Lab 6: Metapopulation modeling

NRES 470/670

Spring 2022

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 transitioning from unoccupied to occupied! (via **immigration**).

extinction (or extirpation) is the process of a patch transitioning 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 metapopulation occupancy can be expressed as:

$\Delta f = I - E$ (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.*

Classical metapopulation models:

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.

If most patches in the landscape are unoccupied, then the majority of the metapopulation is available to be colonized. If most patches in the landscape are already occupied, then most of the metapopulation is closed to colonization. We can express this mathematically:

$I = p_i \cdot (1 - f)$ (Eq. 2)

If most patches in the landscape are occupied, then the majority of the metapopulation can potentially go extinct. If most patches in the landscape are unoccupied, then most of the metapopulation is closed to extinction. We can express this mathematically:

$E = p_e \cdot f$ (Eq. 3)

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

$\Delta f = p_i(1 - f) - p_e f$ (Eq. 4)

This model (and the following models) assumes 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 #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.

$p_i = i \cdot f$ (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.

All other elements remain unchanged from the island-mainland model.

Variant #3: rescue effect.

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

$p_e = e(1 - f)$ (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).

All other elements remain unchanged from the island-mainland model.

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 *collection of interconnected habitat patches*. We can keep track of patch abundance in a metapopulation model. In fact, 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 **global extinction**, we can also study **global abundance** and global abundance trends across the entire metapopulation.

Exercise 1: classical metapopulation models in InsightMaker

HINT: *use the Gotelli book!!!*

1a. Build an InsightMaker model to represent the basic island-mainland metapopulation model described above. The total fraction of occupied patches f should be represented as a [Stock] (make sure this stock can not go negative!) and there should be two [Flows]: one for *colonization* (I) and one for *extinction* (E). Initialize f at 0.25 (set the initial value of the stock to 0.25). The extinction and colonization probabilities (p_e and p_i) should be represented as [Variables]. Set p_e to 0.2 and p_i to 0.35. Use the description of the island-mainland model (above) to complete your model (drawing the appropriate links, setting the equations for I and E). Run a simulation for 100 years and make sure that f reaches an equilibrium value between 0 and 1. Clone your Insight and provide a link to your working InsightMaker metapopulation model in TopHat.

1b. Using your Insightmaker model above (submitted in 1a), test to see if the equilibrium state that the model reaches (constant f over time) is **stable** or **unstable**? Explain how you got your answer. [NOTE: remember that to test for stability of equilibria, start with the initial value of the stock set at it's equilibrium value. From there, try setting the initial value slightly above and below the equilibrium. Does it return to the equilibrium state in all cases? If not, it is unstable...]

1c. Compare the equilibrium value of f from your simulation (the one submitted in 1a.) with the equilibrium value of f computed by applying Equation 4.4 from the Gotelli book: the two values should match. Show how you computed your answer using Gotelli's equation 4.4 (you may submit an image if that's easier!).

1d. Working with a clone of the model you submitted in part 1a, please change your InsightMaker model to reflect *internal colonization* (see above). Set the parameter i to 0.3 and run a 100 year simulation. Compare the equilibrium value of f from your simulation with the equilibrium value of f computed by applying Equation 4.6 from the Gotelli book: the two values should match. Show how you computed your answer using Gotelli's equation 4.6 (you may submit an image if that's easier!).

1e. Working with a clone of the model you submitted in part 1a, please change your InsightMaker model to reflect the *rescue effect* (see above. Restore the colonization model to represent "propagule rain" (constant colonization rate for vacant patches). Set the parameter e in the "rescue effect" model to 0.75. Compare the equilibrium value of f from your simulation with the equilibrium value of f computed by applying Equation 4.8 from the Gotelli book: the two values should match. Show how you computed your answer using Gotelli's equation 4.8 (you may submit an image if that's easier!).

1f. Working with a clone of the model you built above (1e), please change your InsightMaker model to reflect the *rescue effect* AND *internal colonization* (both processes operating in the same model). Set the parameter i to 0.3. Set the parameter e to 0.75. Try some alternative parameterizations for the e and i parameters and simulate for 100 years. Provide **two plots** illustrating two qualitatively different alternative equilibrium 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]).

Exercise 2: a spatial metapopulation model!

Agent-based models (individual-based models) are well-suited for considering spatial context. In addition to being a flexible system for stock-flow modeling, Insightmaker also has the capability of running agent-based simulation models.

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 but most patches are pretty small. 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 die.

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 or TA! 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 100 times (or 50 times, if your browser crashes!), monitoring the total metapopulation occupancy. What is the approximate risk of regional (global) extinction of this metapopulation over 100 years? Briefly describe how you got your answer.

2b. Use InsightMaker's *sensitivity testing tool* to run the model 100 times (or 50 times, if your browser crashes!), monitoring the total metapopulation abundance. Using the results, briefly describe (i) the abundance trend over time (that is, the trend in overall metapopulation abundance) and (ii) your uncertainty about the final abundance at year 100. Justify your answer.

2c. 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). [see note above about how to change the max dispersal distance]

    ii. Improve existing habitats, doubling the mean per-patch carrying capacity (labeled "Mean K per population").

    iii. Restore habitat, effectively doubling the number of patches (labeled "metapopulation").

Which management strategy would be most effective for ensuring that the metapopulation does not go extinct? Please justify your answer with 1-2 supporting figures.

##Checklist for Lab 6 completion

- Please submit all answers *using TopHat*!

Due Apr. 15 at 11:55pm

- Short answers, model URLs, and figures (where appropriate): all on Top Hat
  - **Exercise 1**
    * *InsightMaker link (1a.)*

    * *Short answer (1b.)*

    * *Short answer (and optional image) (1c.)*
    * *Short answer (and optional image) (1d.)*
    * *Short answer (and optional image) (1e.)*
    * *Short answer (and optional image) (1f.)*
  - **Exercise 2**
    * *Short answer (2a.)*
    * *Short answer (2b.)*
    * *Short answer and 1-2 images (2c.)*