INTRODUCTION

In the African savanna ecosystem, many species of large herbivores share similar habitats. How can they all coexist rather than one, or a few, species outcompeting all the others? Niche partitioning is a mechanism that facilitates coexistence. An organism's niche is its place and role in an ecosystem, including where it lives and how it obtains the resources it needs to survive. If competing species use the environment differently, or partition resources, they can coexist in the same area.

NICHE PARTITIONING BY TIME AND GRASS HEIGHT

One type of niche partitioning is shown with examples from the savanna in the graph in Figure 1. *Panicum maximum* is a typical savanna grass; its growing season starts after the peak rains and continues for six months. When the grass is tall, it has lots of stems and is relatively low quality. More nutritious parts of the plant are closer to the ground and on the new growth after it has been grazed.

Zebras are the first grazers to utilize this resource, and they digest grass via fermentation in their hindgut rather than their foregut like ruminants do. Although hindgut fermentation is less efficient at nutrient and protein uptake than foregut fermentation, it means zebras can digest food much more quickly and thrive when there is ample food available, even if it is less nutritious, like when grass is tall with lots of stems in the months following peak rain. Zebras also have paired upper and lower teeth which enable them to bite off tall stems. Ruminants, such as wildebeests and Thomson's gazelles, have four-chambered stomachs; it therefore takes much longer for them to digest food, and sometimes they regurgitate and rechew their cud. A ruminant can extract more energy from a smaller quantity of food if that food is more nutrient-rich.

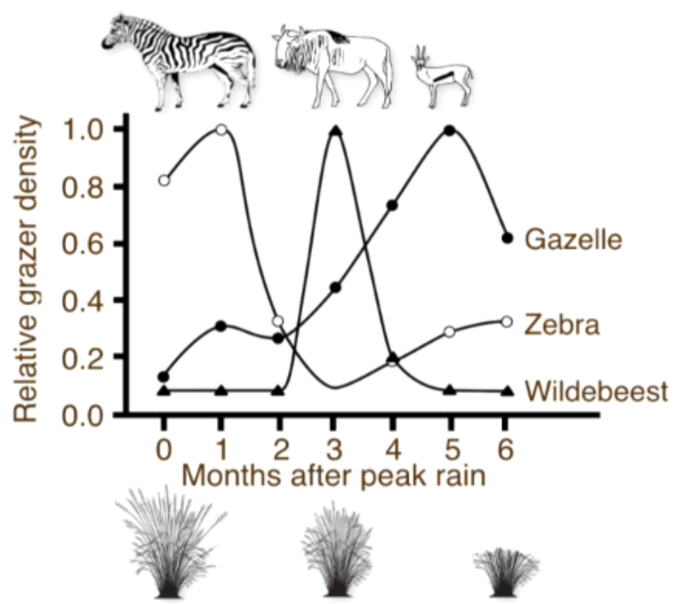

Figure 1. Relative grazer density at different times after the peak rain. Note that the grass pictures below the x-axis show the relative height of the grass at each time point on the graph. The population counts were done on the same area, and numbers were normalized to the maximum count for each species. (Figure courtesy of *Oecologia*, *174*(4), 1075–1083, 2014.)

1. Describe how the density of zebras grazing on *Panicum* grasses changes over time. What characteristics of the zebra explain why zebra numbers are greatest when the grass is tallest and fullest?

2. Describe the trend in wildebeest grazing population density over time.

3. Propose a reason or reasons that the wildebeest population density spikes when it does. Support your idea with evidence from what you know about wildebeest and *Panicum*. (Hint: Grasses continue to grow after being grazed.)

4. How does the gazelle population density change in relation to the changes in the wildebeest population density and the grass morphology over time? Why do you think this is so?

5. Would you describe the interactions between zebras, wildebeests, and gazelles as competition or facilitation between species? Explain with data from above.

TYPES OF NICHE PARTITIONING

6. The example above is only one example of niche partitioning. Watch the *Niche Partitioning* clip and then complete the following table to describe the remaining examples of niche partitioning. The clip is from the 2015 Holiday Lectures on Science, Lecture 3, 3:35 – 7:48.

Mechanism	Description & example
Spatial niche partitioning	
Dietary niche partitioning	
Niche partitioning by plant height	
Niche partitioning by time and grass height	

RECONSIDERING THE GRAZER–BROWSER SPECTRUM WITH NEW DATA

Watch the clip titled *Introduction to Metabarcoding* to learn about new techniques for investigating niche partitioning. The clip is from the 2015 Holiday Lectures on Science, Lecture 3, 10:08 – 13:47.

Using new DNA techniques, scientists are able to more accurately monitor organisms' diets by identifying what plant species each animal eats. You can think of the result as a table with each individual herbivore in rows and plant species in columns. If a specific animal ate that plant, the intersecting table cell is checked.

	Cynodon plectostachyus (Stargrass)	*Solanum indicum* (African Eggplant)	*Tragus berteronianus* (Burr Grass)
Elephant	Yes	Yes	No
Dik-Dik	No	No	Yes

Data like this can be analyzed by using a statistical technique called nonparametric multidimensional scaling (NMDS). Multidimensional scaling (MDS) is a way of calculating similarity between different data points. Here, we are analyzing the diet of every single individual in terms of what it ate and trying to find similarities or differences. Because the original data are a series of yes/no questions (i.e., "Did this individual eat plant x?"), it is a "nonparametric" form of multidimensional scaling (Figure 2). The result is a two-dimensional scatter plot of the variety of plant species found in the diets of individual animals. Points that are closer together have a more similar diet to each other than more distant points.

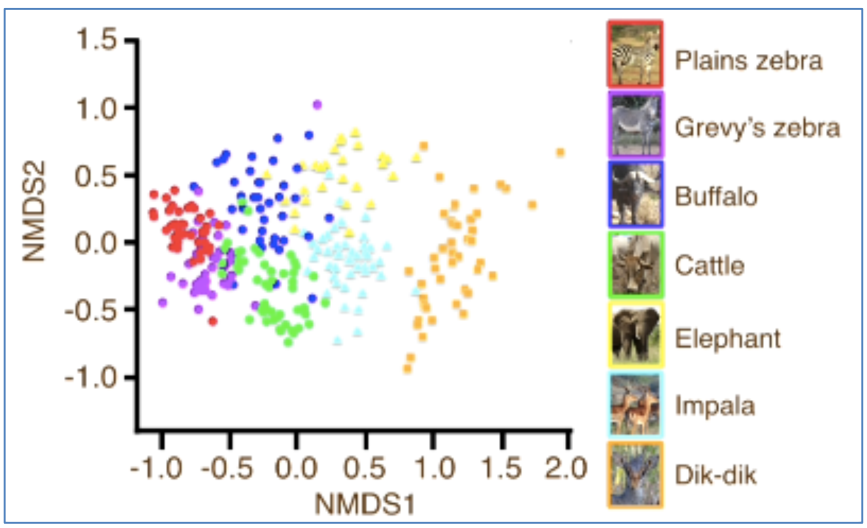

Figure 2: Data comparing herbivore diets during a single wet season. Each colored point represents the diet of a single animal; they are color-coded by species. On NMDS plots, axes do not correspond to any one specific variable, but rather they represent a combination of variables all rolled into one. In this case, the x-axis, NMDS1, is closely related to the grazer-browser spectrum: the higher values correspond to browsers and the lower values correspond to grazers. The y-axis is more complicated, but clearly you can separate out different species (such as elephant and impala) along that dimension. (Figure courtesy of *PNAS*, 112(26), 8019–8024, 2015.

7. How does the diet of the plains zebra compare to that of the Grevy's zebra? Are they eating the same species of grass?

8. How does the diet of the plains zebra compare to that of the impala?

9. What does this new data contribute to our understanding of the grazer-browser spectrum and dietary niche partitioning?

10. Study the data for buffalo, a wild species, and cattle, a domesticated species. How could these data inform management of wild populations near areas with farming and/or ranching of domesticated animals?

11. Note that the data presented above are from a single wet season. Why would it be important to run the experiment again during other seasons?

APPLICATION QUESTIONS

12. Consider each of the following examples and identify the mechanism by which the resources, and thus the niche, are separated (refer to the explanations in the table on page 3).

Mechanism	Description/example
	During the warm daylight hours, bees collect nectar from the flowers on a linden tree. In the evening, different types of moths are on the flowers.
	Pileated woodpeckers and yellow-bellied sapsuckers both consume resources from the same tree. Sapsuckers drill rows of little holes to eat the sap and insects in the sap, while pileated woodpeckers dig deep holes to find insects in the tree trunk.
	Prairie grasses have different length roots: smartweed roots reach to nearly 100 cm, Indian mallow roots reach to 70 cm, and bristly foxtail roots are a clump only about 20 cm deep.

13. Which of the following statements best describes resource partitioning?
    a. Varying prey species maintains biodiversity.
    b. Superior species enjoy success because of competitive exclusion.
    c. Coevolution between two species means they can always share the same niche.
    d. Similar species can coexist because of slight differences in each one's niche.

14. How does niche partitioning promote biodiversity?