

**Lecture 8. Spatially-structured populations.**

Reading:

- Gotelli, 2001, A Primer of Ecology, Chapter 4, pages 81-97.
- Hanski, I. 1996. Metapopulation ecology. Pages 13-43 in Rhodes, O. E., Jr., R. K. Chesser, and M. H. Smith (eds.). Population dynamics in ecological space and time. University Chicago Press, Chicago, Illinois, USA.
- Pulliam, H. R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45-69 in Rhodes, O. E., Jr., R. K. Chesser, and M. H. Smith (eds.). Population dynamics in ecological space and time. University Chicago Press, Chicago, Illinois, USA.

Optional:

- Gilpin, M. E. 1987. Spatial structure and population vulnerability. Pages 125-139 in M. E. Soulé, ed. Viable Populations for Conservation. Cambridge University Press, New York, New York, USA. 189 pp.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Pages 53-68 in Population Regulation and Dynamics, M. P. Hassell and R. M. May, eds. The Royal Society, London, United Kingdom.

Traditional View of Populations

- Panmictic -- no selective mating. Frequency of genes in the population follows Hardy-Weinberg equilibrium.
- Equilibrium -- population reaches a carrying capacity.
- Extinction dependent on N.
- Homogeneous environment/habitat -- no spatial heterogeneity.
- Individuals equal (no heterogeneity of individuals).

We have relaxed some of these assumptions in previous models: stochastic models, age-structured models. However, basically, previous models have been "traditional".

Difficulty of incorporating spatial extension into population models

- Difficult to keep track of locations of organisms in field studies
- Computational problems of dealing with space in a theoretical manner are formidable, requiring computer models

Spatial patterns in populations

Traditional approach is a diffusion equation. Start with a model of local population dynamics:

$$\frac{dN}{dt} = Nf(N) ,$$

where  $N$  is the number of individuals of the species at time  $t$ , and  $f(N)$  is the per capita growth rate of the species. If we now add movement based on a diffusion

equation (Hastings 1990),  $N$  depends on both time and space,  $x$ , and  $N$  is now a density (on space  $x$ ) for the number of individuals. A typical form (Hastings 1990) is

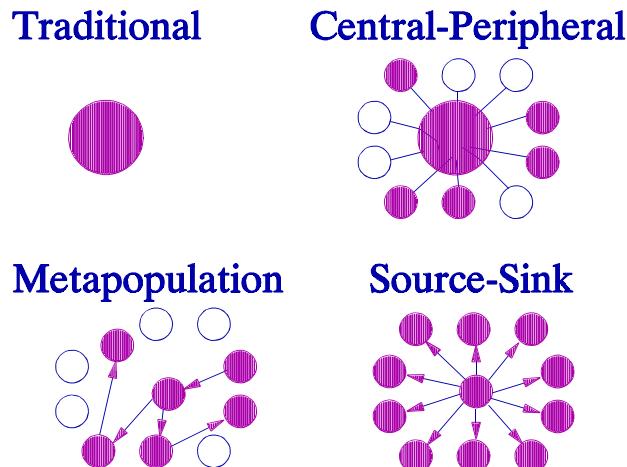
$$\frac{\partial N(x, t)}{\partial t} = \frac{\partial [D \partial N(x, t)]}{\partial x} + N f(N)$$

where  $D$ , which may depend on  $x$ , is a measure of the speed of movement of individuals.

Central-Peripheral (Wright 1943)

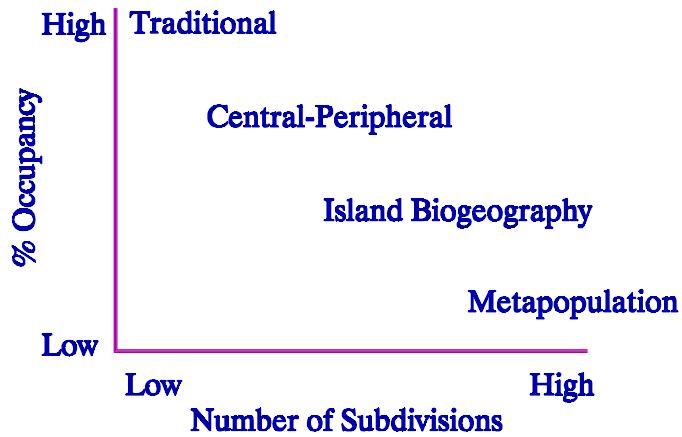
Source-Sink (Gill 1978, Lidicker 1975, Pulliam 1996). Pulliam (1988) argued that active dispersal from source habitats can maintain large sink populations and that such dispersal may be evolutionarily stable. The key idea is that if the source is saturated, an individual without a territory in the source is better off to migrate to the sink, because some chance of breeding is better than none. Van Horne (1983) suggested such a system was operating with populations of *Peromyscus maniculatus* in spruce and hemlock stands of different seral stages in southeast Alaska. The implication of this model is that density is not necessarily a good predictor of habitat quality in terms of maintaining the species.

Metapopulation (Levins 1970, denBoor 1968)



Other examples -- see Fig. 7.2 of Gilpin (1987).

Habitat occupancy rate



Key features of spatial heterogeneity models:

Localized extinction -- each patch has some probability of extinction within the patch.

The patch is re-colonized by immigration (dispersal) from other patches. The percent of patches occupied is a key variable.

Extinction and re-colonization dynamics. The model behavior is critically influenced by the extinction and re-colonization rates. If the extinction rate is  $\gg$  re-colonization rate, the population goes extinct. If the re-colonization rate  $\gg$  extinction rate, the model is really just a single population, and the spatial heterogeneity is covered up.

As a result of the almost complete lack of ecological data to support these models, almost all the evidence comes from mathematical models. These models are hypotheses to be disproved. Currently, the theory (hypothesis) in vogue is a metapopulation.

Features of metapopulations ("population of populations") (Hanski 1996, Weins 1996)

Many local populations ( $>2, 10?$ ).

Each local population has a given extinction probability.

Each local population has traditional dynamics (hence you don't have to forget all you have learned so far).

High probability of extinction generates "winking", no probability of extinction generates "fixed" populations.

Dispersal is responsible for re-colonization of vacant sites.

Spatial subdivisions enhance stability of total population -- "spreading of risk", denBoer (1968).

"the risk of wide fluctuations in animal numbers is spread unequally over a number of subpopulations".

An exception to idea are catastrophes large enough in the spatial scale to blanket the entire metapopulation.

Metapopulation stability requires:

Asynchrony (or otherwise you have just a single large population).

Density-dependence, or a single patch eventually goes to infinity.

Large number of units -- Central Limit Theorem -- to stabilize the system.

Dispersal must not be high enough to synchronize local populations, or otherwise the patches all operate in synchrony, and the result is a single large population.

Dispersal must be sufficient to offset extinction of a patch, or else eventually, all the patches will go extinct.

Gene flow must be great enough to prevent localized selection from generating new species.

Conclusions about metapopulations have basically come from models -- data are lacking for real systems.

An example model -- Levins (1969):

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

where  $p$  = proportion of patches occupied,  $e$  = rate of local extinction with each patch having the same extinction probability, and  $m$  = rate of colonization ( $m$  is a function of dispersal, and is the same for each patch). The spatial configuration of the patches is ignored in this model. The equilibrium condition is  $mp(1 - p) - ep = 0$ , so  $p = 1 - e/m$ . The model also assumes nothing about within patch population dynamics, only that a patch goes extinct and is re-colonized. At any time, a patch is either at  $K$  carrying capacity, or extinct (0). This differential equation is structurally the same as the logistic model:

$$\frac{dp}{dt} = (m - e)p \left[ 1 - \frac{p}{1 - \frac{e}{m}} \right].$$

Thus,  $K$  corresponds to  $1 - e/m$ , and  $r$  corresponds to  $(m - e)$ . This model was motivated by an insect pest control problem: populations over a wide area fluctuated in asynchrony. Hence, to eradicate the pest, you have to treat all areas simultaneous, because if you ignore the areas not currently a problem, they eventually re-colonize all the other patches. "As a conceptual and mathematical tool, the Levins model was something new in population ecology, and a necessary first step towards quantitative research in this area." (Hanski and Gilpin 1991:5).

What are some reasonable time scales for this kind of model?

What factors affect the parameters  $e$  and  $m$ ? Body size? Reproduction and survival rate?

Extension to this model: Hanski (1991) defined  $m$  as a function of distance (isolation) from other patches,

$$m = m_0 e^{-aD}$$

where  $D$  is average distance between patches and  $m_0$  and  $a$  are parameters. Likewise,

$$e = e_0 e^{-bA}$$

with  $e_0$  and  $b$  parameters and  $A$  the average patch area. Then, the equilibrium proportion of patches occupied is

$$p = 1 - \left( \frac{e_0}{m_0} \right) e^{-bA + aD} .$$

This extension still doesn't take into account individual patch characteristics, i.e., patch heterogeneity. Hastings (1991) has published much more complex models. However, he has made no attempt to relate them to biology, again probably because so little is known about extinction and re-colonization rates.

Another extension of this model is to incorporate stochasticity to estimate metapopulation persistence times (Hanski 1991).

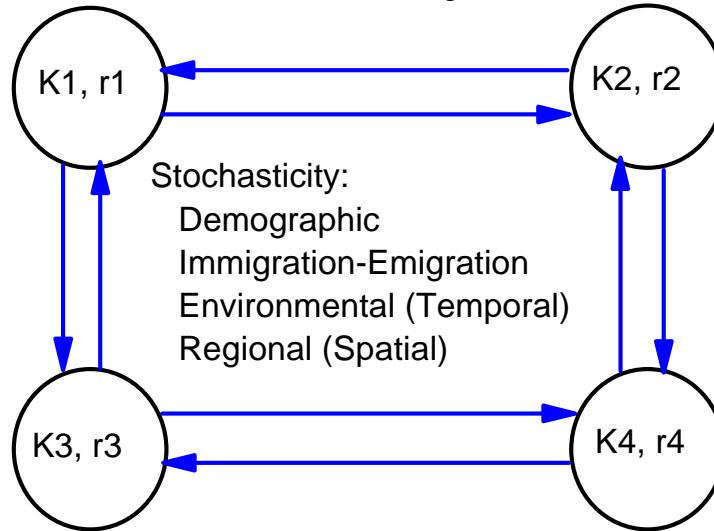
The lowest form of stochasticity is suggested by previous examples of stochastic population models. Demographic stochasticity of patches or local populations, which Hanski (1991) refers to as immigration-emigration stochasticity.

Still more stochasticity can be incorporated by variation in population dynamics across the patches, which Hanski (1991) refers to as regional stochasticity. Regional stochasticity results in the "spreading of risk" concept of den Boor (1968). "Species with high dispersal rate but little regional stochasticity are expected to have long metapopulation persistence times, while species with low dispersal rate but much regional stochasticity have short metapopulation persistence times." (Hanski (1991:33-34). Dispersal is most advantageous when there is little regional stochasticity, and least advantageous when there is much regional stochasticity (Gadgil 1971 in Hanski 1991).

In summary, 4 forms of stochasticity might be incorporated to achieve realistic estimates of metapopulation persistence:

- 1) demographic stochasticity within patches,
- 2) immigration-emigration stochasticity of patches,
- 3) environmental stochasticity within patches, and
- 4) regional stochasticity between patches.

In the following diagram, demographic stochasticity would operate in each of the 4 patches, immigration-emigration stochasticity would cause the immigration and emigration to vary randomly between the patches, environmental stochasticity would operate in that each patch would vary through time (but could all vary the same through time), and regional stochasticity would cause the 4 patches to vary independently of each other. Note that 2 additional sets of diagonal links between the patches have been left out of the diagram.



Some causes of metapopulation extinction (Hanski 1991:34-35):

- 1)  $e > m$ , i.e., there is no solution to Levins equation.
- 2) alternative equilibria.
- 3) immigration-emigration stochasticity, i.e., all the patches go extinct at the same time.
- 4) region stochasticity, i.e., catastrophes that wipe out large portions of the range of the population.

Empirical observations to support spatial population models. The main deviation from the theory is due to problems with local extinctions. Populations tend not to wink on and off as portrayed by the metapopulation model. Harrison (1991) suggests few empirical observations fit the Levins model well. The more likely situations are:

- 1) mainland-island and source-sink spatial populations in which persistence depends

- on the existence of one or more extinction-resistant populations. As an example, the checkered white butterfly in Central Valley, California, as its source as riparian areas. Some patches have  $e = 0$ , other patches have  $e > 0$ .
- 2) patchy populations, in which dispersal between patches or subpopulations is so high that the system is effectively a single extinction-resistant population. In this case  $m \gg e$ .
  - 3) non-equilibrium metapopulations, in which local extinction occurs in the coarse of a species overall regional decline. This suggests a modified view of metapopulation dynamics in which local extinction is more an incidental occurrence than a central feature. A natural example of this phenomena are mammal populations in the sky island country of the south-west, where mammals were isolated on mountain top habitat during post-Pleistocene warming. A more frequent example is human-caused fragmentation of natural habitats.

Hanski (1994) describes a procedure to fit observed metapopulation data with maximum likelihood. The model is fitted to presence-absence data from a metapopulation at dynamic equilibrium between extinctions and colonizations. However, the confidence intervals on all 3 of the parameters estimated from the data include zero, suggesting that in fact the model provides an uninformative fit to the observed data.

#### Spatial population theory and conservation biology.

Habitat fragmentation is making populations resemble metapopulation theory. If individuals routinely move between habitat fragments, then we have a metapopulation. Theory suggests that isolated patches should have some movement of individuals, even if the movement is in the form of transplants as part of management.

SLOSS is a controversy about the design of reserves. SLOSS is Single Large or Several Small reserves. One large reserve suffers a greater chance of a single catastrophe wiping out the population. In contrast, the probability of extinction of a population in a single small patch may be quite high, and hence several small patches may not provide long-term persistence.

#### Spatial population theory and harvest theory (McCullough 1996)

Spatial controls can achieve high yields and avoid the hazards of overharvest that are possible with harvest quotas without detailed population data. Harvesting of metapopulations holds little prospect because of negative effects on dispersal required for recolonization of patches following local extinction.

#### Summary:

The concept of a metapopulation is imaginative, and does offer some insight into how to manage populations given that habitat is being fragmented. The models suggest some interesting hypotheses. However, real data don't appear to support the simplest models.

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