligned}$$

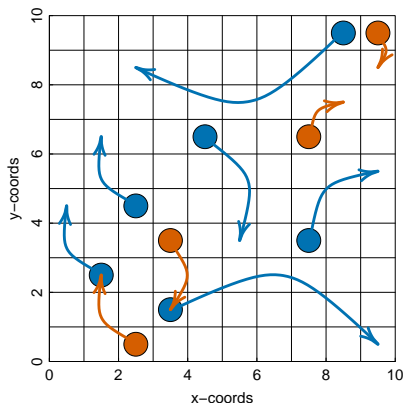
This means that we must have $\frac{e_i}{c_i} = \frac{e_j}{c_j}$ for all i, j pairs of species.

Example of lottery model dynamics



An arbitrary number of species S can persist as long as they all share the same colonization to extinction ratio.

Hierarchical competition



Levins and Culver (1971) and Hastings (1980) modeled hierarchical competition whereby dominant species (red) could colonize patches occupied by subordinate species (blue).

Hierarchical competition

The hierarchical competition model for two species is:

$$\frac{dp_1}{dt} = c_1 p_1 (1 - p_1) - e_1 p_1$$

$$\frac{dp_2}{dt} = c_2 p_2 (1 - p_1 - p_2) - e_2 p_2 - c_1 p_1 p_2$$

Solving at equilibrium yields:

$$\hat{p}_1 = \frac{c_1 - e_1}{c_1} = 1 - \frac{e_1}{c_1}$$

$$\hat{p}_2 = 1 - \frac{e_2}{c_2} - \left(1 - \frac{e_1}{c_1}\right) \left(1 + \frac{c_1}{c_2}\right)$$

Hierarchical competition

The interior equilibrium is biologically feasible if $\hat{p}_1 > 0$ and $\hat{p}_2 > 0$:

$$c_1 > e_1$$

and:

$$c_2 > \frac{c_1}{e_1} (c_1 + e_2 - e_1)$$

The dominant can persist as long as its colonization rate is greater than its extinction rate. The subordinate can persist if its colonization rate is **sufficiently larger than that of the dominant**.

This is the famous **competition-colonization tradeoff**, which allows coexistence.

Hierarchical competition

This interspecific requirement imposed on the subordinate by the dominant species is called **limiting similarity**: species cannot have colonization rates that are too similar for persistence to occur.

Another important result is that **overyielding** will occur in this model because the total proportional abundance will always increase with the number of species S .

Algorithm to build S species communities

The hierarchical competition model for S species is:

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^S p_j \right) - e_i p_i - \left(\sum_{j=1}^{i-1} c_j p_j p_i \right)$$

One can build an arbitrarily complex community by obtaining the equilibrium abundance of each species sequentially starting with the dominant.

Begin by setting the equilibrium abundance \hat{p}_j of species j to some arbitrary value, here using a geometric series:

$$\hat{p}_j = z(1 - z)^{j-1}$$

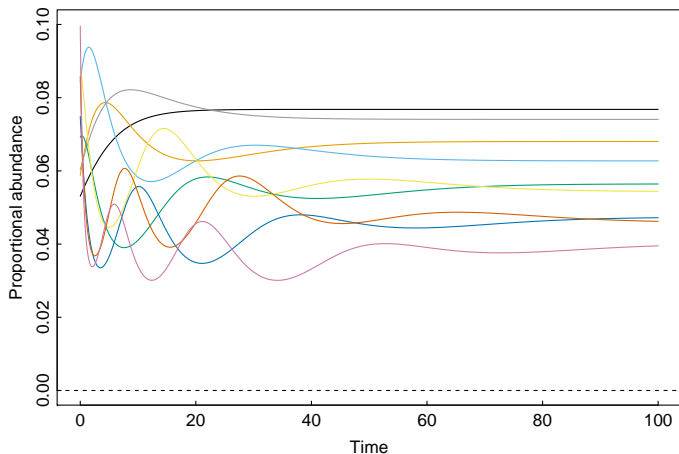
Algorithm to build S species communities

Then select the extinction rates e arbitrarily for all species and find the minimum colonization rate required for species i to persist:

$$c_i = \frac{\sum_{j=1}^{i-1} \hat{p}_j e_j + \left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) m_i}{\left(1 - \sum_{j=1}^{i-1} \hat{p}_j\right) \left(1 - \sum_{j=1}^i \hat{p}_j\right)}$$

Solve this equation for species $i = 1$ to $i = S$ to assemble a stable community.

Example of hierarchical competition model dynamics



S species can persist as long as subordinates have colonization rates that are sufficiently larger than that of the dominants.

References

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