

GUILDS: THE MULTIPLE MEANINGS OF A CONCEPT

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INTRODUCTION

Root (161) defined a *guild* as "a group of species that exploit the same class of environmental resources in a similar way." With this intuitively appealing, seductively simple definition, he commenced the development of what has become a Gordian knot of ecological thinking. Root saw the term as a way to group "together species without regard to taxonomic position, that overlap significantly in their niche requirements." He also felt that one advantage to the guild concept was that it "focuses attention on all sympatric species involved in a competitive interaction, regardless of their taxonomic relationship" (161, p. 335).

Nearly 20 years later, Terborgh & Robinson (195, p. 90) cited the concept of guild as the new perspective in ecology: "Guilds will become the standard currency of ecologists in their efforts to understand community relationships of many kinds." Yet few authors have critically examined the implications of Root's definition or provided an operational definition for it in their studies. Also, many authors have developed meanings for the term that seem quite different from Root's emphasis and intent. For example, Balon (6) used the term to classify "reproductive styles" in fish, while Bambach (7) used charac-

teristics of basic body plans and physiological systems (Baupläne) of fossil marine invertebrates as a partial basis for his guilds.

One reason the concept of guild is so appealing and so often invoked is that after observing any natural system long enough, workers studying particular groups of organisms have difficulty placing their subjects into strictly defined subunits of communities or ecosystems, such as trophic levels. They also realize that their particular taxonomic group is not the only one using a particular resource. This observation leads to a resource-centered classification of community components rather than one based on taxonomic affinities, an emphasis consistent with Root's guild concept. This tendency is not new. For example, Elton (48, pp. 63–68) alluded to a guildlike niche in animal communities when he stated "we might take as a niche all the carnivores which prey upon small mammals, and distinguish them from those which prey upon insects." Interestingly, the literature of the period 1967–1973 contains several references to guildlike phenomena developed without knowledge of Root's definition. For example, Evans & Murdoch (50) stated, "We have been impressed by the evidence that the feeding activities of the organisms impose a pattern on the community which overrides taxonomic composition." Their studies dealt with terrestrial arthropods, but aquatic insects were the subject of a similar convergence in thinking (35).

When Root codified this common experience by adopting a familiar term, not surprisingly many community ecologists wholeheartedly embraced the term, but they flavored it with their own experiences and shades of personal meaning. Despite the apparent common need for a term such as *guild* to describe a resource-oriented, organizational unit within communities that transcends taxonomic boundaries, current opinion regarding the guild concept is mixed. Some view guilds as natural units worthy of detailed study, while others deny that guilds exist except in the minds of ecologists. We believe this multiplicity of viewpoints arises because few workers have critically addressed the dimensions of the word. Thus the literature is full of the self-assured use of the word *guild* but lacks a systematic account of the concept's implications.

In this chapter we review the various explicit and implicit meanings attributed to the term *guild*. Related terms, such as *functional group*, are compared with the guild concept. We also consider the ways that *guild* has been used to describe natural ecological units. Finally, we analyze the usefulness of the concept, its validity as a level of organization in nature, and its prospective use as a basis for management decisions.

Our review emphasizes studies of invertebrates, especially arthropods. Because the concept of guild is prominent in studies of vertebrates, however, we also refer to those vertebrate studies that provide general points about the guild concept.

HISTORICAL USAGE, SHADES OF MEANING, AND SYNONYMS

To obtain some quantitative sense of the prevalence of the term *guild* in the ecological literature, we conducted a bibliographic search of the citation frequency of Root's original paper (161) (Figure 1A). The citation frequency has gradually but unevenly increased over the years. A noticeable decline occurred around 1983, followed by a spate of citations paralleling a reawakening of interest in community ecology (42, 53, 63, 80, 91, 192). Root's monograph discussed much more than guilds, but inspection of these 358 papers revealed that the usage of the term *guild* was most often the only reason for citation. In fact, the real scientific content of Root's manuscript seems to have been overshadowed by the new definition.

Because not all authors who discuss guilds cite Root, we conducted a search of titles and abstracts for the word *guild* (Figure 2). Of the 432 references found through 1986, only about 100 treated invertebrates. The infrequency of the term in the invertebrate literature in part stems from the alternative use of the term *functional group*, coined by Cummins (35) for

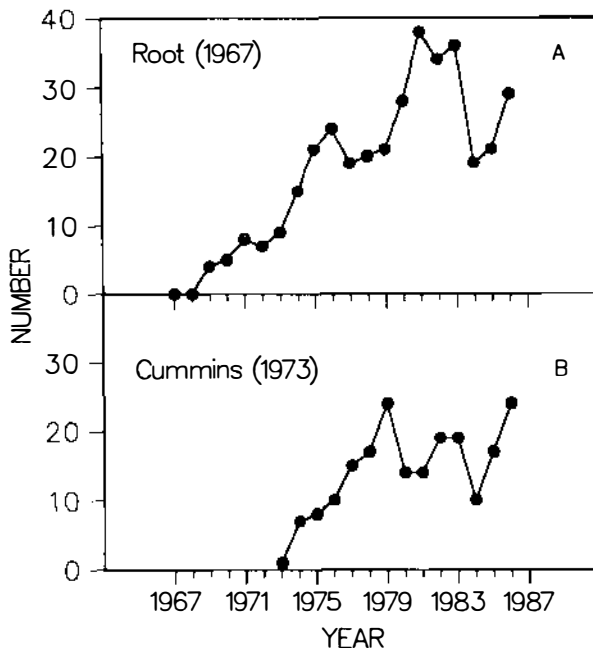


Figure 1 Number of times Root (161) (A) and Cummins (35) (B) were cited each year between 1967 and 1986. Data compiled from *Science Citation Index* (84a).

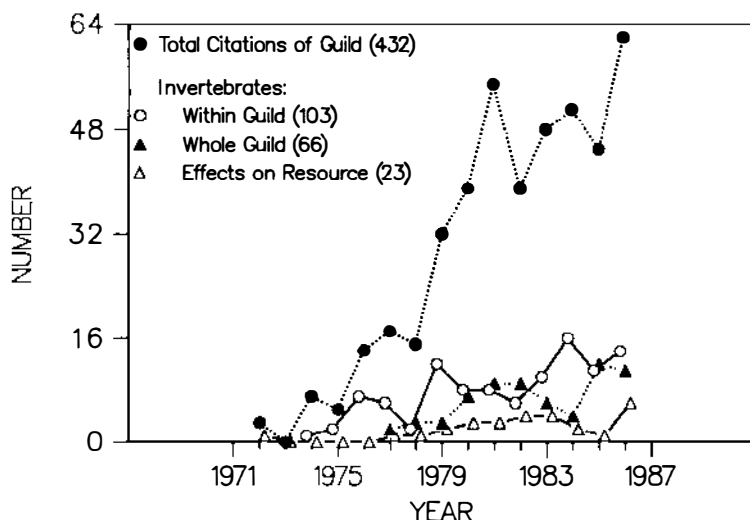


Figure 2 Number of papers published per year containing the word *guild* in either the title or abstract. Total citations include papers for any animal taxon. We placed papers on invertebrates into three categories, which are not mutually exclusive. Within-guild papers addressed patterns of resource partitioning or competition. Whole-guild papers addressed factors affecting overall abundance of one or more guilds. The third group of papers examined the effects of guilds on resource abundance or ecosystem processes. Data were compiled from a computer search of BIOSIS. Papers containing the phrase *functional group* but not the word *guild* are not included, because we would not have been able to extract guild-related papers from those citing chemical functional groups.

aquatic invertebrates (Figure 1B). MacMahon et al (106) attempted to differentiate these two terms because they seemed so similar, and by 1984 the terms were accepted as synonymous (38). In fact, some authors used functional groups as descriptors of guilds (154).

Problems with understanding of the guild concept occurred early. Therefore MacMahon et al (106) attempted to define *guild* explicitly in a general discussion of community and ecosystem theory. Later, Jaksic (85) took a similar approach and argued for a distinction between true (resource-based) community guilds and taxonomically based assemblage guilds. Although he indicated that workers should use quantitative techniques to define guilds, rather than a priori classifications, several attempts to do so have met with mixed success.

CONCEPTS AND ECOLOGICAL IMPLICATIONS OF GUILDS

Ecologists have used the guild concept in three ways. Their different perspectives have strongly influenced the specific questions addressed and the

avenues of inquiry used to consider them. One perspective views the guild as the ecologically appropriate context for the study of interspecific competition. In the extreme of this viewpoint, guild members are the only individuals likely to compete. A second viewpoint is strongly utilitarian and uses guild classifications to simplify the complex and numerous interactions among species that characterize real communities and ecosystems. A vast amount of species-specific information is thus condensed into a few "black boxes" that have generalized attributes. The third perspective views guilds as natural ecological units that recur across communities; this perspective is not always distinct from the other two. Root emphasized the first and third perspectives, whereas Cummins emphasized the last two. In this section we discuss each of these views and consider their ecological implications.

Guilds as Arenas of Interspecific Competition

Ostensibly, a major advantage of a guild approach is that the importance of competition to community structure can be assessed only if interactions between the entire cast of participating characters are understood. Before the development of the guild perspective, studies of interspecific competition and resource partitioning generally focused on taxonomically related species (reviewed in 152). Insights generated from these studies catalyzed more than 50 years of research on the process of competition, but the emphasis on members of the same taxocene limited inferences regarding the importance of competition to whole communities or ecosystems. The demonstration that ants compete with rodents and birds as well as with other ants (17) illustrates the value of this idea.

Root's original idea is now so firmly established in the ecological literature that guilds are often considered "arenas of intense interspecific competition, with strong interactions within guilds but weak interactions between members of different guilds" (142). Many of the comparative and experimental studies of resource partitioning and interspecific competition now define the species of interest as members of the same guild (e.g. 41, 54, 87, 109, 146, 153, 155). The emphasis of many recent papers is on whether and how competition shapes guild structure—i.e. the composition, relative abundance, and number of species observed within guilds (e.g. 4, 22, 97, 107, 175, 176). Because of this emphasis the guild concept is used to discuss all of the aspects of competition and niche related to a wide variety of ecological phenomena including size-ratio differences between guilds (and the related Dyar's constant) (49, 145) and even global patterns of ecological equivalents (195).

Community and Ecosystem Analysis

COMMUNITY STRUCTURE If guilds represent the basic building blocks of ecosystems, communities should share similarities that transcend species

composition. Elton (48) discussed this idea as early as 1927. He argued that "although the actual species of animals are different in different habitats, the ground plan [in terms of ecological types] of every animal community is much the same." Others extended Elton's basic idea by recognizing that the use of a natural, functional classification could facilitate comparison of communities that are either overwhelmingly complex in terms of number of species (147, 161, 162, 189) or poorly known taxonomically (5, 36).

Furthermore, if each guild exploits different types of resources, guild composition of communities should reflect the availability of resource types. This idea has permeated the literature on most ecosystem or habitat types [e.g. oceans (115, 189), fresh water (148, 201, 206), trees (127, 191), grasslands (50, 87), other plants (100)], but it appears to have most strongly influenced the study of freshwater benthic invertebrate assemblages. The functional classification of Cummins (35; see also 120) is almost universally used by ecologists studying freshwater invertebrates and is apparently based on the hypothesis that "the relative dominance of invertebrate groups shifts with differences in available sources of energy" (37, pp. 147–148; see also 39, 74, 125, 199).

The idea that guilds are groups of functionally similar species also leads to the idea that ecosystems contain many functionally redundant species all capable of performing the same ecosystem function (132, 134). If so, guild structure may be more predictable and stable than either the abundance of individual species or species composition (50, 75, 134, 162, 196). Presumably, density compensation within guilds should maintain overall guild abundance at or near carrying capacity, while the fortunes of different species within a guild vary individually in response to factors other than resource availability—e.g. weather, predators, local conditions (162).

ECOSYSTEM ANALYSIS Another important implication of the guild concept is that it provided a conceptual bridge that might unify community and ecosystem approaches to ecology. If different guilds exploit different kinds of resources, the processes of energy flow and material cycling that occur within ecosystems should closely correspond to community structure in terms of guild composition. Focusing on interactions between guilds and their resources offered a means of describing the structure and dynamics of food webs (5, 16, 36, 134) more realistically than was possible with traditional food-chain models (e.g. 103, 132). This last idea may largely explain why functional classifications are now used so frequently by ecosystem ecologists (3, 60, 106, 117, 121, 126, 171, 187).

Guilds as Natural Ecological Units

The concept of guild has engendered the idea that communities are comprised of a limited number of relatively discrete functional subunits (16, 36, 118,

162). This idea, if true, has profound implications for the study and understanding of natural ecosystems. Root (161, p. 336) suggested that guilds represented major ecological categories that have been “molded by adaptation to the same class of resources.” Root & Chaplin (164; see also 163) subsequently introduced the term *adaptive syndrome* to describe a “coordinated set of characteristics that are associated with . . . specialization on a . . . resource.” They proposed that consumers have only a limited number of ways to obtain the resources they need, and that natural selection has molded the morphological and behavioral traits of species to fit one of these “occupations.” Other ecologists have proposed similar ideas (108, 189). In general, the structure of the environment (habitat) is thought to impose selective pressures that cause sympatric species to evolve similar adaptive solutions for resource exploitation (see 108).

This type of reasoning is part of the basis for the guild classification that Root proposed (161). Others have subsequently constructed similar classifications. For example, Steneck & Watling (189; cf 7, 209) based a functional classification of marine invertebrate herbivores on the concept of adaptive zones (*sensu* 183, 188). They argued that relatively few adaptive zones exist in an evolutionary landscape and that one or more species occupies each of these zones.

Convergent evolution is also an important concept here, because it is often cited as the means by which similar adaptive syndromes or “ecological equivalents” arise among different taxa in geographically isolated ecosystems (26, 132, 135, 195). Morphological or behavioral equivalents are thought to represent the manifestation of similar evolutionary pressures to produce individuals that perform similar ecological roles.

APPLICATIONS

In ecology, the fit between concept and reality is often poorly known because new ideas are generated faster than empirical information becomes available. Fortunately, however, the abundance of guild-related studies conducted during the past 20 years permits us to evaluate the utility of some of the ideas and concepts described above. We explore five related questions:

1. What *a priori* criteria have ecologists used to classify guilds?
2. Are invertebrate assemblages organized into a few natural, relatively discrete ecological groups?
3. Is the guild composition of natural communities predictable based on the resource availability?
4. Are guild structure and abundance more stable than species composition?
5. Have guild classifications facilitated understanding of ecosystem processes?

Although space limitations preclude an evaluation of whether guild theory has enhanced the understanding of competitive relationships (see 4, 29, 98, 101, 168 for review), we discuss in conclusion the adequacy of the guild concept as a framework for understanding such interactions.

A Priori Classifications: Assigning Species to Investigator-Defined, Resource-Based Guilds

Table 1 lists some of the criteria used to define ecological groupings of invertebrate and other taxa. Although specific criteria for classification depended on author and situation, most classifications were based on presumed differences in the use of food resources. In some cases, groupings were largely based on the broad trophic categories of herbivore, detritivore, and predator (75, 127). In others, larger trophic groups were divided into guild-like groups based on feeding specializations or exact time or site of feeding. Regardless of the level of resolution, the classifications appear similar in that the taxa were grouped by differential use of a priori, investigator-defined sets of resources.

Guildlike classifications have frequently been used to classify invertebrate consumers over the past 20 years. For example, Evans & Murdoch (50) recognized that some herbivorous insects were specialized leaf-and-stem or flower feeders, whereas others belonged to a more general herbivore group. Root (162) formally introduced the term *guild* into the entomological literature when he divided folivores on collards into "three distinct guilds based on mode of attacking the plant" (i.e. pit feeders, strip feeders, and sap feeders). Several other presumed guilds of terrestrial insects have since been suggested, including chewers (strip feeders), miners, suckers (sap feeders), gall formers, seed feeders, predators, parasites, wood borers, stem borers, nectivores, omnivores (scavengers), fungivores, epiphyte grazers, and dung feeders (e.g. 19, 51, 57, 79, 82, 96, 100, 126, 127, 139, 155, 174, 191). Some authors even recognized a tourist (i.e. visitor) guild (127), even though such a grouping has no obvious basis in similarity of resource use.

Similar groupings have been erected for aquatic consumers. Cummins and coworkers (35, 37, 38) recognized six guilds (functional feeding groups) of freshwater invertebrates based on both food resource and mode of feeding: large particle shredders, small particle collectors, scrapers of algae and other attached organic material, macrophyte piercers, engulfers (predators), and parasites. Like Root, Cummins suggested that mode of feeding corresponds closely to the nature of the resource class. The resource class was defined based on the size of the material and its location (e.g. attached organic matter, deposits of fine or coarse detritus, suspended material). The mode of feeding was defined by the morphological structure of the mouthparts and the behavior of the consumer.

Table 1 Examples of criteria used to define functional groupings in the entomological and ecological literature

Consumers	Criteria ^a	Ref.
Grassland insects	Food habits	50
Model organisms	Energy source	205
Arthropods	Trophic position	75
Herbivorous insects	Exploitation of the same resource in the same way	162
Aquatic invertebrates	Morphobehavioral mechanisms of food acquisition	35
Flies, ants, dragonflies, drosophilids, bark beetles	Taxonomic relationship	41
		119
		128
		175
		30
Forest insects	Trophic level, feeding type, and reproductive rate	65
		33
Marine polychaete worms	Set of relations among food particle size and composition, mechanism involved in food intake, and motility patterns associated with feeding	171
		89
Phytophagous insects	Feeding types	52
Marine benthos	Ways in which [species] exploit their substratum environment and nature of their effects on the substratum	100
Grasshoppers	Coexisting species that use resources in a similar fashion	209
Spiders	Hunting manners	87
Marine herbivorous molluscs	Use of certain aspects of the environment in similar ways	137
Whole communities (40 studies)	Sets of species in a given ecosystem with the property that every pair in the set has some food resource in common	189
Marine benthos	Food source, space utilization, and Baupläne	210
Arthropods in trees	Feeding habits	7
Exopterygote insects	Trophic categories	127
Stream insects	Trophic and functional categories and habitat preferences	191
Mayfly larvae	Gut contents	19
Multispecies assemblages (29 studies)	Preference for a common set of key resources	54
		64
Aquatic insects	Fatty acid composition	70
Protozoa	Type and size of food	2

Table 1 (*Continued*)

Consumers	Criteria ^a	Ref.
Cicadas	Closely related species (usually co-ordinal or confamilial) that are both sympatric and synchronously active and that forage on similar items in similar ways	109
Marine invertebrates	Mobility, size, and taxon	15
Soil arthropods	Principal food source, mode of feeding, reproductive rate, defense against predation, or distribution	126

^aCriteria are listed as closely as possible to that given in the original citations.

Unambiguous classification of species into guilds requires that species fit within some set of morphological or behavioral criteria that define an adaptive syndrome. However, explicit criteria have seldom been used. Species have often been assigned to groups based on either loosely defined criteria or assumptions regarding their feeding biology. Although a few authors clearly acknowledged these problems (e.g. 9, 23, 50, 127, 191), many others did not.

One reason for these assumptions is that the biology of most of these species is poorly known. As a consequence, many authors assumed that species were in the same guilds as taxonomically related species (e.g. 50, 127). These assumptions were often justified by the generalization that genera or families represent major ecological themes and species are minor variations on those themes (e.g. 206; see also functional group assignments in 120). The validity of such generalizations is largely untested, however, and species in at least some genera exhibit pronounced variation in resource use and clearly belong in different guilds (e.g. 64, 70, 156, 191, 197).

Operational placement of species into guilds has often been hampered by pronounced polyphagy and ontogenetic shifts in the diet of species (70, 191). Some studies have placed opportunistic taxa into a separate, generalist guild [e.g. ants (75) and snails (73)]. Species that are moderately opportunistic or that have different diets depending on life stage or sex (e.g. mosquitoes) are more problematic. The individuals of these species are logically members of two or more guilds.

If opportunistic feeding is common, at least two serious implications arise regarding the conceptual and pragmatic utility of the guild framework. First, the idea that the consumptive strategies of different species can be understood in terms of a few adaptive syndromes is compromised. Secondly, operational comparison of community structure becomes problematic because the percentage of the consumptive activity of opportunistic individuals that should be

apportioned to each guild is seldom apparent (e.g. 74). This problem appears especially significant in freshwater systems. So many species of aquatic insects exhibit some degree of omnivory (e.g. 27, 64, 70, 130) that Hutchinson (83) termed them "selective omnivores." Extreme omnivory may not be as significant for terrestrial taxa. Nonetheless, variability in diet within terrestrial taxa can be sufficient to affect interpretations of the guild structure of terrestrial communities (e.g. 191, 204). These problems notwithstanding, the material actually assimilated by consumers may differ sufficiently that taxa can be functionally distinguished from one another (e.g. 61, 67). If invertebrates generally exploit different sets of resources based on biochemical criteria, however, the criterion of similar way of using resources imposes severe practical difficulties for guild classification.

Adams (2) contended that groups of sympatric species were frequently referred to as a guild based on little or no objective evidence. To check the validity of assignments, he applied a technique called psychophysical unfolding to 38 published data sets (17 invertebrate assemblages). This technique determines whether the resource-use preferences of a group of species can be resolved to fit a single resource axis, a criterion Adams believed was necessary for guild membership. Based on his analyses, 28 sets of species appeared to be properly classified as guilds in the sense that species within groups partitioned a single resource dimension. Sets of species that did not fit his criterion included the guilds described by Moran & Southwood (127; see also 191).

Although Adams determined that many species groups were real guilds as defined by his criteria, he skirted the more important issue of what were the proper criteria for defining guilds. To Adams, guild membership depended on the criteria of sympatry and resource partitioning along a single niche axis. To Root (161), Moran & Southwood (127), and others, guilds were groups of species occupying similar functional roles within communities. The disparity between these definitions prompts several questions. Over what spatial scale, if any, should sympatry be a criterion for guild membership? In how many ways should species be functionally similar? Should guilds be defined in terms of a single resource dimension (e.g. food) or multiple dimensions? We believe that lack of consideration of these questions is the basis for significant confusion in the literature.

A Posteriori Descriptions: Are Guilds Natural Ecological Groupings?

If guilds are naturally occurring ecological groups, a posteriori detection of groups of ecologically similar species within assemblages of consumer species should be possible. Over the past 10 years, a few studies have attempted to describe the guild composition of naturally occurring groups of consumers. With multivariate statistics, it is possible to represent the distributions of

species in niche space and look for ecological groupings of species. Inger & Colwell (84) and Pianka (142) used nearest-neighbor analysis of pairwise species overlaps and principal component analysis (PCA) to examine amphibian and reptile assemblages. Others used cluster analysis and PCA to delineate guilds of birds (77, 78, 95) and assemblages of grasshoppers (86, 87) and mayflies (70).

Yodzis (210) used graph theory to determine whether 40 community food webs contained guildlike sets of species, i.e. cliques. He defined a clique as "a set of species with the property that every pair in the set has some food source in common." Cliques are therefore hierarchical in nature, but a dominant clique contains no other cliques and might therefore be regarded as a trophic guild that need not meet the criterion of similar way of using resources. Yodzis found that the number of dominant cliques increased with species richness and that cliques overlapped less than expected by chance, i.e. guildlike groupings of species occurred.

Although these analyses suggest that ecological aggregations of functionally similar species may exist in nature, interpretations are not usually straightforward. The cluster and ordination analyses, for example, implied that species were clumped in niche space. In all cases, however, the structure of these assemblages was clearly hierarchical, and the boundaries suggested by some authors seemed artificial (e.g. 78). Also, some analyses can produce artifacts and thus promote incorrect inferences. Based on an apparent relationship between food web connectance and the point correlation coefficient, for example, McNaughton (118) suggested that species of grass were organized into guilds (*sensu* 142). His conclusions, however, were based on an artifact created by his analysis (68, 99).

Predictability and Stability of Guild Structure

If guilds are the basic building blocks of ecosystems, guild structure should be predictable in both space and time. This idea is conceptually appealing to many ecologists who either explicitly or implicitly accept the view that populations exist in dynamic balance with available resources. To date, however, the collective evidence that communities are so highly organized is equivocal. In this section we review studies that examined (a) whether guild composition is similar in systems with similar resources, (b) whether guild composition shifts predictably with spatially varying resource availability, and (c) whether guild composition shifts temporally.

SPATIAL PATTERNS Moran & Southwood (127) compared the guild composition of arthropod assemblages on trees from Britain and South Africa. Stork (191) conducted a similar analysis of arthropods on trees in Borneo and compared his results with those of Moran & Southwood. These studies

showed that in terms of species richness, the relative composition of the major guilds was similar across sites and species of broad-leaved trees. Guild composition varied considerably between sites, however, both in relative numbers and in biomass of individuals. For example, sap suckers represented 55, 18, and 12% and chewers represented 6, 9, and 14% of total individuals from trees in Britain, South Africa, and Borneo, respectively. Corresponding biomass values were 39 and 13% for sapsuckers and 15 and 32% for chewers from trees in Britain and South Africa. Stork did not report biomass values. Moran & Southwood also found that guild structure varied significantly between broad- and narrow-leaved trees; narrow-leaved trees had proportionately more chewers and sap suckers and fewer predators.

A few data sets have been used to compare convergence in restricted groups of species. Lawton (96) showed that convergence in resource use is not strong among the herbivore species on bracken from England and the southwestern United States. Bracken in Arizona and New Mexico was undersaturated with species. Some parts of bracken in the southwestern sites were never used, and no equivalent species existed. Lawton also observed no evidence for either niche expansion or density compensation in the assemblages he studied. In contrast, Morton & Davidson (129) expected the Australian ant fauna to be more abundant and diverse than the North American fauna because of the absence of competing rodents (cf 17). They found however, that the two faunas were similar in terms of species richness and abundance. Furthermore, the Australian ant fauna did not appear to be in equilibrium with resources. These results imply that similarities in the structure of insect faunas may stem from factors other than the use of a similar resource class and that faunas may differ strongly even when their resources are similar.

A much larger set of comparative studies on guild composition exists for invertebrate consumers in stream ecosystems. This abundance of studies appears to be due to acceptance by many stream ecologists of functional groups (35) as an appropriate means to describe consumer assemblages. In addition, the 1980 publication (199) of a general conceptual model for river ecosystems has prompted worldwide evaluation attempts.

Although many studies of guild structure in stream ecosystems have been published (e.g. 8, 12, 21, 24, 25, 34, 44, 45, 59, 71, 73, 74, 76, 92, 93, 105, 111, 112, 114, 122, 124, 125, 140, 141, 160, 166, 167, 185, 198, 208), their combined results are as equivocal as those for terrestrial systems. Some studies reported positive correlations between guild abundance and resource availability (8, 74, 140). A few reported patterns of guild abundance more or less consistent with presumed patterns of resource availability but did not quantitatively describe relationships between resource abundance and guild abundance (e.g. 12, 34, 44, 167). One study showed that the relative abundance of guilds could shift among sites even though food resources did not

appear to do so (25). Several other studies showed that the relative abundance of different guilds did not vary as expected with respect to either presumed or measured differences in resource availability (45, 73, 111, 114). The strongest trend in these studies was for invertebrate consumers to respond rather similarly as a whole to variation in the resource spectrum. Hunt & Shure (82) also noted similar responses among terrestrial invertebrates.

A common problem in interpreting data from both terrestrial and freshwater studies was that resources were often more ambiguously defined than the presumed guilds (see above). Of the few quantitative studies, most used crude measurements of resource availability. Considering the importance of resource quality to growth and fitness of invertebrates (55, 61, 184), the quantification of resources used in many of these studies may not adequately characterize resource availability. It is therefore impossible to evaluate critically whether the observed differences in the relative abundance of guilds between sites was in fact related to differences in resource availability. It is probably significant that the strongest and most consistent associations between guild and resource abundance were observed when resource availability could be measured with reasonable confidence (e.g. for predators and prey).

Several factors other than food resources could influence guild composition and hence confound comparisons. The character of the foraging substrate (e.g. shape and size) appears to affect proportions of different guilds. For example, Moran & Southwood (127) showed that for tree arthropods the proportion of guilds was associated with shape of leaves. Coyle (32) found that the amount of litter affected the abundances of different spider guilds. Robinson (159) found that the three-dimensional architecture of the habitat also affected the proportion of spider guilds. Proportions of stream invertebrate guilds were found to vary with particle size of the stream bed (12, 185). In contrast, no differences in spider guild proportions could be attributed to the shape of leaf litter (190).

TEMPORAL DYNAMICS If resource availability varies with time, guild structure might shift as resources change. Several authors have addressed seasonal shifts in guild structure, general stability of guild structure, or long-term successional patterns. Georgian & Wallace (54) concluded that the life histories and hence production dynamics of species in a periphyton-grazing guild tracked the seasonal availability of algae in streams. Similar arguments have been given for other groups. Cummins (36, 37) argued, for example, that a tendency for shredders to start growth in autumn evolved in response to the pulsed autumnal inputs of leaf material into streams. Other factors, including seasonal changes in temperature (e.g. 165) and durational stability of habitats (186) may also affect the seasonal dynamics of guilds, however. For example, Rader & Ward (153) suggested that the growth periods and production

dynamics of a guild of "scraper-collectors" was best explained by life history adjustment to physical factors (presumably seasonal flooding); this interpretation was in direct contrast to that of Georgian & Wallace (54). Although the phenologies of some species within some guilds may be tightly coupled to temporal variation in resources, it is unclear how well guilds as a whole track resources. The answer to this question probably depends in part on how narrowly guilds are defined.

Few studies have explored successional shifts in guild composition of invertebrate faunas after disturbance. Some (18–20) showed that for arthropods associated with plants, most groups increased in density with successional stage. On the other hand, the relative abundance of different groups varied with time. Epiphyte grazers increased in relative abundance, while sap suckers declined. These trends appeared to be consistent with changes in resource availability. Minshall et al (123) also observed an apparent trophic reorganization in the invertebrate fauna of a stream after a catastrophic flood. Algal grazers appeared first, followed by detritus collectors and then predators. The appearance of different groups did not seem to track closely the availability of resources, however. Gore (56) observed a similar pattern of differential colonization after construction of a new stream channel, although he did not compare guild abundances to availability of resources.

Successional shifts in the guild composition of more narrowly defined taxocenes have also been noted. Hanski & Koskela (66) observed that dung specialists (coprophages) were the first beetle species to colonize droppings and that more generalist species (saprophages) appeared later. The arrival of saprophages apparently coincided with the appearance of fungal hyphae, a required food source. Parmenter & MacMahon (138) noted a significant difference in the guild structure of the beetle fauna across a successional gradient on reclaimed strip mines. Recently reclaimed plots had fewer herbivores, dung feeders, and predators and more fungivores and insect-carrion feeders than undisturbed plots. Trophic structure also appeared to track changes in resource availability (138).

Results of several other studies imply that functional equilibria may be characteristic of many natural communities. For example, the trophic composition of a grassland insect fauna did not change even though species composition shifted over time (50). Heatwole & Levins (75) also suggested consumer assemblages exist in trophic equilibrium. They reported that the arthropod assemblages on the defaunated mangrove islands studied by Simberloff & Wilson (179, 181, 182, 207) rapidly returned to an equilibrium structure in the proportion of species in different trophic groups.

Wallace et al (202) recently conducted a whole-stream manipulation similar to the mangrove experiments conducted by Simberloff & Wilson. They noted that two years after experimental poisoning, the guild composition of a stream

had returned to predisturbance structure in terms of standing biomass even though strong differences in taxonomic composition persisted. Wallace et al concluded, as Heatwole & Levins (75) had, that functional equilibria had been established even though the original species composition had not. As a whole, these results suggest that invertebrate assemblages are strongly organized around functional roles and that guilds may be the basic building blocks of communities. The validity of these conclusions is clouded, however, by contrary observations in other systems and potential errors in interpretation caused by statistical artifact. For example, Root (162) tested the idea that compensatory shifts in arthropod species on collards would promote the kind of stability reported by Evans & Murdoch (50). He found little evidence that guild structure was more stable than species composition. In general, guild structure varied in concert with the abundances of a few dominant species, a result also observed for disturbed stream systems (71).

Simberloff (178, 180) questioned the conclusions of Heatwole & Levins (75) because the observed equilibrium could be explained as a passive consequence of random colonization from a large species pool. Cole (28) similarly criticized the conclusions of Evans & Murdoch (50). Teraguchi et al (194) also noted that although the trophic structure of insect assemblages of defaunated patches rapidly returned to that found in surrounding old-fields, the observed patterns could have resulted from random colonization. These problems in interpretation may also apply to the conclusions of Wallace et al (202). If colonization is largely a random process, the guild structure of a recovering community may simply reflect the overall guild composition of the surrounding species pool. The recolonization of several streams differentially disturbed by the eruption of Mount St. Helens (71) is consistent with this interpretation of the colonization process. Even though the streams differed in the types and amounts of resources available to consumers, their guild composition was nearly identical five years after disturbance. For these assemblages, overall species composition appeared to vary randomly, and the presence of a few dominant species strongly influenced overall guild structure.

Recently, the analysis of guild composition has also been applied to fossil assemblages. Bambach (7) assigned species from fossil marine faunas (mostly invertebrates) to guilds to examine changes in "ecospace utilization." Based on these data he concluded that the increase in species richness between the Paleozoic and Cenozoic eras resulted from an addition of guilds and that resource partitioning (species packing) within guilds generally remained unchanged. Presumably, community structure was tracking changes in resource availability via radiation of new species into new adaptive syndromes. Unfortunately, the absence of direct data on resource availability prevents critical evaluation of this idea.

Ecosystem Analyses

Ecosystem science has gained prominence because the simulation modeling of ecosystem functions promises a quantitative predictability that is only now becoming common in ecology. Additionally, the creation of a model has heuristic value in the sense that an investigator must develop a blueprint of the system, and this activity reveals voids in knowledge of system components and processes.

A common finding during ecosystem analysis is that one cannot hope to model all of the species individually. Thus, the need to aggregate species into functional units, or guilds, emerges rapidly. Botkin (16) correctly asserted that during the modeling process, aggregating a variety of organisms into biologically based "black boxes" could reduce an ecosystem's bewildering complexity to "mathematically tractable proportions." This aggregation is implicit in ecosystem treatises that do not even mention the term *guild* (e.g. 133). The guild concept provides a convenient, supposedly biological basis for simplifying ecosystem models. Whether guilds have aided in the elucidation of ecosystem processes, however, remains unclear.

That guilds are often based on food resources makes them useful for ecosystem studies because of the universal emphasis on the flow of matter and energy. Even in the theoretical literature, the convenience of a group such as a guild is clear, e.g. in theories related to food web design and nutrient cycling (143), theories on diet selection as an ecosystem process (47), and in the application of ecological theories to insects (116). McNaughton (118), using cybernetic analysis, has even suggested that "organized blocks" of species can act as guilds.

Many examples illustrate the usefulness of a guildlike approach, especially for its heuristic value. Recent reviews of the role of arthropods in below ground detrital food webs have emphasized a functional group approach (172) and have led to the development of simulation models (126). Studies of detritus processing by aquatic macroinvertebrates have similarly used a functional group approach (3, 117, 121), as have analyses of secondary production in aquatic insects (11). Guildlike approaches were used to examine arthropod herbivory in forests (170) and streams (60) by dividing taxa into groups such as folivores, sap-feeders, and grazers and by emphasizing the plant as a heterogeneous resource in space and time (60, 170). Wallwork (203) similarly grouped oribatid mites and emphasized that any one species can participate in several food-based "feeding types" simultaneously (203). Recent studies of trophic interactions have criticized the reliance of the Lindeman model (103) on history of energy flow rather than on an assessment of present resource states; these studies imply the usefulness of guilds but do not require a guild approach per se (31). Despite this wealth of examples of the utility of the guild concept, guild theory does little to elucidate ecosystem

structure and functioning, and most papers have not adequately addressed how to allocate the polyphagous activities of guild members among trophic levels. The utility of the guild concept does not prove that guilds exist in nature or that systems are organized around groups of organisms such as guilds. Given these shortcomings, the uncritical use of the guild concept in the literature of applied ecology is surprising. This adoption has implications for the care with which we transfer ecological information to management-oriented individuals and agencies.

APPLIED ECOLOGY AND THE CONCEPT OF GUILD

As the guild concept caught on, it was so thoroughly embraced that it took the form of a theory or truism. The concept was subsequently suggested as a basis for assessing environmental impacts of anthropogenic disturbances as required by law in the United States (National Environmental Policy Act of 1969) and elsewhere.

Although invertebrates are not the usual objects of these applied studies and recommendations, the political pressure created by proposals to use guilds for management purposes, coupled with the poor understanding of the problems associated with the term's ambiguity, is instructive. In time, similar proposals will be made for the management of beneficial and appreciated invertebrates such as butterflies. The guild or functional group approach is already used for management-related studies by members of United States governmental agencies such as the National Park Service. Also, recent studies of the response of invertebrates to anthropogenic disturbances have used a guild-based approach (32, 73, 110, 136, 138).

The early applied work often attempted to develop fool-proof guild classification schemes. Johnson (88) presented a dichotomous key to ecological characteristics of plants that was to "provide a clear-cut placement of plant species into a specific guild thus eliminating much of the subjectivity of classification." The method, based on growth form, leaf persistence, ability to fix nitrogen, and other quantifiable components, identified 95 guilds. Simultaneously, Severinghaus (173) classified mammalian and avian guilds into 30 and 31 divisions, respectively. Short & Burnham (177) followed with a classification of wildlife guilds that relied strongly on the physical strata and vegetative structure used by vertebrates. They formally applied a variety of statistical analyses to a matrix of species and habitats and produced a system that was supposed to be useful in modeling the relationships between wildlife species and their habitats.

Severinghaus (173) strongly implied that guilds were objectively defined, real assemblages of organisms that interacted as natural units. Landres (94) responded by stating that the guild approach is useful for environmental impact assessments but may not represent a real level of organization in

nature. Additionally, Landres suggested that a theoretical basis for guilds was lacking. About that time, Hairston (62) argued that, at least for the salamanders that he studied, guilds may not exist. In a recent monograph (63), however, he used a guild concept as a major organizing theme. Verner (200) railed at the suggestion that management techniques could be developed using a single indicator species for each guild rather than all guild members. He also appealed for the use of a matrix approach to define guilds, in which the rows and columns consisted of primary feeding and nesting zones. Note that the emphasis in the literature had changed since 1967. Initially guilds were discussed generally for their importance in dynamic processes such as competition. By the 1980s, however, guilds were defined on the basis of a series of habitat-characteristic variables, with the implied assumption that co-occurrence in one of these habitats assured competition. A further change from the original view of guilds occurred when Verner (200) coined the phrase *management guild* to classify a group of species that respond in a similar way to a variety of changes likely to affect their environment. In essence his definition relied on the summed response of the organisms to a change in their habitat, rather than on their role. This approach was challenged (113) because it masked individual species responses.

By 1985, despite the wide variety of usages and inconsistency of approaches in management, DeGraaf et al (40) concluded that the guild concept had become a useful tool for looking at competition, niche separation, and functional relationships within the community. These authors then produced a guild classification for North American birds based on food, feeding substrate, and foraging technique. In a sense this classification was the extreme application of previous methods that were used for subdividing guilds within local taxocenes (95).

Szaro (193) registered serious reservations about the wide variety of characteristics used to define guilds and postulated that guilds based on the analysis of one or two niche dimensions were too simplistic to describe nature. He decried the a priori, investigator-defined nature of guilds recommended for management purposes and urged extreme caution before wholehearted acceptance of the guild concept as a basis for management decisions. Roberts (158), apparently unaware of Szaro's paper, again suggested a matrix approach to guild definition, in which he included layers of vegetation and other features of the environment that are used for feeding and breeding. He admitted that the ease of use of guilds was previously exaggerated but stated that the concept is still worthwhile. Block et al (14) emphasized the use of guild-indicator species in resource management.

This series of papers highlights a problem that plagues the guild concept wherever it is used: Definitions are loose and are inconsistent among investigators (or even among studies by the same investigator), and guilds are seldom analyzed before they are accepted as existing in nature. The guild

concept seems to have developed a life of its own, and its disciples forget that it rests on verbal arguments, not on experimental data.

CONCLUDING REMARKS

Guilds are most useful when they include a variety of interacting taxa. This perspective in ecology has fostered great interest and is consistent with Root's (1961) original intention. For a variety of reasons, however, guilds are still most often studied, we believe inappropriately, within a narrow taxocene. In recent explicit review of guilds and their utility in ecology, Terborgh & Robinson (1995) suggested that the "special value of the concept as applied to ecology is that guilds can be more or less objectively defined independently of the particular species that comprise them." Nonetheless, they later cited examples to show that guild members share the same resources, occur in the same or overlapping microhabitats, and are taxonomically related. They stated that taxonomic relatedness has been assumed "because of limitations of time, methodology, and the expertise of the investigators." This series of statements suggests that the taxocene remains the first constraint on guild membership simply for practical reasons. We believe that such a constraint is biologically inappropriate.

Guilds are most useful when species co-occur in space and time. If they are offset in either dimension, a guild approach may yield heuristic value, but the farther the separation, the less likely it is that species or individuals will influence each other in measurable ways. Thus, we doubt that a fossil and a living species would truly be in the same guild, nor would a red oak, leaf-eating insect species in the Ozarks and one in Virginia.

A caveat is in order. Our approach emphasizes the interaction of guild components. The functional classification approach to the guild concept uses a broader community perspective, in which direct comparison of the components of similar communities in different places or at different times is desirable. Such a perspective does not use or require a detailed analysis of the effect of and participants in a specific interaction.

The crux of Root's (1961) original definition, that guild members use the resource in the same manner, is not always useful. The problem of defining "similar manner" is complex. In spiders, for example, an assemblage of species that all capture prey in shrubs might be divided into separate guilds such as web-builders, stalkers, ambushers, and so on (1, 69, 146), even though they are all generalist predators of the same types of arthropod prey with, in fact, substantially overlapping diets. From another perspective, species with a wide variety of strategies for hunting arthropods may form a single guild specifically because they are all generalist predators, regardless of how they get their prey. For example, Polis & McCormick (1994) defined a guild of scorpions, solpugids, and spiders on desert flats. In fact, a less

parochial community viewpoint might also require the inclusion of lizards, some birds (169), and a variety of insects in a ground-dwelling, generalist, arthropod-eating guild. Regardless of the manner used, these disparate species interact as each obtains the same resource.

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 that specific perspective.

The viewpoint stated above emphasizes that the definition of guilds should be related to the interaction of organisms in nature. 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. Recent use of the guild concept is related to community interactions, especially competition. We reiterate that we do not relate guilds solely to competition, nor do we infer that competition is only an intraguild phenomenon. Clear examples demonstrate interguild competition (e.g., 13, 72, 90, 209) and relationships other than competition, such as mutualism.

The "same resource" should be clearly defined; the resource definition probably depends on the specific ecological questions being addressed, rather than on some natural rule of definition. For example, all 10 arthropods living as phyllophages of beech (*Fagus silvatica*) have been termed a guild (131). This approach groups species that feed on one specific part of one plant species. In contrast, the parasites of insect species have been differentiated by the hosts' life history stage; each stage is said to support a different guild of parasites (43, 149–151). Is a life-cycle stage equivalent to a plant part? Perhaps for some questions it is and for others it is not. In a granivore guild the same part (seed) of several species is involved, and in a grazer guild several parts (leaves, flowers, stems) of numerous species may be the unit resource. Clearly, a single resource ranges from a specific morphological part of one species, to one life history stage, to nearly all parts of several species, depending on the specific question being asked and the particular organisms being studied.

The problems stated above show why *guild* is such an elusive term. The definition of a guild depends on many user-defined parameters that have no absolute guidelines. Even though there have been some recent theoretical excursions into the nature of guilds (2), their properties (175), and their basis as the foundation of communities (63), confusion (perhaps better stated as multiple viewpoints) remains. Ecologists should be mindful of the problems attendant to the use of this concept.

The heuristic value of the general concept of guild continues unabated, however; even general ecology textbooks organize whole sections (46, pp. 326–91) of community discussions around the elusive guild concept. The

value of the concept stems partly from the intuitive appeal of guilds as a classification system based on the attributes of community components. We agree that the concept is useful and will use it ourselves, but we hope to make our assumptions and definitions explicit.

The concept of guild may be a perfect example of a problem that was recently elucidated by Loehle (104):

Proper hypothesis testing is the subject of much debate in ecology. According to studies in cognitive psychology, confirmation bias (a tendency to seek confirming evidence) pervasively influences actual problem solving and hypothesis testing, often interfering with effective testing of alternative hypotheses. On the other hand, these psychological factors play a positive role in the process of theory maturation by helping to protect and nurture a new idea until it is suitable for critical evaluation. As a theory matures it increases in empirical content and its predictions become more distinct. Efficient hypothesis testing is often not possible when theories are in an immature state, as is the case in much of ecology. Problem areas in ecology are examined in light of these considerations, including failure to publish negative results, misuses of mathematical models, confusion resulting from ambiguous terms such as "diversity" and "niche," and biases against new ideas.

The guild concept has been subject to the sins of confirmation bias and theory tenacity. Although its empirical content has increased, we believe that the concept is a useful but artificial construct of the minds of ecologists. The immaturity of the guild hypothesis may be responsible, inevitably, for the lack of adequate testing of this notion.

To us, *guild* still describes all organisms that use the same investigator-defined resource; the usefulness of the concept depends more on the investigator's acuity and care than it does on the organisms and their interactions in nature.

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