Resource Partitioning and Why It Matters

By: John N. Griffin (*Department of Zoology, University of Florida*) & Brian R. Silliman (*Department of Zoology, University of Florida*)

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Similar species commonly use limiting resources in different ways. Such resource partitioning helps to explain how seemingly similar species can coexist in the same ecological community without one pushing the others to extinction through competition. Understanding resource partitioning among species may help us to predict how ongoing species declines will impact the functioning of ecosystems.

The Diversity of Life

One of the most striking features of life on Earth is its amazing diversity. There are so many species, in fact, that even after centuries of exploring different ecosystems, describing species, and cataloguing them, the total number of species on planet Earth is still unknown. Estimates range from 5–30 million, but we have only named and described a mere 2 million (the most obvious ones!). Individual ecological communities can hold almost unbelievable numbers of species. For example, it is not uncommon to find 100 species of coral on a reef in Fiji or Hawaii or 150 species of fish feeding on or sheltering among the same corals. Biodiversity is not something that is just observable in tropical paradises — a close look at birds in a local park or the fish caught in a local pond will reveal numerous species.

How is this tremendous diversity of life maintained (i.e., why do so many species coexist), and what are the effects of the rapid loss of species we are currently experiencing on the functioning of ecosystems? An understanding of resource partitioning may be key to answering both of these questions.

Similar Species Compete for Limiting Resources

There are only a limited number of ways of "making a living" within ecological communities. For example, on a coral reef, there are hard-skeleton corals that gain food from capturing planktonic animals in their tentacles and, in exchange for providing a suitable habitat and nutrients, gain extra sources of energy from sugar-synthesizing symbiotic algae. Within groups of species that make a living in a similar way, species compete for the same resources. These resources, which include nutrients and habitat, are the raw materials needed by organisms to grow, live, and reproduce. However, resources are not unlimited, and individuals from different species commonly compete for resources (interspecific competition).

Complete Competitors Cannot Coexist

Classic experiments and mathematical models show that two species cannot coexist on the same limiting resource if they use it in the same way: The superior competitor will always win out. If ecologically similar species (like corals on a reef or plants in a field) compete with one another for limiting resources, what stops the best competitor from out-competing all the others? The answer may lie in species "doing their own thing" — specializing in their use of resources and thereby limiting their competition with others.

Dividing the Resource Pie

Species can divide up a limiting resource, such as food, water, or habitat (in other words the resource "pie"), by using different slices or even using the same "slice" but in different places (i.e., they are dining in different restaurants, to take the analogy one step further) or at different times ("do you have a table free at eight o'clock?").

How Do Potential Competitors Partition Resources in Nature?

Careful and detailed study has revealed some of the many ways in which potential competitors show differences in patterns of resource use.

Perhaps the most obvious way that species can partition resources is in terms of *what* they consume. This is often underpinned by differences in their morphological adaptations that allow differential resource use. For example, a detailed study of bumblebees in the mountains of Colorado (Figure 1) neatly shows how different species can be best adapted to specific forms of a resource (Pyke 1982). Bumblebee species all compete for nectar from flowers, but crucially these flowers vary in the length of their corolla. Matching this variation, different bumblebees in this area appear to be adapted to specific species of plant that have different corolla lengths in their flowers. Careful observations of bumblebee visits to different flowers revealed clear resource partitioning — different species preferred different length corollas in accordance with their proboscis length (i.e., long proboscis, long corolla; short proboscis, short corolla).

Ecologists have found it relatively easy to document the various differences in the ways that ecologically similar *animal* species use their environment and resources. In many cases nothing more than a pair of binoculars and careful observation is required. Studying resource partitioning in *plants* can be much more challenging, and the relative lack of such examples has led many ecologists to wonder whether plants really do show resource partitioning; after all, they all require a limited suite of resources (light, water, and nutrients). However, ecologists do not give up easily, and recent work has shown that coexisting plant species often differ in the forms of nitrogen (e.g., ammonium versus nitrate or organic v. inorganic) they prefer (Kahmen *et al*. 2006). Differences in rooting depth and light-use optima have also been documented. Nevertheless, how common or important resource partitioning is in plants remains uncertain and is an active area of current research.

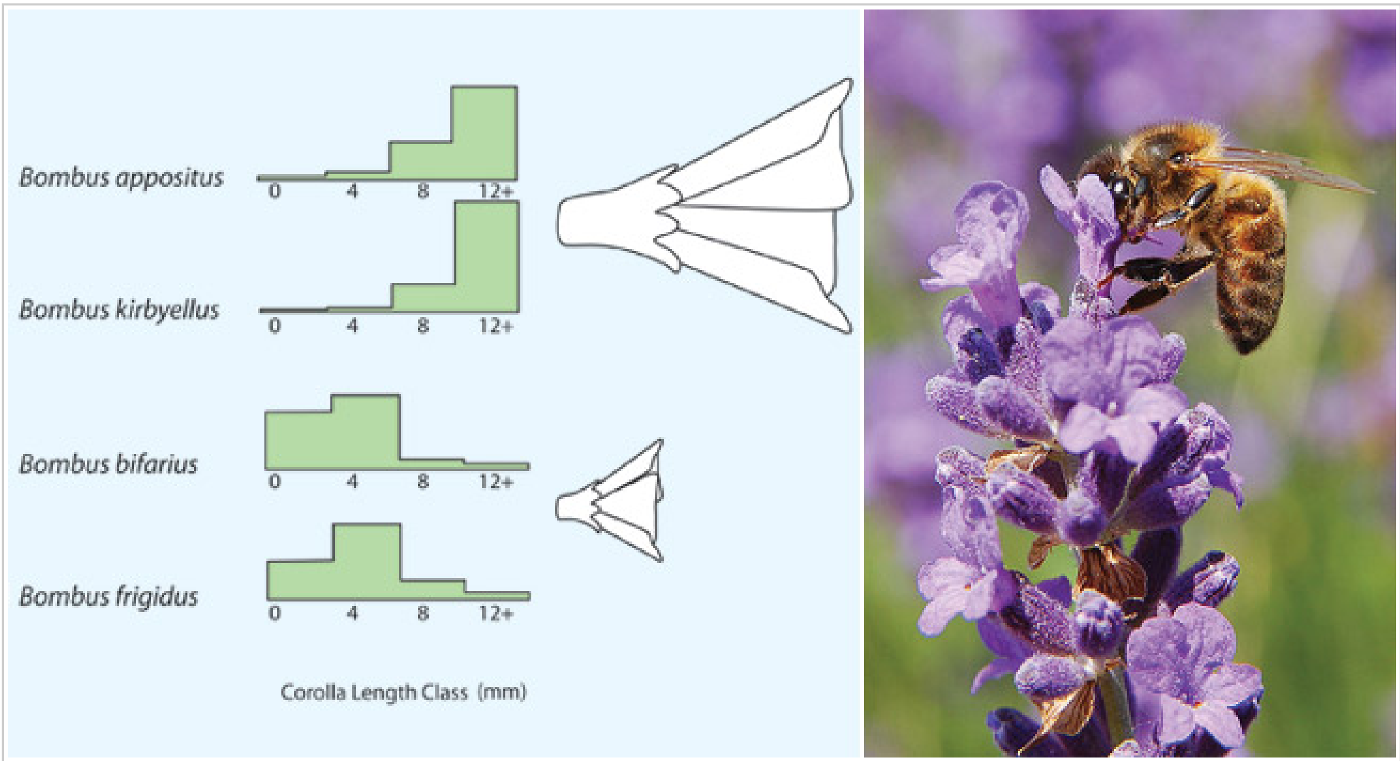

Figure 1: Resource partitioning among bumble bees (*Bombus* spp.)

Species have proboscises of different lengths, enabling them to specialize in the exploitation of plants with different length corollas. Species with similar length proboscises occur at different altitudes (Pyke 1982).

Same Slice, Different Restaurant

When species use a resource similarly in one respect (i.e., they show "overlap" in their use of a resource along one axis), they commonly show differences in some other respect (along another axis). For example, the bumblebee study mentioned above was conducted over sites varying in altitude. Pyke (1982), the author of this work, found that although several bumblebee species had similarly long proboscises and so could forage on similar species of plant, they were differentially specialized to altitude, so that sites at different altitudes were dominated by a different pair of long- and short-length proboscis species. Another striking example comes from tree-dwelling *Anolis* lizards on the Caribbean island of Bimini (Schoener 1974; Figure 2). In this case, species either foraged in the same places (as determined by the thickness of branches they perched on) or ate similar sized prey, but in no cases did two species do both of these. In contrast, individuals of the same species commonly showed a high degree of overlap along both of these resource axes (Figure 2).

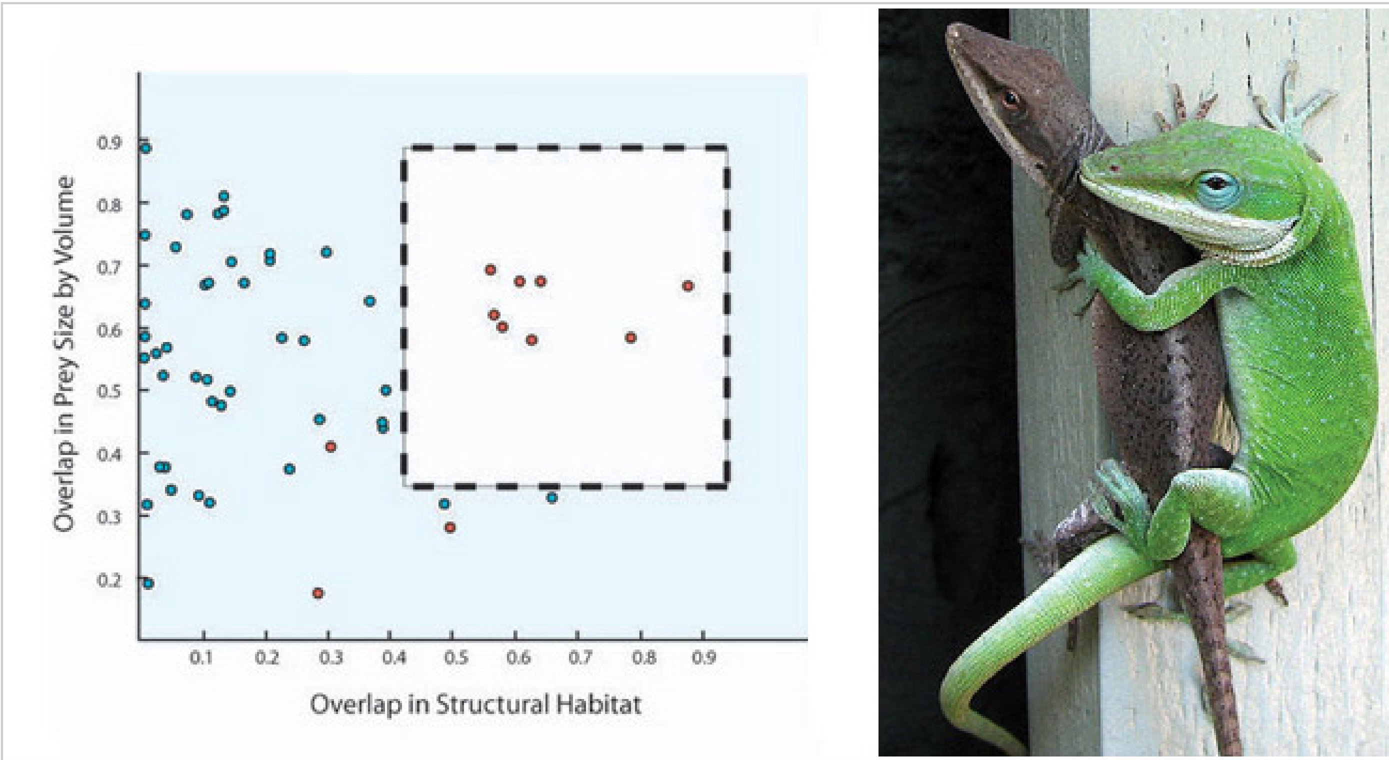

Figure 2: Similarity in structural habitat and prey size in pairs of individual *Anolis* lizards from the Caribbean island of Bimini

Pairs of classes that do not belong to the same species (interspecific) do not show high overlap along both axes (i.e., there are no interspecific pairs in the dashed box).

Is Resource Partitioning a Solution for Coexistence?

Ecological theory shows that interspecific competition will be less likely to result in competitive exclusion if it is weaker than intraspecific competition (Chesson 2000). Resource partitioning can result in exactly this! By consuming slightly different forms of a limiting resource or using the same limiting resource at a different place or time, individuals of different species compete less with one another (interspecific competition) than individuals of the same species (intraspecific competition). Species, therefore, limit their own population growth more than they limit that of potential competitors, and resource partitioning acts to promote the long-term coexistence of competing species. Other theories have been put forward that attempt to explain the coexistence of large numbers of species in local communities, and assessing their importance relative to resource partitioning is likely to be an active area of research for years to come. There is no doubt, however, that mechanisms reducing interspecific relative to intraspecific competition act to promote coexistence, and resource partitioning can achieve this.

Competition Can Drive the Evolution of Differences

So far we have discussed the phenomenon of resource partitioning and its role in reducing interspecific competition and therefore promoting coexistence. Where does resource partitioning come from in the first place (i.e., what causes species to be able to partition resources)?

Competition can limit the growth, and ultimately the reproductive success, of individuals. It can consequently serve as a selection pressure driving differential reproductive success and the evolution of traits that enable organisms to use resources differently compared to their competitors. This process has been clearly demonstrated in the evolutionary events that have followed the colonization of volcanic islands. For example, a single species of seed-eating finch originally colonized the Galapagos Islands and was faced with a diverse range of seed types and sizes. However, the beak of the founding species only allowed it to eat a small subset of the available seed types and sizes. The advantages gained by individuals that were able to exploit slightly different seed types drove evolution of many new species, each with different shaped beaks enabling them to specialize in a particular size of seed (Grant 1986).

There is convincing evidence that competition (and not another selection pressure such as predation) drove — and maintains — differences in beak sizes between these species. When species occur on their own on an island (i.e., there is no interspecific competition), they have similarly sized beaks and presumably exploit similarly sized seeds. When several species occur on the same island however, they show clear differences in beak shapes, showing that it is interspecific competition that maintains differences between species and resultant resource partitioning (Figure 3).

An interesting new twist has been added to this story of the evolution of resource partitioning. Around 25 years ago the island of Daphne Major, originally host to just a single species of Darwin's finch (*Geospiza fortis*) was invaded by another, larger beaked species (*G. magnirostris*). Amazingly, researchers have documented a rapid evolutionary shift in the sizes of beaks in *G. fortis*. In response to severe competition for larger seeds it has evolved to take full advantage of small seeds. This study is particularly important because the researchers were able to document the process of character displacement, and by monitoring the levels of resources, show that competition was the most likely possible cause (Grant & Grant 2006).

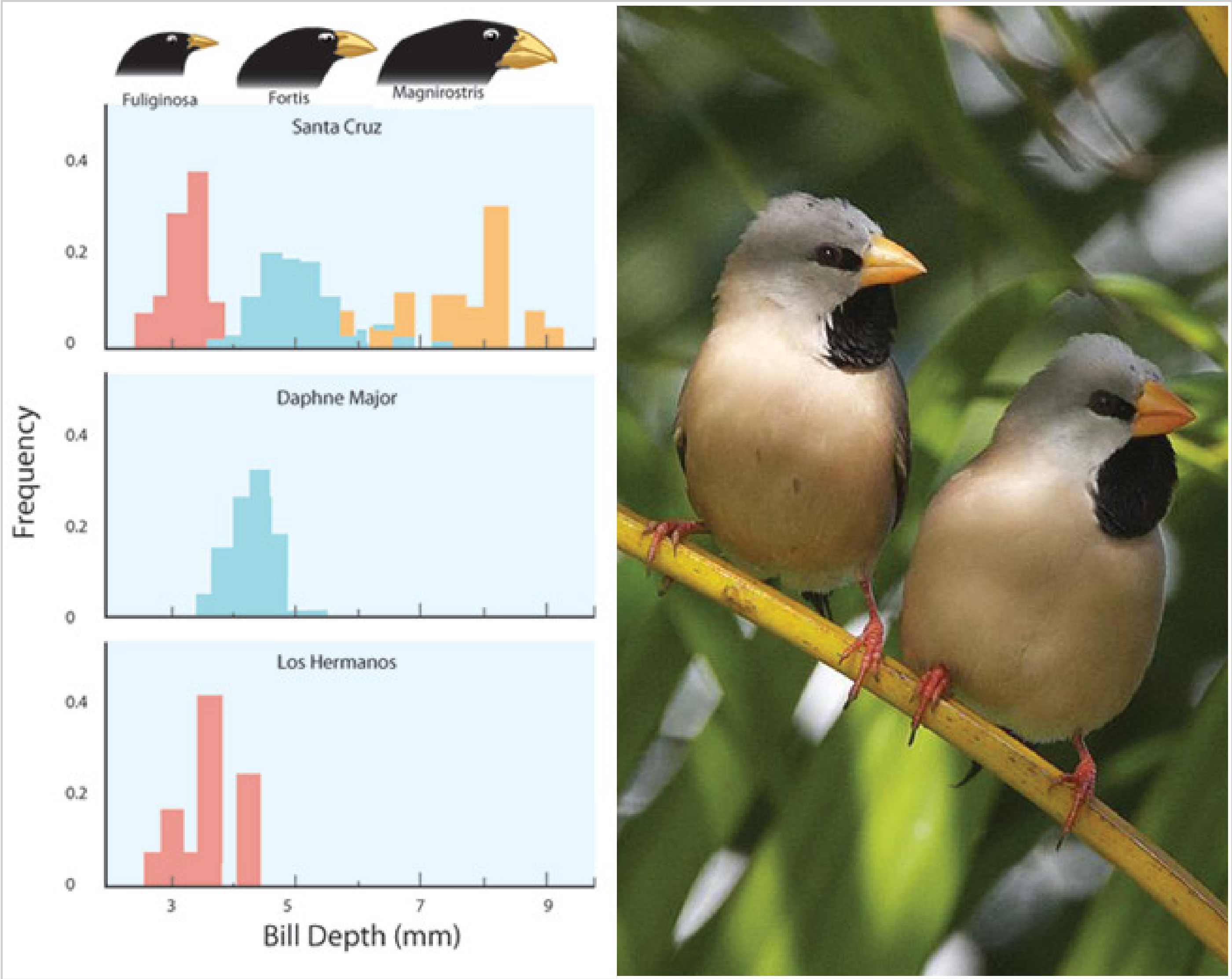

Figure 3: A classic example of character displacement

When multiple species of Darwin's finches co-occur on an island, they show differences in bill depth (and eat different sized seeds) compared to when they are alone on an island.

Resource Partitioning, Species Extinction, and the Functioning of Ecosystems

Humans are causing widespread extinctions of species on local and even global scales. Recently, ecologists have realized that resource partitioning may have important implications for our understanding of the effects of losing species on the functioning of entire ecosystems.

Groups of ecologically similar species may all contribute toward the same, aggregate ecological processes; for example, grasses in a meadow all contribute towards overall primary production and predatory spiders in the same meadow may all contribute towards the control of plant herbivores. Maintenance of such ecological processes is important for the overall functioning of ecosystems, including ecosystem services that humans benefit from.

Resource partitioning can help scientists understand how aggregate ecological processes will be impacted by species extinction. If species show a high degree of resource partitioning, when a species is lost so too is the capacity of the ecological group to exploit the particular slice of the resource pie that the deleted species was adapted to exploit. For example, extinction of a species of grass that was uniquely specialized to use ammonium as a source of nitrogen would leave ammonium in the soil unused. Because this slice (ammonium) of the resource pie will not be exploited, the overall rate of new growth of meadow grass (primary production), as well as associated processes like uptake of carbon dioxide and production of oxygen, will be reduced.

A vast number of recent experiments show that species extinction, on average, reduces levels of ecosystem processes (Cardinale *et al*. 2006). Resource partitioning is thought to play an important role in causing this effect, although ecologists are only just beginning to directly test this (Griffin *et al*. 2008, Finke & Snyder 2008). There is an important application of this ongoing work — by considering the degree of resource partitioning among species scientists may be able to predict those ecosystems that are most vulnerable to the loss of species.

Summary

The long-term coexistence of ecologically similar species, and thus the astounding diversity of life on Earth, has long fascinated ecologists. Resource partitioning may hold the answer to the coexistence of species that make a living in similar ways (i.e., species are able to "stay out of the way of each other" and reduce interspecific competition by using resources differently). Indeed, the benefit of tapping into resources that another competing species cannot use as effectively can be so great that following the addition of a competitor, new traits can literally evolve right in front of the eyes of scientists!

The astounding diversity of species on Earth is at least partly attributable to the various ways in which potentially competing species have evolved specialized traits and intricately partitioned resource exploitation. Ecologists are beginning to realize that the very resource partitioning that helps maintain species diversity may also leave the overall functioning of ecosystems highly sensitive to species extinction.

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