22 *NICHE BREADTH AND RESOURCE PARTIONING*

Objectives

- Compute niche breadth for two organisms coexisting in a community.
- Compute niche overlap for the two coexisting organisms.
- Use the Solver function to evaluate how breadth and overlap between the two species can be maximized and minimized.

Suggested Preliminary Exercise: Interspecific Competition

INTRODUCTION

A **community** is an assemblage of different species that coexist in time and space (Gotelli 2001). Community dynamics can occur at any spatial scale. That is, we can study the interaction of different species within a community on our front lawn, inside the gut of a deer, in a pond after a rainstorm, or in a temperate rain forest.

Given that resources are not infinite within any ecosystem, a fundamental question in ecology is, How many species can occur together within a given community? The **competitive exclusion principle** states that if two species compete for critical resources in an environment, one of two outcomes results. Either both species coexist, or one species outcompetes the other and drives the other species to extinction (at least in that community). Coexistence can occur only if the species niches are different enough to limit competition between them. Thus, ecologists interested in community dynamics often ask, How do the different species partition the resources in this community? To answer this question, we need to know how organisms utilize their environment. One way to do this is to measure the **niche parameters** for one species and then compare it to the niche parameters of another.

As a hypothetical example, consider two species that occur together in a community. Both species consume a food resource that varies in size, such as seeds. Suppose both species 1 and species 2 consume a wide variety of seed sizes, but eat similar kinds of seed sizes. A graph of their resource consumption might look like Figure 1. Since both species eat a variety of seed sizes, *intraspecific* competition may not be that significant because individuals may not have to compete directly with members of their own species for a certain size of seed. However, the overlap in curves between species 1 and 2 suggests that *interspecific* competition may
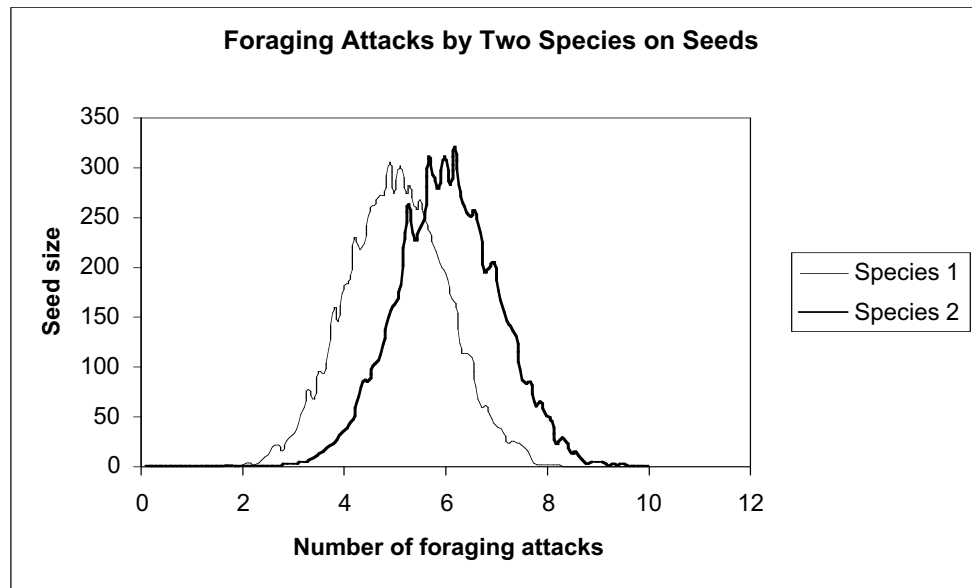
Foraging Attacks by Two Species on Seeds

Figure 1   The two species whose foraging habits are charted here are competing for the same food resource and would not be able to coexist comfortably.

be significant. The competitive exclusion principle suggests that such competition may lead to the local extinction of one species.

Alternatively, assume that species 1 and species 2 consume different seed sizes, with a graph of seed consumption as shown in Figure 2. In this situation, *intraspecific* competition may be significant because each species specializes on only a small range of seed sizes in their diets. However, since the species do not overlap in their consumption of seeds of a certain size, *interspecific* competition is likely to be low, and the two species may coexist.

How can we determine quantitatively the degree to which two species can compete for a similar resource? We will consider two measures: niche breadth and niche over-
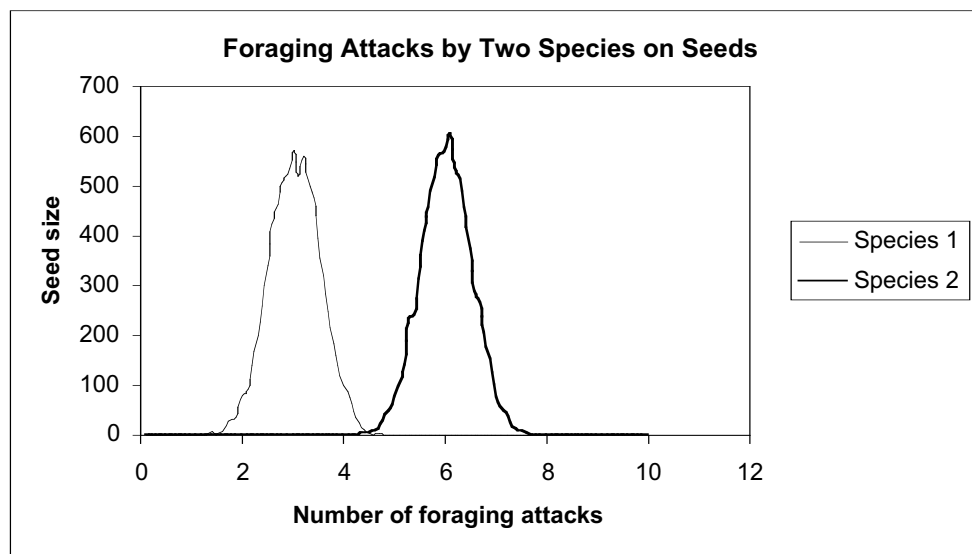
Foraging Attacks by Two Species on Seeds

Figure 2   Individuals of the two species in this graph would face greater competition from members of their own species than from members of the second species.

lap. **Niche breadth** is a parameter that attempts to measure how specialized or unspecialized a species is within a given environment. A specialist that feeds on only one or two food sources will have a much smaller niche breadth than a generalist that feeds on many kinds of food items. Niche breadth is measured by observing how individuals in the community make use of the same set of resources. Food, for example, is a resource that can be measured by identifying the kind of food taken or the size of food taken. Habitat is also a resource whose use can be measured for niche analysis.

There are many ways to quantify niche breadth (Krebs 1999). One common measure is the Levins measure (1968), which measures how uniformly resources are being utilized by each species. The equation is

$$B = \frac{1}{\sum p_i^2} \qquad \text{Equation 1}$$

where B is the Levins measure of niche breadth and p_i is the proportion of individuals found using resource i. To derive measures of niche breadth for a species, an ecologist typically counts the number of resource items used by a set of individuals of that species.

Suppose we observed two species of lizards and quantified the food intake of 1000 individuals in both species. One species, the whiptail lizard (*Cnemidophorus tigris*), has a diet that consists of 20% grasshoppers, 30% termites, 20% insect larvae, 20% beetles, 5% vertebrates, and 5% roaches (data drastically modified from Pianka 1986). The second species, the side-blotched lizard (*Uta stansburiana*) has a diet that consists of 10% ants, 20% grasshoppers, 25% beetles, 15% termites, 10% insect larvae, 10% arthropods, and 10% spiders. The niche breadth for the whiptail lizard would be

$$B = \frac{1}{.20^2 + .30^2 + .20^2 + .20^2 + .05^2 + .05^2} = 4.65$$

and the niche breadth for the side-blotched lizard would be

$$B = \frac{1}{.10^2 + .20^2 + .25^2 + .15^2 + .10^2 + .10^2 + .10^2} = 6.06$$

Often, these measures are standardized on a scale of 0 to 1 by using the formula

$$B_A = \frac{B-1}{n-1} \qquad \text{Equation 2}$$

where B_A is the standardized niche breadth, and n is the total number of food items for the species of interest (in the whiptail example, six food types were observed in total, so $n = 6$).

In contrast to niche breadth, the parameter **niche overlap** measures the degree to which two different species overlap in their use of a particular resource. Estimating niche overlap is a way to answer the question, How do the different species partition the resources in the community? It might be obvious that some species do not overlap at all in their use of resources. For example, a hummingbird and an owl are very unlikely to compete for the same food resources, so measures of niche overlap seem trivial when it comes to food. However, estimating niche overlap and resource partitioning is often of interest when a number of species use resources in similar ways. Such a group of species is called a **guild**. Seed-eating finches on the Galápagos Islands are an example of a guild.

If species overlap in niches to a great extent, they may influence each other's population growth through interspecific competition. As with niche breadth, niche overlap can be measured in a variety of ways (Krebs 1999). One measure, developed by MacArthur and Levins (1967), is calculated as

$$M_{jk} = \frac{\sum p_{ij} p_{ik}}{\sum p_{ij}^2} \qquad \text{Equation 3}$$

where M_{jk} is the MacArthur and Levins niche overlap measure *of species k on species j* (keep track of the notation used), p_{ij} is the proportion that resource i is of the total resource that species j utilizes, and p_{ik} is the proportion that resource i is of the total resources that species k utilizes. Both summations are over the index i. Note that when we calculate niche overlap this way, the effect of species j on species k can be different from the effect of species k on species j. This formula was originally developed to estimate α and β coefficients in the Lotka-Volterra interspecific competition model (Exercise 10). However, most ecologists now agree that overlap measures are not appropriate for competition coefficients (Krebs 1999). A similar, but symmetrical, measure of overlap was developed by Pianka (1986), and is calculated as

$$O_{jk} = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ij}^2 p_{ik}^2}}$$
                                                                          Equation 4

where O_{jk} is Pianka's measure of overlap between species j and species k, p_{ij} is the proportion that resource i is of the total resources used by species j, and p_{ik} is the proportion that resource i is of the total resources used by species k. This measure ranges from 0 (no resources used in common) to 1 (complete overlap).

In our lizard example, we can plug in the numbers and calculate M to determine the extent to which whiptail lizards are overlapped by side-blotched lizards, and the extent to which side-blotched lizards are overlapped by whiptail lizards. We can compute Pianka's measure of overlap, O, as well. The results give us some indication of how food resources are partitioned between the two species in the community. Keep in mind that these measures suggest a potential for competition between species, which in turn may affect the diversity of species present at a site, but they do not provide direct evidence that the presence of one species can influence the population dynamics of the second.

PROCEDURES

In this exercise, you'll set up a spreadsheet to calculate both niche breadth and niche overlap of two hypothetical species. A primary goal is to be able to determine, in Questions 3 and 4, how diets must change in order to either maximize or minimize niche breadth and niche overlap.

As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION
A. Set up the model community.	
1. Open a new spreadsheet and set up column headings as shown in Figure 3	
2. For each species, fill in the numbers of foraging attacks shown in Figure 1 for resources 1 through 10.	We'll focus on two species and assume that we can record how many times we observe foraging attacks on 10 major food resources, listed in cells A6–A15. Glancing at the raw data, which species do you think has a broader niche breadth?

	A	B	C	D	E	F	G	H	I	J
1	*Niche Breadth and Resource Partitioning*									
2										
3										
4			Species 1				Species 2			
5	Resource	# users	$\#^2$	p	p^2	# users	$\#^2$	p	p^2	$p\,1^*p\,2$
6	1	7				0				
7	2	1				0				
8	3	286				38				
9	4	71				24				
10	5	0				30				
11	6	0				140				
12	7	0				5				
13	8	0				0				
14	9	0				0				
15	10	0				0				
16	$Y =$	365				237				
17										
18	$n =$					$n =$				
19	$B =$					$B =$				
20	$B_A =$					$B_A =$				
21	$M_{12} =$					$M_{21} =$				
22	$O =$					$O =$				

Figure 3

3. Use the **SUM** function in cell B16 and F16 to count the total number of foraging attacks observed for species 1 and 2, respectively.

Enter the formula **=SUM(B6:B15)** in cell B16.
Enter the formula **=SUM(F6:F15)** in cell F16.

4. In cells C6–C15, enter a formula that squares the number of foraging attacks on prey item 1 for species 1.

Enter the formula **=(B6^2)** in cell C6. Copy this formula down to cell C15.
The columns labeled $\#^2$, p, and p^2 are simply steps that you need to compute in order to estimate niche breadth and overlap at a later point in time. The **^** symbol indicates that the value in cell **B6** is to be raised to a power (in this case, the power of **2**).

5. In cells D6–D15, calculate the proportion (p) of the total number of attacks for each resource type.

Enter the formula **=B6/$B$16** in cell D6. Copy this formula down to cell D15.

6. In cells E6–E15, square the values in column D.

Enter the formula **=D6^2** in cell E6. Copy this formula down to cell E15.

7. Sum your column values in cells C16–E16.

Enter the following formulae:
- Cell C16 **=SUM(C6:C15)**
- Cell D16 **=SUM(D6:D15)**. This result should be 1.
- Cell E16 **=SUM(E6:E15)**

8. Calculate $\#^2$, p, and p^2 for species 2.

Enter the following formulae:
- Cell G6 **=(F6^2)**
- Cell H6 **=F6/$F$16**
- Cell I6 **=H6^2**.

Copy these formulae down to row 15.

9. In cell J6, multiply p (species 1) by p (species 2), and copy your formula down to cell J15.

Enter the formula **=D6*H6** in cell J6.

10. Sum cells J6–J15 in cell J16.

Enter the formula **=SUM(J6:J15)** in cell J16.

11. Save your work.

Your spreadsheet should now resemble Figure 4.

	A	B	C	D	E	F	G	H	I	J
4			Species 1				Species 2			
5	Resource	# users	#^{2}	p	p^2	# users	#^{2}	p	p^2	$p1*p2$
6	1	7	49	0.019178	0.000368	0	0	0	0	0
7	2	1	1	0.00274	7.51E-06	0	0	0	0	0
8	3	286	81796	0.783562	0.613969	38	1444	0.160338	0.025708	0.125634
9	4	71	5041	0.194521	0.037838	24	576	0.101266	0.010255	0.019698
10	5	0	0	0	0	30	900	0.126582	0.016023	0
11	6	0	0	0	0	140	19600	0.590717	0.348947	0
12	7	0	0	0	0	5	25	0.021097	0.000445	0
13	8	0	0	0	0	0	0	0	0	0
14	9	0	0	0	0	0	0	0	0	0
15	10	0	0	0	0	0	0	0	0	0
16	Y =	365	86887	1	0.652182	237	22545	1	0.401378	0.145333

Figure 5

B. Calculate niche statistics.

With the basic calculations in place, you are now ready to calculate n, B, B_A, M_{12}, M_{21}, and O. Take a moment to review the equations presented in the Introduction to this exercise.

1. In cells B18 and G18, enter formulae to calculate n for each species.

Enter the formula **=COUNTIF(B6:B15,">0")** in cell B18.
Enter the formula **=COUNTIF(F6:F15,">0")** in cell G18.
These formulae count the number of entries in cells B6–B15 and F6–F15 that are greater than 0, hence providing information on n.

2. In cells B19 and G19, enter formulae to calculate B for each species.

Enter the formula **=1/E16** in cell B19.
Enter the formula **=1/I16** in cell G19.

3. In cells B20 and G20, enter formulae to calculate B_A for each species.

Enter the formula **=(B19-1)/(B18-1)** in cell B20.
Enter the formula **=(G19-1)/(G18-1)** in cell G20.

4. In cells B21 and E21, enter formulae to calculate M_{12} and M_{21}, respectively.

Enter the formula **=J16/E16** in cell B21.
Enter the formula **=J16/I16** in cell G21.

5. In cells B22 and G22, enter a formula to calculate O.

Enter the formula **=J16/SQRT(E16*I16)** in cells B22 and G22.

6. Save your work.

C. Create graphs.

1. Graph the overlap statistics for the two species.

2. Save your work.

Use the column graph option and label your axes fully. Your graph should resemble Figure 5.
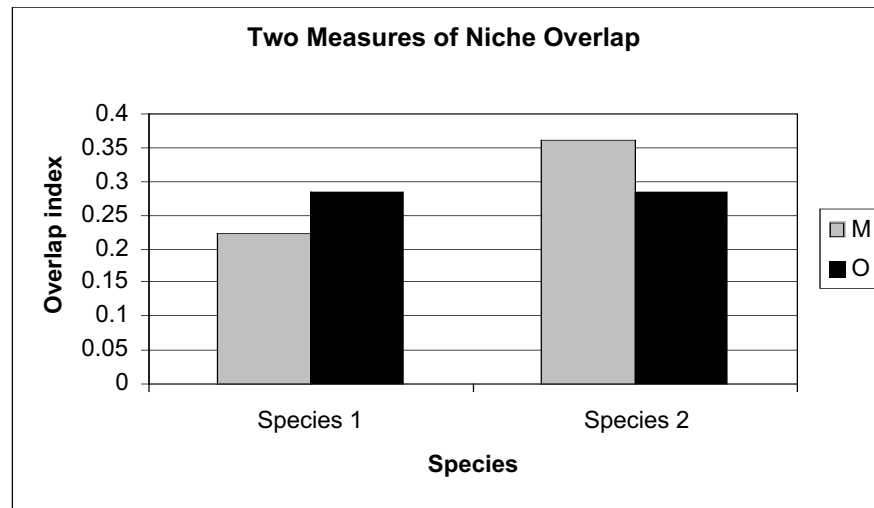
Two Measures of Niche Overlap

Figure 5

Using Solver

Questions 3 and 4 ask you to use the function **SOLVER** to mathematically *optimize* specific niche parameters. To access Solver, go to Tools | Solver and select Solver. (If Solver does not appear in the menu, go to Tools | Add-ins and select the Solver add-in. Your computing administrator may need to help you with the installation.) The dialog box in Figure 6 (see Question 3) will appear. In general, Solver works through the following steps:

- In the Set Target Cell box, enter a cell reference or name for the target cell. The target cell must contain a formula.
- To have the value of the target cell be as large as possible, click Max. To have the value of the target cell be as small as possible, click Min. To have the target cell be a certain value, click Value of, then type the value in the box.
- In the By Changing Cells box, enter a name or reference for each adjustable cell, separating nonadjacent references with commas. The adjustable cells must be related directly or indirectly to the target cell.
- In the Subject to the Constraints box, enter any **constraints** you want to apply. For instance, we will constrain the number of foraging attacks and the total observations. Table 1 lists of the operators that can be used in writing constraints.
- When you click Solve, Solver will run through several different scenarios with varying combinations of parameters, evaluating each combination given the constraints you identify. When the Solver finds a solution, a dialog box will

TABLE 1. Operators Used as Constraints in Solver	
Operator	**Meaning**
<=	Less than or equal to
>=	Greater than or equal to
=	Equal to
int	Integer (applies only to adjustable cells)
bin	Binary (applies only to adjustable cells)

appear, asking you whether you want to keep the solution or to restore the
original values.
• To keep the solution values on the worksheet, click Keep Solver Solution in the
Solver Results dialog box. To restore the original data, click Restore Original
Values.

QUESTIONS

1. Fully interpret your results from cells B18–B22 and cells G18–G22. What general
conclusions can you draw about how the two species coexist in the community?

2. In counting the number of resource "hits" for each species and using this infor-
mation to calculate niche breadth and overlap, what assumptions are you mak-
ing about the availability of different resources in the environment?

3. Under what conditions would niche breadth, *B*, for species 1 be maximized?
Under what conditions would niche breadth for species 1 be minimized?

To answer this question, you could plug in some numbers for resource utiliza-
tion, varying your scenarios from conditions in which a single item is utilized
versus all 10 resources utilized equally versus all 10 resources utilized unequal-
ly. However, you can readily use the Solver function described at the end of the
exercise to answer this question.

• To use the Solver, select cell B19, then go to Tools | Solver and the dialog box
shown below.
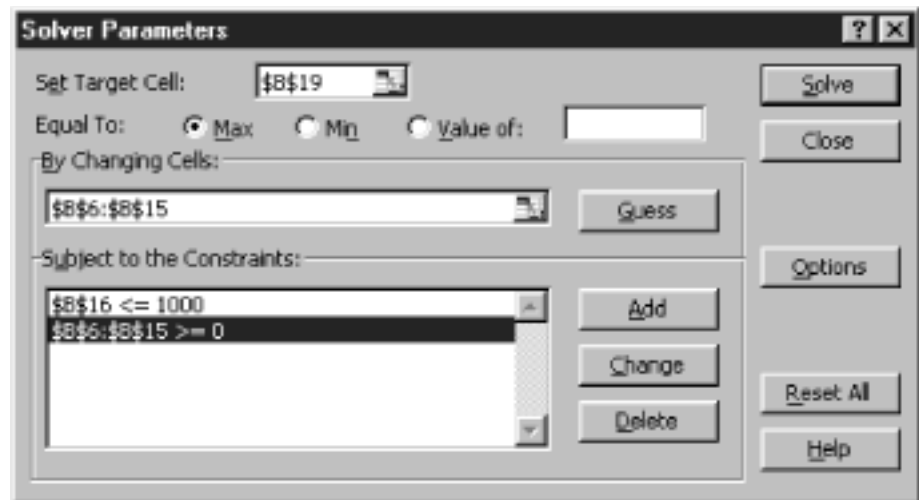
• To maximize the niche breadth of species 1, we want to set Target Cell B19 (B,
niche breadth) to a maximum by changing cells B6–B15. You can use your
mouse to click on cells for these entries, or you can directly type in the cell ref-
erences in the appropriate locations. If you do the latter, make sure you type in
absolute cell references (e.g., Set Target Cell to $B$19, not B19).
• The spreadsheet will figure out how to change the diets in order to maximize
niche breadth, but we will *constrain* the numbers that the spreadsheet uses in
the calculations. First select the Add button and add a constraint that the num-
ber of foraging attacks for each resource must be greater than or equal to 0.
Then select the Add button again and constrain the total number of observa-
tions to 1000 (cell B16 must be less than or equal to 1000).
• Once you've entered the constraints, click the Solve button. The program will
return a solution, with new values entered automatically in cells B6–B15.

You can either keep the Solver results (which pastes the Solver values into your spreadsheet), or simply interpret the results and cancel the Solver results to return to your original spreadsheet values. (You might want to copy your spreadsheet into a new worksheet if you wish to keep the Solver answers and your original cell entries). Note that you can also find minimums or specify a certain value that you want to be solved.

4. Assuming that species 2 cannot change its resource use, what diet should species 1 consume to minimize niche overlap with species 2? Again, you can use the Solver and set cell B22 to a minimum (and constrain the foraging observations to a total of 365, the original number of observations).

5. Ask an interesting question pertaining to niche overlap or niche breadth. Use your model to answer your question. Provide graphs to support your answer.

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