

Lecture 24: Community Ecology: Species Richness and Community Dynamics

Thanks to Jim Nichols and John Sauer for some slides that I have modified and extended

Metrics Ecologists Use in Increasing Spatial Scale and Complexity

Population of a Species

Abundance and Relative Abundance

Population Dynamics Parameters (Earlier Lectures in Class)

Metapopulations of a Species

Abundance by Patch (Multi-State Models Lectures)

*Patch Occupancy and Patch Dynamics

Communities

*Species Richness and Community Dynamics

Remaining Lectures

Metapopulations of Species Lectures 26-27.

Not in Text. I will provide some notes.

Patch Occupancy

**Communities Lectures 24-25 Chapter 20 in
Williams et al. (2002)**

Species Richness

Community Ecology: Species Richness and Community Dynamics

Species Richness Estimation

- Data Structure and Designs
- Modeling and Estimation
- Example

Community Dynamics Estimation

- Data Structure
- Modeling and Estimation

Common Measures of Species Diversity

- Diversity/evenness measures

- Simpson's Index

$$D = \frac{1}{\sum_1^N p_i^2}$$

- Shannon Index

$$H = -\sum_1^N p_i \ln p_i$$

- p_i = proportional abundance of species, N is no of species

- Applied to data sets without regard to sampling issues, pretending that N is known.

Species Richness

- Species richness is simply defined as the number of species in the community.
- Often the number of species counted in a community with no consideration that species detection probability is less than 1!
- Therefore this empirical estimate must be negatively biased

Comparison of Communities: Failures of Index-based Measures

- Species richness
 - Influenced by incomplete detection
 - Miss some species during counting
- Diversity measures
 - Require
 - Estimates of abundance
 - Detection of all species
 - Greatly influenced by sampling

Estimating Species Richness

- Detection issues apply to species richness estimation in the same way they apply to population size
 - Miss species during counting
 - Differs due to habitat, observers, weather, etc
- Counts (C) of number of species underestimate actual species richness!
- Recall: problems in estimating change over time or space from indices. One needs to make the unrealistic assumption that detection probability is constant.

Population – Community Analogy

- Population
 - Comprised of individuals
 - Abundance changes via rates of birth, death, and movement
- Community
 - Comprised of species
 - Richness changes via rates of local colonization and extinction

Sampling Communities

There are many taxa that one may want to list species from and count in community ecology surveys. Mammals, birds, fish, amphibians, reptiles etc. all have their unique sampling challenges

To start with let us assume that all the species of birds, for example, in a community are theoretically sightable from point counts.

Later I will come back to the sampling complexities for different taxa.

Procedures for Estimating Species Richness

Adapt Capture-Recapture Models

- Applied to counts from replicate points, times, observers.
- Species are analogous to individuals
- Sites, times or observers are analogous to capture occasions
- Estimate N , now the no. of species

$$\hat{N} = \frac{C}{\hat{p}}$$

Estimating Species Richness: Species Detection Probability

$$p_{ij} = 1 - (1 - p_{ij}^*)^{n_{ij}}$$

p_{ij} is the probability of detecting species j at occasion i . It is the probability of detecting at least one individual.

p_{ij}^* is the probability of detecting one individual

Species detection probability is therefore a function of the number of individuals and also how hard each individual is to detect.

This guarantees heterogeneous detection probabilities and the need for models which allow this!!

Review of Closed Capture- Recapture Models

I shall go back to some of our earlier class notes for a quick review...

CAPTURE-RECAPTURE MODELS

LINCOLN-PETERSEN MODEL (two samples)

$$\hat{N} = n_1 n_2 / m_2$$

Think of having two observers making their own species lists.

n_1 is how many seen by 1, n_2 how many seen by 2

and

m_2 is how many they have seen in common.

PETERSEN MODEL ASSUMPTIONS

1. Closure

2. Equal Catchability (This is the big problem with this application)

3. No Mark Loss

What to do about heterogeneity?

- Move to having at least 3 samples!!
- This brings us to the general closed models.
- These would be based on the capture histories of each species over sampling occasions.
- eg suppose 5 observers make species lists then 11010 might be the detection history for black capped chickadee at 5 BBS points in NY State
- Remember to replace animal by species in this new application.

Table 3.1. Capture-recapture models for closed populations that allow for unequal capture probabilities.

Monograph with minor changes.

<i>Model*</i>	<i>Source of variation</i>	<i>in</i>	<i>capture probability</i>	
	Heterogeneity	Trap response	Time	Estimator availability
M_o				yes
M_h	X ^a			yes
M_b		X		yes
M_{bh}	X	X		yes
M_t			X	yes
M_{th}	X		X	yes
M_{tb}		X	X	yes
M_{tbh}	X	X	X	no

*This set of 8 models comes from Otis et al. (1978).

^aXs denote the sources of variation in capture probability incorporated in the models.

2. M_0 : THE EQUAL CATCHABILITY MODEL

- * The simplest model but usually unrealistic
- * There are two parameters in this model
 - N - the population size
 - P - the probability of capture, which is constant over all animals over all periods.
- * M.L. Estimators found iteratively using the programs **CAPTURE** or **MARK**.
- * Estimators can be highly biased if heterogeneity or trap response is occurring. Variation in capture probabilities, due to time, are less troublesome.

3. M_b : TRAP RESPONSE MODEL

- This model makes the following **assumptions**:
 1. Every unmarked animal in the population has the same probability of capture (**p**) for all samples.
 2. Every marked animal in the population has the same probability of recapture (**c**) for all samples after it has been captured once.
- There are **three parameters** in the model:
 - N** - the population size
 - p** - the probability of capture for unmarked
 - c** - the probability of capture for marked
- M.L. estimators found iteratively using programs **CAPTURE** or **MARK**.

4 M_h : THE HETEROGENEITY MODEL

- This model allows capture probabilities to vary by animal, due to heterogeneity, but there is no trap response or time variation.
- The parameters in the model are:
 - N - the population size
 - p_j - the capture probability of animal j for $j = 1, \dots, N$
 - p_j s are assumed to come from distribution $F(\mathbf{p})$, otherwise the model is overparameterized.
- Estimators include:
 - Burnham's Jackknife
 - Lee and Chao's Coverage Estimator
 - Norris nonparametric MLE (Mixture Model)
- Burnham's estimator is widely used, but it has a questionable theoretical basis. It is given by program **CAPTURE**.

5. M_{bh} : THE HETEROGENEITY AND TRAP RESPONSE MODEL

- This model allows capture probabilities to vary due to heterogeneity and trap response, but not time.
- The parameters in the model are:
 - N - the population size
 - p_j - the unmarked capture probability for the j th animal
 - c_j - the marked capture probability for the j th animal

The (p_j, c_j) are assumed to come from some bivariate distribution $G(p, c)$.

6. M_t : THE TIME MODEL

- This is the traditional **Schnabel model** that only allows for time variation in capture probabilities.
- The parameters in the model are:
 - N - the population size
 - p_1, p_2, \dots, p_k - the unmarked capture probability of all animals in each sample.
- Programs **CAPTURE** or **MARK** provides the MLEs of N and the p s.

These estimators are not robust to heterogeneity and trap response.

7. OTHER TIME DEPENDENT MODELS

- Model M_{tb} - now has estimator available in CAPTURE
- Model M_{th} - now has estimator available in CAPTURE
- Model M_{tbh} - is only a conceptual model and has no estimators of N available.

Procedures for Estimating Species Richness

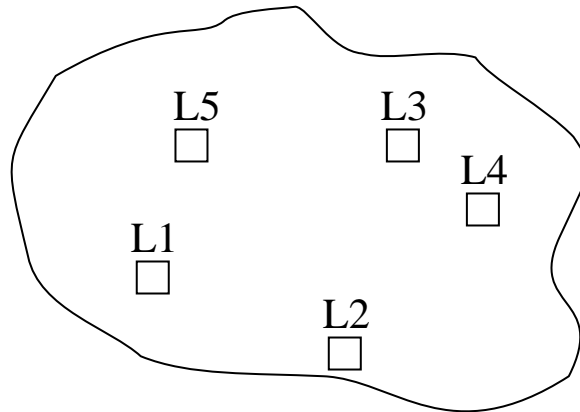
- Well-developed estimation procedures based on the capture –recapture approach.
 - We know that species vary in detection rates
 - Individual heterogeneity: Models allow for heterogeneity in species detection rates (M_h)
 - Other factors influencing p (M_{bh} , M_{th})
 - Computer programs

Sample Situations/Designs

- Have replicated counts
 - Over space
 - Over time
 - Over observers
- Don't have replicate counts
 - Use empirical species abundance distribution in a modified heterogeneity model.

Replicated counts (over space) at single time

Quadrat samples



Model issues:

M_h (detection probs vary by species)

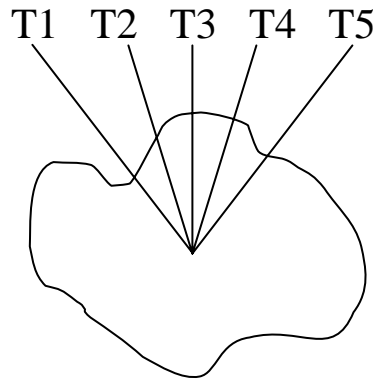
M_{th} (spatial variation in detection prob)

Short interval: Closed population model

-Estimate N

Replicated counts (over time) at single site

Multiple species lists



Short interval: Closed population models

-Estimate N

Useful Models

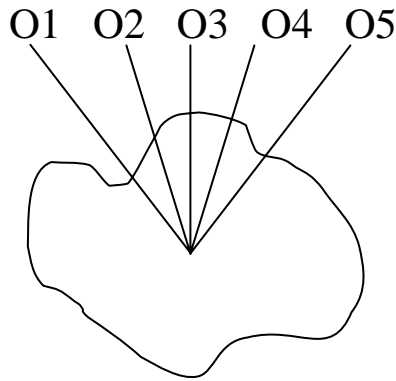
M_h (detection probs vary by species)

M_{bh} (Same observer more likely to redetect a species)

M_{th} (conditions vary across sample periods)

Replicated counts (over observers) at single site

Multiple species lists



Model issues:

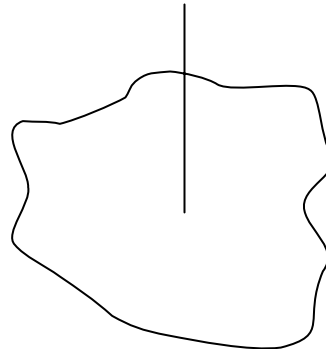
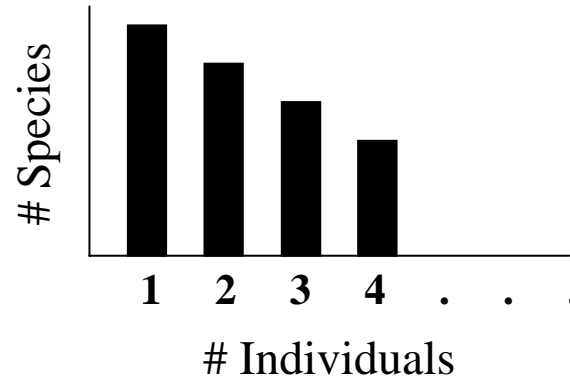
M_h (detection probs vary by species)

M_{th} (detection probs also vary across observers)

Short interval: Closed population models

-Estimate N

Summary of
information
used in
SPECRICH



**Empirical Species Abundance Distribution Approach
(Burnham and Overton 1979)**

Empirical Species Abundance Distribution Estimation Approach

- This uses the first 5 frequencies and the total number of detected species
- f_1 is the # of species where one individual was detected. f_2 is the # of species where two individuals were detected.
- It is a modification of the Mh model. Use SPECRICH to compute interactively on the Patuxent Software archive Web Site.

Analysis of Data

- Capture history format (preferred input)
 - Over replicates (time or space or observers)
 - Each species encountered or not encountered
 - e.g., 5 sites :00101
 - Programs CAPTURE, MARK
 - Use heterogeneity models (e.g. Burnham and Overton M_h)
 - Can use reduced input format:
 - $f(i)$: freq of species occurring i times in M_h



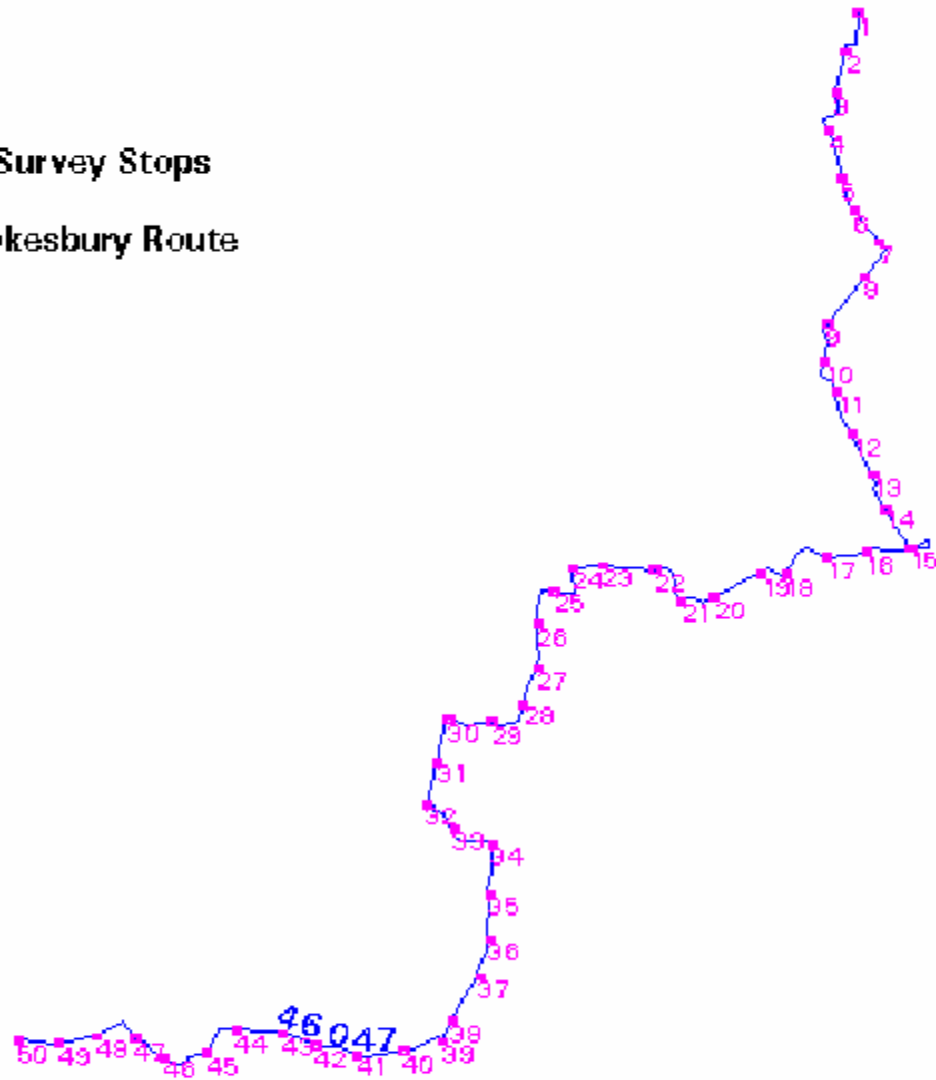
North American Breeding Bird Survey

- Started in 1966
- Roadside survey
 - Conducted in June, 1 survey/route/year
 - 24.5 mi roadside survey “routes” conducted by volunteer observer
 - 50, 3-min point counts along route
- Sum of counts for each species over 50 stops form the index of abundance for the route

Application to BBS

- Count locations are sites
- Estimate richness at route level (done)
- Analyze subsets of species (e.g., forest birds **could be done**)
- Could Provide Some Examples on Species Richness, and associations with habitat variables

Breeding Bird Survey Stops
Maryland's Cokesbury Route



Survey Route in MD, Data from 1966 and 1992

Estimating Species Richness

- Data: Capture history condensed from 50 stops (capture occasions)
- Use program CAPTURE (M_h)
- Results:
 - 1966: Count: 64 spp; Estimate=75 (5.62)
 - 1992: Count: 50 spp; Estimate=83 (11.61)
- Notes-Look at raw counts vs estimates. Also there is no evidence of a change in N between the two occasions. (Size of SEs)

Programs for Species Richness

SPECRICH (Patuxent)

- Capture frequency only (reduced form input)

<http://www.mbr-pwrc.usgs.gov/software.html>

No Species observed=100

First 5 frequencies $f_1=50$, $f_2=20$, $f_3=10$, $f_4=5$,
 $f_5=9$.

$$\hat{N} = 167.0384$$

$$SE(\hat{N}) = 14.0147$$

Will be needed for one homework problem.

Programs for Species Richness

SPECRICH2 (Patuxent)

- Summarized capture history input for M_h
- Observed species, observed frequencies

<http://www.mbr-pwrc.usgs.gov/software.html>

Programs for Species Richness

CAPTURE through MARK

- All M_h varieties (most general)
- Unsummarized capture histories

CAPTURE on the WEB

<http://www.mbr-pwrc.usgs.gov/software.html>

Jackknife Procedure Lecture 8 shows format will be needed for one homework problem

Summary

- Capture-Recapture estimators that allow for heterogeneity are useful and are better than just using the counts.
- There are a variety of sampling protocols which give rise to various estimators.
- Not adjusting and using the species counts as indices would be dangerous due to possible changes in detection probability over space, time or observers.

Practical Issues

- Species pools need to have a “reasonable” number of species for these estimators to work (>10 ?)
- If a species has a detection probability of 0, it will not be part of the sampled species pool and no adjustment can account for this.
- Suggests that one needs to think very carefully about how to sample the community. More on this later.

Practical Issues

- Birds may often be able to be sampled using one relatively simple technique like point counts---but even there some species may have 0 detection rate—not singing in a dense forest setting.
- Mammals and other taxa often need species specific sampling methods to find them. Therefore one would need multiple sampling methods on each occasion or at each location to apply these methods.

Practical Issues

What are community ecologists interested in?

- Species richness changes over space and time. A kind of summary measure for use in monitoring studies?
- Detailed species lists so one can look at associations of species
- Common species, rare and endangered species and how they are changing over time and space.
- Keystone species so one doesn't have to focus on the whole community. Not clear if this approach works.
- There are a myriad of very complex quantitative questions confronting community ecologists.

Important References

Williams et al.(2002). Chapter 20.

Burnham and Overton (1979)

Boulinier et al. (1998ab)

Nichols et al. (1998ab)

The last 3 references are in the Williams et al.
(2002) Book.

Next Class: Community Temporal and Spatial Dynamics

- Read ahead in Ch 20 if you are interested.
- Many quantities of interest.
 - Change in N over time or space
 - Local Colonization by new species
 - Local Extinction
- Will Use Robust Capture-Recapture Design
 - Estimate richness with closed models in a year
 - Estimate local colonization and extinction between years