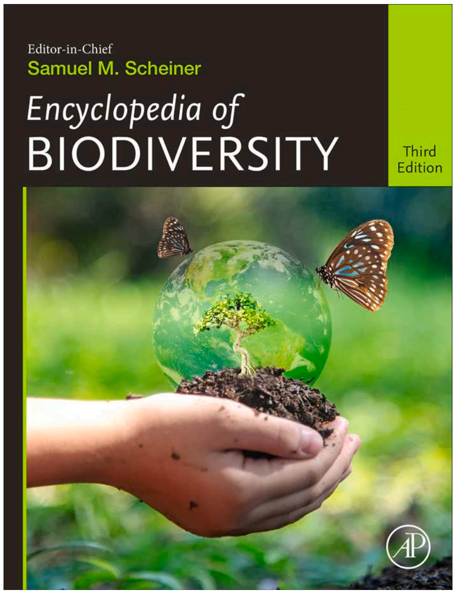

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Guilds

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Abstract

Investigating entire natural communities is a formidable task because one must take a high diversity of species into account. To focus on a more manageable unit, ecologists usually restrict their attention to some portion of the larger system, such as the "plant" or "bird" community. Such "taxon"- defined communities, however, are rather unwieldy, and they may contain a heterogeneous mix of interactions. Thus, most beetle communities contain predators, herbivores, and scavengers but ignore the bugs, caterpillars, flies, and gastropods that share many of the beetles' resources. The guild concept, which groups species according to the manner in which they exploit a common resource, provides a manageable, functional unit for studying patterns of adaptation and the organization of natural communities. The existence of species with mixed requirements and different evolutionary histories, however, makes it difficult to determine standard procedures for defining guilds. The indefinite boundaries that surround most guilds are a fundamental outcome of evolution, which is also at play in all of our attempts to group species into communities, trophic levels, and other ecological categories. Discovering how to draw valid conclusions from entities with vague boundaries is a special challenge to ecologists and provides us with a quest of broad significance.

Glossary

Adaptive syndrome A coordinated set of adaptations.
Community An assemblage of populations that coexist in an area.
Eltonian niche The role, or occupation, of a species in a community.
Exploitative competition An adverse interaction which results from organisms depleting their shared resources.
Family A category, in the classification of evolutionary lineages, of related organisms that ranks above a genus and below an order. A family usually contains many genera.
Grinnellian niche The requirements and behaviors expressed by a species wherever it normally occurs.
Hutchinsonian niche The set of environmental conditions, or opportunities, that will permit a species to exist indefinitely. The set of opportunities that are available to a guild can be referred to as a "nook."
Individualism of species Refers to the observation that the distributions and abilities of most species do not exactly coincide because each species is the product of a unique evolutionary history. Coevolution favors integration of traits of distinct species and convergence among non-related species may occur, but rarely these processes lead to the formation of groups of species distributed as a unit or superorganism.
Taxon A general term used to indicate groups of related organisms at any level in a taxonomic hierarchy. In the classification of evolutionary lineages, the term can refer to species, genera, families, orders, etc.

Key Points

- Define ecological guild.
- Describe the usefulness of the guild concept.
- Discuss the lack of clear boundaries for guilds.

Introduction: The Definition and Properties of Guilds

Guilds are groups of species that exploit the same class of resources in a similar way (Root, 1967). This simple definition has several implications that are best explained by way of an example. Consider the birds that probe for insect prey on the bark of tree trunks (Figs. 1 and 2). In many parts of North America this guild is composed of small woodpeckers (family Picidae), nuthatches (family Sittidae), and treecreepers (family Certhiidae). The guild also contains the black-and-white warbler (*Mniotilta varia*, family Parulidae), whose relatives are primarily adapted for gleaning insects from foliage. Guilds thus contain species with very different phylogenetic histories and, as a consequence, with different propensities for dealing with the special requirements associated with exploiting a particular resource. Thus, the woodpeckers and treecreepers have evolved stiffened tails to act as props in climbing tree trunks, whereas the nuthatches and warbler have evolved modifications of the foot to assist in moving on vertical surfaces.

In addition to the core members of the guild which take the bulk of their food by foraging on trunks and limbs, there are many species, such as titmice (family Paridae), that occasionally feed by probing bark. The presence of these infrequent bark probers illustrates that guilds can have a hierarchical structure with members that range from strict specialists to occasional opportunists. As a consequence, the size and makeup of the guild will depend on where we draw the line with respect to the proportion of a species' diet that is obtained while probing bark.

The hierarchical structure of guilds is also reflected in how broadly we interpret the "in a similar way" portion of the definition. For instance, there are ants that forage for insect prey on tree trunks. These insects have the potential of influencing the food supply

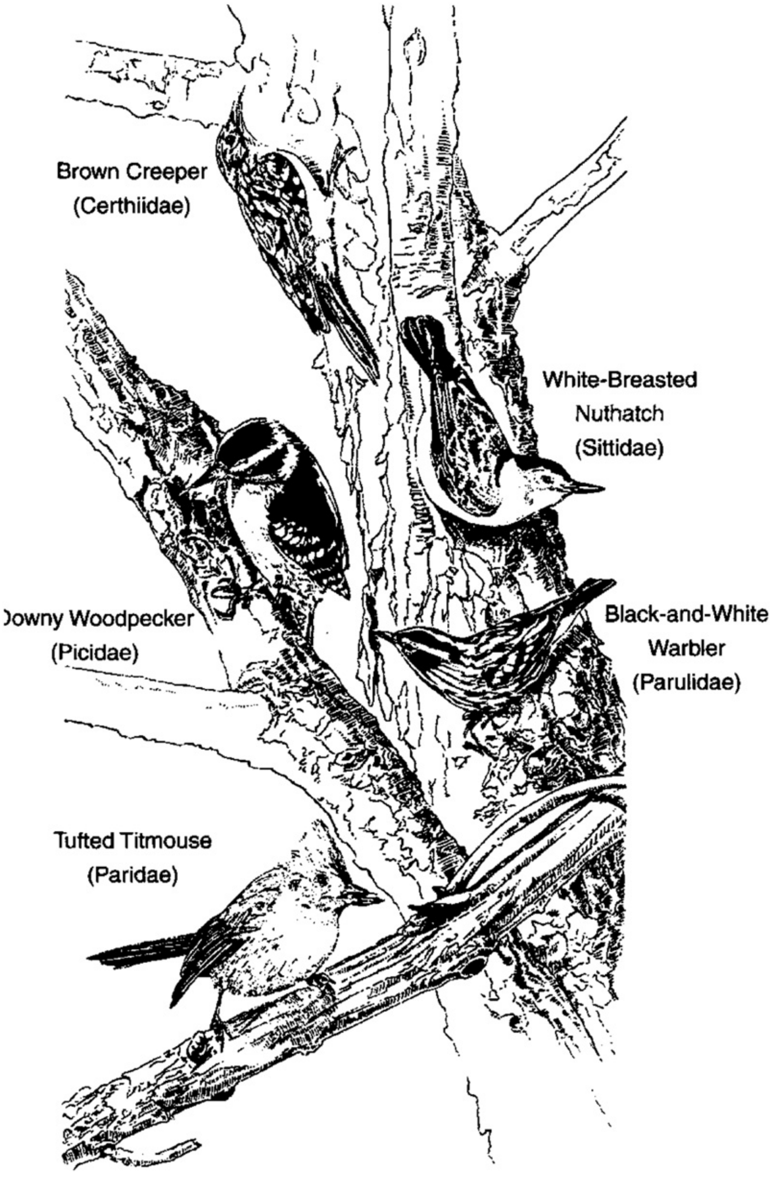

Fig. 1 A few members of the bark-probing guild in North America.

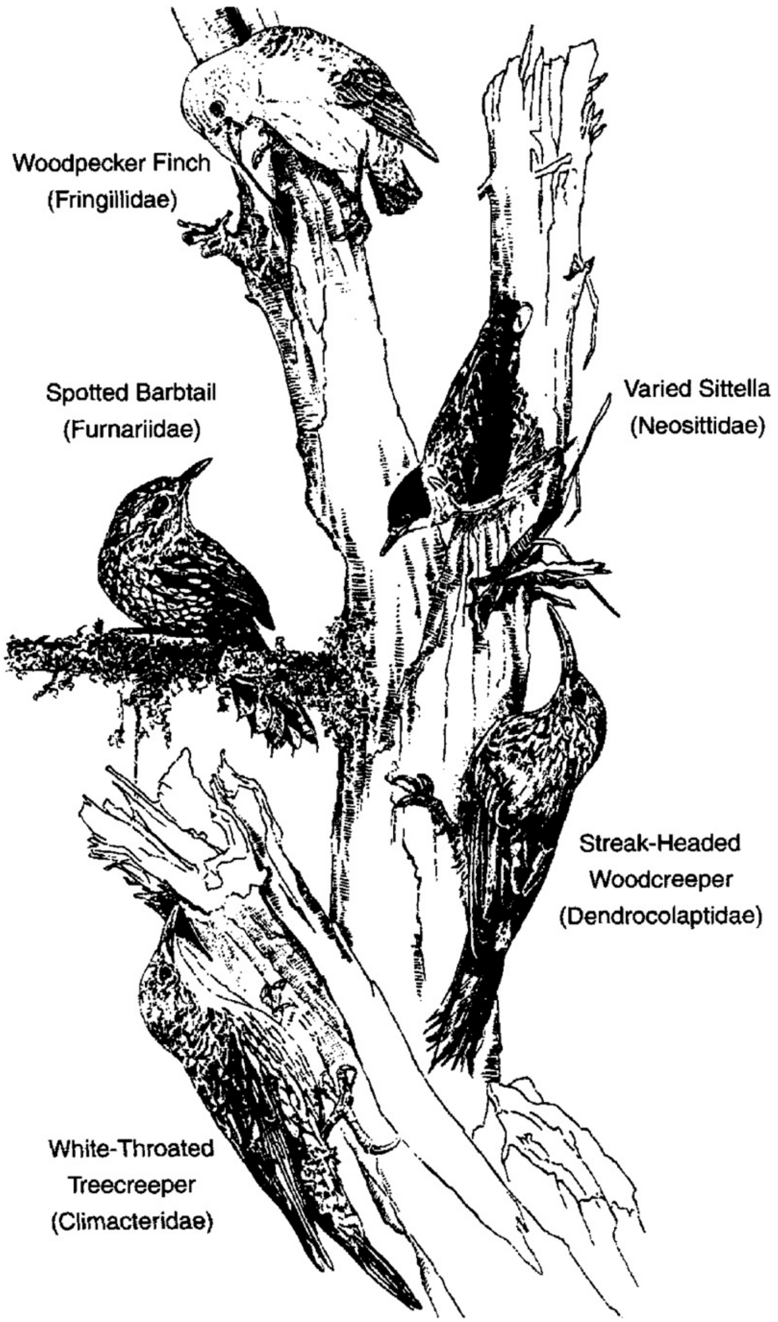

Fig. 2 Birds from different regions and lineages that have independently evolved the bark-probing habit. The dendrocolapids and furnaniids live in the American tropics and the climacterids and neosittids live in Australia. The woodpecker finch is one of the Darwin's finches that inhabit the Galapagos Islands.

available to the bark probers. Their foraging style, however, is fundamentally different: Ants rely on their small size to enter bark crevices, whereas the birds employ their relatively large mass to lever out embedded prey and to flake bark. In this example, it can be seen that the scope of a guild's delimitation needs to be matched to the question being asked. The broader definition, which includes ants, might be most useful if our primary concern is competition, and the narrower concept, which excludes ants, might be more appropriate if our primary interest is in the evolution of adaptations. Furthermore, the birds eat the ants, which introduces further complications if the ants are lumped into the same guild with the birds.

During the northern winter, the black-and-white warbler migrates to the American tropics, where it joins another representation of the bark-probing guild which includes the tropical woodcreepers (family Furnariidae, subfamily Dendrocolaptinae) and barbtails (family Furnariidae) shown in Fig. 2. The warbler's experience illustrates that guild membership can vary in space and season.

The opportunities provided by the existence of bark-dwelling arthropods, many of which are in a cryptic resting stage, has been exploited by bark probers that evolved from several phylogenetic lineages throughout the world. Thus, the Australian manifestation of the bark-probing guild contains Australasian treecreepers (family Climacteridae) and sittellas (family Neosittidae). On Madagascar, the bark-probing role is filled by the nuthatch-vanga (family Vangidae), and on the Galapagos Islands the woodpecker finch (family Fringilliade) uses cactus spines to probe for prey under bark.

In classifying the ways that organisms exploit resources, guilds hold a rank that is similar to genera in phylogenetic schemes. One may also think of a guild as a group of species that occupy similar niches. Indeed, one of the original motivations for introducing the guild concept was to clarify confusion regarding the niche concept, which was used to describe three quite different entities: (i) the Hutchinsonian niche, which refers to the set of conditions that are sufficient for a species to exist in a particular habitat; (ii) the Grinnellian niche, which refers to the requirements and behaviors that are expressed wherever a species normally occurs; and (iii) the Eltonian niche, which refers to the role or occupation of a species in a community. The Eltonian niche was usually viewed as a relatively broad category (e.g., sap-feeding insects and predators of small mammals) which could contain several species and occur in a variety of habitats. In creating the guild concept, we provide an alternative category which clarifies some of the ambiguities associated with the Eltonian niche. For instance, by substituting guild for the Eltonian niche, we can avoid the contradictions that occur when several similar species are said to occupy the same "niche," a category that is supposed to be a property of individual species according to the Hutchinsonian and Grinnellian concepts. Accordingly, species exploit niches and guilds exploit "nooks"—the adaptive space that is presented by resources with similar characteristics. In this sense, guild is similar, as a concept, to the idea of ecospace that is used primarily in paleontology.

There are many types of guilds in addition to those that are based on food resources. For instance, animals can be grouped according to their use of tree cavities for nest sites and plants can be grouped according to their shared use of agents for pollination (e.g., moths or hummingbirds) and seed dispersal (e.g., fruit-eating birds or wind). In the case of plant-eating insects, there has been a tendency to define "mixed" guilds that group species according to a combination of overlapping functions. Frequently, the "feeding guild," defined on the basis of the insects' mode of feeding and the plant tissues they ingest, is combined with the "sheltering guild," defined on the basis of the insects' use of different plant structures as lairs for protection from enemies and adverse conditions. As a result, we often find that plant-chewing insects are divided into categories such as "leaf-miners," "leaf-rollers," "shoot-borers," and "stem galls" that have been shaped by the interaction of nutritional and protective functions. In searching for patterns, it is important to take all these mixed functions into full account.

It should also be kept in mind that species can belong to more than one guild. For instance, the woodpeckers mentioned previously are members of both the feeding guild that probes bark and the nesting guild that utilizes tree cavities. Many insects shift from one guild to another during the course of development because larvae and adults are adapted to perform such different functions. Thus, most butterfly species have caterpillars that are in the leaf-chewing guild and adults that are in the nectar-drinking guild. In this sense, the participation in multiple guilds or the ontogenetic changes in the resource use by a single species echoes some key issues in the study of ecological networks, in which the patterns of interaction of a given species can assign it to multiple interacting groups (modules) or change across the development of an individual.

The Utility of Guilds in the Search for Organization and Patterns

Guilds Provide a Natural Unit of Manageable size for Comparative and Evolutionary Studies of Species Interactions

Even fairly simple communities, such as old fields in the temperate zone, can harbor more than 1500 species of insects belonging to more than 175 families. Such diversity obscures our view of fundamental processes, such as competition, mutualism, and evolution, because most species interact only rarely. This requires that we sort out the insignificant interactions to appreciate the true intensity of the critical interactions. For instance, most species of plant-eating insects in an old field rarely come into direct contact with one another because they are adapted for feeding on different plant species. As a consequence, the use of standard sampling methods, such as sweeping vegetation with a net or collecting the moths that are attracted to lights, which combine the insects on different plant species, would blur our understanding of competitive interactions between plant feeders. Furthermore, the existence of many types of species presents technical difficulties. Thus, to measure the density of all the plant feeders in a community might involve censusing deer, rabbits, mice, sparrows, snails, grasshoppers, caterpillars, aphids, galls, and tiny mites. Clearly, each of these categories of plant feeders require somewhat different methods based on different assumptions, relating to different spatial scales, and having different biases. To avoid these difficulties, ecologists often restrict their attention to some portion of the community. The guild concept is ideally suited to this purpose.

In defining a guild, we create a community detachment whose members share resources that are exploited in a similar way. In many situations, guilds have an advantage over partitioning on the basis of taxonomy because the members of a taxon may be utilizing a variety of resources in a variety of ways. For instance, a bird community may contain rodent-eating owls and seed-eating sparrows but take no account of rodent-eating weasels and seed-eating mice. This is not to imply that guilds are necessarily invalid if all their members are drawn from the same major taxon; frequently, certain styles of exploiting resources are only "available" to organisms with capabilities that evolved in particular taxa. As discussed previously, birds possess the beak and body mass required to probe tree bark. Focusing on a guild has the added advantage of improving our ability to conduct accurate censuses on all the guild members because by sharing the same resources they are likely to be found in the same microhabitats and, by behaving in a similar way, they are more likely to have similar reactions to being observed or captured. Furthermore, the resources, by virtue of belonging to the same class, can be more accurately measured and compared. As a consequence, we are in a position to draw closer comparisons and conduct more realistic experiments when we are working with a guild.

By observing how a guild changes along spatial gradients, we can seek patterns in the relationships between environmental factors and variations in population density, reproductive rate, body size, dispersal ability, investment in predator or herbivore defenses, and a variety of other traits within a group of species that are comparable because they use similar resources in a similar way. Such comparisons also permit us to examine how species are "packed" onto the guild's resource base in relation to disturbance, elevation, and latitude.

Comparisons of similar guilds can reveal interesting patterns. For instance, there is a much smaller range of sizes of plant-chewing insects that live in abodes, such as mines and leaf rolls, compared to that of plant chewers that feed in exposed locations. This pattern reflects the limitations on body size that are imposed by the small spaces provided by plant structures that are pliant enough to be penetrated or rolled.

Much can be learned by comparing the same guild in regions that have been isolated from one another so that their biotas have undergone independent evolution (Figs. 1 and 2). In such comparisons, the discovery of close resemblance provides insights into the process of convergent evolution. In particular, we can observe (i) if certain types of characters are more responsive to evolutionary pressures, (ii) if certain combinations of traits are associated with each other in different regions, and (iii) the degree to which convergence is limited by deep ancestral traits in the various phylogenetic lines that make up the guild.

Guilds Partition Biotas Into Entities Appropriate for Detecting Community Organization

Ecologists have long debated the significance of exploitative competition in organizing communities. An important line of inquiry in this debate concerns the constancy of a community's functional relationships. The reasoning is as follows: If communities are competitively organized, we expect to find that important functional relationships are predictable in space and time because the waxing and waning of populations of one species would be countered by compensatory changes in the populations of other species that use the same resource. Furthermore, these compensatory responses are expected to be most intense within groups of species that have similar methods of using the shared resources. Finally, we might expect to find that similar types of communities have similar functional profiles because the imperatives associated with using similar resources have sorted and shaped species into convergent groups. Guilds provide a means of partitioning a community into functional entities in which these compensations might be detected.

Much of the search for community organization has focused on plant–insect associations. One reason for doing this is that the basic resources (the biomass of foliage, stems, roots, flowers, and seeds produced by a particular plant taxon) are well circumscribed and relatively easy to measure. The constancy of the association's functional profile can be judged by changes in the guild spectrum—the proportion of total herbivore biomass that is engaged in exploiting different plant parts in various ways. A matrix for sorting insect herbivores into guilds is presented in Table 1. In all likelihood, such a scheme will need to be revised to suit the needs of a particular investigation.

Evidence for community organization based on guilds has been elusive. For instance, Cornell and Kahn found extensive variation in the guild spectra associated with 28 tree species in Great Britain and Root and Cappuccino found no evidence for compensatory changes in the densities of species within guilds that feed on goldenrods. These failures draw us to question our assumption that the intensity of competition is likely to be most severe within guilds. Different types of resources are linked in nature. Thus, in plant–insect associations, the consumption of leaves will reduce the future availability of seeds and the sapping of juices from stems will reduce the nutritional quality of foliage eaten by leaf chewers. Similarly, the caterpillar eaten by a foliage-gleaning bird is unavailable as a moth to bats that forage in the air. Linked resources link guilds and open the possibility for exploitative competition to play out its effects across a complex network of species, leading to competition between guilds. Having said that, the effects of a given guild may generate positive effects to other guilds in the community. For example, a guild of seed dispersers may increase the reproductive success of multiple plant species which, in turn, may increase the availability of resources for multiple guilds of herbivores. Because the ecological networks are often characterized by short pathways connecting species and due to the non-linear nature of ecological interactions, the effects propagating between guilds may be strong and unexpected.

Table 1 A Provisional matrix for defining guilds of insects that feed on terrestrial plants

Manner of feeding	*Resource*							
	Buds and leaves	*Pliant stems*	*Flowers*	*Pollen*	*Fruits*	*Seeds*	*Wood and bark*	*Crusts of algae, molds, etc.*
Chewers								
Exposed	✓	✓	✓	✓	✓	✓		✓
Concealed	✓	✓	✓		✓		✓	
Sap-tappers	✓	✓	✓		✓	✓		
Gall-makers	✓	✓	✓		✓			
Grazers				✓				✓

Among the distinct types of interactions, competition has been one key interaction in the study of guilds because species withing a guild use similar resources. Having said that, competition could be operating in a weak and spread way across multiple species, which would be difficult to detect by only studying variations in guild spectra. In plant–insect associations, however, there is evidence from long-term experiments and extensive surveys that plants in natural communities are rarely devastated by herbivores and that competition between plant-eating insects is a sporadic occurrence. These results, considered in conjunction with the highly variable guild spectra that have been reported by Cornell, Root, and Strong, suggest that most plants could support more herbivore species (i.e., plants provide Hutchinsonian niches that have not been filled) and that the structure of these associations is idiosyncratic, largely determined by the characteristics of a few dominant species that happen, for a variety of historical reasons, to have evolved to become members of the community.

Guilds Provide a Framework for Describing and Comparing the Trophic Structure of Ecosystems

The trophic structure of ecosystems is often described in terms of broadly defined levels consisting of primary producers, primary and secondary consumers, decomposers, and so on. Ecological networks, on the other hand, are usually described in terms of individual species. Various attempts have been made to develop a scheme based on guilds that can be used to describe trophic structure with an intermediate degree of refinement; thus, herbivores might be subdivided into browsers of woody plants, grazers of grasses, sap-tappers on succulent foliage, borers in stems, and so on. To accomplish this requires that the entire community be partitioned so that all its members can be placed into a standard set of feeding guilds that have a widespread occurrence in nature. When ordered in this way, it is hoped that insights about a number of patterns and processes in ecosystems, such as patterns of energy flow, patterns of interaction within communities, and frequencies of different lifestyles can be gained by drawing comparisons between systems. In practice, however, such schemes have been little used, probably because it is almost impossible to develop a "key" to the guilds of the world that is flexible enough to accommodate a wide array of taxa and yet sufficiently circumscribed that different ecologists will assign species to guilds in the same manner.

The Individualistic Nature of Species and the Vague Boundaries of Ecological Categories

The process of defining guilds raises some fundamental questions. Are guilds distinct entities that reflect the outcome of natural processes or are they merely artificial groupings that we invent to divide diversity into more comprehensible units? In other words, are the opportunities provided by the environment discontinuous so that species are sorted into clearly defined groups on the basis of their requirements and lifestyles? Furthermore, are similar openings (or nooks) available in different regions? What is the role of coevolution in shaping the emergence of guilds? Are organisms constrained from filling these opportunities by their evolutionary histories? We can begin to address these difficult questions by comparing the characteristics of the core and marginal members of various guilds.

If we census the habits of all the species that utilize a particular resource, we usually find that there is a wide variation in the level of their dependency on the resource. The most dependent species—the core users—usually possess obvious specializations. Thus, in the bark-probing guild (**Fig. 1**), the treecreepers, woodpeckers, and nuthatches, which take the bulk of their diet from bark, have specialized feet and tails for moving on vertical surfaces (Richardson, 1942). In our census, however, we usually encounter a host of species that use the resource only rarely. These marginal users are either generalists or they are specialized along other lines that compromise their ability to use the resource in question. For instance, bark-probing titmice often forage on horizontal surfaces, such as the tops of limbs and branches, where they take much of their prey by hammering apart acorns, galls, and similar objects that they hold against the perch with their foot. These habits are reflected in the distinctive foraging maneuvers that titmice display during their infrequent forays onto tree trunks. Other species, such as gnatcatchers (Polioptilidae), vireos (Vireonidae) , and wood warblers (Phylloscopidae), which are primarily adapted for gleaning insects from tree foliage, make clumsy efforts to take insects from bark on rare occasions.

Here we confront the individualistic nature of species—a fundamental issue, originally raised by Gleason, that complicates all of our efforts to define functional groups of species. Thus, the various taxa that can utilize a particular resource have evolved "individualistically" along independent paths. As a result of their separate histories, these taxa have different constraints and proclivities, which result in different levels and styles of specialization. As a consequence, guilds often have ambiguous boundaries consisting of several species of generalists and inept opportunists that are specialists on other resources. Since the degrees of dependency grade into one another, the line one draws to define the membership in a guild can be somewhat arbitrary.

The indefinite boundaries of guilds are merely one expression of a more general issue confronting ecologists. Community ecology and biogeography are, by their very nature, concerned with levels of organization that consist of multiple species. In their efforts to discover the processes operating at these levels, workers have developed several systems for classifying species into groups on the basis of similarities in their (i) response to physical or site conditions to define communities; (ii) possession of particular adaptive traits to define life-forms and adaptive syndromes; (iii) response to seasonal cues to define phenological aspects; (iv) geographic distributions to define biogeographic provinces, biomes, life zones, and plant formations; and (v) diet to define trophic levels. Ecologists recognize and discuss these entities because they find that several species fall into clusters on the basis of these various types of classification. As with guilds, however, we also encounter species with intermediate characteristics that tend to blur the boundaries of these various categories. This is because all the traits that underlie these classifications are subject to the same individualistic evolution that can produce the marginal members of a guild. Thus, vague boundaries are an inherent property of any species assemblage—a fact that requires ecologists to cultivate certain habits of mind in forming arguments.

Conclusion: Attitudes Concerning Vaguely Bounded Categories

Here, the usefulness of guild concept to ecology and evolution was illustrated. In the last section, it is emphasized a key point: a guild is often vaguely bounded. In this final section, a roadmap to the use of the guild concept is provided. People are generally uneasy about categories, such as guilds, that are subjectively defined because the criteria one chooses to define the operational boundaries will have an impact on our ability to observe patterns. Thus, if a guild is defined too broadly, the characteristics of a miscellaneous collection of marginal species could obscure interesting similarities between the core members. On the other hand, if a guild is defined too narrowly, we could overlook the full range of influences that stem from extracting a particular resource in similar ways. Similar problems emerge for describing many patterns in ecology and, more broadly, in science, especially in problems associated with determining groups of elements in the system that are more similar to each other than to other elements in the same system.

There have been a variety of attempts to address this problem by using quantitative procedures, such as cluster analysis, principal components analysis and modularity analysis in network ecology, to delimit the membership in guilds. The raw material for these analyses comes from "activity censuses" which measure the relative frequency that species utilize different resources in different ways. The groupings that are sorted out by these procedures, however, may seem abstract and artificial, because guilds are not only defined by the identity of resources used but also by the way organisms use these resources.

Despite these difficulties, the continued and widespread use of subjectively defined categories attests to the need of such concepts in ecology. The best results are obtained when we follow some simple guidelines. In the case of guilds, the classifications that provide the most insights are based on a thorough knowledge of the species' natural history. Open-minded observations and journal keeping are good starting points to form an intuition for distinguishing resources with properties that require special means for their efficient exploitation. For instance, insects on bark constitute an appropriate resource for a guild of bird-sized predators because the core members must move on vertical surfaces and extract prey from narrow crevices or under bark—maneuvers that are difficult for birds that lack the necessary specializations.

After a guild has been tentatively defined, it helps to conduct activity censuses at different sites and in different seasons to discipline intuition and provide a quantitative basis for determining guild membership. (For sedentary organisms such as plants, one would count the incidence of the traits that define the guild along transects laid out in appropriate habitats.) When the investigators are satisfied that a guild "makes sense" with respect to the questions that are being asked, the criteria that will be used to delimit the boundaries should be clearly described and fully justified. At this point, it may be useful to assign classes of membership; for instance, core species might be those that engage in the activities that define the guild on at least 50% of occasions, and marginal or accidental species might be those that engage in such activities on less than 10% of occasions. Many of these steps seem obvious, but they are often left out of guild classifications, especially in cases in which the investigators are attempting to partition entire communities in such a way that each species can be assigned to a single guild. Such classifications are often used to compare the functional organization of communities in which only the most general of categories can accommodate the great diversity of species that must be placed.

Part of the art of becoming an ecologist involves developing a set of attitudes for coping with the complications that stem from the individualistic nature of species. One of the most important of these is an ability to match the question one is asking with the most appropriate grouping of species—the set that will reveal valid patterns that act in nature. Thus, the guild definition that is most useful for exploring convergent evolution may be quite different from the one that is best for observing compensatory shifts in the densities of interspecific competitors. In addition, we need to be on steady guard against the natural tendency to drift into thinking that the entities we have invented are "real." Guilds are not a fixed feature of nature. They are a convenience that we can use to cope with diversity, reveal patterns, and facilitate discussion. As a consequence, guilds can be modified as long as they provide a valid base for addressing a question and their limits are explicitly defined and justified.

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