

# THE GUILD CONCEPT AND THE STRUCTURE OF ECOLOGICAL COMMUNITIES

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## THE GENESIS AND APPEAL OF GUILDS

### *The Original Definition*

The term *guild* holds a central place in community ecology:

A guild is defined as a group of species that exploit the same class of environmental resources in a similar way. This term groups together species without regard to taxonomic position, that overlap significantly in their niche requirements. The guild has a position comparable in the classification of exploitation patterns to the genus in phylogenetic schemes. . . . To be considered a member of the foliage-gleaning guild in the oak woodland, the major portion of a bird species' diet had to consist of arthropods obtained from the foliage zone of oaks. As a result, birds that occasionally use the foliage zone were excluded even though they may have exerted some influence on the guild's food supply. (130, p. 335)

Root thus defined the first of many ecological guilds—the foliage-gleaning bird guild in oak woodland.

*Precursor and Parallel Concepts*

The word “guild” had appeared earlier in the ecological literature. Root (130) cited an earlier use of “Genossenschaften” (134), translated as “guild” in the English edition, to refer to four groups of plants that depend upon other plants for their existence—lianes, epiphytes, saprophytes, and parasites. Another early use of “guild” (25), following Drude’s “Artengenossenschaften,” was for a group of species that has migrated from one area to another. We know only one recent use (160) in this sense. Because Root considered the term guild “the most evocative and succinct term for groups of species having similar exploitation patterns” (130, p. 336), and because prior uses seemed not to have become established, he adopted it for his purpose.

Root (130) cited Salt (131, 132) and Turpaeva (151) as using functional classifications based on “feeding groups” in their comparative analyses of communities. Salt (131) suggested classifying a local avifauna on the basis of location of feeding site, type of food taken, and foraging method (searching or drilling). In fact, this is how some researchers divide avifaunas into foraging guilds today. Salt did not explicitly and consistently use foraging method in generating all feeding groups, as Root did. He noted a similarity between the classification of birds by feeding habits and familial classification, because in some families feeding behavior is quite uniform. His focus differed from Root’s. Salt (131, 132) was primarily interested in adaptations of animals to their physical environment. Root (130) considered guild associates to be molded by adaptation to the same class of resources, but also by competition among themselves, and this latter aspect struck an especially responsive chord. This is not surprising; by the time of Root’s paper, Hutchinson’s seminal paper (77) and the work of MacArthur and his colleagues (e.g. 96) had generated enormous new excitement about the role of interspecific competition in structuring communities (13, 105).

Turpaeva’s groups (151) of detritus-feeding benthic invertebrates were even more in the spirit of Root’s guilds, in that each group had a distinctive mode of capturing resources (e.g. swallowing, filtering), and she, like Root, emphasized heightened competition for food between members of the same group. She noted an isomorphism between division by microhabitat and division by feeding method because the food-gathering behavior of each species adapts it primarily to food in one microhabitat. This isomorphism differs from Root’s view in that he entertained the possibility that different ways of getting a resource could lead to more than one guild within a microhabitat. However, it is unclear if Turpaeva viewed the isomorphism as peculiar to her particular assemblage or as a general trait of nature.

A parallel term for guild is “functional group,” coined (36) and widely used (67) for aquatic invertebrates. Initially, the classificatory basis was almost wholly resources (particle size), with no attention paid to how resources are garnered, though the motivation was “to address important process-oriented

ecological questions" (36, p. 631). MacMahon et al (98) attempted to distinguish "functional group" from "guild" by defining the former to be species performing the same function, but by 1984 the terms were often used synonymously (67). A classification at that time of functional groups of aquatic insects incorporated ways of using a resource (e.g. shredders, scrapers, piercers) but did not refer to "guilds" (108). There is surely still confusion. For example, Menge et al (107) depicted functional groups rather than guilds on the grounds that guilds are simply groups of species using the same resource, whereas functional groups focus on the method of foraging! In fact, the original "guild" paper focussed on the method of using resources, while the original "functional groups" paper focussed on resources themselves.

Because most studies of guilds considered food as the resource, the burgeoning literature on trophic web structure used entities very much like guilds. The resemblance was inevitable because many tabulated trophic webs lumped groups of species using the same food into "trophic species" or the like (120), while much research on guilds de-emphasized "in a similar way" and emphasized the same food. Noting this resemblance, Yodzis (164) compared concepts from food web studies to the guild. A clique is a set of species in which every species pair shares some resource, and a dominant clique is a clique that is not a subset of another clique. Yodzis suggested dominant cliques might be viewed as "trophic guilds" but are not guilds in the original sense because how resources are used is not considered; thus a dominant clique or trophic guild might contain several guilds defined on the basis of method of feeding. Burns (20) appropriated "trophic guild" for a different group—an aggregation of species with similar trophic resources; this use corresponded to the traditional concept of "trophic level," which he saw as too imprecise.

Conflation of trophic structure concepts with the guild concept has led to profound confusion about the status and importance of the latter. For example, Heatwole & Levins (68) detected an emergent community property (133) in the apportionment of mangrove island insect communities into crude trophic categories—herbivores, predators, scavengers, etc. In fact, the apparent regularity of this apportionment is probably an artifact of the statistic used to characterize differences in apportionment (142). Others (1, 31, 69, 112) resuscitated this argument in the context of the role of guilds, referring to the original papers as being about guilds, though neither of them mentioned guilds or addressed in more than cursory fashion how resources are gathered.

### *The Motivation Behind the Concept*

Root (130) suggested three advantages of using guilds in the study of ecological communities:

1. Guilds focus attention on all sympatric competing species, regardless of their taxonomic relationship.

2. "Guild" eliminates the dual usage of the term "niche" as meaning both the functional role of a species in a community and the set of conditions that permits a species to exist in a particular biotope. This duality had led to controversy, which Root hoped to resolve by limiting the term "niche" to the latter purpose and recognizing that groups of species having very similar ecological roles within a community are members of the same guild, not occupants of the same niche.

3. Guilds are useful in comparative study of communities. Since it is usually impossible to study all species living in an ecosystem at once, guilds enable us to concentrate on specific groups with specific functional relationships. This is preferable to studying taxonomic groups, within which different species may perform unrelated roles.

Investigators often cite the first and third advantages when studying guilds. The almost universal need to limit research on communities to manageable units makes the use of guilds so attractive. More recently, as the term has become popular, a fourth goal is often articulated for study of guilds—they might represent the "basic building blocks" (67) of communities, and the partitioning of communities into guilds might reveal a structure not attributable simply to species numbers and identities (67, 148). The view that species in communities fill fixed, basic functional roles is one of the most venerable in ecology, stretching back at least 200 years (104). This view, in turn, has spawned attempts to depict different communities in terms of these roles and thus to demonstrate their underlying similarity. "The view that there exist fixed ecological roles is supported by the observation that ecological communities often bear striking resemblances to each other even though their constituent species have very different evolutionary origins" (104, p. 256–57). Until the last decade, discussions of this sort were mostly cast in terms of niches, which were construed as individual species' functional roles. However, the recognition that different species may have very similar functional roles, and Root's proposition that groups of such species, namely guilds, can be compared among communities, led to a shift from niches to guilds as the potential fundamental units of communities. If guilds really are fundamental units, the nature of guilds forming a community might be an emergent property, the elusive grail of community ecologists (133). This hope has generated the prediction that "guilds will become the standard currency of ecologists in their efforts to understand community relationships of many kinds" (148, p. 90).

## THE IMPORTANCE OF CLEARLY DEFINING AND DELINEATING GUILDS

"Guild" has come to be used in many different senses, as we will document in later sections. Often, it seems to be used colloquially to mean all species using

some resource, with rather little attention paid to how the resource is used. This usage probably arose because no other term has taken this meaning, yet much current ecological research is aimed at such groups of species. Colloquial usage of scientific terms that were originally narrowly defined is hardly unique to *guild*, and the fact that its first ecological usage was metaphoric almost ensured that it would acquire a variety of meanings. So long as all readers bear in mind a distinction between the narrow and colloquial definitions, the word can perhaps usefully fill the lexical void just noted and still function in precise scientific discourse. However, the inadvertent confounding of different meanings of guild can lead to confusion and misunderstanding.

Root (130) viewed members of a guild as molded by adaptation to the same resources and by competition. This is itself a statement of belief in how ecological communities are structured. Use of the same resources need not imply competition for them. For example, Duggins (50) studied three congeneric sea urchins occupying virtually the same habitat and eating similar food. Experiments showed that addition of the largest species, *Strongylocentrotus franciscanus*, did not decrease the populations of the other species and, if anything, resulted in an increase in gonad size, a good measure of fitness. Apparently, interspecific facilitation of two sorts overshadowed possible consumptive competition (*sensu* 136). First, *S. franciscanus* is especially adept at snagging drift algae, which the other two species then share. Second, presence of *S. franciscanus* results in decreased abundance of the predatory starfish *Pycnopodia helicanthoides*, which consumes or drives out the other two species. Ironically, this example seems to conform closely to the primary dictionary definition of *guild*: "a confraternity, brotherhood, or association formed for the mutual aid and protection of its members, or for the prosecution of some common purpose" (117, p. 1225). Thus, if guilds are to be used to test hypotheses on the relative importance of various processes in structuring communities, they should be defined independently of the mechanisms by which the members may interact, lest the entire enterprise drift toward circularity (cf 99, 100).

It is only natural, during a decade in which the ecological and evolutionary role of competition has been intensely argued, that the *guild*, originally conceived as molded by interspecific competition, would generate considerable interest and debate. The view of guilds as coevolved entities, as "arenas of intense competition" (122), is one reason the clear delineation of guilds is critical. An alternative view of ecological communities as groups of sympatric species shaped primarily by response to autecological pressures (e.g. 60, 157) implies that guilds are groups of independent species sharing a resource but not likely to be subject to much coevolution. This view necessarily detracts from the importance of identifying guilds. If this view is correct, or correct for some species assemblages, then perhaps the term "functional group" for

species that perform a certain functional role in the ecosystem is more appropriate, and functional groups, not guilds, deserve more attention. Perhaps, in the original spirit in which the term was coined, guilds as coevolved entities are the exception rather than the rule in ecological communities. Only studies of groups of species using similar resources in similar ways, whatever they would be called, will resolve the question of how prevalent competitively driven coevolution is in nature.

Many studies of guilds seek determinants of community organization in particular competitive interactions. The search for such determinants has been a cornerstone of recent community ecology. Morphological patterns and ecological data implying niche partitioning within guilds frequently result from such searching (e.g., 9, 11 12, 47, 62). The interpretation of such data and the results drawn from them rest heavily on guild assignments. Lack of stated, unambiguous criteria for these assignments can potentially lead to ambiguous results and controversial interpretations. For example, Diamond (47) studied several guilds of New Guinea birds and concluded that a series of competitively determined assembly rules governs the distribution of all species on islands. While he listed some reasons for grouping certain species into guilds, he did not refer to supporting ecological studies, nor did he discuss the possibility that other species share these resources or why they were excluded from particular guilds. These guilds form a small part of the New Guinea avifauna, but their choice was not rationalized. When Gilpin & Diamond briefly discussed membership in one guild (fruit pigeons), they based it on "extensive dietary data published by Crome (1975) and other authors" (58, p. 335). Crome studied seven species of frugivorous pigeons in Queensland, made no claims concerning guild membership, and suggested that "a characteristic of tropical rainforests is the importance of fruit as food for birds, so much that large groups such as parrots, pigeons, manakins, and hornbills are adapted to a partly or wholly frugivorous diet" (32, p. 155). Indeed, in a later study of a wider (though by no means exhaustive) assemblage of birds in the same region, Crome (33) divided bird species on the basis of their height in the canopy, foraging site, and foraging behavior, and found six other avian species with which the fruit pigeons of his previous study should be grouped. Thus, the exclusive treatment of fruit pigeons as a guild bears further discussion. A large part of the heated debate on assembly rules (30, 48, 58) rested precisely on how to delimit the guilds within which patterns would be sought. Had a thorough rationale for guild membership been available at the outset to readers, much of this "unpleasant" and "bitter" debate (64) might have been avoided.

The study of single guilds within a whole fauna (e.g. 100) is not uncommon. While investigators usually at least partly justify guild designations, they often give the reader no clue about other sympatric species. Although

frequently appealing intuitively, and quite possibly biologically sound, such guilds cannot be critically evaluated. It is true that studies of complete faunas are often technically impossible, or impractical, while guilds are small, manageable units, more amenable to ecological study. A brief outline of the sympatric species and their trophic or other relationship to the guild studied may, however, give other investigators a better grasp of the system studied and potential alternative designations. Root (130) himself listed the other bird species that occasionally take insects, or those that are insectivorous but differ in foraging behavior, and explained his guild designation. This enables readers to evaluate this study critically. Case et al (22) discussed only four of the guilds of West Indies birds but reported the species that are not included in these guilds and mentioned their habits. Cody's study of South African forest birds (28) is similarly detailed. Thus, while not designating guilds for the other species, they afforded the reader the chance to assess their conclusions.

## WHICH SPECIES ARE GUILD ASSOCIATES

### *Guilds in the Original Sense*

The guild concept was specifically meant to relate to species using the same class of resources, but the possibility of different partitions based on different resource classifications was explicit: "For instance, the Plain Titmouse (*Parus inornatus*), while belonging to the foliage gleaning guild with respect to its foraging habits, is also a member of the hole nesting guild by virtue of its nest-site requirements" (130, p. 335). However, the emphasis in animal community ecology has increasingly been on food resources as generating interspecific competition: "In any study of evolutionary ecology, food relations appear as one of the most important aspects of the system of animate nature" (77, p. 147). Accordingly, in most guild designations the shared resource is food. Exceptions are not infrequent: e.g. habitat guilds (61, 86), nesting guilds (89, 102, 159), reproductive guilds (5). Some guild designations are not based on resource use and clearly violate the definition of guilds: body mass guilds and mobility guilds (63) are striking examples.

Many studies define a guild as the group of species (usually within a taxon) that inhabit a certain microhabitat. For example, Sedgwick & Knopf (139) defined as a guild the group of birds directly dependent on the grass-herb-shrub layer of vegetation for foraging, nesting, or both. The way they are dependent ("in a similar way") played no role in this guild designation. Similarly, Cruz studied effects of microhabitat change on the avifauna of a neotropical mahogany plantation by dividing it into guilds using different heights of vegetation. He concluded that "removal or reduction in the understory vegetation probably will cause pronounced decreases in the members

of the understory guild" (34, p. 286). The resource here is in fact the microhabitat.

Some authors, in delineating guilds, attempt to stay close to the original criteria of both the same resource and a similar way. For example, Bush (21) assigned all intestinal helminth parasites of birds to four guilds based on how they garner resources (absorbing across their body surface or engulfing material), where they gather resources (absorbing organ in the mucosa or lumen of the gut), and what the resources are (gut tissue or gut contents). The guilds largely parallel taxonomy at either the phylum or class level because feeding biology differs greatly between the groups. However, cestodes include some species in a mucosal absorber guild and others associated with acanthocephalans in a luminal absorber guild. Osborne et al (119) partitioned bird species at one site into 18 guilds based on their primary food, foraging substrate, and foraging behavior. Humphrey et al (75) described a guild of nine surface-gleaning, primarily beetle-eating bats. They provided extensive dietary data, while detailed field research by Bonaccorso (7) documented both behavior and diet of these species plus sympatric bats.

### *The Guild as a Taxonomic Group*

One advantage of the guild concept stressed by Root (130) is that it focusses attention on all sympatric species involved in a potentially competitive interaction, regardless of their taxonomic relationships. While most previous studies of interspecific competition had considered only sympatric congeners, on the assumption that closely related species tend to compete most strongly, Root cited several studies demonstrating intergeneric competition, and he applied this term to groups of bird species in different families.

Despite its formal definition, guild designations still tend to include closely related species. Schoener (137) terms a group of closely related species using the same resource a "taxon-guild." Taxonomically limited guild designations stem, in part, from insufficient biological data. For example, Hanski & Koskela (66) defined six guilds of dung-inhabiting beetles; they adopted a conservative within-genus approach in the absence of detailed information on the feeding and breeding biology of most species. Likewise, Walter & Ikonen (156) in their study of nematophagous arthropods rationalized the use of genus level groupings. They argued that feeding behavior (as well as other functional parameters) is rarely predictably similar beyond the generic level, and they advocated intensive behavioral studies. Lambert & Reid divided the herpetofauna of Colorado into guilds and reasoned that, "as a set of rather specialized consumer species, the guilds inevitably reflect taxonomy" (91, p. 145). Partly, of course, the tendency to delineate closely related guilds springs from the knowledge and taste of researchers, who are often particularly expert in restricted taxa.



MacNally & Doolan suggested an alternative guild definition: "a set of closely related species (usually coordinial or confamilial) that are both sympatric and synchronously active, and that forage on similar items in similar ways" (100, p. 34). They argued that by limiting guilds to closely related species we also limit other differences, because closely related species often overlap in foraging methods, habitat preference, etc. Thus, MacNally (99) formalized the guild as a taxonomic construct but did not circumvent the ambiguity inherent in judging degree of similarity in foraging method and food. This definition is limited to feeding guilds.

### *Guilds of Distantly Related Species Sharing Resources*

The expectation that competition will be strongest among congeners has an illustrious pedigree: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera" (37, p. 87). Nevertheless, as Darwin noted, this pattern is by no means invariable, and examples abound of distantly related taxa engaging in consumptive competition. An oft-cited example is granivorous rodents and ants of American southwestern deserts (15, 19, 40). In this instance suggestive dietary data were buttressed by controlled experimental removal. Similarly, introduction and removal experiments showed that insects compete with frogs for pond periphyton (113), while lizards and spiders compete for insect prey (138), as do ducks and fishes (54, 70). Non-experimental evidence implied competition for nectar among all bees and finches (135) and between wasps and a parrot (4, 10, 111), for insect prey between lizards and birds (163), and for zooplankton between flamingoes and fishes (76).

Oddly, though an entire symposium was devoted to competition between distantly related taxa (125) and most recent papers (e.g. 71) repeat a litany of well-known examples, almost all point to the phenomenon as an oddity worth noting, and there has yet to be a thorough review of the phenomenon. Without such a review, it is difficult to surmise to what extent consumptive competition is predominantly between closely related as opposed to distantly related species.

Rarely have researchers formally identified distantly related species as guild associates. Jaksic (79) argued that difficulty in studying interactions among very many species leads researchers to study "community ecology" within taxonomic groups that they know well—lizard "communities" (121), bird "communities" (143), small mammal "communities" (83), etc.—and for the same reason many ecologists describe guilds within arbitrarily chosen taxonomic boundaries. Jaksic suggested a distinction between "true" (resource-based) community guilds, which unite species exploiting an investigator-based resource in a similar manner, and taxonomically based

assemblage guilds. He proceeded to study guild structure of predators in various regions, grouping falconiforms, owls, snakes, and carnivores as potential guild associates, through a study of the actual prey composition of the different species (80, 81); he recognized 50% overlap as the minimum value for guild association.

Some guilds thus defined encompass species from different orders and even different classes. For example, the insectivore guild of Spain comprises one falconiform, two strigiforms, and four carnivores (81). However, the authors conceded that this guild may be divided into three groups: avian predators and two carnivore groups. The distinction between "groups" and "guilds" stems from the use of the arbitrary 50% overlap threshold and from the fact that prey were not weighted according to their mass. Thus, a red fox with 90% of its prey items insects is liable to appear as an insectivore, despite having over 80% of its mammalian prey items rabbits, with a mean weight of 900 g, so that mammals constitute the bulk of its diet. Similarly, the insectivore guild of Chile appears to comprise one falconiform and one owl (81), with insects constituting 64.8% and 76.8% of their diets, respectively (80). Closer scrutiny, however, reveals that diurnal birds and lizards which are over 20% of the falcon's prey, by count of items, comprise, unsurprisingly, only 1% by count of the owl's diet. Conversely, over 15% of the owl's prey items were identified mammals; this is three times as much as in the falcon's diet. The weight of these vertebrate prey must be much greater than that of the insects taken, so partitioning vertebrate prey must be more significant than this guild assignment implies. Without information on prey weights, this analysis must be questioned.

Even though many instances are known in which taxonomically distant species share a resource and probably (or surely) compete, Jaksic's is one of the few attempts to classify such species as guild associates. It is quite possible that differences in foraging behavior, possibly in relation to morphological differences between distantly related species (such as birds and mammals, or even different families in the same order) reduce the ecological overlap between them; this notion is discussed in later sections. If this were so, the relative rarity of published multitaxon guilds would not simply result from lack of knowledge or difficulties in studying wide ranges of species, but would reflect nature.

## QUANTITATIVE METHODS OF PARTITIONING A COMMUNITY INTO GUILDS

Most studies of guilds do not use quantitative methods to divide a group of species into guilds, relying instead on taxonomy plus intuition. Root viewed the guild as having fuzzy borders; the precision of specifying guild boundaries

would be inherently subjective and would rest on the sensitivity and judgment of the investigator: "As with the genus in taxonomy, the limits that circumscribe the membership of any guild must be somewhat arbitrary" (130, p. 335). It is often difficult to determine which species were considered for membership in a particular guild and which omitted, and why. For example, MacNally & Doolan (100) used MacNally's definition (99) to produce a guild of nine cicadas, though the precise criteria for limiting the guild are obscure. The study focussed on structure *within* this guild, and one result exemplifies the ambiguity. A "tall forest subguild" of three species was detected and subsequently became a "tall forest guild" (p. 43). The fact that results rest heavily on particular guild assignments plus an unease with qualitative procedures has fostered attempts to produce objective algorithms that automatically delineate guilds.

Quantitative methods used for guild assignment include nearest neighbor statistics (78, 162), cluster analysis (33, 93), principal components analysis (72, 141, 150), canonical correlation (55), and Monte Carlo techniques (84). All of these approaches, though explicit, do not unambiguously determine guilds because the investigator sets arbitrary levels for clustering. Various Monte Carlo methods (e.g. 146) can allow tests of hypotheses such as whether potential guild associates have diets more similar than would be expected given specified randomizations of the data (e.g. 82), but the level of nonrandomness required to qualify for membership in the same guild is still arbitrary. Further, so long as the basic data for these analyses consist of relative amounts of some resources used by each species, the classification depends on which resources are selected for analysis (148) and neglects the "similar way" aspect of guild assignment.

Adams (1) suggested psychophysical unfolding as a means of delineating and, incidentally, defining guilds. For a set of candidate guild associates offered the same set of resource states, preference data were examined to see if they could be "resolved" to fit a single axis. If so, all species were construed as forming a guild. If not, at least some of the species were interpreted as using the resources in a different way. The degree of resolution to a single axis was tested by Monte Carlo methods, so there remained the arbitrary decision of how much deviation from perfect resolution is required to disqualify a group as a single guild. This approach is attractive in that it formalizes the definition of "similar way," and it accords with a long tradition of ordering groups of species along single axes (e.g. bill length, body weight, size of seed eaten) and seeking patterns in that order that might be interpreted as reflecting competition (12, 47). But there is no consensus on whether the abstract definition of "similar way" corresponds to the commonsensical interpretation.

It seems unlikely that any of these quantitative methods of apportioning

species to guilds will become widely accepted. Intuition usually seems to play an important role. For example, Emlen (53) studied six avian foraging guilds. These included two guilds of terrestrial grain gleaners, one comprising doves and the other comprising galliforms. These two guilds appear to differ only in their members' systematics. Emlen apparently separated them on the basis of differences in structure and body size that he judged important, but he did not discuss why. Similarly, for MacMahon's research in North American deserts, "the guilds chosen here were selected on the basis of subjective familiarity with desert mammals" (97, p. 144). Probably the investigator's understanding of the biology of the species in question will continue to guide guild assignment, but unless more explicit discussion of the criteria is routinely provided, conclusions will be suspect and arguments will abound.

## AMBIGUITIES IN PARTITIONING A COMMUNITY INTO GUILDS

Root's (130) definition of a guild as a group of species using the same class of resources in a similar way leaves two basic points wide open for interpretation: What constitutes the same class of resources, and just how similar should a similar way be.

### *Same Class of Resources*

The definition of the same class of resources has probably been the less equivocal. The standard practice has been to define general classes of resources—insects on leaves (e.g. 130), fruit (e.g. 144), seeds (e.g. 14)—and then to study groups of species exploiting these resources. The species are usually a subset chosen for a certain foraging behavior, or simply winnowed on the basis of taxonomy.

But the same class of resources may be defined more or less broadly. "For example, seeds are a resource for a variety of desert consumers. Is the resource class all of the seeds on an area? Seeds of only some of the plant species? Seeds of particular sizes? Seeds in particular microsites? Clearly any of these might be the appropriate resource class, depending on the investigator's frame of reference" (98, p. 302). Correspondingly, some workers based guild assignments on study of actual food items taken by potential guild associates (80, 81). However, over a wide range of body sizes, there is a general correlation between sizes of consumers and their resources (e.g. 59). Also, species that may decrease overlap by different foraging methods, and so qualify as members of different guilds, may still overlap substantially in prey items taken. For example, the largest members of different predatory guilds may use many of the same prey. Conversely, species that feed in similar ways

on similar resources may exhibit low or no overlap in use of specific prey items because they differ greatly in body size and, therefore, prey-handling capabilities. A large raptor is likely to take rabbits and thus overlap more in its resource use with medium-sized mammalian carnivores than with a small raptor that takes small rodents. Should we then consider the large raptor and the carnivore, but not the small raptor, members of one guild? How narrowly can one define the same class of resources? At an extreme, are rabbits a resource class? We think not. One could conceivably construe a single prey species as a resource class if a predator were so highly adapted to it that it is nearly restricted to this species. Among vertebrate predators, this condition is, at best, extremely rare. The likelihood of assigning more than one such species to the same guild must be negligible. Because different species' resource distributions tend to comprise more than one prey species, and different predators' ranges of prey species tend to overlap only partially, the class of resources is best viewed as the sum of the prey spectra of the different predators.

A more difficult exercise is defining a guild on the basis of shared resources in cases of omnivory or either opportunistically or regularly changing diet. Can organisms be viewed as adapted generalists and thus placed in an omnivore or generalist guild? For species whose diet changes with resource availability, does guild membership change accordingly? Species whose life history stages use different resources raise a similar question. So can migratory species. For example, DuBoway (49) assigned seven dabbling duck species on their breeding grounds in North Dakota to one guild on the grounds that they forage in close proximity and take similar food items, although four foraged primarily by dabbling and three by "head-under," so they might have been construed as forming two guilds (see next section). On their wintering grounds in California, six of these species are again found together (the seventh is replaced by a single similar species), but they are generally more specialized in food, habitat, and behavior, and these traits often differ from those of the summer. For example, *Anas strepera* primarily dabbles in the summer but forages head-under in the winter. Primarily a dabbler in the summer, *Anas clypeata* in the winter has two distinct foraging modes and food types: alternately dabbling in the water column on small swimming invertebrates or "tipping-up" on the bottom for seeds and chironomid larvae. Diet, habitat, and behavioral overlaps between pairs of species are significantly less in winter than in summer. Should the guild partition be the same in the two seasons? There is no consensus on guild assignments in such matters. Because, as noted in the section on precursor and parallel concepts, guild designation without consideration of how resources are gathered is very similar to determining a food web, it is not surprising that most of these situations are also seen as problematic in depicting food webs (120).

*In a Similar Way*

Root (130) himself addressed the question of how similar is "similar." He excluded the western flycatcher (*Empidonax difficilis*) from the foliage gleaning guild on the basis of differences in its foraging behavior: This bird hunts by searching a large area from a "sentinel" position on an exposed perch. Most prey are taken in long, sweeping aerial attacks on flying insects or arthropods that alight momentarily on the foliage, so the western flycatcher concentrates on active insects (130). Thus, by its foraging method this bird, an important avian insectivore in the oak woodland, is likely to capture a greater proportion of Hymenoptera and Diptera (130). In fact, the blue-gray gnatcatcher, the member of the foliage gleaning guild that was the focus of Root's (130) study, also takes hymenopterans and dipterans and was observed also hawking flying insects. Its more typical foraging method—hopping from perch to perch and closely scrutinizing leaves—allows for a higher proportion of stationary or slow moving prey. The different, though partially overlapping, foraging methods of these two birds that coexist in the oak woodland, both exploiting insectivorous prey found on leaves, reduce (but do not eliminate) the overlap between prey species taken, and so merit their separation into two guilds.

Many studies of avian species follow Root (130) in assigning guild membership through foraging method. Case et al (22) discussed four major foraging guilds: frugivores, foliage gleaning insectivores, flycatching insectivores (including hawking, sallying, and gleaning forms), and nectarivores. Similarly, Cody (28) perceived three major foraging guilds: foliage insectivores, sallying flycatchers, and slow-searching omnivores. However, assessment of similarity in foraging behavior remains quite subjective. Landres & MacMahon (93) divided oak woodland avifauna into foraging guilds that are relatively more specialized, and include foliage gleaning, wood gleaning, wood probing, air sallying, and ground sallying. Other studies deemphasize foraging behavior and use coarser categories of feeding guilds; they seem to incorporate the nature of the resources but not the way resources are gathered. For example, Martin (102) divided island avifaunas into three guilds: granivore, omnivore, and insectivore. Meserve (109, 110) studied three feeding guilds of the Chilean semi-arid small mammal community: herbivore, insectivore, and granivore. Strand (145) described two guilds of California reef fishes: herbivores and predators. It appears that the investigator's notion of similarity, based probably on the particular system studied, strongly affects guild designations.

Different investigators have divided the same or ecologically closely related taxa into guilds in different ways that reflect a different grasp of this term, and a different impression of the importance of the "similar way" in guild definition. Consider predator guilds as an example. At one extreme

Jaksic (79) considered grouping taxonomically related species into guilds, a clear abuse of Root's (130) original definition of the term. Following MacMahon et al (98), Jaksic believed that the criterion for "similar manner" should be based on the effect of resource use on the resource itself: ". . . it does not matter whether an organism removes a tree leaf for nesting material, for food, or as a substrate to grow fungi which in turn are eaten; the leaf is gone and the leaf users belong to a common guild" (98, p. 301). Consequently Jaksic et al (80) and Jaksic & Delibes (81) described predatory guilds whose members include mammalian carnivores, falconiforms, owls, and snakes. A "similar way" does not play much of a role in these guild definitions.

A narrower definition of predatory guilds, to include only extant and extinct mammalian predators, was used by Van Valkenburgh (152, p. 407): "As defined here, the guild of large land predators includes the nonaquatic, nonvolant mammal species within a community that take prey and potentially compete for food." Van Valkenburgh (152) limited guild membership to species above jackal size (7 kg) because she expected heightened competition among large predators, but also because these are better represented in the fossil record.

Dayan et al (46) based guild designations of recent carnivorous mammals on limb morphology, which reflects locomotor function and affects foraging behavior. Underlying these guild designations was the assumption that similarities in locomotor behavior imply greater ecological overlap and thus the potential for increased competition. The three guilds are cursorial carnivores of open areas (canids), plantigrade, relatively slow species (mustelids and viverrids), and species that stalk their prey (felids). These carnivores differ also in their killing behavior. Mustelids and viverrids kill by using an upper canine to drive apart two cervical vertebrae, a specialized method allowing them to take prey that are quite large relative to themselves. Felids kill similarly, further assisted by their ability to seize prey with their forepaws. Canids are more omnivorous than the other carnivores. They use a series of slashing bites or shred prey in their mouth. Consequently, canids while hunting alone take prey that are relatively small. Dayan et al hypothesized that these differences in foraging behavior reduce overlap between prey species composition of the three guilds; members of different guilds are less likely to encounter, pursue, or take overlapping prey items than are members of the same guild. However, much as with Root's birds, some overlap may well occur. Thus "similar way" plays a key role in these guild designations. Unfortunately, basic data on food habits of the different species are unavailable. A coevolutionary morphological response within each guild is evidenced (42–45), and this pattern does not obtain when all species are placed in one guild, but the case for inter-guild resource partitioning remains indirect and not empirically tested.

To test the significance of differences in foraging methods one must study a resource-based grouping of species that show different foraging behaviors and whose resource use pattern is at least reasonably well understood. The granivores of North American deserts constitute exactly such an assemblage and exemplify problems in partitioning a biota into guilds.

## AN EXAMPLE—GRANIVORES OF THE AMERICAN SOUTHWEST

Rodents, ants, and birds all eat seeds in the same areas (19). Many of the birds eat seeds opportunistically and/or seasonally, but most habitats support at least a quail and a dove that are resident granivores. Their impact on rodents and ants has scarcely been studied. The rodents consist of (a) heteromyids (kangaroo rats, kangaroo mice, and pocket mice) that are highly specialized physiologically and morphologically for eating seeds, and are primarily or exclusively granivores, and (b) cricetids that are opportunistic omnivores, lacking such specializations (14, 19). The percentage of seeds in cricetid diets is unknown. One kangaroo rat, *Dipodomys microps*, has a mixed diet of leaves and seeds that varies spatially and temporally (35).

Brown (11, 12, 14) and Davidson et al (40) lumped all heteromyids plus some cricetids in one guild. Bowers & Brown (9), aiming for a finer partition based on the trophic classifications of Morton (114), placed *D. microps* in a separate herbivore guild, the other heteromyids in a granivore guild, and the cricetids in an omnivore guild. Kangaroo rats and kangaroo mice jump bipedally, while pocket mice and the cricetids are quadrupedal (12). Kangaroo rats forage mostly in open areas between scattered perennial plants and hop quickly between widely spaced seed clumps, while pocket mice forage mostly on more evenly distributed seeds under shrubs (14, 19). "Rodent species feeding under shrub canopies and those feeding in open habitats may share only the subset of seed resources that cross habitat boundaries. This subset may be particularly insignificant for buried seeds that are less likely to be moved by physical forces" (19, p. 216). Because of these behavioral differences, we viewed bipedal and quadrupedal heteromyids as separate guilds and suggested that *D. microps* is a guild associate of the other kangaroo rats because it is at least partly granivorous and its foraging behavior and morphology resemble that of its congeners (41). We separated cricetids based on their different physiology, morphology, and behavior; the cricetids, lacking the large external cheek pouches of the heteromyids, appear to forage differently from heteromyids (126). Hallett (65) assigned the cricetids and pocket mice to one guild and kangaroo rats to another. Brown & Heske (18) also called the kangaroo rats a separate guild, on the grounds that they are ecologically and taxonomically similar. These classificatory dilemmas em-



body how subjective guild assignments can be. Even if cricetid diets were studied more thoroughly, the decision on how much dietary overlap qualifies species for guild association would be arbitrary.

The ants have also been variously apportioned into guilds. Some researchers (24, 106) perceived a guild of seed-foragers and an omnivore guild containing only *Novomessor cockerelli*. Others (23, 40) included the latter species in the seed-eating guild. Davidson et al (40), based on Davidson (38, 39), nevertheless distinguished within this guild between species that forage in columns and those that forage individually. The former tend to feed on energetically rich clumps of seeds, while the latter feed primarily on dispersed seed. However, unlike the rodents, the ants seem not to include species that forage particularly close to shrub cover (39). Ant species also differ in how they grasp and carry seeds (24). In sum, as with the rodents, one might argue, based on diet and foraging behavior, for at least three guilds (omnivore, single forager, column forager) among these species.

These rodents and ants are the most frequently cited example of competition between distantly related organisms: "the competitive interaction among the rodents may be weaker than that between rodents and ants" (51, p. 343). Though Brown & Davidson (15, Figure 1) and Davidson et al (40, Table 1) emphasized the broad overlap in sizes and species of seeds eaten by the two groups, in fact the differences are enormous. For seed size, a Smirnov 2-sample test between ants and rodents yields  $T_2 = 0.387$ ,  $P \ll 0.01$ . For seed species, a variety of null models would be possible, but it is difficult to imagine any of them not finding rodents and ants remarkably different. For example, of 20 seed species recorded by Davidson et al (40), 13 are eaten only by ants or only by rodents. If one omits the 8 seed species eaten by only one granivore species, 5 of the remaining 12 seed species are eaten only by ants or only by rodents. A controlled experiment (15, 17) was equivocal (16, 57, 74): Removal of rodents resulted in a significant increase in ants only for the genus *Pheidole*, while, over the long term, rodent presence may facilitate ants by favoring growth of small seeded annual plants, the main resource for the ants. Even Brown & Davidson "no longer place so much confidence" (16, p. 1424) in this particular experimental implication that ant removal led to an increase in rodent density. However, experimentally demonstrating competition in the field even when it exists is extraordinarily difficult. The ambiguous results may stem from a reduction in competition effected by different foraging methods.

These ants and rodents may greatly lessen competition even though sizes and species of seeds overlap. As noted above, heteromyids are seed specialists while cricetids are omnivores, so overlap between these groups is reduced. The pocket mice specialize in seeds near shrub cover, while no ants do. Ants forage only on the surface, while the rodents, especially the kangar-

roo rats, can dig for buried seeds, which may remain in dense clumps long after surface seeds are gone (19, 127). In sum, though all these ants and rodents have been lumped together with birds in one guild (118, 137), they probably do not form one guild *sensu* Root (130). Possibly they form six. The differences in foraging behavior may suffice to reduce competition between species in different groups substantially.

## PLANT GUILDS

Guilds defined for plants usually have not been tied to resources as obviously as animal guilds have, perhaps because of the difficulty in reconciling plant diversity with notions that resource partitioning structures communities. Field work in plant communities indicates that at most three or four resources are limiting in any community (149). "In terms of many of the theories of resource competition, it seems hard to imagine how hundreds of plant species may coexist when limited by a few resources, all of which are required for plant growth" (149, p. 8). Also, perhaps because researchers are animals, differences in ways that plants use resources do not seem as obvious as they do for animals. Some classifications seem little more than versions of life forms and other traditional schemes (cf 88) of classifying plants by vertical stratification. For example, Wilson (161) pointed to the difficulty in defining guilds *sensu* Root (130) in plant communities and suggested that some plant communities may be structured into guilds by stratification, especially of forests into canopy, small-tree stratum, herbs, etc. Resources, such as light and space, that might be partitioned by such stratification are tacit. Some designated tropical tree guilds (73)—shade-tolerant shrubs, understory trees—fall in this category. Others were defined on the basis of habitat—species restricted to slopes or swamps. Yet others may comprise species with similar, specialized conditions for regeneration. There is no single resource classification here; rather, the goal seems akin to the division of the entire community into "basic building blocks." Platt (124) assigned plants to a "fugitive species guild" on the grounds that they exploit a common resource (open space with increased soil moisture) in a similar manner, but he did not define what that manner was or suggest what might have constituted different manners. Fowler (56) doubted that a grassland plant community is divisible into well-defined guilds, on the grounds that all component species interact weakly and quite equally with one another.

Pollination guilds very much in the spirit of Root's definition are clearly possible for plants pollinated by animals. Because distantly related plants can compete for the same pollinators (90), pollination guilds can be taxonomically diverse. For example, Murray et al (115) discussed two tropical pollination guilds spanning several families. Here the resource was pollinating birds,

shared by the guild associates: One guild is pollinated by long-billed hummingbirds and the other by short-billed hummingbirds. Wheelwright (158) conceived of plant guilds more narrowly, defining the Lauraceae as a guild that share avian seed dispersers and insect pollinators: "a group of species providing similar fruit resources and attracting the same seed dispersers. They also share similar floral morphologies and flower visitors" (158, p. 466). The original guild definition might have apportioned these species into guilds according to two separate classifications, and in each of these Lauraceae might have associated with heterofamilial species.

Fowler (56) designated warm- and cool-season grasses as two distinct "temporal guilds" and pointed out that, in her system, the cool-season species are all  $C_3$  plants while the warm-season ones are all  $C_4$  plants. The different photosynthetic pathways seem not so much different ways of getting a resource (light) as different ways of using it once it is captured. In much the same way, cow and horse digestive systems process grass differently, though the animals may be gathering the same resource in the same way. Digestion is not foraging. The parasitic habit of some flowering plants may lead to guilds more in the spirit of animal guilds whose associates gather similar foods in a similar way. No doubt detailed consideration of how parasitic plants find and use their hosts would lead to the demarcation of more than one such guild, but it seems clear that even hemiparasites are using at least some different resources than those of free-living plants and are garnering their resources very differently from free-living species.

Possibly because competition-structured guilds are so difficult to detect for plants, Atsatt & O'Dowd (3) used the term in a different sense entirely, one quite close to the dictionary definition of "guild." They identified "plant defence guilds" as groups of plant species that aid one another in defense against herbivores. For example, some plant species may have nectaries that attract predatory or parasitic insects to an entire plant assemblage. Or groups of plant species may contain alternate herbivorous insects that all function as hosts for a parasitoid that could not complete its life cycle on just one of them. This usage of "guild" has not prevailed.

## GUILDS AS FUNDAMENTAL COMMUNITY BUILDING BLOCKS

The niche is usually viewed as a property of populations or species, but Elton (52) occasionally discussed niches as traits of groups of species not unlike guilds (67). As noted in the section on The Motivation Behind the Concept, Root hoped to reserve "niche" for the habitat requirements of a species and establish "guild" as the functional role of a group of species. This hope is unfulfilled, but "guild" and "niche" have come to have different connotations,

“niche” referring to roles of species and “guild” to groups of species with similar roles. However, Terborgh & Robinson refer to “guild niches” (148, p. 89) as the sum of the niches of guild associates. Both guilds and niches in the “guild niche” sense have been prime candidates for fundamental elements of communities. Pianka suggested the possibility of a “periodic table of niches” (123, p. 264) completely analogous to the periodic table of elements, with entries that are groups of species corresponding to broadly delineated guilds (flycatchers, insectivorous bats, etc). Elton (52) anticipated the notion of community convergence of ecological roles and function, arguing that the divisions of different communities into roles is quite similar even when species compositions differ (67). Terborgh & Robinson (148) construed the many efforts at demonstrating morphological convergence as essentially in the same vein, with morphology reflecting ecological function. Various studies compared the structure of parallel guilds in different regions, and even in different periods. Van Valkenburgh (153, 154), for example, compared locomotor and trophic diversity within guilds of extant and extinct large predatory mammals, while Terborgh & Robinson (148) compared the partition into guilds of several tropical forest bird assemblages. Apparent constancy in proportions of species with different roles (e.g. 29, 68), quite similar to “guild signatures” (85), has been perceived as possibly indicating fundamental structural constraints on the relationship of basic community building blocks.

May was quite sanguine about this idea, seeing “the convergence of the structure of entire communities of plants and animals in spatially separate but climatically similar regions” (103, p. 151), of which the six identical guilds of insectivorous birds perceived by Cody (26, 27) in similar habitat of California, Chile, and South Africa were a prime example. Terborgh & Robinson (148), though optimistic, recognized two key problems that might lead researchers to see convergence that would suggest fundamental community units—first, it is not clear what aspects of communities to compare; and second, degree of similarity is largely in the eye of the beholder, and few descriptions entail statistical tests. Orians & Paine (118) were much more skeptical. They found little evidence of community convergence in the way terrestrial or benthic marine communities are structured into guilds; they see most anecdotal evidence of coevolutionary convergence as more parsimoniously explained by more or less similar physiological responses of individual species to similar environments.

Because this search for convergent community properties has focussed so heavily on ecological roles as integral to community constraints, and thus to how communities are likely to converge, guilds inevitably became one currency of this search. One would naturally start by focussing on which groups of species use the same resource (e.g. nectar) in different regions with

different biotas. If one either omits the "similar way" part of the definition of "guild," or interprets it quite loosely, groups of species that use a resource more or less in the same way can often be construed as convergent guilds (e.g. sunbirds, honeycreepers, honey-eaters, and hummingbirds). However, observing similar sets of guilds defined in this way does not confirm a strong convergence in fundamental community properties. Evolutionary constraints may well restrict similarity of foraging methods between distantly related species to the extent that whether or not they are viewed as convergent guilds is a judgment call. Sunbirds usually perch and hummingbirds usually hover while feeding. Whether such differences in how they use a resource would lessen resource sharing could only be determined if they co-occurred. Preliminarily, all one can say is that birds have evolved to use nectar in different biogeographic regions. This is not to say that objective tests of convergence are impossible. For example, Niemi (116) found similar direction of morphological evolutionary change between congeneric shrub- and forest-dwelling peatland birds in both North America and Europe. But the division of species into more or less subjectively defined guilds in different regions does not seem to have aided the search for convergent emergent properties; this search remains frustrating (133).

## GUILDS IN ENVIRONMENTAL ASSESSMENT

The popularity of the guild concept inevitably led to its use in environmental assessment and management (67). The key notion was that, if a guild consists of species using the same resources in similar fashion, "actions that affect environmental resources will similarly affect the members of the guilds using those resources. Once the impact on any one species in a guild is determined, the impact on every other species in the guild is known" (140, p. 187). The guild concept thus became inextricably linked with the idea of indicator species (94), except that indicators were transformed to "guild-indicators" (155) rather than indicators of entire communities. The assumed solid status of the guild concept in academic ecology justified the relatively easy but controversial management practice of using censuses of single species' populations as indicators of population trends of other species and of habitat quality. Severinghaus also suggested that one might predict the effect of an environmental action on a guild in one region from its effect on a similar guild in another region.

Traditional methods of classifying birds into guilds led to different partitions and, no matter what the partition, guild associates differ sufficiently in ways other than resource use that they need not respond identically to habitat change (92, 155). Verner (155) went so far as to suggest that, if guilds are to be used in management, they should be transmogrified to reflect Severing-

haus's supposition. He defined a "management guild" as exactly those species that respond similarly to changes in their environment. Yet guilds are normally assigned, as noted in the section on Guilds in the Original Sense, on habitat and feeding grounds, in the absence of empirical research on how they respond to environmental changes (147). Further, if guilds as traditionally defined really do include species that most strongly compete with one another, one might expect that a common response among all guild associates to physical environmental change overlays compensatory, opposite-direction population changes among specific pairs of guild associates. It is therefore difficult to believe that a guild member can unambiguously represent a guild, even if all species have been studied for their individual responses to habitat change.

Probably because of its innate economic appeal (6), the use of guilds for management is remarkably persistent, in spite of the above objections and several critical studies of specific communities (e.g. 6, 101, 147). The guild concept seems to have taken on a life of its own (67). Roberts (129, p. 473) argued that, "Guilds can be used to select evaluation species to extrapolate information to nonstudied species." Karr (87) recommended comparing proportional representation among guilds of birds and fishes ("guild signature" [85], "guild spectrum" [31]) to indicate the health of biological systems, while warning against simplistic use of aggregate statistics such as various diversity indices to indicate environmental quality. However, it is difficult to imagine that guild signatures, guild indicators, and other guild-based short-cuts would not be used in exactly this way. Already, "response guilds" and the claim that individual guilds can indicate community-wide effects of disturbance are appearing in newspapers (e.g. 2). It would be sad if environmental managers, assuming ecologists know how to assign species to guilds easily and understand how guild associates behave with respect to one another and the surrounding milieu, based decisions about the fates of populations and communities on what is, in fact, an incompletely understood concept that is used inconsistently.

## CONCLUDING REMARKS

Hawkins & MacMahon suggest that behavior—the way resources are used—is important only for descriptive cataloging of the components of a community: "If one uses guilds only as a classification scheme for community components, however, then a similar manner of resource use is an important criterion. Root's original intention seems to be related to classification" (67, p. 443). On the other hand, they feel that foraging method is irrelevant if one is seeking to understand how species interact in nature: "To state the question with a bit of hyperbole, does it matter that a particular insect species is

captured by a silken spider web as opposed to a bird's beak? The ecosystem and community consequences are similar—one less insect of that species—and manner is irrelevant from the specific perspective” (67, p. 443).

We cannot accept this view. It is important to bear in mind that all species using a resource are potential competitors if that resource is limiting. But, as we noted in the desert granivore example, even if a resource is limiting—a point that is usually not demonstrated—to a great extent different ways of using a resource can reduce, though not necessarily eliminate, the effect that different species using that resource have on one another. It is quite possible that the “similar way” part of the original definition is just as important as the “same class,” but it is certainly much more difficult to study and has thus received far less attention. Because related species often use resources in similar fashion, partitions into guilds, *sensu* Root, probably will often reflect taxonomy. But taxocenes taken as guilds without extensive information on which resources they use and how they use them should be viewed as, at best, preliminary constructs. Similarly, distantly related species are not automatically guild associates simply because they use similar resources.

That a search of titles and abstracts revealed 432 references to “guild” through 1986, most of them since 1980 (67), means that this word answered a felt need among ecologists. Had “guild” not come along, an analogous word would have. A major theme of ecology was resource partitioning and potential competition between species, and no prior term quite expressed the concept of the group of species that comprise the potential competitors or partitioners of some resource. We show in the section on Precursor and Parallel Concepts how “functional group” has evolved almost simultaneously to carry the same connotations, but the metaphor of the “guild” must have seemed more elegant than this term, because “guild” became far more popular. It is interesting and perhaps instructive that the metaphor was not quite apt from the outset, emphasizing competitive aspects of individuals doing the same thing, rather than the mutual aid and protection functions that typified craft guilds. Possibly the reason “guild” was the word that became popular, and not other more or less contemporaneous and synonymous terms, is the economic basis of its referent. A key attraction of the notion of communities regulated by competition among their populations may be its suggestion that unfettered capitalism is “natural” and has self-regulatory traits analogous to those of a supposed “balance of nature” (8, 95). If this is so it may not be surprising that the strong connotation of mutualism in the word “guild” was deemphasized. Others (8, 128) have argued that a similar deemphasis of ecological mutualism relative to competitive interactions and predation reflects a social background and worldview as much as the nature of nature.

The problem with “guild” now is that it has too many connotations. Root's original definition was very precise, but others adapted the term to their own

needs so that different authors may connote very different things. Even researchers who know the original paper, supporting meticulous research and strict definition, lapse into idiosyncratic, casual use of the term. For the same reasons that the term caught on in the first place, it is still needed, but it is well on its way to becoming a panchreston, a term of such flexible meaning that its use is as likely to generate confusion as to communicate information. However, if "guild" is used in the narrow sense, the notion of the group of all species using a resource is an anonym. The need for a word for such a group is so great that this meaning has almost co-opted "guild;" now that "guild" is used in a very broad sense in textbooks as the basis for community ecology (51), it will be difficult for the narrow meaning to recapture it and save it for scientific use. If the term is to be used fruitfully in research, two conditions must be met:

1. A clear statement is always required of the criteria and considerations that have led to a particular guild assignment, in order to enable other investigators to consider the validity of this designation. To say "We divided the birds into four guilds based on microhabitat use," or "We divided the birds into six guilds based on the habitat and dietary information in Smith and Wesson (1913)," is insufficient. The role of foraging method should be emphasized because of its potential importance in effecting differences in resource use.

2. Sympatric related biota should always be listed and an explanation provided for why they were excluded from a designated guild, in the many cases where the grounds for this exclusion are not self-evident and consist of intuition or simply taxonomy.

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