

Lab 6: Metapopulation modeling

NRES 470/670

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Some definitions

In this lab we will build spatially structured population models for the first time. The simplest type of spatially structured population model is the **classical metapopulation model**. In this model, we have a **landscape** with a certain number of habitable **patches**. Patches are either **occupied** (coded as 1) or not (coded as 0). We are not keeping track of abundance (N) any more- we are just keeping track of whether each population is occupied or not, and how many total occupied populations we have in our metapopulation.

A metapopulation is best considered **a population of populations**. If a population is composed of individuals, a metapopulation is composed of populations!

colonization is the process of a population going from unoccupied to occupied!

How can a metapopulation become colonized? The answer is **immigration** of course.

extirpation (or extinction) is the process of a patch going from occupied to unoccupied.

regional extinction represents extinction of all patches in the metapopulation.

More formally, here are some terms we will consider:

I is the total fraction of patches that are colonized by immigrants per time period (colonization rate, or “immigration” rate)

E is the total fraction of patches that go extinct per time period (extirpation rate)

f_t is the fraction, or proportion, of patches that are occupied at time t . This is also known as the **occupancy**

Therefore, the change in occupancy can be expressed as:

$$\Delta f = I - E \quad (\text{Eq. 1})$$

p_i is the probability of colonization for any given (unoccupied) patch.

p_e is the probability of extinction for any given (occupied) patch.

A basic metapopulation model:

The more sites are available for colonization, the higher the rate of colonization!

$$I = p_i \cdot (1 - f) \quad (\text{Eq. 2})$$

The more sites are occupied, the higher the rate of extinction!

$$E = p_e \cdot f \quad (\text{Eq. 3})$$

Combining equation 1 with the above equations, we get our first metapopulation model:

$$\Delta f = p_i(1 - f) - p_e f \quad (\text{Eq. 4})$$

This model assumes the following:

- Homogeneous patches (all patches are created equal)
- Spatial context does not affect extinction and colonization parameters
- No time lags
- Very large number of patches

- Extinction and colonization parameters are not dependent on the fraction of patches occupied.

Variant #1: island-mainland model

Colonization occurs via immigration from a constant external source – a constant **propagule rain**

This is the simplest metapopulation model. p_i and p_e are fixed, totally constant.

This is actually the model we have already constructed!

Variant #2: internal colonization

Now, colonization can only happen via immigration from within the metapopulation itself. So when few populations are colonized, colonization is low because of a lack of potential immigrants in the metapopulation.

$$p_i = i \cdot f \quad (\text{Eq. 5})$$

i represents the strength of internal colonization (how much the probability of patch-level colonization increases with each new occupied patch in the metapopulation).

Variant #3: rescue effect.

Now, the extinction rate can be reduced by immigration from other populations in the metapopulation!

$$p_e = e(1 - f) \quad (\text{Eq. 6})$$

e represents the strength of the rescue effect (maximum patch-level extinction risk, which occurs at complete metapopulation vacancy).

Variant #4: both internal colonization AND rescue effect!

This one is pretty self-explanatory!

What is a metapopulation?

The term *metapopulation* is often used to refer to models where we don't care about abundance, we only care about occupancy- as in the model described above. However, a metapopulation is simply a *population of populations*. We can keep track of patch abundance in a metapopulation model. In fact, if we want, each patch can contain a stage-structured, density dependent population if we really want!

Just as we can use metapopulation models to study the probability of **regional extinction**, we can also study **regional abundance** and regional abundance trends across the entire metapopulation.

Exercise 1: basic metapopulation terms and concepts!

HINT: use the *Gotelli book!!!*

1a. An endangered population of 100 frogs lives in a single large pond. One proposal for conserving the frog population is to split it into three populations of 33 frogs, each in a separate pond (located far enough away from each other so you can reasonably assume that extinction risks are independent of one another). You know from your demographic models that decreasing the frog population from 100 to 33 individuals will increase the annual risk of extinction from 10% to 50%. In the short run, is it a better strategy to retain the single population or to split it into three? Show your calculations, and explain your reasoning!

- 1b. Consider the simplest (island-mainland) metapopulation model. Under what conditions is the occupancy rate f constant over time? Explain your reasoning.
- 1c. Build an InsightMaker model for the basic island-mainland metapopulation model. The total fraction of occupied populations f should be represented as a [Stock] (this stock can not go negative, nor can it go above 1!) and there should be two [Flows]: one for *colonization* and one for *extinction*. Initialize f at 0.9. The extinction and colonization probabilities (p_e and p_i) should be represented as [Variables]. Set p_e to 0.15 and p_i to 0.4. Provide a link to your working InsightMaker model as part of your lab write-up.
- 1d. On the basis of your Insightmaker model, what happens to f over the course of the simulation? Does the metapopulation go extinct (regional extinction)? Does f reach an equilibrium? If so, is this equilibrium **stable** or **unstable**? Explain your reasoning.
- 1e. Compare your InsightMaker results (provide a plot) with the results from applying Equation 4.4 from Gotelli. Show your work. Do the two answers match?
- 1f. Change your InsightMaker model to reflect *internal colonization*. Set the parameter i to 0.1. Provide a link to your InsightMaker model as part of your lab write-up.
- 1g. Compare your InsightMaker results (provide a plot) with the results from applying Equation 4.6 from Gotelli. Show your work. Do the two answers match?
- 1h. Change your InsightMaker model to reflect the *rescue effect*. Restore the colonization model to represent “propagule rain” (constant colonization rate for vacant patches). Set the parameter e to 0.25. Provide a link to your InsightMaker model as part of your lab write-up.
- 1i. Compare your InsightMaker results (provide a plot) with the results from applying Equation 4.8 from Gotelli. Show your work. Do the two answers match?
- 1j. Change your InsightMaker model to reflect the *rescue effect* AND *internal colonization*. Set the parameter i to 0.1. Set the parameter e to 0.25. Provide a link to your InsightMaker model as part of your lab write-up.
- 1k. Is this model *stable*? explain your reasoning. Under what conditions do you get perfect 100% occupancy?

Exercise 2: a spatial metapopulation model!

As we already know, agent-based models are well-suited for considering spatial context.

I have already prepared an agent-based metapopulation model for you. You can access and clone this model [here](#).

Each population/patch in the metapopulation is represented by an “individual”, or “agent”. These individuals cannot move (they are patches of land, after all), but they can influence each other via immigration and emigration!

The landscape is 200 km by 200 km. Each simulation run, patches are initialized randomly in the landscape. The **metapopulation size** (total number of patches) is initialized at 10.

Each patch potentially contains a population of animals. If it has ≥ 2 individuals living in it, it is considered “occupied”.

Each patch has its own carrying capacity (K)- some patches have very low carrying capacity, and some have very high carrying capacity. The distribution of K among populations is approximately *lognormal*. This means that there are usually a few very large populations in the landscape. The minimum K is 2 (minimum to support an “occupied” population).

Abundance dynamics are density-dependent, and population growth is computed as a function of **r_max**, **local carrying capacity**, and previous-year local abundance using the **Ricker** growth model:

$$N_{t+1} = N_t e^{r_{max}(1 - \frac{N_t}{K})}$$

This is one of the most commonly used models for discrete logistic population growth (very analogous to the logistic growth model we have already seen!).

Population growth in each patch is also driven by migration to and from nearby populations. A fixed proportion of each population disperses each year (**dispersal rate**, set to 25% initially), and the **maximum dispersal distance** is set initially at 50 kilometers. If no neighboring population exists within that distance, all dispersers perish.

There is, of course, demographic stochasticity in this model!

Graphical summaries are available, which illustrate the spatial configuration of the patches, the total metapopulation occupancy, the Total metapopulation abundance, and the total numbers of immigrants/emigrants.

Take some time to open the model (clone it!) and get familiar with the parameters and model behavior. If you don't understand something, ask your instructor! Make sure you have the following starting parameters:

Metapopulation size: 10 patches r_max: 0.11 maxdist (maximum dispersal distance): 50 kilometers dispersal rate: 0.25

NOTE: there is one parameter (max dispersal distance, maxdist) you will need to pay attention to, but it is not represented by a value slider (I couldn't get it to work that way, unfortunately). To alter the maximum dispersal distance, you need to open the equation editor for the [Immigrants] variable, and change the value in the top line, which should look something like this:

```
maxdist <- 50
```

2a. Use InsightMaker's *sensitivity testing tool* to run the model 50 times. What is the approximate risk of regional extinction of this metapopulation? What is the abundance trend (that is, overall regional, or metapopulation, abundance) over time? What is the trend in occupancy over time? Provide plots to justify your answer.

2b. Change the dispersal rate to zero. Run a few simulations to examine the model behavior. Re-run the sensitivity testing tool to examine expected patterns in occupancy and abundance over time. How did the trend in abundance and occupancy change relative to the scenario with 25% dispersal? What about the probability of regional extinction? Justify your answer, including figures. Do these results match with your expectation of what would happen? Why or why not?

2c. Change the dispersal rate back to 25 % and change the number of patches to 25. Run a few simulations to examine the model behavior. Re-run the sensitivity testing tool (note that InsightMaker will run slower with more patches!) to examine expected patterns in occupancy and abundance over time. How did the trend in abundance and occupancy change relative to the scenario with 10 patches? What about the probability of regional extinction? Justify your answer, including figures. Do these results match with your expectation of what would happen? Why or why not?

2d. Change the metapopulation size back to 10 patches and change the maximum dispersal distance (maxdist) to 100 km (remember you need to open the equation editor for the [Immigrants] variable to do this). Run a few simulations to examine the model behavior. Re-run the sensitivity testing tool to examine expected patterns in occupancy and abundance over time. How did the trend in abundance and occupancy change relative to the scenario with a dispersal distance of 50 km? What about the probability of regional extinction? Justify your answer, including figures. Do these results match with your expectation of what would happen? Why or why not?

2e. Imagine that this metapopulation represents the last remaining patches of habitat for an endangered butterfly. You have identified three possible management strategies: You could:

- i. Improve the intervening, or "matrix", habitat, effectively doubling the maximum dispersal distance (individuals are able to disperse more effectively over longer distances).
- ii. Improve existing habitats, doubling the mean per-population carrying capacity.

iii. Restore habitat, effectively doubling the number of patches.

Which management strategy would be most effective for ensuring that the metapopulation does not go extinct (prevent regional extinction)? Justify your answer with supporting figures.

2f. [thought question] Is it possible for r_{max} to be positive and yet for the total regional abundance to exhibit a persistent declining trend? Explain your reasoning, using at least one biologically realistic example. You can use the agent-based metapopulation model in InsightMaker to help test your ideas, but this is not required.

Checklist for Lab 6 completion

- Please bundle all your responses into a single Word document and submit *using WebCampus!*
- Where appropriate, URLs for your InsightMaker models should be pasted in your lab submission (MS Word document). See details below...
 - After you save the model you should see a link on the top left-hand corner, “Insight Access”. Click on that link, and a new window will pop up. Under “allow update access”, add a username (i.e., kevintshoemaker or waldenTA). click on the “Add User” button, and then click on “Submit”. Finally, copy and paste the URL into the Word document.

Due Mar. 30 at 10 am.

- Word document with short answers, model URLs, and figures (where appropriate)
 - **Exercise 1**
 - * *Short answer (1a.)*
 - * *Short answer (1b.)*
 - * *InsightMaker model (1c.)*
 - * *Short answer (1d.)*
 - * *Short answer (1e.)*
 - * *Short answer (1f.)*
 - * *Short answer (1g.)*
 - * *Short answer (1h.)*
 - * *Short answer (1i.)*
 - * *Short answer (1k.)*
 - **Exercise 2**
 - * *Short answer (2a.)*
 - * *Short answer (2b.)*
 - * *Short answer (2c.)*
 - * *Short answer (2d.)*
 - * *Short answer (2e.)*
 - * *Short answer (2f.)*