

Lab 6: Metapopulation modeling

NRES 470/670

Spring 2020

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 patch is occupied or not, and how many total occupied patches we have in our metapopulation.

A classical metapopulation is best considered a **population of patches** – patches which may or may not be occupied. A patch is composed of individuals, and a metapopulation is composed of patches!

colonization is the process of a patch going from unoccupied to occupied! (via **immigration**).

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

regional (or global) extinction represents extinction of all patches in the metapopulation.

More formally, here are some terms we will consider:

f_t is the fraction, or proportion, of patches that are occupied at time t . This is also known as the **metapopulation occupancy**. This is the primary [Stock] in our classical metapopulation models.

I is the total fraction of the metapopulation that is colonized by immigrants in a given time period (colonization rate, or “immigration” rate)

E is the total fraction of the metapopulation that goes extinct per time period (extirpation rate)

Therefore, the absolute change in occupancy can be expressed as:

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

Q: If f_t is the [Stock], what would I and E represent in a stock-and-flow modeling framework (e.g., InsightMaker)? And what are the [Variables] (i.e., are there ‘per-patch’ rates that are analogous to per-capita rates?)?

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

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

A basic metapopulation model:

The more sites are available for colonization (not currently occupied), the higher the rate of patch colonization!

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

The more sites are occupied, the higher the rate of patch 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 (and the following models) assume the following:

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

Variant #1: island-mainland model

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

This model (and only this model) assumes that per-patch extinction and colonization rates (p_i and p_e) are not dependent on the fraction of patches occupied (f).

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

In this scenario, colonization can only happen via immigration from within the metapopulation itself. So when few patches 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).

In this model, the colonization rate is zero if all patches are unoccupied (there are no sources of immigrants to colonize any patches!)

In this model, the colonization rate approaches i as nearly all patches become occupied.

Variant #3: rescue effect.

Now, the extinction rate can be reduced by immigration from other patches 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).

In this model, the extinction rate approaches 0 as all patches become occupied [note, this may not be realistic, as it implies a perfectly successful rescue effect!]

In this model, the extinction rate approaches e as the metapopulation approaches global extirpation (fewer immigrants to ‘rescue’ a patch from extinction).

Variant #4: both internal colonization AND rescue effect!

This one is pretty self-explanatory. But it has some interesting emergent properties!

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 patches*. 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 (assume the ponds are 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%. Over the next 3 years, is it a better strategy to retain the single population or to split it into three (and “spread out the risk”)? Show your calculations, and explain your reasoning! [NOTE: you may want to refer to the ‘spreading the risk’ topic in the Metapopulations lecture and video. Also, recall that to compute the probability of three independent events of probability p , you simply multiply the probability by itself three times: $P(\text{three events}) = P(\text{one event})^3$].

1b. Build an InsightMaker model for the basic island-mainland metapopulation model. The total fraction of occupied patches f should be represented as a [Stock] (this stock can not go negative!) and there should be two [Flows]: one for *colonization* (I) and one for *extinction* (E). 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. Clone your Insight and provide a link to your working InsightMaker metapopulation model as part of your lab write-up.

1c. 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. [remember that to test for stability of equilibria, set the initial value of the stock at it's equilibrium value. From there, ‘perturb’ the initial value by setting it above and below the equilibrium. Does it return to the equilibrium state in all cases?]

1d. Compare your InsightMaker results at equilibrium (provide a plot) with the results from applying Equation 4.4 from Gotelli. Show your work. Do the two answers match (i.e., do your results from applying the equation match with the equilibrium from your InsightMaker model)?

1e. Change your InsightMaker model to reflect *internal colonization*. Set the parameter i to 0.1. Clone the model and provide a link to your InsightMaker model as part of your lab write-up.

1f. Compare your InsightMaker results at equilibrium (provide a plot) with the results from applying Equation 4.6 from Gotelli. Show your work. Do the two answers match?

1g. 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 in the “rescue effect” model to 0.25. Clone the model and provide a link to your InsightMaker model as part of your lab write-up.

1h. Compare your InsightMaker results at equilibrium (provide a plot) with the results from applying Equation 4.8 from Gotelli. Show your work. Do the two answers match?

1i. Change your InsightMaker model to reflect the *rescue effect* AND *internal colonization* (both processes operating in the same model). Set the parameter i to 0.1. Set the parameter e to 0.25. Clone your model and provide a link to your InsightMaker model as part of your lab write-up.

1j. Try some alternative parameterizations for the e and i parameters in the model you built for question 1i. Provide two plots illustrating two qualitatively different alternative stable states (e.g., provide one figure illustrating complete colonization over time [f=1] and another illustrating an equilibrium at an intermediate level of patch occupancy [e.g., f=0.25]). Make sure you indicate which parameters were used for each plot.

Exercise 2: a spatial metapopulation model!

Agent-based models (individual-based models- we skipped this lecture, so you are not expected to know this!) 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 time a simulation is initiated, patches are placed randomly in the landscape. The **metapopulation size** (total number of patches) is initialized at 10 (but you can change this quantity using a slider bar).

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 patches is approximately *lognormal*. This means that there are usually a few very large patches in the landscape. The minimum K is 2.

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 patches. A fixed proportion of the population in each patch disperses each year (**dispersal rate**, set to 25% initially), and the **maximum dispersal distance** is set initially at 50 kilometers. If no neighboring patch 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 Mean K per population: 10

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 (global) extinction of this metapopulation over 100 years? What is the abundance trend (that is, overall regional abundance) over time? Provide plots to justify your answer.

2b. Imagine that this metapopulation represents the last remaining patches of habitat for an endangered butterfly. You have identified three possible management strategies: Starting from the initial conditions specified at the beginning of this exercise, 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-patch 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.

2c. [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 (i.e., describe a scenario under which this may actually occur in the real world). 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).

Due Apr. 12 at midnight.

- Word document with short answers, model URLs, and figures (where appropriate)

– **Exercise 1**

* *Short answer (1a.)*

* *Short answer (1b.)*

* *Short answer (1c.)*

* *Short answer (1d.)*

* *Short answer (1e.)*

* *Short answer (1f.)*

* *Short answer (1g.)*

* *Short answer (1h.)*

* *Short answer (1i.)*

* *Short answer (1j.)*

– **Exercise 2**

* *Short answer (2a.)*

* *Short answer (2b.)*

* *Short answer (2c.)*