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5: Defining and measuring functional aspects of biodiversity

NEO D. MARTINEZ

5.1 Introduction

Concern with biodiversity from genes to ecosystems focuses primarily on what these entities are and where they are located. A more recently emphasized research agenda concerns what these living entities do or what their ‘function’ is (e.g. Grassle et al., 1991; Solbrig, 1991; Younès, 1992). Research in this area is barely a half decade old and there is only a small and immature body of literature that explicitly addresses relationships between biodiversity and function. Furthermore, this literature lacks generally accepted definitions of central and frequently reiterated terms. For example, practically no one defines ‘function’ in the context of biodiversity. Also, only one brave author explicitly defines ‘functional diversity’ (Steele, 1991) and the level of acceptance of this definition is unclear. As Lawton and Brown (1993, p. 261) comment, ‘We lack even a preliminary theoretical framework to guide our observations and experiments in this area and to avoid a morass of special cases.’ A ‘careful reading’ of Schulze and Mooney’s (1993) edited volume of eminently authored papers on biodiversity and ecosystem function ‘makes it clear that in fact we know embarrassingly little’ about this subject (Huennke, 1994).

Despite this lack of clarity, there are several consistent concepts explicitly and implicitly embraced by investigators of relations between function and biodiversity. For example, there is nearly universal acceptance that function has something to do with ecological processes. The first section of this chapter (Section 5.2) elaborates the meaning of ecological and ecosystem function because ‘much confusion arises from our imprecise use of those terms’ (Huennke, 1994). The section continues by developing a preliminary conceptual framework that uses several prominent themes in the literature that explicitly focus on functional aspects of biodiversity. Two aspects in particular are discussed: ecological function addresses the relationships between living entities and ecological processes; and functional diversity addresses the variety of these relationships. After these concepts are distinguished, they are more fully developed by reviewing relevant research.

While several hypotheses are alluded to in the first section, the second section (Section 5.3) more systematically examines a wide range of hypoth-
eses that relate biodiversity and function. The purpose of investigating these relationships is taken to be the generation and testing of such hypotheses. Conceptual difficulties with prominent hypotheses employing redundancy and keystone concepts are identified and ways to ameliorate the difficulties are examined. Further discussion identifies other hypotheses that relate biodiversity to ecological function which have been largely ignored in previous research. The third section (Section 5.4) provides a detailed example of the definition and measurement of certain indices of functional diversity using current food-web research. This example also demonstrates how such measurements are used to test hypotheses such as those that relate diversity and stability. The fourth section (Section 5.5) revisits functional redundancy and replaces the concept with more precise and scientifically useful terms. The conclusion (Section 5.6) considers the future of research in this area and the types of generality that may be achieved by employing more rigorous approaches to functional aspects of biodiversity.

5.2 What is functional about biodiversity?

5.2.1 Defining ‘functional’ within the context of biodiversity

Following Franklin (1988), Noss (1990, p. 357) was one of the earliest authors to explicitly distinguish functional from structural aspects of biodiversity: ‘Structure is the physical organisation or pattern of a system, from habitat complexity as measure within communities to the pattern of patches and other elements at a landscape scale. Function involves ecological and evolutionary processes, including gene flow, disturbance, and nutrient cycling.’ Structure typically refers to an amount or arrangement of substance within a particular space. Function typically refers to how such substances change over time. Biodiversity has been evaluated primarily in terms of criteria (e.g. taxonomic, phylogenetic) that qualify the morphological and genetic structure of organisms and also implicitly, or explicitly, address evolutionary processes (e.g. Chapters 3 & 4). Still, there are many other processes that organisms interact with. Interactions between biodiversity and ecosystem processes such as material and energetic stocks and flows have received the most attention (e.g. Schulze & Mooney, 1993; Naeem et al., 1994). Other processes of interest include ecological stability (MacArthur, 1955; May, 1973; Ehrlich & Ehrlich, 1981; Tilman & Downing, 1994), behaviour (Stone et al., 1994), economic activities (Mikluski, 1994; Solow, 1993), and ecosystem services (Westman, 1977; Ehrlich & Ehrlich, 1981).

After familiarizing ourselves with the multitude of concepts concerning biodiversity or the variability of life from genes to ecosystems, we might hope that qualifying ‘biodiversity’ with ‘functional’ would restrict it to a more tractable concept. However disappointing, the assertion here is that the functional aspects of biodiversity are a broad and vague concept that
needs substantial added specification in order to become scientifically more useful. This vagueness follows from the many uses of ‘function’ in the English language. Webster’s Dictionary (Woof, 1979) ascribes a variety of meanings to function from a person’s occupation to a social gathering, not to mention a mathematical operation. Perhaps the most relevant definition with regard to biodiversity is: ‘the acts or operations expected of a person or thing, referable to anything living, material, or constructed, implies a definite end or purpose that the one in question serves or a particular kind of work it is intended to perform.’ ‘Functional,’ in turn, is defined as ‘used to contribute to the development or maintenance of a larger whole.’

The teleological implications of definitions involving purpose pervade discussions of function in biology and ecology. Several theories considered in this chapter that relate biodiversity to function also hinge on purpose. For example, consider the redundancy hypothesis that many species needlessly perform functions identical to other species in ecological systems. Walker (1992) compares redundant species to passengers in an automobile and juxtaposes the passengers to non-redundant drivers. Lawton and Brown (1993) compare functionally redundant species to words of a sentence that can be deleted without changing the meaning of the sentence. Eliminating the passengers and redundant words does not interfere with the purposeful activity of travelling from point A to point B or communicating an idea. However, other activities, such as a driver talking with someone or a sentence flowing in a particular way, are interfered with. The teleological implications are expressed by the unstated but tacitly accepted hierarchy where one activity (going from point A to point B) is generally considered more important or purposeful than another (talking with someone). An activity lower in this hierarchy is redundant if elimination of the entity engaged in the activity does not interfere with the more important activity, also called its ‘proper function’ (Solbrig, 1992). In an alternative theory to redundancy, Ehrlich and Ehrlich (1981) compare species to rivets in an airplane where each is functionally important. Though loss of a few may not be missed, the loss of many leads to catastrophic failure. Each of these examples employs entities designed by humans for widely accepted purposeful activities or functions. Theories that make use of such anthropocentric analogies are encumbered by scientifically indefensible notions of purpose and proper function.

Teleology has a long and problematic history in biology (Mayr, 1988). In recognition of this, Lawton and Brown (1993) eschew teleological purposes of ecological function and instead assert that ecosystems simply process materials and energy. Following Lawton and Brown, this chapter replaces the notion of purpose with process (an activity by which some effect is obtained). Doing so avoids the distracting discussion of which activities are most important and instead encourages explicit specification of the activity of interest. The replacement of purpose with process retains the intuition that
if something is functional, it must do something. Here, only entities that interact with ecological processes are considered to be functional. Ecological processes include more than just material and energetic or ecosystem processes. Ecological processes also encompass information exchanges represented by gene flows and communication represented by certain bird songs. Wider and more explicit consideration of these and other ecological processes such as mutualism, competition, pollination, and population dynamics broadens the framework for addressing ecological function beyond one that only admits ecosystem processes.

5.2.2 A framework for investigating functional aspects of biodiversity

Perhaps the most useful role of a scientific framework is to facilitate consistent determination of which hypotheses are corroborated or refuted by certain observations. This role is achieved through the definition of terms and development of concepts in a manner that can be widely accepted. Redefining function to imply ecological processes instead of purpose is an important precursor to describing a framework for investigating relationships between biodiversity and ecological function.

Further explication of function might not be necessary if we accept Lawton and Brown's (1993, p. 255) suggestion that "ecological processes" and "ecosystem function" [are] synonymous. However, this synonymy assumes that interest in a process (e.g. primary productivity) is restricted to entities whose function is to engage directly in the process (primary producers). This assumption is warranted in many, but not all, cases. Interest in primary productivity could also be focused on nitrogen-fixing bacteria that are not primary producers but do interact with primary productivity by increasing the supply of nitrogen to primary producers (Vitousek & Hooper, 1993). In other words, there are different ways that living entities affect a process besides engaging in it. These include increasing or decreasing the rate of a process. Such associations and relationships seem well described as interactions with processes. Therefore, a function in this context may be defined as an interaction with a process. This definition allows entities that do not interact with a process to be accurately characterized as non-functional relative to that process. More examples below demonstrate that in order to specify a function, both process and interaction should be described.

Biodiversity interacts with ecological processes in many ways. Perhaps most basically, living entities enable or disable the occurrence of ecological processes. For example, communities with high species diversity may contain pollinators for a certain plant (pollination occurs) whereas the pollinators may be absent in communities with lower species richness (pollination does not occur). One of the more commonly examined ways biodiversity interacts with ecological processes is its influence on the rates of processes. Increasing
some aspect of biodiversity may increase, decrease, or leave unaffected the rate (Naem et al., 1994) or stabilize that rate (Tilman & Downing, 1994). A different measure could focus on the product of a process such as stocks of minerals or nutrients (Vitousek & Hooper, 1993; Tilman & Downing, 1994). For example, the stock of vegetative biomass could be measured instead of primary productivity. An increase in this stock could result from an increase in primary productivity or allochthonous inputs or from a decrease in decomposition. Besides affecting rates, changes in biodiversity can also alter the temporal dynamics and spatial patterns of processes.

This categorization of interactions leads to the following definition of ecological functions: interactions with ecological processes. Ecological processes are those activities that result from interactions among organisms and between organisms and their environment. Frost et al. (1995, p. 229) ‘define ecological function in terms of the effects of a given species on the population growth rates of all species in the community.’ Interactions with processes generalize Frost et al.’s definition to entities other than species and functions other than those that involve population processes. Hypotheses that relate biodiversity to ecological function can be tested by measuring both biodiversity and interactions with processes in the same system. Application of this framework to other examples relating biodiversity to ecological function is discussed below.

A particular aspect of measuring a function is measuring the diversity of the function, i.e. functional diversity. Measurements of relationships between biodiversity and functional diversity require more than measuring a particular interaction with a process (e.g. the magnitude of herbivory, the occurrence of pollination). It also involves distinguishing between different types of interactions with processes. For example, Cornell and Hawkins (1993) describe four functional groups of insect herbivores: well-concealed endophytics (gall formers and stem, flower, fruit, and seed borers); poorly concealed endophytics (casebearers and leaf miners), exophytics (leaf chewers); and mixed exophytics/endophytics. One could also add intracellular herbivores (microbial parasites and diseases) to expand the included taxa to protists and viruses. Each of these groups has a different and somewhat distinct type of herbivorous interaction with the process of primary productivity. Here, functional diversity is defined as the variety of interactions with ecological processes. The number of types of herbivorous interactions within a community is a measure of its functional diversity.

Another important issue involves specification of the scale of interest (Allen & Starr, 1982; O’Neill et al., 1986). Scale is specified by range or extent of phenomena of interest as well as the grain or resolution of the observations within the range. For example, the range of concern with the functional diversity of herbivorous insects may be defined as that between the present and the last ice age. Furthermore, the resolution of interest may be 1000 year intervals. Variations of diversity over a few tens of years and before the last
ice age may not be of interest. Specification of the scale of interest is critical to an understanding of what theories and data may be reasonably employed to address phenomena. Explicit scales of interest are also very useful for clarifying the level of generalization that theories and observations warrant. For example, theories developed within the scale specified above may have little to do with why a small plot of land may have a functionally more diverse set of herbivores this year than were observed last year.

5.2.3 Biodiversity and ecological function

Specification of function in terms of processes and interactions lays a foundation for defining, observing and comparing relationships between biodiversity and ecological function. For example, consider the process of herbivory, the consumption and subsequent respiration of live primary production. Ecological entities can interact with herbivory as do many insects, by engaging in it or, as do many plants, by producing the material consumed. Entities such as parasitoids can also interact with herbivory by consuming herbivores. The role each of these entities plays with respect to herbivory can be defined as one of their functions. The effects of biodiversity on herbivory could be investigated by observing how the species richness of plants, herbivores, and consumers of herbivores vary with rates of herbivory. All else equal, increasing plant species richness may decrease herbivory due to increased heterogeneity of the herbivores’ trophic resources (Gilbert, 1980). Increasing parasitoid species richness may also reduce herbivory by increasing predation pressure on the herbivores (Hawkins et al., 1993). Of these functional groups, perhaps only increasing species richness of herbivores increases the rate of herbivory. The effects of varying diversity within each of these functional groups on herbivory could be compared within a community. Among communities, it would be more convenient to choose only one of these functional groups and compare its diversity with rates of herbivory.

As previous chapters have demonstrated, defining and measuring biodiversity is not a simple matter. A definition of biodiversity that explicitly uses the structure-function dichotomy embraced here is, ‘the spatial and temporal variability of the structure and function of living systems’. We could measure biodiversity in terms of genetic polymorphism or in terms of species diversity that takes into account both the presence and relative abundance of species (Magurran, 1988). As is commonly done, Tilman and Downing (1994) measure plant biodiversity simply in terms of species richness. They measure function in terms of the rate of primary productivity. Only the species that engage in primary productivity were examined and the researchers found a positive correlation between species richness and stability of primary productivity during drought, which led them to accept the rivet hypothesis and reject the redundancy hypothesis. Vitousek and Hooper
Fig. 5.1 Eight possible simple relationships between biodiversity and ecological function (after Vitousek & Hooper, 1993). (a) Describe mostly positive relationships between diversity and function. (b) Describe mostly negative relationship between diversity and function.

(1993) describe several frequently reiterated potential relationships between species richness and ecosystem function (Fig. 5.1a). They define ecosystem function in terms of the stocks of soil organic matter, soil nitrogen, extractable calcium and soil acid saturation and suggest that several studies are consistent with a modified rivet hypothesis (Fig. 5.1, type 2), where increasing species richness asymptotically increases ecosystem function.

Beyond these details of relating biodiversity to ecological function is the more fundamental choice of which processes to focus on. Are biologists interested in material, energetic, or population processes? What about behavioural or genetic processes? Is there any limit to the number of processes that occur in ecological systems? Even if there is such a limit, would the different ways biodiversity can interact with ecological processes result in an infinite amount of different functions of biodiversity? No precise answers to these questions are proposed here. However, a reading of the literature demonstrates that there are very many ecological processes that interact with biodiversity in many different ways. A large set of functions that has received
much attention has been termed ecosystem services (e.g. Westman, 1977; Ehrlich & Ehrlich, 1992), which may be defined as ecological functions that are beneficial to humans. Westman (1977) recommended quantifying many of nature’s services (Table 5.1) represented by ecosystem functions ‘that enable humans to obtain the food, fibre, energy, and other material needs for survival.’ Ehrlich and Ehrlich (1992) related a similar and overlapping set of ecosystem services of biodiversity (Table 5.2).

These comments about the relationship of biodiversity to ecological function focus on function. The problems of measuring biodiversity will not be dwelt upon. There are many measures of biodiversity (e.g. alpha-diversity, beta-diversity) and likewise function (e.g. rate of flows, stability of processes) that do not necessarily correlate with each other. While authors emphasize different measures, none are generally accepted as preferred or better than the others. They are simply different. Without clear and generally accepted preferences, it is unlikely that the disposition of hypotheses (redundancy, rivet, etc.) will be clearly articulated and generally accepted. Instead it appears that their disposition will depend on the processes, interactions and the scales invoked during examination and possibly the system investigated.

The scientific challenge to investigators of biodiversity and ecological function is to discover hypotheses that apply to the broadest range of systems experiencing the widest variety of conditions. The first paragraph in this subsection suggests that the rate of a consumptive process is positively correlated with the diversity of the entities engaged in the process and negatively correlated with the diversity of the entities consumed. Another example is Vitousek and Hooper's (1993) proposal that a type 2 relationship generally applies to interactions between species diversity and biogeochemical functions (Fig. 5.1a). Such discoveries lay the groundwork for delineating general mechanisms that determine relationships between biodiversity and function in all, or at least many, ecological systems. However, even Vitousek and Hooper's unusually well-articulated example does not clarify why stock-based measures are used as opposed to flow-based measures (e.g. Naeem et al.,

<table>
<thead>
<tr>
<th>Table 5.1 List of ‘nature’s services’ provided by ecosystem functioning discussed by Westman (1977).</th>
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<tbody>
<tr>
<td>Sulphate reduction</td>
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<tr>
<td>Carbon dioxide fixation</td>
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<tr>
<td>Oxygen release</td>
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<td>Waterfowl support</td>
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<td>Ground-water storage</td>
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<td>Soil binding</td>
</tr>
<tr>
<td>Water purification</td>
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<tr>
<td>Streamside fertilization</td>
</tr>
</tbody>
</table>

.121
Table 5.2 Ecosystem services discussed by Ehrlich and Ehrlich (1992).

<table>
<thead>
<tr>
<th><strong>Climate and water</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Maintenance of the gaseous composition of the atmosphere</td>
</tr>
<tr>
<td>Climate control</td>
</tr>
<tr>
<td>Maintenance of biotically necessary moisture levels</td>
</tr>
<tr>
<td>Water recycling</td>
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<tr>
<td>Hydrological regulation</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Soils, nutrients, and wastes</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Generation and maintenance of soils</td>
</tr>
<tr>
<td>Conversion of nitrogen, phosphorus, and sulphur into forms usable by higher plants</td>
</tr>
<tr>
<td>Weathering of underlying parent rock</td>
</tr>
<tr>
<td>Holding soils in place</td>
</tr>
<tr>
<td>Disposal of wastes</td>
</tr>
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<table>
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<tr>
<th><strong>Maintaining biogeochemical cycles</strong></th>
</tr>
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<tbody>
<tr>
<td>Carbon</td>
</tr>
<tr>
<td>Nitrogen</td>
</tr>
<tr>
<td>Phosphorus</td>
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<td>Sulphur</td>
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<tr>
<th><strong>Pest control and pollination</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Control of pest and disease that attack crops or domestic animals</td>
</tr>
<tr>
<td>Pollination of 90 different crops in the United States alone</td>
</tr>
</tbody>
</table>

1994). Also, it would seem that there are other biogeochemical functions in the same soils examined that are not consistent with type 2 relationships. More specific description of the processes and interactions referred to as biogeochemical functions would help clarify the generality and testability of their type 2 hypothesis.

5.2.4 Functional diversity, similarity, groups, and guilds

Functional diversity is very closely related to ecological guilds, functional groups, and functional similarity. Steele (1991, p. 470) defines ‘functional diversity’ as ‘the variety of different responses to environmental change’. He explicitly includes biotic change as environmental change, suggesting a high degree of synonymy between ‘responses to environmental change’ and ‘interactions with ecological processes’. If a living entity responds to biotic change, then that change could easily be seen as an ecological process. Processes themselves are changes over time and ecological processes are biotic and abiotic changes. For example, soil nutrient cycles could be described as changes in the stocks and flows of nutrients in the biotic and abiotic components of the soil over time. However, this redefinition is rather clumsy in light of the wide acceptance of nutrient cycles as ecological processes (e.g. Noss, 1990; Lawton & Brown, 1993; Vitousek & Hooper; 1993).
The 'responses to' part of Steele's definition connotes a one-way interaction—the reaction of an entity to a process or environmental change. 'Interactions with', as used here, more explicitly embraces two-way interactions (reciprocal reactions). This appears to more accurately describe relations between living entities and ecological processes. For example, a nitrogen-fixing bacteria may react to an increase in molecular nitrogen by converting more of that nitrogen into nitrate. This not only increases the nitrate available to the bacteria but it also decreases the nitrogen in the environment and thus, the nitrogen available to other organisms. If we accept that interactions include responses and that ecological processes include biotically consequential environmental changes, then the definition advanced here can be seen as including the special case of interactions and processes that Steele describes.

The most problematic aspect of Steele's definition is his explicit exclusion of ecological diversity from the notion of functional diversity. Functional diversity is considered a fourth category of biodiversity distinct from genetic, species, and ecological diversity (Steele, 1991, p. 470). This distinction is not elaborated further and seems difficult to sustain. For example, vegetation dynamics in a landscape is both a change in the biotic environment and an ecological process. There seems to be no major distinction between Steele's biotic and abiotic environmental changes that living entities respond to and the ecological processes invoked by many investigators of functional diversity. Zak et al. (1994) define microbial functional diversity in terms of the utilization of substrates by a bacterial community. Such utilization is perhaps more often thought of as an ecological process than an environmental change. Cowling et al. (1994) measure plant functional diversity in terms of growth forms that 'attempt to categorize species on the basis of known differences in ecophysiological processes' (p. 145). Following these authors, no significant distinction between ecological and functional diversity is claimed here.

Functional diversity can be further clarified by comparing it with functional similarity. This similarity is inherent in the notion of functional groups. That is, identification of a functional group means that its members are functionally similar and also that entities excluded from the group are functionally different. 'Functionally similar' means that entities have similar interactions with the same process(es) (Chapin et al., 1992). The interactions may be specified qualitatively (e.g. consumers that prey on the same species) or quantitatively (e.g. consumers that consume similar amounts of the prey). Functional diversity refers to differences among functional groups. The most widely accepted, albeit tautological, measure of functional diversity may be the number of functional groups in an ecological system. Also, the most widely accepted measure of functional redundancy may be the number of functionally similar entities within a functional group.

Vitousek and Hooper (1993) make a corresponding distinction between
'diversity among functional groups and [diversity] within them.' The diversity of herbivorous interactions represents diversity among functional groups. In a previous example, diversity among functional groups refers to exophytic, well-concealed endophytic, poorly-concealed endophytic and mixed exo-/endophytic herbivores. Systems with more functional diversity have more of these functional groups represented than systems with less functional diversity. Diversity within these groups could be described in terms of the variable types of primary production consumed by organisms or in terms of their taxonomic diversity. An example that employs variability of consumption could distinguish between pollination related exophytic consumers (e.g. hummingbirds, butterflies, etc.) and non-pollination related exophytic consumers (e.g. grasshoppers, aphids, etc.). While this quantitative distinction maintains an emphasis on the function of herbivory, taxonomic distinctions broaden the emphasis to include evolutionary processes. This example brings up two important points. First, functional diversity within functional groups is often based on more finely resolved distinctions among interactions with a process than the distinctions that determined group membership. Second, distinctions within functional groups may, and often are, based on interactions or processes different from those used to group members.

Like Vitousek and Hooper, several other researchers examining biodiversity and function describe 'one approach [they] find particularly useful [that] subdivides the species in an ecosystem into two levels on the basis of function: (1) different functional types (e.g. feeding guilds, plant growth forms) and (2) functionally similar taxa within a functional type' (Solbrig, 1991, p. 38). A description of functional types presents a typological scheme that enables classification of living entities into functional groups. As suggested by the functional groups exemplified above, 'any typological scheme applied to the functional diversity of species will be, to some degree, arbitrary' (Solbrig, 1991, p. 38). It is important to recognize that the number of functional groups is highly contingent upon the processes and interactions chosen. Still, once these choices are made, the number of functional groups can be very useful.

Perhaps the most useful functional typology in ecology has been based on the notion of guilds (Simberloff & Dayan, 1991). Guilds are functional groups of organisms whose members exploit environmental resources in a similar way (Root, 1967). Like functional groups and 'as with the genus in taxonomy, the limits that circumscribe the membership of any guild must be somewhat arbitrary' (Root, 1967, p. 335—quoted in Simberloff & Dayan, 1991). The development of the guild concept over the years provides many lessons for research on functional groups such as the importance of clear definitions and delineations (Simberloff & Dayan, 1991). Simberloff and Dayan (1991, p. 137) explain the preference for the term 'guild' over 'functional group' as almost a haphazard coincidence: "'Functional group" has
evolved almost simultaneously to carry the same connotation, but the metaphor of the "guild" must have seemed more elegant than this term. This blurring of the distinction between guilds and functional groups is largely due to the departure from the original emphasis of guild on exploitation of food resources towards inclusion of other ecological processes (habitat exploitation, taxonomic relatedness, etc.).

Before moving on to the quantification of functional diversity, a few general comments on the entities being measured is warranted. The distinction between structure and function leads to questioning the functional relevance of biogeochemical stocks (Vitousek & Hooper, 1993), body size (Cousins, 1991) and growth forms (Cowling et al., 1994). Strictly speaking, these entities appear to be distinguished on structural criteria such as physical arrangements rather than process-oriented criteria. As is common in biology, structural differences often imply functional differences but such implications are best made explicit if function is the main focus of research. For example, it would be helpful to know whether energetic (Harvey & Godfray, 1987), hydrologic (Le Maitre et al., 1995), or competitive (Simberloff & Boecklen, 1981) processes are being addressed by investigators of body-size and growth-form distributions. Without such specification, the purported functional relevance of more structurally defined (e.g. physical appearance) functional groups is difficult to assess.

5.2.5 Quantifying functional diversity

Functional diversity can be quantified by determining which and how many functional groups are represented in an ecological system. First, a typology of functional groups should be developed based on a variety of interactions with an ecological process. Once this typology is arrived at, representation of a functional group is expressed by the occurrence of interactions with the process that defines the group. Membership of living entities in functional groups is evaluated quantitatively (e.g. quantities of prey consumed) by characterizing the interaction with a process both qualitatively (which prey were consumed) and quantitatively (how much was consumed). Such measurements can be analyzed for the number of functional groups in standard statistical procedures that quantify the similarity and difference between entities according to the qualified and quantified functions. Since a guild is a type of functional group, Simberloff and Dayan's (1991, p. 125) review of quantitative analyses of guild membership applies quite well to assigning functional group membership:

Quantitative methods used for guild assignment include nearest neighbour statistics (Inger & Colwell, 1977; Winemiller & Pianka, 1990), cluster analysis (Crome, 1978; Landres & MacMahon, 1980), principal component analysis (Holmes et al., 1979; Short & Burnham, 1982; Toda, 1984), canonical correlation (Folse, 1981)
and Monte-Carlo techniques (Joern & Lawlor, 1981). 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. Strauss, 1982) can allow tests of
hypotheses such as whether potential guild associates have diets
more similar than would be expected given specified
randomisation’s of the data (e.g. Jaksic & Medel, 1990), 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 (Terborgh & Robinson, 1986).

Such analyses arrive at a delineation and enumeration of functional groups.
The number of functional groups is comparable among systems in as much as
the criteria for measurement are consistent among systems.

Zak et al. (1994) provide a cogent example of measuring functional diversity
and comparing it among systems. They measure functional diversity of
soil bacteria in six plant communities in the Chihuahuan Desert in the
southwestern United States in terms of 128 specific carbon sources used. A
functional portrait of each community is based on the activity of the soil
bacteria allowed to grow on each of the sources. Three communities
(mesquite-playa fringe, herbaceous bajada, black grama grassland) had the
highest functional diversity measured both in terms of the number of carbon
sources utilized and in terms of substrate diversity. The number of sources
utilized is analogous to the species richness measure of a community.
Substrate diversity is analogous to community diversity measured in terms of
both species richness and the evenness of abundance among species. Indeed,
Zak et al. used a classic community diversity index, the Shannon index, to
measure substrate diversity. Substrate diversity takes into account both the
number and evenness of substrates used. It is lower when substrates are used
equitably than when the same number of substrates are used more variably.

Zak et al. (1994) employed all the basic components of the framework
developed here. They identify the process of carbon utilization. The variety of
interactions with the process are identified in terms of the variety of
substrates on which bacteria are active. Functional diversity is quantified in
terms of which different substrates are utilized by the communities. Scale-is
given explicit attention and is-standardized by the consistent soil sampling

As with comparing communities based on measuring biodiversity in terms
of species richness, measuring functional diversity in terms of the number of
functional groups does not completely quantify how different ecological
systems are from one another. In a taxonomic example, consider a system
with three closely related species of grasses. Is this system as diverse as
another three-species system with one grass species, one forb species and one
tree species? In terms of species richness, the answer is yes. However, sometimes it may be desirable to measure biodiversity in a manner that weighs more distantly related species greater than closely related species. Indeed, the title of this volume emphasizes this desire to understand not only the quantities of different living entities, but also how different the entities are from one another. Zak et al. (1994, p. 1104) make this point about functional diversity: 'Measures of substrate richness, evenness and diversity do not provide information about the types of substrate that are utilized by the bacterial community. Two sites could exhibit identical substrate richness, evenness or diversity but still catabolize totally different substrates.'

The same methods for measuring differences among species are directly

![Diagram](image_url)

**Fig. 5.2** Measures of functional diversity of soil bacteria from several plant communities investigated by Zak et al. (1994). The abbreviations correspond to plant communities: F, mesquite-playa fringe; B, herbaceous bajada; G, black grama grassland; C, creosotebush bajada; P, playa grassland; S, Sporobolus grassland. Functional diversity is based on overall substrate utilization using (a) cluster analysis based on presence or absence of activity and (b) principal components analysis based on levels of activity.
applicable to functional groups (Gaston, 1994). Measures of the difference between species are typically based on phylogenetic or evolutionary distance (Cousins, 1991). To measure the difference between functional groups, species’ evolutionary relatedness is simply replaced by functional similarity. Zak et al. (1994) measure functional similarity using cluster and principal component analyses based on Jaccard’s similarity index. These analyses show that the mesquite-playa fringe, herbaceous bajada, and black grama grassland communities are functionally different from one another while the other three communities were found to be functionally similar to each other (Fig. 5.2).

While ecosystem services typically focus on whether or not a function is performed and, if so, to what degree, the diversity of ecosystem service functions has received some recent interest. For example, Solow (1993) describes a measure of functional diversity that is derived from genetic diversity by ‘assuming that genetically similar species tend to share more characteristics, including medicinal ones, than do dissimilar species.’ By associating an economic option value with medical possibilities, Solow transforms a measure of taxonomic diversity into a measure of the functional diversity of ecosystem services.

A more detailed example of quantifying functional diversity is discussed below. First, the purpose of measuring functional aspects of biodiversity is discussed.

### 5.3 Hypothesis specification and testing

While no purpose or goal of biodiversity is assumed here, scientists do have goals which should be explicitly stated since this facilitates evaluation of their accomplishments. One would also hope that goal specification would help in accomplishing goals more efficiently but this is not always the case (Feyerabend, 1993). As is implied throughout this chapter, the purpose of measuring functional aspects of biodiversity is to test hypotheses that relate biodiversity to ecological function. The purpose of a scientific framework is to enable reproducible conclusions as to whether or not certain observations are consistent with explicit hypotheses (e.g. Table 5.3). Hypothesis-driven research agendas have been elaborately embraced in calls to study the relationship between biodiversity and ecological function (Solbrig, 1991; Grassle et al., 1991; Younès, 1992), although these references lack general definitions that would provide a framework to examine the hypotheses. We now turn to general hypotheses that relate biodiversity to ecological function. Then, hypotheses that relate biodiversity to functional diversity are discussed.
5.3.1 Prominent hypotheses relating biodiversity and function

Some of the earliest theories relating biodiversity to ecological function focused on population processes. MacArthur (1955) asserted that populations of species would be more stable in communities with more species because these communities provide a greater variety of trophic resources. Increasing this variety reduces the dependence of species on the population fluctuations of their individual resources. However, this theory is challenged by the assertion that the number of trophic resources per species is independent of the number of species in the community (Pimm, 1982; Cohen & Briand, 1984). May (1973) argued that increasing species diversity could decrease the stability of populations because greater numbers of interactions in large communities increase the likelihood of destabilizing positive feedback loops whereby populations explode to infinity or go extinct. According to May's mathematics, these instabilities could be avoided if more diverse communities did not have more interactions on a per species basis. The assertion that the

Table 5.3 Examples of hypotheses that address functional aspects of biodiversity (from Solbrig, 1991).

<table>
<thead>
<tr>
<th>HYPOTHESIS B.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Keystone' species are essential for maintaining species richness in communities under all environmental conditions</td>
</tr>
</tbody>
</table>

**Alternative Hypothesis B.1a**

The effect of a keystone predator on the species richness of a community is dependent on the abiotic environmental disturbance regime

**Alternative Hypothesis B.1b**

The effect of a keystone resource species on species richness of dependent species is dependent on the temporal variability in total resource availability

**Alternative Hypothesis B.1c**

Keystone species play a more important role in marine than in terrestrial ecosystems and this role is more important in the lower latitudes

<table>
<thead>
<tr>
<th>HYPOTHESIS B.2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both the richness of functional types and species richness of functional analogues within functional types will respond the same way to a change in resource availability</td>
</tr>
</tbody>
</table>

**Alternative Hypothesis B.2a**

The number of different functional types in a community is unaffected by the total resource availability (possibly indexed by the net productivity of the community) or by the number of different types and forms of the resources

**Alternative Hypothesis B.2b**

The number of potentially competing species within a given functional type is unaffected by the total amount of resources available to that functional type

<table>
<thead>
<tr>
<th>HYPOTHESIS B.3</th>
</tr>
</thead>
<tbody>
<tr>
<td>The number of functionally analogous species within functional types has no effect on ecosystem function or stability</td>
</tr>
</tbody>
</table>

continued on p. 130

129
Table 5.3 (continued)

Hypothesis B.4
Local species diversity is determined by local environmental properties and processes, not by the number, dispersal ability, life history adaptations, or reproductive strategies of species in the regional pool. Communities with the same degree of spatial heterogeneity, and the same dynamic equilibrium between the opposing processes of competition and mortality-causing disturbances should exhibit the same level of species diversity.

Alternative Hypothesis B.4a
The representation of the regional pool of species (within a functional type) in assemblages of locally coexisting species of that functional type is unaffected by the local disturbance regime or potential level of productivity.

Alternative Hypothesis B.4b
In local communities, the proportion of a regional species pool that is due to species within a functional type or taxon is independent of the dispersal ability of the organisms involved.

Alternative Hypothesis B.4c
In local communities, taxonomic richness within a specific functional type or higher taxon is independent of the reproductive biology and genetic structure of the taxa.

Hypothesis B.5
Spatial heterogeneity of the regional landscape has no effect on the number of functional types or coexisting species in a local community.

Alternative Hypothesis B.5a
The rate of increase of the species/area curve is independent of the disturbance regime or average productivity of a ‘mosaic’ landscape.

The number of trophic interactions per species was independent of species diversity (Pimm, 1982; Cohen & Briand, 1984) was seen as consistent with May’s stability criteria (May, 1983). However, the assumptions necessary for this result such as linear deterministic population interactions and population equilibria may not be biologically reasonable (Law & Blackford, 1992; Haydon, 1994).

More recent theories relating biodiversity to ecological function have drifted towards anthropocentric analogies exemplified by the rivet and redundancy hypotheses. These hypotheses have the strength of being applicable in principle to any function. However, as discussed previously, the analogies assume that an unstated and relatively narrowly defined function is widely accepted among investigators. The rivet hypothesis is quite similar to MacArthur’s theory that diversity contributes stability to ecological systems, while the redundancy hypothesis is similar to May’s theory. Species richness does not affect stability as long as May’s criteria are adhered to. His theory has also been interpreted as going beyond redundancy by asserting that diversity could be destabilizing and therefore have a negative rather than a neutral relationship to ecological function.

Given that function may refer to any ecological process, there seems to be
no *a priori* restrictions on hypotheses that relate biodiversity to ecological function. We could assume that an increase in biodiversity correlates with an increase in the quantity of ecological function, but exceptions easily come to mind. For example, highly oligotrophic lakes such as Lake Tahoe have hundreds of species of producers (phytoplankton) in each square metre. Still, these systems produce much less net primary production than a monocultural sugar cane field. We could guess that, due to the great variety of life, more biotic diversity leads to more functional diversity (e.g. Cody, 1991), but this is not necessarily the case. Cowling *et al.* (1994) found that arid and semi-arid sites in southern Africa relatively rich in species had less functional diversity in terms of 21 above-ground growth forms. However, this result could be criticized by asserting that the growth forms represent structural diversity instead of functional diversity.

The rivet and redundancy hypotheses previously described have received much attention in the literature. Another frequently considered hypothesis concerns the functional importance of ‘keystone species’ that by definition are not redundant (Chapin *et al.*, 1992): ‘A keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance’ (Power & Mills, 1995). It is these taxa to which policy makers and scientists are asked to pay particular attention because their presence is relatively inconspicuous compared to the effects of their extirpation. Keystone species are often described as strong interactors as compared to weakly interacting redundant species. The litmus test for a keystone species is to experimentally remove its population from an enclosed ecological system and observe the effects (Paine, 1980). If unexpectedly large changes in abundance or composition of the community ensue, the species is considered a strong interactor and therefore a keystone. If the removal does not result in such changes, it is a weak interactor and may be considered redundant. The number of strongly interacting populations in a community is thought to be small compared to the large number of weakly interacting populations (Paine, 1992).

Since keystone species or strong interactors (‘drivers’ in Walker’s (1992) automobile analogy) are many fewer than the weak interactors (‘passengers’), diversity *per se* may not be critical to ecological function (Paine, 1992). Instead, a small number of strong interactors is all that is needed. In this context, ecological function is closely related to stability and typically refers to the maintenance of species composition and relative abundance within a community. However, similar to the teleological aspects of the rivet and redundancy hypotheses, the keystone hypothesis suffers from unstated and inaccurate assumptions (Mills *et al.*, 1993). Perhaps most basically, the keystone species designation applies to populations, not whole species. It is a population that is removed from an enclosure, not the larger group of organisms asserted by Power and Mill’s definition and implied by ‘species removal’ experiments. This leads to confusion, such as whether the classic
keystone seastar *Pisaster ochraceus* (Paine, 1980) is a keystone in all the intertidal systems in which it is found (Foster, 1991). This difficulty may be avoided by explicit acknowledgment and critical evaluation of the disparity between the scales at which experiments are conducted and the scales at which the results are presumed valid.

Another difficult aspect of the keystone hypothesis is the clause, ‘much larger than would be expected from its abundance.’ What one expects from abundance depends on how abundance is measured. Since abundance, both in terms of population numbers and in terms of biomass, is used for the keystone designation, there is considerable flexibility in one’s expectations. Consider a removal of Douglas fir *Pseudotsuga menziesii* trees from a forest monoculture that leads to large changes in the forest community. Based on the large abundance of fir biomass, such large changes would be expected. However, based on the small number of trees in comparison with orders of magnitude more microbes and insects, the large community changes could be unexpected which would lead the fir to be considered a keystone. This flexibility combined with the extremely subjective and therefore problematic notion of human expectation casts serious doubts as to the utility of the keystone concept.

Other uncertainties have prompted abandonment of the keystone/weak-interactor dichotomy in favour of more formally measuring the interaction strength of the group of organisms in question (Mills *et al*., 1993). As with explicit measurements of function, measurements of interaction-strength eliminate many uncertainties. For example, interaction-strength measurements do not include the problematic judgement of whether the strength is disproportionate to expectations.

### 5.3.2 Less prominent hypotheses relating biodiversity and function

Chapin *et al*. (1992) and Lawton and Brown (1993), among many others, consider the rivet and redundancy hypotheses to be extremes of a continuum. Still, there are other hypotheses that do not lie within these extremes. One may be called the uniqueness hypothesis, which asserts that whenever a species is lost, a particular function of an ecological system is largely eliminated (Fig. 5.1a, type 4). In other words, a function can be found for practically every species which leads to its designation as a keystone species. For example, Daily *et al*. (1993) observed that a single species of woodpecker provides the only habitat available for several other species in an ecological system in the Rocky Mountains. If this warbler is extirpated, all of this ecological engineering function (Jones *et al*., 1994) would apparently be lost. Beaver (*Castor canadensis*) are similar in that their elimination leads to the local extinction of many other species (Pollock *et al*., 1995). While these may be considered merely examples of relatively uncommon keystone species, it has been claimed that each species of herbivorous insect has several
parasitoid species that specialize and therefore critically depend on it (Price, 1977). It is also plausible that all species have host-specific endosymbiotic or exosymbiotic viral, microbial and metazoan endemics whose survival depends on the host.

The redundancy, rivet, and uniqueness hypotheses appear to cover a comprehensive range of simple hypotheses that assert positive relationships between ecological processes and biodiversity. A different set of hypotheses that have not received as much attention assert negative relationships between ecological processes and biodiversity (Fig. 5.1b). One such hypothesis may be called the inverse rivet hypothesis (Fig. 5.1b, type 5). Consider the hydrologic processes in a catchment basin and how vegetation may affect the yield of water emerging from the catchment. Le Maitre et al. (1995) show that invasions of alien wooden plants into a catchment reduces the water yield from that catchment. The invasions increase the species richness of a system and decrease an ecosystem service function. As invasions progress, water yield progressively decreases.

In other cases, the negative effects of biodiversity on ecological function may be more immediate, leading to an almost complete loss of ecological function with a slight increase of biodiversity from an already very low value (Fig. 5.1b, type 8). This may be most obvious in hydroponic plant growing systems where additional species are often pathogens whose presence reduces or eliminates plant growth. Other examples include crop systems whose low diversity must be maintained by insecticides, fungicides, herbicides, cultivation, and other methods to prevent consumer and competitor species from establishing and reducing the growth of crop species available for harvest. This example may follow the type 5 or type 6 relationship in Fig. 5.1b.

Perhaps the most heretical hypothesis to consider is that an ecological function could be maintained at a high level during the progressive decrease and ultimate elimination of species diversity (Fig. 5.1b, type 7). An example could be the amount of water that filtrates down to the water table below a sand dune ecosystem. Le Maitre et al. (1995) show that species diversity interacts with hydrological processes. It is plausible that plants on a sand dune filter particulates and pollutants out of precipitation that percolates down to a water table. However, as the diversity and the biomass of species decrease, the sand below the biota may begin performing the filtration function, resulting in a negligible change in filtration despite the eventual elimination of the biota. In other words, the sand may be functionally equivalent to the biota in narrow terms of water-filtration; and the filtration capacity of the biota-sand system may be well above that necessary for maintaining a certain water quality in the water table.

Each of these eight hypotheses (Fig. 5.1, types 1–8) address the relationship of ecological function to taxonomic or species diversity within functional groups, whether it be in terms of positive, neutral, or negative interactions with ecological processes. The framework has been useful in developing
hypotheses not yet seriously considered in the literature. However, it should be apparent from the previous hypotheses and examples that biodiversity may have all or perhaps none of the hypothesized relationships to ecological function, depending on which processes, interactions, and measures of biodiversity are emphasized.

5.3.3 General notes on hypotheses relating biodiversity to ecological function

In the search for general relationships between biodiversity and ecological function, it should be recognized that almost any function can be specified in an inverse form. For example, rather than maintaining a habitat hospitable to a particular species, an ecological function could be defined as maintaining a habitat inhospitable to it (or hospitable to its consumers and competitors). Merely repurposing the function like this may reverse which hypotheses are rejected or corroborated. For example, Vitousek and Hooper (1993) consider the relation between species richness and biogeochemical functions. They fit a type 2 response (Fig. 5.1a) to function in terms of percent soil organic matter. A type 6 response (Fig. 5.1b) would logically fit the same data if function was evaluated in terms of percent inorganic matter. This is why the framework developed here is based on a priori identification of function in order to reproducibly evaluate specific hypotheses.

A hypothetical alternative to a priori identification of a function of interest is the a priori identification of a species of interest. In this case, one or many species may be identified and the functional effects of their addition or loss to the system can be investigated. Still, the practically infinite number of functions cannot all be investigated. Therefore, even this purported alternative demands a priori identification of functions to be observed.

Another difficulty with these general hypotheses is that species are not all the same and no consistent ranking of species along an X-axis of Fig. 5.1 is apparent. Species have different effects which could greatly affect which hypotheses are corroborated or rejected (Hughes & Noss, 1992). For example, whether an asymptote is reached or not may depend on the order of species along the species-richness axis in Fig. 5.1. If species that are almost entirely responsible for a function are on the right side of the species-richness axis, an asymptote may not be apparent. An asymptote would be apparent if those same species were arranged on the left side of the species-richness axis. This difficulty can be somewhat ameliorated by establishing a generally acceptable convention for arranging species along the X-axis. Hypotheses concerning aspects of function not easily described by the Y-axes in Fig. 5.1 (e.g. temporal dynamics) and other measures of biodiversity (e.g. landscape diversity) also deserve consideration.
manner. However, it is important to realize that this class of problems has already been addressed by evolutionary biologists in debates about species concepts.

Mishler and Brandon (1987) describe such problems as an issue of specifying grouping and ranking criteria: ‘All species concepts must have two components: one to provide criteria for placing organisms together into a taxon (“grouping”) and another to decide the cut-off point at which the taxon is designated a species (“ranking”)’ (p. 404). These two components apply to functional groups as well as taxonomic species. The grouping criterion for trophic species is the similarity in a taxon’s sets of trophic consumers and resources. The ranking criterion is complete similarity. If a group of organisms has a single different consumer or resource different from that of another group, these groups belong to different trophic species. The challenge for distinguishing ontogenetic trophic species is to develop ranking criteria that allow consistent determination of ontogenetic classes among taxa as diverse as microbes, fungi, plants and animals.

To measure functional diversity, the framework is specifically applied to the function of interest at a particular scale which specifies the extent and resolution of observations. Let us choose a lake volume over a year as the spatial and temporal bounds of our system of interest. Furthermore, we will target trophic species as aggregates of taxonomic species and trophic interactions as either present or absent at the desired level of resolution. As an example we will address Little Rock Lake, Wisconsin (Martinez, 1991).

In the interest of scientific advancement, one of the initial considerations is whether there are any specific hypotheses regarding food webs that may be tested by observing the trophic structure in Little Rock Lake. Pimm et al. (1991) specify a suite of patterns that apply to food web structure that may be tested. The only hypothesis we consider here, has been called the ‘link-species scaling law’ that asserts that the number of trophic links in a food web is roughly twice the number of trophic species (Cohen & Briand, 1984; Cohen et al., 1990). Another initial step is identification of which taxa participate in trophic interactions. Virtually all taxa participate in trophic interactions, so the first measurement may include an all-taxa survey of the organisms within the lake. An initial, albeit limited, survey documented 182 taxa in Little Rock Lake (Martinez, 1991).

5.4.2 Conducting the measurement

Ideal documentation of the food web would include testing the hypothesis that each taxon consumes each other taxon against the hypothesis that no such trophic interaction occurs. This would involve over 33000 (182^2) tests. However, basic knowledge of natural history can greatly reduce this number. For example, since 60 of the taxa are algae, phytoplankton, or otherwise producer taxa that are apparently physiologically unable to trophically
consume other taxa, we can eliminate the 10920 (60 multiplied by 182) hypotheses that these producers consume any of the taxa within the web. Further specification of basic natural history, such as which taxa are known solely to consume primary producers or secondary producers, further reduces the hypotheses in need of further investigation. Several ecologists who were studying the organisms in Little Rock Lake were asked to provide their educated guesses as to the trophic interactions involving the organisms of their speciality that were likely to occur over a typical year. This resulted in roughly 2500 links being designated. These links were checked against available data such as gut contents of fishes and also cross-checked with available literature and other specialists studying identical taxa in other ecological systems.

Contrary to the discussion in the previous section [5.4.1], five of the 182 taxa are ontogenetically immature stages of fishes and three more of the taxa are immature zooplankton. This represents a classic bias of ecologists toward more highly resolving vertebrates, which make up only six Linnean species, compared to the invertebrates that constitute over one hundred Linnean species in Little Rock Lake. Such bias in taxonomic resolution should be avoided. Fortunately, the ontogenetic species are a small fraction of all the species in the Little Rock Lake web and should not interfere with the heuristic purposes for which the web is used here.

Aggregation of the 182 taxa results in 93 distinct trophic species. The trophic species web has 1036 links. Both of these quantities measure among group functional diversity of the web. That is, there are 93 different functional groups of taxa in the web as well as 1036 functional groups of trophic links among these groups. An increasingly popular way of comparing the functional diversity of webs with different numbers of species is dividing the number of links by the square of species richness to calculate a measure of ecological complexity called directed connectance (the fraction of all possible trophic links including cannibalism and mutual predation that are realized; Martinez, 1991; Warren, 1994). Directed connectance equals 0.12 in the 93 trophic species web.

Besides these among-group measures of functional diversity, we can also calculate within-group functional diversity given the functional portrait that is a food web. For example, we can define new functional groups called specialists and generalists. Generalists are trophic species that consume a higher than average fraction of species. This average is equal to directed connectance or 0.12 in Little Rock Lake. Within the specialist group, there are 64 trophic species that consume less than 0.12 of the species in the web, while the remaining 29 trophic species consume more than 0.12 of the species. Another such measure calculates the fraction of trophic species within functional groups at basal, intermediate and top trophic positions (Briand & Cohen, 1984). The basal group includes species with consumers but no resource species (e.g. many plant species). The intermediate group includes
species that have consumers and also consume. Top species consume but have no consumers. The variation of these measures with overall species richness is actively debated (e.g. Martinez, 1994). In Little Rock Lake, 13% of the trophic species are basal, 86% are intermediate and only 1% are top. Interestingly, the variation of these fractions with the number of trophic species addresses the relationship between within- and among-functional group diversity.

Besides these sorts of within-group measures based primarily on trophic processes, one can also expand the measures to invoke evolutionary processes by examining taxonomic diversity within functional groups. The most taxonomically diverse trophic species are among phytoplankton whose taxa are largely lumped according to size class and taxonomic lineage (e.g. large diatoms). These groups are highly diverse because they appear to consume no other organisms and therefore, unlike intermediate and top species, basal species cannot be distinguished by differences among their organismal trophic resources. Also, because these organisms are small, there is little information about their consumers other than consumers who engulf their resources. There may be a rich group of highly specialized bacterial consumers of phytoplankton that could be used to distinguish the trophic roles of phytoplankton. However, such bacteria were not investigated and there is little, if any, locally based information that can inform this issue. Certainly, the hypothesis that phytoplankton within a trophic species have identical sets of trophic interactions would be important to test if the functional diversity of phytoplankton was an issue of special interest.

At a different level, one could also measure the within-functional group diversity by counting among the 182 taxa to discover how many are within top, intermediate and basal functional groups. The count is 1, 121, and 60 richness. Variation of the number of taxa in these groups with species diversity is also actively debated (e.g. Havens, 1992; Martinez, 1993a; Murtaugh, 1994). This variation addresses the relationship between within-functional group diversity in terms of number of taxa in functional groups and biodiversity in terms of species richness.

Again, this sort of descriptive reorganization of functional data such as a food web, could go on forever. We could look for the most trophically unique taxa (e.g. those who share the fewest predators or prey with all other taxa). We could examine vulnerability (the fraction of species that consume each taxa or trophic species) in the same way as we examined generality. Such explorations can be very useful for hypothesis generation. However, we now turn to the previously discussed hypotheses that could be tested by measuring the functional diversity of Little Rock Lake.

5.4.3 Testing hypotheses with the measurements

Among the objectives for measuring functional diversity was the testing of
the link-species scaling law that predicts that the number of trophic links in a food web is roughly twice the number of trophic species (Cohen & Briand, 1984). Analysis of the Little Rock Lake food web demonstrated that there are over 1000 trophic links among the 93 trophic species. This is highly inconsistent with the link-species scaling law that estimates less than 200 links for this web. This discrepancy suggests that the ‘law’ should be rejected as inapplicable to Little Rock Lake.

One possible reason for the discrepancy is that the number of links in Little Rock Lake are highly over-estimated due to the inclusion of extremely rare links that are typically excluded from the webs that the law was based on. This possibility was examined by reducing the detail or resolution of the web to be more similar to less speciose and less resolved webs. These sensitivity analyses were conducted via a hierarchical cluster analysis that varied the ranking criterion from complete similarity to progressively less similarity (Martinez, 1991, 1993b). The analysis progressively aggregates the most trophically similar taxa in order to represent the web with progressively fewer species (Fig. 5.3). Once the web was aggregated to include 30 or less ‘trophospecies,’ webs began to look much more like that which would be estimated by the link-species scaling law which was based on webs with 30 or fewer species (Cohen & Briand, 1984) even though all original links were included in the aggregated webs. This consistency suggests that no overestimation is necessary to observe the large number of links in Little Rock

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**Fig. 5.3** Number of trophospecies or clusters of taxa as a function of the minimum trophic similarity among taxa within clusters, based on an analysis of the food web of Little Rock Lake, Wisconsin. As less trophic overlap is required for taxa to be within a cluster, fewer clusters or trophospecies are present in the web. Dashed line represents a hypothetical result discussed in the text. Trophically equivalent taxa are aggregated into trophic species in the vertical portion of the curve at the 1.0 similarity coefficient. From Martinez (1991).
Lake. If the links were over-estimated in the original web, the more aggregated webs should also have relatively many links.

This aggregation addresses the arbitrariness of functional group delineation. The decision to base trophic species on complete similarity of trophic consumers and resources is an arbitrary but pragmatic and easily applicable criterion. One clear result of this application is the immediate reduction of the number of 182 taxonomic species to 93 trophic species. Changing the ranking criterion from 100% to, for example, 90% similarity reduces the 93 trophic species to fewer numbers of trophospecies (Fig. 5.3). As Simberloff and Dayan’s (1991) discussion of guilds argues, choosing 100% instead of 90% is an arbitrary decision in the definition of trophic species as functional groups.

It is interesting to imagine what less arbitrary functional groups might look like in Fig. 5.3. For example, imagine that there were 20 relatively distinct functional groups of taxa in Little Rock Lake and that each taxon shares 80% of its trophic consumers and resources with other taxa in its group. Also imagine that the taxon within each group shares less than 10% of their consumers and resources with taxa in the other functional groups. While there could still be 93 trophic species at 100% similarity, there would be a steep drop to 20 trophospecies at 80% similarity (see dashed line, Fig. 5.3). There would be no decline to fewer trophospecies until at least 10% similarity. That no such step functions at lower than 100% similarity was observed and suggests that no such relatively distinct and less arbitrary functional groups are present in Little Rock Lake.

A hypothesis that rectifies the discrepancy between the numbers of links in small webs and that of Little Rock Lake is the constant connectance hypothesis that links increase as the square of the number of species (Warren, 1990; Martinez, 1992). This hypothesis is consistent with both the Little Rock Lake web and the much less speiose webs (Martinez, 1992). Many recent data have corroborated the predictions resulting from this hypothesis (Martinez, 1993a, 1995; Warren, 1994).

An important scientific component of testing hypotheses is bringing the results of the test back to bear on theory that originally motivated the test in a way that leads to new hypotheses. The rejection of the link-species scaling law in favour of constant connectance affects the key variables employed in the stability–diversity debate that relates population processes to biodiversity. Loosely translated, May’s (1973) stability criterion holds that the product of average interaction strength ($i$) and square root of species richness ($S$) multiplied by connectance ($C$) must stay below one ($i(SC)^{1/2} < 1$) for the population processes of a multi-species system to be stable. Assuming constant $i$ with increasing $S$ means that $C$ must decrease to maintain stability if this criterion constrains food-web structure. Maintaining a constant ratio of trophic links ($L$) to species ($L/S$) maintains this stability because $C$ equals $L/S^2$ which means that $SC$ equals $L/S$. In other words, as long as $i$ and $L/S$ are constant, stability is maintained and $C$ varies inversely with $S$. However, the constant $C$ hypothe-
thesis suggests that $i$ should decrease with increasing $S$ to maintain stability (Warren, 1994; Martinez, 1995). This new hypothesis can be studied by conducting interaction strength experiments among communities with variable species diversity. Such experiments could empirically illuminate whether $i$ varies with $S$ in the manner suggested by the constant $C$ hypothesis. These experiments would also be an exciting contribution to the study of the relation between ecological function and biodiversity.

This food web example demonstrates the utility of measuring functional aspects of biodiversity within a framework that tests hypotheses that relate biodiversity, ecological function and functional diversity. The rejection of earlier hypotheses, their replacement with more empirically consistent and successfully predictive alternatives, along with the generation of new testable hypotheses, represents basic scientific progress.

### 5.5 Functional redundancy revisited and replaced

Walker's (1992) automobile passengers and Lawton and Brown's (1993) unnecessary words in a sentence are quite consistent with Webster's (Woolf, 1979) definition of redundancy as superfluous or needless repetition. It is, again, the teleological and subjective notions of superfluousness and needlessness that degrade the scientific utility of redundancy. Taxa within a trophic species are functionally similar or repetitive because they interact with the same process in a similar manner. These taxa may even be called trophically equivalent (Cohen, 1989) because there are no topologically apparent differences among them. Is such similarity, repetition or equivalence (along with people's blood cells and second kidneys) superfluous or unnecessary?

'Redundancy', 'superfluous', and 'needless' are value-laden terms that have pejorative and anthropocentric connotations that seem out of place in a science that purports to be an objective activity. An economic organization would be widely presumed to be flawed if it retained many redundant workers. It seems revealing that, whereas the dichotomy between structure and function has been useful throughout biology, ecologists alone are drawn towards characterizing functional similarity, repetition or equivalence as redundancy. For example, even though red blood cells in a human may be functionally repetitive and equivalent to the point of no measurable functional response to removal of several cells, 'redundant' is rarely if ever used to describe red blood cells. Why should ecologists much more readily consider redundancy in an analogous situation with species? At a time when conserving biodiversity and other social activities (e.g. politics, economics) appear in conflict, scientists should be wary of advancing terms that serve particular ends that irreversibly disturb and destroy the objects of their study. The finding that many species are functionally redundant would seem to contribute a scientific patina to efforts to weaken conservation efforts. Therefore redundancy warrants heightened scrutiny.
While the motivation behind the term 'functional redundancy' can be questioned, the scientific utility of the term should be decided on whether it accurately describes the current scientific understanding of living entities' functions in ecological systems. Consider the type 3 and 7 responses in Fig. 5.1 that are purported examples of functional redundancy. There are at least two distinct situations that lead to these responses, neither of which are accurately described as redundancy. The first is that the species removed or added are simply non-functional. They do not interact with the process measured. Such species do not repeat the function and therefore cannot be redundant. For example, a species of grasshopper could be excluded from a pollination experiment that results in no change in pollination rates. The grasshopper is not redundant if it does not interact with pollination even though type 3 or 7 responses would be observed. The second is a situation that Frost et al. (1995, p. 224) describe as functional complementarity, which occurs when 'processes are maintained at constant levels despite stresses that induce shifts in the [entities] driving those processes.' Here, we have bonafide repetition by functionally similar and compensatory (Frost et al., 1995) entities, but the classification of 'superfluous', 'needless' and hence, 'redundance' appears to be a scientifically illegitimate determination.

Functionally inconsequential repetition seems to retrieve the most scientifically defensible connotations of functional redundancy and would accurately describe a situation where addition or removal of the repetitive entity has no functional effect. In order to defend the assertion of functional inconsequence, a scientist must be able to assert that all the functions of the redundant entity have been accounted for. This appears to be a theoretical and practical impossibility. The most a scientist can defend is a description of a specified set of functions and an investigation of observable differences among the manners in which entities interact with the processes responsible for the specified functions over the scales investigated. Not only are all processes impossible to investigate, but it is impossible to investigate any one process at every scale. Given these limitations, functionally inconsequential repetition can only be demonstrated for certain functions over certain scales. However, such highly qualified inconsequence appears more accurately described by functional similarity left unqualified.

Functional redundancy and inconsequence implies great certainty regarding the future of ecological systems. Billions of years ago, a single mutation in a single organism may have been largely responsible for the conversion of Earth's reducing atmosphere to an oxidizing atmosphere which resulted in the vast majority of species going extinct. Scientists do not appear to have any certainty that similar mutation or recombination of genetic material will not result in another global calamity or prevention thereof. Describing a living entity as redundant or inconsequential claims that that entity has no such potential. This claim, however likely to be correct, appears to be beyond scientists' ability to determine with absolute certainty. Hobbs
and Mooney (1995) more specifically make this point about vegetation dynamics:

Clearly, changing conditions or particular episodic events can lead to hitherto relatively unimportant species suddenly becoming very important. This applies equally to minor native components of the vegetation and to non-native species which have previously been present only at low abundances. Such results suggest that care has to be taken when the issue of ecological redundancy is raised (Solbrig, 1991; Walker, 1992). The change in *Microseris douglasii* from a minor component representing 1–2% of the vegetation cover at the start of the study to a dominant with over 70% cover at the end (11 year) illustrates that redundancy depends on the time scale involved.

Another scale-related difficulty with redundancy and inconsequential repetition can be illustrated using an extreme example concerning leaves on a tree. Removing one leaf may be compensated by the tree growing more leaf area that eventually replaces all known and perhaps all unknown functions of the removed leaf. Still, during the time when the leaf area was reduced, the photosynthetically active area of the tree is reduced along with particulate adsorbing capacity and all other functions associated with the lost leaf surface area. This demonstrates that even loss of a leaf of a tree is not functionally inconsequential. Loss of the leaf results in loss of function even though the loss may be small in effect and consequence. Indeed, leaves of trees are functionally similar in many ways but even in this extreme case, redundant and inconsequential appear to be inaccurate characterizations of the biophysical situation. Investigators could come up with even more extreme cases such as a single bacterium in a soil system but this does not escape the assertion that the loss of any living entity results in the loss of some amount of function, however small in scale.

These arguments demonstrate that functional redundancy has anthropo-centric and pejorative connotations, that it implies an ability of ecologists to see into the future with absolute certainty, and that it misrepresents scientists’ understanding of living entities’ interactions with ecological processes. Furthermore, it appears that other terms such as functional similarity, equivalence and compensation do not suffer from these problems and more accurately describe what scientists can defend in terms of living entities’ known interactions with ecological processes. For example, type 3 and 7 responses are more accurately described as functional inconsequence than as functional redundancy. Trochically equivalent taxa within trophic-species may be called functionally inconsequential because the taxa represent topologically inconsequential repetition. It is inaccurate to call such taxa functionally repetitive and inconsequential repetition without qualifications such as, ‘with respect to binary trophic interactions and the topology of trophic-species webs observed over a certain spatial and temporal scale.’
Without such qualifications, such taxa are accurately described as functionally similar.

5.6 Conclusion: prospects for general theory relating biodiversity to function

Research on functional aspects of biodiversity runs the risk of losing its scientific utility by becoming so variably defined that determination of whether hypotheses are accepted or rejected will depend more on whimsical semantic interpretations than on reproducible determinations of whether or not certain observations are consistent with hypothesized predictions. Such a loss would limit both scientific achievement and the ability of society to rationally assess the consequences of the rapid and widespread loss of biodiversity at all scales. In contrast, the development of a successfully predictive and general theoretical core that relates biodiversity to function could do much to enhance scientific achievement and increase human society's abilities to rationally address our current biodiversity crisis. This chapter aims to accomplish this more positive end by embracing more precise, accurate and explicit terminology and avoiding teleologic, anthropocentric, and politically-charged terms used to relate biodiversity to function.

The framework developed in this review leads to the suggestion that ecologists do 'more of the same' regarding function and biodiversity, and continue to specify their consideration of function by more rigorously articulating and restricting the processes that they consider. The focus on ecosystem functions restricts consideration to energetic and material processes that are somewhat separate from population and evolutionary processes. Still, as the discussion of Vitousek and Hooper's (1993) work demonstrates, such restriction needs to be more extreme and precise in order to articulate reproducibly testable theory. Instead of specifying biogeochemical processes, it may be more useful to specify 'the consumption of live primary producers by metazoan primary consumers.' Even leaving out 'live' from this phrase which describes the process of interest could result in confusing herbivory with decomposition. Leaving out 'metazoan' could confuse herbivory with pathogenic consumption by disease organisms such as bacteria and viruses.

Such extreme restriction may be thought to limit the generality of hypotheses in a scientifically counter-productive manner. However, a framework based on more precisely defined processes and interactions provides a means to organize research beyond the current 'morass of special cases' (Lawton & Brown, 1993). Instead of a 'morass' of research specialized upon each ecological function, research on many different functions can be usefully integrated if the functions represent different interactions with the same processes. Such integrated research could lead to a scientific understanding of the relations between biodiversity and particular processes. Such understanding would be demonstrated by successfully predictive hypotheses that (Peters,
1991) relate biodiversity and a particular process. After this understanding is achieved for several processes such as primary productivity and nitrogen cycling, similarities in the relation between biodiversity and both processes could be discovered. Further work may achieve greater generality by illuminating patterns common to larger classes of processes such as the cycling of plant nutrients and eventually back to ecosystem processes or, even more ambitiously, ecological processes in general. This chapter does not dismiss these more grandiose and somewhat ill-defined conceptual leaps but merely recommends achieving the same goal via smaller and more well-defined steps.

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