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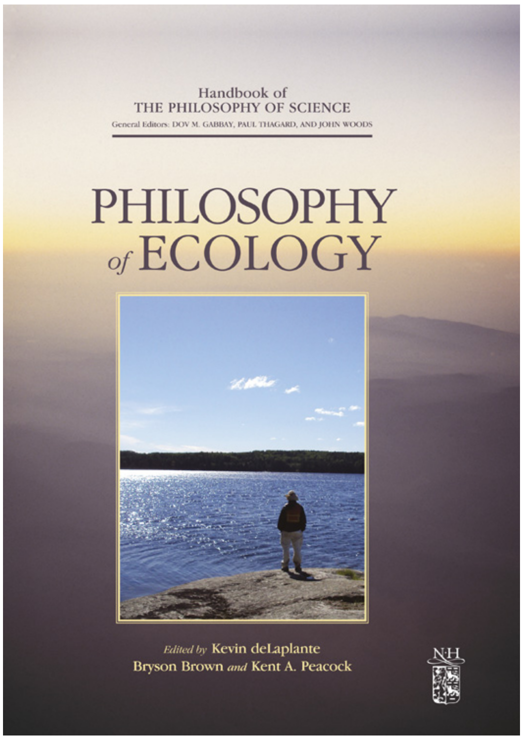

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THE BIODIVERSITY–ECOSYSTEM FUNCTION DEBATE IN ECOLOGY

Kevin deLaplante and Valentin Picasso

1 INTRODUCTION

Population/community ecology and ecosystem ecology present very different perspectives on ecological phenomena. Over the course of the history of ecology there has been relatively little interaction between the two fields at a theoretical level, despite general acknowledgment that many ecosystem processes are both influenced by and constrain population- and community-level phenomena. However, recent years have seen a growing interest in theoretical models and experimental studies aimed at investigating the relationship between biological diversity and higher-level community and ecosystem properties, such as invasibility and productivity. This research on the relationship between biodiversity and ecosystem functioning has spawned a large and growing literature that holds great promise for productive engagement between community ecology and ecosystem ecology. Indeed, some have argued that the synthetic viewpoints developing out of this research represent a genuine "paradigm shift" in ecology [Naeem, 2002].

However, this research has also generated heated debate among ecologists over experimental methodology and interpretation of research results. The debate burst into the public sphere in 2000 when a group of critics of the biodiversity-ecosystem function experiments accused proponents of misrepresenting the scientific debate to the public for political purposes. One media source described it as a "full war among ecologists" [Kaiser, 2000]. Recent writings have been more conciliatory in tone, but the incident points to a broader socio-political context that has played an important role in both motivating and enabling research on biodiversity-ecosystem function relationships, a context that connects research in this field to debates in conservation science and environmental policy. A comprehensive overview of this debate needs to take account of this socio-political context.

Young ecologists beginning their research careers are often unaware of the intellectual history of their field, or the relevance of this history for understanding the scientific and socio-political environment within which their work is situated. The primary aim of this paper is to provide an historical and conceptual overview of the biodiversity-ecosystem function debate that will help to illuminate research that is currently being conducted in this field.

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The biodiversity-ecosystem function literature employs concepts like "biodiversity", "ecosystem" and "function" that are themselves subjects of considerable debate in the foundational literature in ecology and in the philosophy of ecology and biology. It is a central thesis of this paper that a proper understanding of the biodiversity-ecosystem function debate requires an appreciation of this broader intellectual history. Consequently, one of the tasks of the paper is to critically assess the status of these concepts as they are used in ecology generally and in the biodiversity-ecosystem function literature in particular. In this respect the paper serves not only as an introduction to the biodiversity-ecosystem function debate, but also as an introduction to a number of central debates in the philosophy of ecology more broadly.

2 BACKGROUND: THE DIVERSITY-STABILITY DEBATE

The contemporary biodiversity-ecosystem function debate is best viewed against the background of the long-standing debate in ecology over the relationship between the diversity and stability of ecological systems.

Commentators on the history of the diversity-stability debate commonly distinguish three historical periods in the history of ecology, each characterized by a particular theoretical and empirical perspective on diversity-stability relationships, with the most recent third period identified with a shift toward what we now call "biodiversity-ecosystem function" relationships [Ives, 2005; McCann, 2005].

As we will see, the history of the diversity-stability debate has important lessons for contemporary research on biodiversity and ecosystem function.

2.1 The 1950s and 1960s

The view that diversity is positively correlated with stability was endorsed by a number of prominent ecologists in the 1950s and 1960s, including Eugene Odum [1953], Robert MacArthur [1955] and Charles Elton [1958].

Odum related the notions of diversity and stability to the flow of energy through the trophic links in an ecological network. A system with greater redundancy in energetic pathways will be more stable than one with lesser redundancy. For Odum, diversity is interpreted as diversity of network connections, and stability as stability of energetic throughput and organizational structure—the more stable system is the one that suffers the least change in energy flow with the removal of a random species. However, these ecosystem concepts have a rough correspondence to population and community concepts via the identification of network nodes with species populations and network connections with trophic links.

MacArthur [1955] followed Odum in understanding stability as a measure of "the amount of choice which the energy has in following the paths up through the food web". He sketched a series of food webs and described the ramifications of energy partitioning for stability using information theory. Formally, MacArthur's notion of stability is a measure of the response of a community to a perturbation

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that influences the density of at least one of the species. MacArthur gives a semi-formal argument that recapitulates Odum's conclusion—in general, more diverse communities will be more stable than less diverse communities.

Elton's [1958] arguments draw on a wider range of theoretical and empirical evidence, but he agrees that diversity and stability are positively correlated. Elton noted that both simple Lotka-Volterra models and simple laboratory microcosms suffered from instability, and argued that simpler food webs are more vulnerable to invaders. Elton's definitions of stability vacillate within his discussion, but they reflect his general interest in dynamic instabilities that drive destructive oscillations and population explosions in food webs.

To sum up, the broad consensus during this period was that stability of ecological systems is positively correlated with diversity, and indeed that diversity is a causal factor in generating stability.

2.2 The 1970s and 1980s

This consensus did not survive the next two decades. By the end of the 1980s the general consensus was that diversity is not, in general, positively correlated with stability. How did this shift in attitudes come about?

In the early 1970s mathematical ecologists began to systematically study diversity-stability relationships in model communities [Gardner and Ashby 1970; May 1973; Pimm 1980]. The conclusion of these studies undermined the conventional wisdom about diversity and stability.

The most influential work of this period was Robert May's seminal 1973 book *Stability and Complexity in Model Ecosystems.* May argued that diversity actually begets instability. More specifically, he showed that the chances of a randomly constructed Lotka-Volterra community being stable decreases with both the number of species in the community and the connectance among species, where connectance is measured by the probability that a pair of species interacts.

May's argument employed a very specific definition of stability: it is the probability that the population size of every species in the community would return to equilibrium if there were an arbitrarily small perturbation in the population size(s) of one of the species. It is important to note that this so-called "neighborhood stability" (or "Lyapunov stability") is an all-or-nothing property; for a given perturbation, either every population returns to equilibrium or it doesn't. May presents his results in terms of the probability that a community, randomly selected from a certain hypothetical population of communities, is neighborhood-stable.

Stuart Pimm [1980] came to a similar conclusion in his influential analysis of stability properties of food webs. However, Pimm's analysis employs a different definition of stability. He questioned the ecological relevance of May's "arbitrarily small perturbations" and chose to model instead the effects of a more significant perturbation, the permanent removal of one of the species in the community. This "species-deletion stability" is defined as follows: it is the probability that the

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removal of one species will not lead to any further local extinctions. Pimm's analysis showed that, indeed, communities with more species were less "species-deletion stable" than communities with fewer species.

These theoretical results were taken to have broad significance for ecology and lead to a general rejection of the diversity-stability hypothesis among ecologists. The significance of these results can be challenged, however.

Consider, for example, that a negative diversity-stability relationship *is an immediate statistical consequence* of the definitions of stability used by both May and Pimm. If every species population must return to equilibrium after a perturbation (May), or if every species population must survive the permanent deletion of one species (Pimm), then the criteria for stability *necessarily* becomes more and more strict as you add more species to the community. The conclusion is independent of any particular feature of ecological communities; indeed, it can be viewed as an artifact of probability theory.

This fact can be viewed as undermining the empirical significance of the conclusions; the stability definitions that are employed in the analysis turn what ought to be an empirical hypothesis into a probabilistic *tautology* in idealized systems that are unlikely to be realized in nature anyway [Mikkelson, 1999].

Moreover, it can be argued that these strict, population-level concepts of stability don't faithfully capture the original notions of stability expressed in the writings of Odum, MacArthur and Elton, which more often referred to functional properties of whole communities or ecosystems.

It is this intuition—that a proper test of the diversity-stability hypothesis should focus on functional properties of communities and ecosystems—that motivates more recent work on diversity-stability relations.

2.3 The 1990s

The 1990s saw a revival of the diversity-stability hypothesis in experimental studies that indicated a positive relationship between diversity and the stability of various functionally defined properties of communities and ecosystems. The leading figure in this revival was David Tilman [Tilman and Downing, 1994; Tilman *et al.*, 1996], though many researchers have since contributed to research in this field.

The general conclusion of these more recent studies is that increasing species diversity may well decrease the stability of individual plant populations, but it may simultaneously *increase* the stability of higher-level community and ecosystem properties. This is because the increased fluctuations in population size induced by increased diversity aren't in phase across all populations—while some populations are decreasing, others may be increasing. Within a more diverse community there is a greater chance that downward fluctuations will be balanced by upward swings elsewhere in the community, resulting in greater stability of community and ecosystem properties that are averaged over individual population sizes.

These studies typically employ one of two measures of stability*: resistance to invasion* by new species, or *temporal stability* of an ecosystem property like

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biomass or productivity. Here, "temporal stability" is the mean value of a variable divided by its standard deviation, both calculated over time; it is a measure of the degree of variability of a property over time. These concepts of stability self-consciously reflect the concerns with resistance to invasion and temporal variability that dominated pre-1970s thinking about diversity-stability relationships. Note that this shift in stability measures inspired a corresponding shift in terminology, from talking about the stability of *population sizes* to the stability of *ecosystem functions*.

Another feature of the recent literature on diversity-stability relations is a recognition that "diversity" itself has many possible measures other than species richness. There is considerable interest, for example, in studying relationships between the *functional diversity* of a community and the stability of ecosystem functions. Functional diversity represents the diversity of functional traits or groups. Examples of functional traits include properties like leaf size, seed size, dispersal mode, canopy structure, and capacity for symbiotic fixation of nitrogen. Examples of functional groups include trophic groups (*e.g.*, producers, consumers, decomposers), animal guilds (*e.g.*, granivores, sap suckers, leaf miners, pollinators) or plant groups (*e.g.*, legumes, cool season grasses, warm season grasses, woody forbs).

Consequently, recent work has moved toward a broader investigation of relationships between different measures of *biodiversity* and the stability properties of *ecosystem functions*. Thus do we arrive at the nomenclature of contemporary **biodiversity-ecosystem function** studies.

2.4 Diversity-Stability Relationships and Environmental Policy

We noted in the introduction that the biodiversity-ecosystem function debate burst into the public sphere in 1999 when a group of critics of the biodiversity-ecosystem function experiments accused proponents of misrepresenting the scientific debate to the public for political purposes [Kaiser, 2000]. We discuss the details of this event in section 4; here we wish to emphasize the general point that diversity-stability hypotheses do have implications for environmental policy, and this fact is relevant in evaluating how ecologists interpret and report research findings.

Consider, for example, (1) increasing concern over loss of biodiversity induced by environmental deterioration and loss of habitat, and (2) the growing perception that human impacts on the biosphere may significantly alter the behavior of ecosystems and threaten vital ecosystem services. Diversity-stability hypotheses are relevant to environmentalist and conservationist arguments in both areas of concern by linking issues in one area to issues in the other. If one believes that certain types or levels of biological diversity are necessary to maintain the stability of ecosystems and correlated ecosystem services, then one can easily develop an argument for placing a high instrumental value on biodiversity, and thereby motivate environmental policies that promote the conservation and restoration of biodiversity.

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This observation highlights an important fact: *ecological research on diversity-stability relationships is conducted in a socio-political environment that favors certain outcomes over others.* People who endorse environmental protection policies often look to ecology for scientific support for their agendas. Indeed, ecologists themselves may be motivated for similar reasons to look for evidence that supports a positive diversity-stability relationship.

In the 1970s and 1980s the majority view among ecologists was broadly skeptical of diversity-stability hypotheses. It was easy to regard ecologists who continued to defend a positive relationship between diversity and stability in light of the evidence mounting against it as either stuck in an outmoded paradigm, engaged in wishful thinking, or overly beholden to environmentalist interests.

In the 1990s it once again became scientifically respectable to defend diversity-stability hypotheses, but many ecologists remained wary of the influence of environmental advocacy on the interpretation and presentation of scientific results. As will be shown in greater detail later, these concerns came to a head in 1999 when critics complained that an Ecological Society of American *Bulletin* presented a biased and politically motivated account of the biodiversity-ecosystem function research results.

2.5 Diversity-Stability Relationships and the Holism-Reductionism Debate in Ecology

The study of diversity-stability relationships also takes place in a context framed by the historical schism in ecology between holistic and reductionistic research traditions and worldviews. A belief in a positive diversity-stability relationship is commonly associated with some kind of commitment to holism, while skepticism is more commonly associated with reductionism. Thus, in addition to biases arising from environmental policy considerations as outlined above, we must also consider biases arising from philosophical predispositions toward holism or reductionism in ecology.

These claims require some elaboration. In ecology, holistic and reductionistic theses come in several varieties, but they can generally be divided into one of two categories depending on whether their focus is *ontological* or *epistemological.* Ontology pertains to the nature of reality, of what exists. Epistemology pertains to knowledge and the justification of beliefs about the world (in a scientific context, issues concerning scientific methodology fall into this category). For example, ecologists may differ on the ontological constitution of communities and ecosystems (*e.g.*, whether they have “emergent causal properties” at the community and ecosystem level), and they may differ on the best way to represent and analyze ecological systems in ecological theories (*e.g.*, whether community- and ecosystem-level phenomena can be exhaustively explained in terms of the behaviors of their component parts). The latter is an epistemological issue, the former an ontological issue.

There are at least two reasons why a belief in a positive diversity-stability

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relationship is commonly associated with holism:

1. There is an historical association between diversity-stability theses and traditional notions of the "balance of nature", the view that ecological systems are naturally driven toward an equilibrium state in which community composition persists and population sizes are (roughly) stable. In its original formulation with the Greeks, the balance of nature was explained in terms of teleological principles governing nature as a whole. In the Medieval period the common explanation was divine providence [Egerton, 1973]. In the modern period the favored explanations have referred either to density-dependent regulation or the stabilizing effects of network redundancy (as articulated, for example, in the arguments of Odum, MacArthur and Elton). Whether these modern explanations are properly described as "holistic" depends largely on how one defines the term, but the point is that the diversity-stability hypothesis has an historical association with worldviews that are widely regarded as holistic.

2. We noted that the diversity-stability hypothesis fell out of favor in the 1970s and 1980s in the wake of theoretical studies that seemed to undermine any positive relationship between diversity and stability. It is notable that this period also saw the rise to prominence of a new "non-equilibrium" paradigm in ecology that rejected the balance of nature hypothesis outright [Botkin, 1990]. This paradigm reconceptualized the default state of nature as one of constant flux and change, and its proponents were often motivated to label the paradigm as reductionistic to contrast it with the holism associated with equilibrium views of nature [Simberloff, 1980]. Proponents of the non-equilibrium paradigm were also inclined to associate the rejection of the diversity-stability hypothesis with the broader move toward reductionism during this time period.

These developments were, and continue to be, significant for research aimed at reviving the diversity-stability hypothesis. The fact is that within mainstream academic ecology—particularly plant ecology—there is a general bias toward reductionistic and away from holistic hypotheses and methods. The default view is to be skeptical of holistic hypotheses. Insofar as a positive diversity-stability relationship is associated with ecological holism one can expect it to face the same default skepticism.

As contemporary research on biodiversity-ecosystem function relationships continues to mature these default attitudes may slowly be changing, but among plant ecologists who continue to strongly identify with reductionism (*e.g.*, neo-Gleasonian views on plant dynamics) one is likely to encounter resistance to any diversity-stability hypothesis that is perceived as appealing to holistic mechanisms or properties to account for experimental results.

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2.6 Lessons Learned

The purpose of this brief overview of the diversity-stability debate in ecology was to show how biodiversity-ecosystem function research may be viewed as both a consequence of and contribution to the long-standing debate in ecology over the relationship between the diversity and stability of ecological systems, and to outline a number of factors that played prominent roles in this debate. There are several lessons that can be learned from this overview for researchers in biodiversity and ecosystem functioning:

1. *Sensitivity to definitions.* The question of whether diversity begets stability is not well-posed until one stipulates a definition of the key terms. We have seen that certain definitions of diversity and stability in certain modeling contexts may yield a negative correlation, while other definitions in other modeling (and experimental) contexts may yield a positive correlation. Thus the relevant scientific question to ask is not "does diversity beget stability?", but rather "does diversity of type D beget stability of type S under conditions of type C?". As we will see, the same lesson applies to debates over biodiversity-ecosystem function relationships.

2. *Biases arising from ideological commitments relating to environmental policy.* Ecological research on diversity-stability relationships is conducted in a socio-political environment that favors certain outcomes over others. In particular, a positive diversity-stability relationship (*i.e.*, one showing a positive correlation between diversity and stability) will be a preferentially desired outcome for those looking for scientific support for biodiversity conservation policies. We should expect the same factors and biases to be in play in contemporary biodiversity-ecosystem function research.

3. *Biases arising from attitudes toward holism versus reductionism in science.* A positive diversity-stability relationship is historically more closely associated with holistic than reductionistic research programs in ecology. Consequently, skepticism about holistic interactions in ecological systems can translate into skepticism about positive diversity-stability relationships. Similarly, a commitment to the reality and ecological significance of holistic interactions in ecological systems can translate into a bias in favor of positive diversity-stability relationships.

3 BIODIVERSITY AND ECOSYSTEM FUNCTIONS: KEY CONCEPTS

As noted in section 2, one of the lessons learned from earlier studies of diversity-stability relationships is the importance of being clear about the definitions of key theoretical terms and their empirical measures. Biodiversity-ecosystem function research is particularly vulnerable to charges that their key concepts, "biodiversity" and "ecosystem function", are either too vague, multi-faceted or value-laden

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to properly serve the needs of empirical science. In this section we discuss the various meanings with which these terms are used in the ecological literature, identify some of the conceptual challenges facing the use of these terms in a scientific context, and clarify their usage in the biodiversity-ecosystem function literature.

3.1 Biodiversity

We begin with the concept of "biodiversity", central to conservation biology and the biodiversity-ecosystem function literature.

3.1.1 Biodiversity and Conservation

The concepts of biological and ecological diversity are as old as natural history, but the term "biodiversity" only appeared in the scientific lexicon in the late 1980s, coinciding with the emergence of conservation biology as an applied science aimed at preserving and conserving biological diversity in the face of a looming biodiversity "crisis" [Soulé, 1985].

Attempts to define "biodiversity" as an object of conservation have always been complicated by the fact that, in this context, the *objects* that comprise biodiversity are associated with conservation *values*, *i.e.*, those aspects of the natural environment that we value and wish to preserve for current and future generations (or for their own sake). In principle this can include any biological entity or process of interest. However, this move runs the risk of making biodiversity co-extensive with all of biology and consequently rendering biodiversity conservation impractical, since everything biological would become a goal of conservation

Definitions of biodiversity are also complicated by the fact that objects of biological and ecological interest don't fall under a single hierarchy of nature (see [Sarkar, 2005] for elaboration on the following). One can distinguish at least two distinct hierarchies: (i) a *taxonomic* hierarchy that includes genes and alleles, genotypes, subspecies, species, genera, families, orders, classes, phyla, and kingdoms; and (ii) a *spatial/compositional* hierarchy that includes biological molecules, cell organelles, cells, individuals, populations, meta-populations, communities and ecosystems (communities plus their physical environments), and extending ultimately to the entire biosphere. Biological entities of interest may not fall cleanly into any specific category in either hierarchy (consider fungi, or asexual species), and at every level of each hierarchy one finds significant variation.

Standard definitions of biodiversity address this problem by focusing on the diversity of entities at three levels of organization—alleles or genes, species, and ecosystems. The reasoning is that if you can preserve allelic diversity then you'll likely preserve most of the variation of interest below the level of the individual; if you preserve species diversity then you'll preserve all of the taxonomic entities above the species level; and if you preserve ecosystem diversity then you'll preserve most kinds of communities [Sarkar, 2005].

This traditional approach to defining biodiversity has been criticized for being overly focused on conserving biological *entities*—individuals, species, communities,

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etc. In addition to entities, conservation efforts are also (or should be) aimed at conservation of unique or valuable biological and ecological *phenomena* that don't fit into either the spatial or taxonomic hierarchies. A standard example is seasonal migration patterns, such as the migration of monarch butterflies in North America from the eastern and western regions of the US and Canada to Mexico and back. This migration pattern would disappear if overwintering sites were destroyed, though the species itself may persist. Conservation of unique biological phenomena isn't guaranteed by conservation of genetic, species and ecosystem diversity.

Conservation science and the associated literature on biological diversity has also been influenced by the rise to prominence of holistic conservation concepts like "biological integrity", "ecosystem integrity" and "ecosystem health". Here the focus is less on preserving individual species and more on preserving or restoring the biotic and abiotic conditions that allow different community and ecosystem types to persist. On this more holistic view, the targets of biological conservation also include ecosystem properties like network organization, characteristic rates of cycling and throughput of energy and materials, and dynamical properties related to adaptability and resilience.

These and other considerations have led many writers to suggest that the concept of biodiversity—in the context of conservation science and policy—is necessarily pluralistic and value-laden [Norton, 2000; Sarkar, 2005]. There is no single correct measure of biodiversity to be discovered but many, each representing different ways of valuing biotic and abiotic resources.

3.1.2 Biodiversity and Ecosystem Function Experiments

Many of the complicating factors noted above (relating to, for example, the association between biodiversity and conservation values) are fortunately not present in the context of the common forms of biodiversity-ecosystem function experiments. In this context we are concerned with determining empirical relationships between biodiversity and various measures of community or ecosystem stability and function. The experimental context requires that all biodiversity concepts be operationally measurable and controllable in such a way that empirically significant conclusions can be drawn. In practice this amounts to a severe restriction on the scope of possible biodiversity measures. Typical experiments focus on one taxonomic group (usually plants, but sometimes microorganisms) and then consider only the species level of biodiversity, leaving the genetic and ecosystem levels out of the discussion. At the species level, various measures of diversity may be used, such as the Shannon-Weiner index which takes into account two components, *richness* (the number of species in an area) and *evenness* (the relative abundance of different species in an area). (See Justus, this volume, for a detailed discussion of diversity measures in community ecology.)

Another class of biodiversity-ecosystem function studies focuses on relationships between *functional diversity* and ecosystem function. Functional diversity includes

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diversity of functional traits and groups. Functional *traits* are "the characteristics of an organism that are considered relevant to its response to the environment and/or its effects on ecosystem functioning" [Diaz and Cabido, 2001]. Examples include leaf size, seed size, dispersal mode and canopy structure. A functional *group* or *type* is a set of organisms sharing similar responses to the environment (*e.g.*, temperature, water availability, nutrients) or similar effects on ecosystem functioning (*e.g.*, productivity, nutrient cycling). Like species diversity, common measures of functional diversity include two components: i) *functional richness* (the number of different functional groups or the proportion of a multi-dimensional trait space covered by a particular suite of species) and ii) *functional composition* (presence or absence of certain functional groups or traits). Although functional diversity can apply to an indefinite number of traits, it is commonly measured by measuring the diversity of *functional groups.*

Though biodiversity-ecosystem function experiments involving functional diversity are becoming more common, it remains the case that for the majority of biodiversity-ecosystem function studies, *the proxy for biodiversity is nothing more than plant species richness*—the number of plant species in a plot. There are several practical reasons for this simplification: species are easy to identify; plant communities are easy to assemble, manipulate and maintain in pots and fields; and many interactions among plants are well documented in ecology. Also, policy makers tend to prefer single numerical measures over complex multidimensional indices to make decisions about conservation [Purvis and Hector, 2000].

Not surprisingly, this simplification imposes serious limitations on the inferences that can be drawn from biodiversity-ecosystem function studies. Claims about the significance of biodiversity *in general* for ecosystem functioning, or about the applicability of observed biodiversity-ecosystem function relationships for ecological systems *in general* (in both experimental and non-experimental contexts), will be extremely tentative at best. This is a potentially serious concern because, as noted in section 2.4, one of the motivations for the biodiversity-ecosystem function research program is the perception that this research has policy implications. Indeed, one of the criticisms of the controversial 1999 ESA Bulletin report was that the authors were too hasty in drawing *general conclusions for environmental policy* from the biodiversity-ecosystem function literature.

3.2 Ecosystem Function

For some ecologists the term "ecosystem function" is suspect because it carries with it associations of holism and teleology that are perceived to be outdated and unscientific. The term seems to presuppose the existence of ecosystems as integrated entities with emergent properties that can properly be said to fulfill "functions". However: (i) the general trajectory of plant ecology over the past thirty years has been away from strongly holistic conceptions of communities and ecosystems, and (ii) the concept of "function" in ecology is historically associated with Clementsian teleology and group-selection mechanisms of community and

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ecosystem development, both of which are now widely viewed by plant ecologists as empirically falsified and/or inconsistent with neo-Darwinian evolutionary theory[1] [Hagen, 1992; Glenn-Lewin *et al.*, 1992].

Defenders of the concept of "ecosystem function" should have something to say in response to objections such as these. In this section we take a closer look at these objections and clarify the meaning of the term "ecosystem function" as it is employed in the biodiversity-ecosystem function literature. We will see that, as with the case of "biodiversity", in the context of biodiversity-ecosystem function experiments the operational meaning of the term "ecosystem function" is usually rather tightly circumscribed, and consequently is less problematic than it might otherwise be. Nevertheless, ecologists need to become more aware of the conceptual issues surrounding the use of "function language" in science if they wish to avoid confusion and misreading of their work.

3.2.1 Modern Science and the Challenge to Natural Functions

Tools and other artifacts have obvious functions (a carpenter's hammer has the function of hammering nails, a coffee maker has the function of making coffee, etc.), but the function of these artifacts is grounded in the intelligent design of human beings—these objects are built and used for a conscious purpose. But do the objects studied by the natural sciences have functions? Do water molecules, chemical reactions, cells, frogs or lakes have functions? If an object is not the product of conscious intelligent design, can it have a function?

Greek and Medieval natural philosophers believed the answer was "yes": in fact, all natural systems have functions, and these functions are essential to any explanation of what they are and why they behave the way they do. Within Aristotle's philosophy of nature, every object has a "final cause" or "telos", which is the goal or purpose of the object, and every object strives to fulfill it's natural goal or purpose. This is what is meant by saying that Aristotle has a "teleological" worldview.

Indeed, Aristotle believed that natural systems possess a set of functions that reflects a hierarchical and teleological conception of the cosmos as a whole. The cosmos is an organic whole composed of many parts nested in various hierarchies. The functions of the parts are partly defined in relation to the role they play within the greater wholes that contain them. Thus, one function of plants is to grow and develop as plants do, but for Aristotle another function of plants is to provide food for animals, and this function is part of the explanation for why plants exist with the properties that they do.

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[1] Among certain biologists and philosophers of biology, group selection has enjoyed a comeback in recent years under the label of "hierarchical" or "multi-level" selection theory [Wilson, 1983; Sober and Wilson, 1994]. However, it remains the case that most biologists and ecologists are *taught* that group selection is either incompatible with Darwinian evolutionary theory or that it occurs only rarely in natural systems, and it is this sociological fact that is relevant to the discussion here.

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Greek and Medieval scholars working out of this teleological tradition agreed that dead, inert objects could not have natural functions of their own—any functions they have must be derived from some form of intelligent agency. For Plato and the Medieval theologians, this agency is derived from the creative work of an external designer (a "demiurge" for Plato, a theistic God for theologians). For Aristotle this agency is not external, but internal, immanent in the fundamental nature of objects. Thus, while not all objects are conscious in the way that higher animals and human beings are, all objects possess "mind-like" qualities in some sense [Lindberg, 1992]. Within this context, traditional ecological notions like the "balance of nature" were articulated in explicitly teleological language, appealing either to the immanent teleology of Aristotle or the external teleology of divine creation [Egerton, 1973].

However, the scientific revolution of the 16th and 17th centuries brought about a dramatic change in cosmological worldview. The "mechanical philosophy" developed by (among others) Bacon, Galileo, Kepler, Hobbes, Boyle, Gassendi, Descartes and Newton was grounded in the notion that the physical universe was entirely made up of small solid corpuscles in motion, and that these corpuscles are inert, devoid of any of the "psychic characteristics" that were common to the earlier frameworks. Within this framework, natural phenomena are explained as the result of mechanical interactions of inert particles. The immanent teleological principles of Aristotle were "squeezed out", and the origin of natural functions was consolidated in the external agency of God.

The more serious challenge to the concept of natural functions arose as scientific explanation became increasingly "naturalized" and explicit references to God were discouraged. Without reference to God or other forms of intelligent agency, how are we to understand natural functions?

3.2.2 Natural Functions, "Function Talk" and the Philosophy of Biology

The view that came to dominate the physical sciences was that appeal to natural functions could not be justified, and reference to them should be eliminated in scientific explanations. By the end of the 18th century the dominant research programs in physics and chemistry were mechanistic in orientation.

In the biological sciences the mechanical revolution had a less dramatic impact on the use of natural function concepts in scientific explanation. To most scientists there seemed no hope of explaining the striking adaptedness of organisms to their environments, or phenomena such as embryonic development, in purely mechanical terms. Darwinian evolutionary theory eventually offered a non-teleological explanation for biological adaptations, but in many areas of biology teleological explanations continued to flourish under the banners of vitalism, Lamarckism and orthogenesis.

It was not until the neo-Darwinian synthesis of the 1930s and 1940s and the discovery of the molecular basis of heredity that overt teleological explanations were eliminated from most areas of biology and the prevailing view in the physical

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sciences was finally endorsed: teleological explanations are illegitimate outside the context of human intentional explanation.

But of course function talk *didn't* disappear in the biological sciences. Biologists and ecologists continue to use expressions like "the function of", "the role of", "for the sake of", "serves as" and "for the purpose of" in discussing biological and ecological entities, processes and mechanisms. Function talk also persists in the social sciences and in medicine. This linguistic fact poses a puzzle: on the one hand, modern scientists officially disavow teleological explanations in science; on the other hand, they routinely use the language of functions in scientific description and explanation. Is this usage justified? And if so, how is it justified? This question has spawned a large philosophical literature on the relationship between function talk and teleology.

Early work by philosophers was uniformly hostile to teleology and attempted to show how function talk can be reinterpreted in non-teleological terms without loss of meaning [Hempel, 1959; Nagel, 1961]. This project had only limited success. The problem is that function talk—and especially reference to "natural functions"—seems to presuppose a degree of *normativity* that resists analysis in purely descriptive terms.

To give a standard example, we might say that the heart can perform a number of functions in virtue of its causal properties: it can produce rhythmic sounds, for instance; it can also be used to train medical students in physiology and dissection. But we also want to say that producing rhythmic sounds or assisting the training of medical students isn't the *proper* or *natural function* of the heart—the proper or natural function of the heart is to pump blood through the circulatory system of an organism. And when a heart fails to pump blood, then it's *malfunctioning.* The concepts of "natural function" and "malfunction" appear to be normative concepts in the sense that they refer not only to what hearts *in fact* do, but what they *should* do. This kind of normative function attribution is quite common in biology, but where and how does the normativity arise in the absence of immanent teleological properties (as in Aristotelian science) or intelligent design by an external agent like God?

More recent work on the philosophy of functions has attempted to *naturalize* the teleology that is evident in normative function ascriptions. The most discussed theory of normative functions is based on the observation that Darwin's theory of natural selection seems to justify a certain kind of teleology [Wright, 1973; Millikan, 1984]. We say that certain traits were "selected for". For what? For the effects of that trait that contributed to its persistence within a population over evolutionary time frames. Hearts haven't persisted in populations because they make rhythmic sounds; they persisted because they perform a particular adaptive function—pumping blood—that contributed to the survival of organisms; they were selected *for* this causal effect. Thus, the selection history of a trait allows us to distinguish between causal effects of a trait that are merely accidental and causal effects that contributed to survival because they performed an adaptive function. This conception of natural functions justifies a certain kind of normative teleo-

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logical language without recourse to intelligent agencies or immanent teleological principles in nature.

However, not all philosophers are happy with theories of natural functions based on evolutionary history. If an organism didn't have any evolutionary history—if, say, it was an entirely new species created in a laboratory—but it still had a heart, wouldn't we still want to say that the heart has a function, and that function is to pump blood? Considerations such as these have motivated philosophers to develop alternative accounts of functions that are not based on evolutionary history (*e.g.*, Cummins [1975]; Boorse [2002])

For current purposes there is no need to survey the (vast) philosophical literature on functions any further (for an extended survey written for biologists see Wouters [2005]), suffice it to say that, while there is currently no consensus theory of functions among philosophers or biologists, there is widespread agreement that function talk is unlikely to be eliminated from biology, and that certain kinds of normative function attributions may be justified without presupposing Aristotelian or theological conceptions of nature.

3.2.3 Functions and Ecology: The Holism-Reductionism Split Once Again

Though biologists and ecologists have conducted their affairs largely in ignorance of the philosophical debate over functions, we should not conclude that philosophical attitudes toward functions and functional explanations have played no role in shaping the practices of scientists. These philosophical attitudes are revealed in general attitudes toward scientific methodology and holistic versus reductionistic research programs.

With respect to methodology, it is a generally accepted principle of modern scientific reasoning that a proper scientific explanation is either causal-mechanical in nature or grounded in general laws that describe uniform regularities; overt appeals to teleological principles in explaining the properties of natural systems are either discouraged or dismissed. This is the legacy that modern science has inherited from the scientific revolution of the 17th century.

In addition, the history of 20th century ecology is marked by a schism between holistic and reductionistic research programs that reveal differing views on the proper role of functions and function language in ecology. Put succinctly, holists are more willing than reductionists to attribute functions to higher-order ecological entities and processes.

Some of the reasons for these predilections should be obvious. In the non-human world, function talk is most naturally applied to well-organized systems with component parts that play distinctive roles in maintaining the structure and behavior of the system as a whole. Organisms are the quintessential example of such integrated systems and consequently function talk is most naturally applied to organisms. There is a long-standing tradition of holistic theorizing in ecology that is grounded in analogies between ecological systems and organisms. The most obvious historical example is the Clementsian concept of the plant community as

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a kind of "super-organism" that has an ontogeny and phylogeny directly analogous to that of individual organisms [Clements, 1916]. Organismal metaphors are also prominent in ecosystem ecology via the language of respiration, metabolism, growth, development and self-organization, and in the work of certain theorists who self-consciously defend non-trivial analogies between organismal and ecosystem development (*e.g.*, [Odum, 1969]). There are also holistic traditions of population and community ecology that emphasize the roles of individual species in contributing to the stability of higher level ecological properties, such as resistance to invasion [Elton, 1958; 1966]. It is within these holistic traditions of ecological theorizing where one is most likely to find the language of functions and functional roles applied to populations, communities and ecosystems.

By contrast, within more reductionistic approaches to ecology that are more strongly under the influence of either neo-Gleasonian individualist conceptions of plant communities and succession [Gleason, 1939; Egler, 1954], and/or the view that ecological principles must at least be consistent with, if not ultimately grounded in, neo-Darwinian evolutionary theory [Pianka 1999; Mayhew 2006], one is far less likely to find the language of functions applied to ecological entities above the levels of individuals and populations. And when it is used the tendency is to have the function language grounded in natural selection history.

There are at least two reasons for this. First, research within these traditions emphasizes the changing, stochastic, non-equilibrium aspects of ecological systems, and by and large rejects the holistic view of communities and ecosystems as coherent, organized entities with emergent causal properties. By rejecting the organismal metaphor they consequently reject function attributions that are predicated on strong analogies between ecological systems and organisms.

Second, attitudes toward function language in ecology have been influenced by the group selection debate that took place in the 1960s [Wynne-Edwards, 1962; Williams, 1966]. The critique of group selection was based on the affirmation that within orthodox evolutionary theory, natural selection acts primarily at the level of individual organisms (or, indeed, the level of individual genes), and rarely if ever at the level of groups. This debate raised awareness among ecologists of the broader implications of the theoretical perspective represented in population genetics and the neo-Darwinian synthesis, and was partly responsible for the rise of evolutionary ecology in the late 1960s and early 1970s. Evolutionary ecologists tend to associate the language of functions with organism-environment relationships relevant to selection and adaptation (*e.g.*, "functional traits"). But if natural selection only acts at the level of individuals within species populations, then the language of functions should only apply at this level (though we note again the point made in footnote 1, section 3.2). Consequently, evolutionary ecologists are inclined to be skeptical of function attributions at the community and ecosystem level.

To sum up, in ecology the language of functions is historically and conceptually tied to philosophical and theoretical debates between holists and reductionists that have played central roles in the intellectual history of the discipline. The

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biodiversity-ecosystem function literature is notable for its heavy use of function talk. It is an open question whether and to what extent differing philosophical attitudes toward functions (and their affiliation with holistic research traditions) influence the work of researchers within this field, but it would be naïve to assume that they play no role at all. There is no doubt, however, that some ecologists (generally, those not directly involved in biodiversity-ecosystem research) may view this research program with suspicion because of its affiliations with what they regard as a discredited ecological holism (*e.g.*, [Goldstein, 1999]).

3.2.4 Functions in the Biodiversity-Ecosystem Function Literature

We have seen that function attributions come with a certain amount of philosophical baggage associated with commitments to holism and the normativity of so-called "natural" or "proper" functions. But not all function talk in biology or ecology carries this baggage. In many cases the term "ecological function" is used synonymously with "ecological process", and merely refers to an ecologically relevant causal process. The biodiversity-ecosystem function literature uses the term "function" in a wide range of senses, some of which are innocuous and with no implications for the philosophical issues described earlier. But this is not always the case. In some cases the language of functions is used in ways that invoke the normative sense of function and that presuppose a certain kind of holism with respect to ecosystems.

Kurt Jax [2005] offers a helpful review of function language in ecology and specifically in the context of biodiversity-ecosystem function research. Jax distinguishes four major uses of the term "function" in ecology:

1. *to characterize processes and interactions between pairs of objects, and the causal relations that sustain them.* This sense of function refers to pair-wise interactions. Examples: a fox eats a mouse; a plant assimilates nutrients. In most cases the term "function" can be replaced by "process" or "interaction" without loss of meaning.

2. *to characterize processes and interactions between a collection of objects, and the causal relations that sustain them.* At this level we are viewing the objects as constituting or as situated within a larger system, and asking how the objects (now conceived as "parts") contribute to or relate to the larger system (now conceived as a "whole"). Examples: biomass production and phosphorus cycling within a lake; community population dynamics. These kinds of investigations are the stock-in-trade of a great deal of ecological research.

3. *to characterize the overall processes that sustain an ecological system as a whole, and the role of the component parts in these processes.* At this level the focus is on whole-system properties and processes. The parts of the system and their behaviors are reconceived as bearers of functions in relation to properties and processes of the whole. Examples: describing a plant

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species as a "primary producer" or a bacterium as a "decomposer"; a species conceived in terms of its Eltonian "functional role" niche.

4. *to characterize those aspects of an ecological system that are useful or important to humans.* Examples: the concept of an "ecosystem service", such as providing oxygen or purifying water. Though this concept of function is most generally used in relation to human needs and interests, in principle it could be applied to other living beings.

Another important distinction that cross-cuts these categories is between functions conceived as "means" and as "ends". When conceiving of functions as "ends" we are simply focusing on the activity or performance of various objects within a temporal sequence or causal chain. When conceiving of functions as "means" we are asking about the role or contribution that an object makes for something else (*e.g.*, "what is the function of biodiversity to ecosystem functioning?"; "what function does species X play in the service of ecosystem property Y?"). Studies that focus on functions as ends are generally unproblematic since they involve nothing more than empirical investigation of a process (like productivity, or drought resistance). Studies that focus on functions as means are more problematic because they require that we consider the "aims", "goals" or "purposes" served by the function, and this brings into play the issues of teleology and normativity discussed earlier. We argued earlier that certain kinds of normative function attributions can be justified in biology, but raised questions about their applicability to ecosystem processes (we return to this issue below).

The question to be asked is this: How is the language of functions used in the biodiversity-ecosystem function literature? And are these uses problematic or unproblematic?

Jax distinguishes three kinds of research questions in the biodiversity-ecosystem function literature that employ different meanings of "function" [Jax, 2005, p. 644]:

1. How does biodiversity relate to *ecosystem processes* (= ecosystem function)?
2. How does biodiversity relate to the *functioning of ecosystems*?
3. How does biodiversity relate to *ecosystem services* (= ecosystem functions)?

The bulk of the experimental work on biodiversity-ecosystem function relations is focused on answering the first question, where the variables of interest (productivity, drought resistance, decomposition of litter, etc.) are treated as ends, not as means to some other end. This usage is largely unproblematic since it is does not invoke the normativity of functions conceived as means to some other end.

The second question employs a sense of "function" that can be problematic when the expression "functioning of ecosystems" (or "ecosystem functions") refers to the overall behavior or performance of an ecosystem, because this usage often presupposes a certain conception of ecosystems as entities in the world. Consider how the expression is used in the controversial ESA article on "Biodiversity and ecosystem functioning" (more on this in section 4):

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> Ecosystem functioning reflects the collective life activities of plants, animals, and microbes and the effects these activities—feeding, growing, moving, excreting waste, etc.—have on the physical and chemical conditions of the environment. (Note that 'functioning' means 'showing activities' and does not imply that organisms perform purposeful roles in ecosystem-level processes.) A functioning ecosystem is one that exhibits biological and chemical activities characteristic of its type." [ESA, 1999, p. 3]

The authors try to head off worries about their use of function language but the last line betrays a normative interpretation of this language. A functioning ecosystem is one that "exhibits biological and chemical activities characteristic of its type". As Jax puts it,

> The aim of investigating "functioning" ecosystems here is clearly not to observe any activities of organisms in a particular area, but specific activities that sustain some "typical" ecosystem. Here "functioning" clearly receives a normative dimension in the sense that it refers to some pre-defined reference states of an ecosystem (those that "exhibit biological and chemical characteristics of its type"). The "functioning" of the ecosystem thus is a desirable state, and the organisms in fact are investigated as if they perform purposeful roles in its perpetuation. This is a legitimate aim of applied ecological research, but it goes beyond a pure description of processes that occur in some aspect of nature. [Jax, 2005, p. 644]

In short, this usage presumes that one can describe ecosystems as functioning or malfunctioning relative to some reference state that characterizes an idealized ecosystem "type". The problem here isn't so much the normativity of the function ascription as the conception of ecosystems and ecosystem individuation that is being presupposed. Very few ecologists believe that ecosystem "types" are part of the furniture of the world. By far the more common view (even among holists) is that the boundaries and variables that characterize an ecosystem *are chosen by observers*, they're not given in nature as such. Consequently, making statements about the functioning of ecosystems demands that observers delimit the ecosystem in question and specify the relevant reference states. The problem, as Jax sees it, is not that this is impossible, but that it is almost never done in a careful, explicit and motivated fashion. As a result, the concept of a "functioning ecosystem" is never operationally defined. This kind of usage lends support to critics who charge that expressions like "ecosystem function" are nothing more than trendy buzzwords that don't belong in the scientific lexicon of ecology.

Jax [2005] identifies a number of other examples in the biodiversity-ecosystem function literature where distinctions between ecosystem processes and ecosystem functions, and between normative and descriptive senses of function, are blurred, resulting in semantic confusions that hinder rather than help the empirical investigation of biodiversity-ecosystem function relationships. We agree that this

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research can benefit from a theoretical framework that encourages greater precision in the use of key concepts and that is more mindful of the historical and philosophical issues associated with the use of these concepts.

3.3 Summing Up

In the preceding sections we presented an overview of conceptual issues related to the use of the terms "biodiversity" and "ecosystem function". We saw that scientific investigations of biodiversity are challenged by a multiplicity of concepts and measures of biodiversity, and by associations of the concept with normative and political goals of conservation ethics and policy. And we saw that scientific investigations of ecosystem function are challenged by historical associations of "function talk" with teleological views of nature, discredited (or at least, marginalized) holistic views of the structure and organization of ecological systems, and by ambiguity in the usage of the term "ecosystem function". Consequently, we should not be surprised to find divided opinions on the status and interpretation of contemporary biodiversity-ecosystem function research.

4 THE BIODIVERSITY-ECOSYSTEM FUNCTION DEBATE

In this section we present an historical narrative leading up to the so-called "war among ecologists" that was reported in the journal *Nature* [Kaiser, 2000]. As we shall see, this more recent debate shares several features with earlier debates over diversity-stability relationships.

4.1 The Socio-Political Context

Concerns about biodiversity loss escalated in the 1980s and 1990s, along with a growing awareness that intact, functioning ecosystems perform a wide range of so-called "ecosystem services", among them the provisioning of food and clean water, crop pollination, pest and disease control, nutrient dispersal and cycling, and seed dispersal. It is not surprising that researchers would be interested to investigate whether loss of biodiversity might interfere with the ability of ecosystems to perform these vital functions, but the research program on biodiversity-ecosystem function relationships that emerged in the 1990s was driven not by scientific curiosity alone, but by an international group of scientific and policy organizations motivated by a range of policy concerns. These organizations included the following:

- *International Council for Science* (ICSU). An NGO founded in 1931, comprised of 112 national scientific bodies and 29 international scientific unions, to promote scientific activity applied for the benefit of humanity. ICSU's broad scientific expertise addresses major issues by creating interdisciplinary bodies and joint initiatives with other organizations.

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- *United Nations Educational, Scientific and Cultural Organization* (UNESCO). Founded in 1945 with the goal of building peace though education, science, culture, and sustainable development.

- *Scientific Committee on Problems of the Environment* (SCOPE). An international scientific organization, comprised of 38 national science academies and 22 international scientific union. SCOPE develops scientific reviews of environmental issues in three cluster areas: "managing societal and natural resources", "ecosystem processes and biodiversity", and "health and environment."

- *International Geosphere Biosphere Program* (IGBP). One of ICSU's interdisciplinary boards charged with studying global change, started in 1987. One of its projects, Global Change in Terrestrial Ecosystems (GCTE), addressed how global change would affect terrestrial ecosystems and feedbacks to the climate system.

- *DIVERSITAS*. Joint initiative by SCOPE, UNESCO, ICSU, and other organizations, started in 1991. It provides an international multi-disciplinary framework for promoting integrative biodiversity science through synthesizing scientific knowledge, promoting new interdisciplinary research, and communicating policy implications.

- *National Science Foundation* (NSF). A US federal agency created in 1950 to promote the progress of science; to advance the national health, prosperity, and welfare; and to secure the national defense. The Directorate of Biological Sciences, Division of Environmental Biology, funded much of the American biodiversity-ecosystem function research of this period.

- *European Science Foundation* (ESF). Association of 75 member organizations (European national research councils) devoted to scientific research in 30 European countries. Established in 1974, it has coordinated a wide range of pan-European scientific initiatives. LINKECOL, a program to promote a synthesis between population, community, and ecosystem ecology, funded most European biodiversity-ecosystem function research between 1999 and 2004.

The reality is this: the biodiversity-ecosystem function research program that emerged in the mid-1990s was driven by an organized effort of the international scientific community, with the explicit goal of providing evidence for the utilitarian value of biodiversity for human society, in order to convince policy makers to take serious action towards conservation of biodiversity. This is the socio-political context in which this research was conducted, a context that from the very beginning was motivated by normative concerns about biodiversity loss and its impact on the planet. Loss of biodiversity alone was enough to motivate scientific and ethical concern, but if it could be established that biodiversity loss negatively impacted

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ecosystem functioning, then one had a powerful economic and self-interested argument that could be used to motivate broad conservation initiatives. We have seen such arguments before, in earlier debates over diversity–stability relationships, but not on the scale witnessed here.

4.2 The Experiments: ECOTRON, Cedar Creek, and BIODEPTH

The initial phase (mid-1990s) of the biodiversity-ecosystem function research program is dominated by three experiments: the ECOTRON (UK), Cedar Creek (USA), and BIODEPTH (Europe).

In these studies, diversity is manipulated by constructing multi-species assembled communities and the effects of these communities on ecosystem function subsequently determined. If the observed response of the multi-specific assemblages differs from the response predicted by simple summation of the single species responses, then it is concluded that diversity *per se* has had an effect on ecosystem functioning.

In the ECOTRON experiment, Naeem *et al.* [1994] assembled communities of plants, microorganisms, and animals (representing trophic levels of decomposers, producers, and consumers) with three different biodiversity levels (9, 15, and 31 species), in replicated controlled growth chambers, and observed an increase of plant productivity and community respiration in the more species-rich communities. They explained this positive association between biodiversity and ecosystem functioning by the mechanism of “niche complementarity”. The idea is that at lower diversity, species are more likely to compete for a given resource, but as diversity increases, different species are forced to exploit the same environmental resource in different, non-competitive ways (*e.g.*, some animals feed off leaves at the tops of trees while others feed off the bottom; or some feed by day while others feed by night; etc.). This is expected to have an effect on overall system function. A simple example: a more diverse community of plants may have a canopy structure that intercepts more light at various heights, thereby capturing more energy that can be converted into biomass.

The second set of experiments was conducted at Cedar Creek, Minnesota, by Tilman and his colleagues. In one experiment they used different nitrogen fertilizer rates to alter the species composition and diversity of native grasslands, and observed an increase in stability with species richness (and fertilizer), which they measured as resistance and recovery after a major drought [Tilman and Downing, 1994]. In a second experiment they assembled communities of native grassland species with different species richness levels (1 to 24 species) drawing species at random from a list, and measured an increase in productivity and nutrient use with greater diversity [Tilman *et al.*, 1996]. A similar “niche complementarity” model was used to explain these results: diverse communities make more complete use of the resource space, increasing the resources available for ecosystem processes.

The third major experiment was the European BIODEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems). Hector *et al.* [1999]

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manipulated replicated artificially assembled grassland communities with varying species richness (1 to 32) at eight different sites (Silwood and Sheffield in UK, Sweden, Portugal, Ireland, Greece, Germany, and Switzerland) and observed a reduction in total plant productivity with decreasing diversity levels. They explained the results by niche complementarity and positive species interactions, as well as the selection effect (see 4.3 below).

These experiments and others were interpreted as providing evidence for a general and positive relationship between species richness and ecosystem productivity. Some were featured in prestigious scientific magazines and general news media, accompanied by calls to support biodiversity preservation.

However, some experiments looking at other ecosystem processes such as soil organic matter decomposition failed to provide evidence for a positive relationship between diversity and ecosystem functioning (*e.g.*, [Griffiths *et al.*, 2001]). Other studies highlighted the greater contribution of functional composition rather than species diversity to ecosystem processes [Hooper, 1997; Tilman *et al.*, 1997a]. Because species diversity and functional composition may not necessarily be correlated, the interpretation of the functional composition effects also became an issue of debate.

4.3 Critical Response (late 1990s)

By the late 1990s, two types of scientific criticism had arisen that challenged the results and interpretation of the previous experiments. First, there were observational studies that appeared to contradict the experimental results (*e.g.*, [Wardle *et al.*, 1997]). And second, there was growing recognition that the design of the experiments made the interpretation of results either ambiguous or impossible to extrapolate to natural ecosystems [Huston, 1997; Huston *et al.*, 2000]. We will consider these objections in turn.

First, most of the high productivity ecosystems in the world appear to have low species richness, an observation that runs counter to the general inference that ecologists wanted to draw from the biodiversity-productivity experiments [Huston and McBride, 2002]. If diversity was positively correlated with productivity, this association should be evident in natural ecosystems. But in community ecology it has long been recognized that productivity is generally a "hump-backed" function of diversity [Grime, 1973], *i.e.*, species numbers will be maximized in environments with *intermediate* productivity. The prevailing rationale for this result was that at low levels of environmental productivity (*e.g.*, poor soils), species diversity in natural ecosystems is low because few species can survive. Diversity increases as more resources become available for species to exploit, reaching a maximum at intermediate levels of productivity. Then diversity declines at higher levels of productivity because dominant species either out-compete others or are limited by growth in size of individual plants. But from this perspective, environmental conditions are the driver of diversity, and not the other way around. Only when the environment is controlled, say the critics, can the relatively small effects of

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species composition on productivity be distinguished [Huston and McBride, 2002].

Second, experiments with randomly assembled plant communities have several hidden effects that are confounded with the diversity effect. The most important of these is the *sampling effect* (now considered an example of the *selection effect*) [Huston, 1997; Tilman *et al.*, 1997b]. As a statistical necessity, the probability of including a highly productive species in a random pool increases as you add new species. Consequently, the increase in productivity may be due to the presence of a single highly productive species, rather than due to an increase in species diversity *per se*. To critics, the sampling effect is better viewed as an artifact of the way the experiments were conducted, not a biologically valid mechanism to explain an increase in productivity with species richness. Other design problems of these first experiments noted by critics included "quasi replication" (low diversity replicates are less represented, and there is more chance that the most productive individual species are not included) and variance reduction effects (high diversity replicates are more similar than low diversity replicates, confounding experimental error with the diversity effect). According to critics, these design problems rendered invalid any general conclusions about the relationship of diversity to ecosystem function based on this class of experiments. Interestingly, Tilman responded by granting that the sampling effect was indeed the simplest mechanism to explain the observed positive diversity-productivity relationship, but given that species extinction processes are poorly understood, and assuming that species loss is random, he asserted that this is a reasonable and legitimate scientific explanation of the effect [Tilman *et al.*, 1997b]. The interpretation of the role of the sampling effect in biodiversity experiments remained a contentious issue. As Grime [1999] put it, the debate "deepened".

4.4 "War among ecologists"

In 1999, a panel of ecologists reported in the Ecological Society of American *Bulletin*, a publication aimed at the general public and policy makers, that there was scientific evidence that loss of biodiversity impacted ecosystem functioning by reducing plant productivity, decreasing ecosystem resistance to environmental perturbations, and increasing the variability of soil nitrogen levels, water use, and pest cycles [Naeem *et al.*, 1999]. The report concluded that, because "both the magnitude and stability of ecosystem functioning are likely to be significantly altered by declines in local diversity," it recommends "the prudent strategy of preserving biodiversity in order to safeguard ecosystem processes vital to society."

A group of critics of the biodiversity-ecosystem function experiments subsequently wrote a letter to the ESA *Bulletin* heavily criticizing the report [Wardle *et al.*, 2000]. As Kaiser [2000] commented in *Science*,

> Huston and the other critics hit the roof. In a commentary published in the July 2000 ESA *Bulletin*, which goes to all 7,700 ESA members, they mince no words, charging that the pamphlet is "biased," "states opinions as facts," and sets "a dangerous precedent"—especially as it

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> appears to represent the position of the entire society. It is "a propaganda document," they claimed, "and an advertisement for some authors' research." By promoting "unjustifiable actions" based on a "house of cards," they wrote, "scientific objectivity is being compromised." [p. 1283]

It is unusual for scientific disagreements to enter the public sphere in so dramatic a fashion. Certainly there were legitimate questions about the design and interpretation of the experiments that the authors of the original report failed to mention, but by itself these methodological facts don't account for the heat of the exchange. The full story has to recognize that basic ecological research has rarely been subject to such anticipation and scrutiny from professional associations, science and policy institutions, and the general media. In addition, the differing sides in this dispute were also professional rivals in a real sense, vying for hefty grant dollars and peer recognition (Consider: Tilman's Cedar Creek experiments have received over 10 million dollars in NSF grants over the past fifteen years). It is the environmental, socio-political and institutional context of the research that encouraged both the publication of the original ESA report and the critical response.

4.5 Conciliation and Synthesis

This story has a happy ending. In the wake of the flare-up over the ESA report, a conference was held in Paris in December 2000 in an attempt to bring everybody to the table and reach a consensus on the status and interpretation of the biodiversity–ecosystem function experiments. This "Synthesis Conference" was an effort to reconcile the different interpretations of the results and to arrive at a consensus framework for guiding new research and for framing the current understanding of the science for the general public. Participants described the conference as "a delight" [Naeem *et al.*, 2002]. "Perhaps it was the rich desserts and the French wine, but there were few signs of acrimony at the conference" [Hughes and Petchey, 2001].

The consensus framework was structured by pointing out the issues that were clear, and identifying questions that remained to be answered, so that the framework might serve as a guide for future research endeavors.

First, it was clear that a large number of species is required to maintain ecosystem functioning, but whether this is because more rich communities have some key species that differentially affect ecosystem function, or whether diversity effects arising from niche complementarity had an effect on ecosystem function, was unclear. This provided a goal for further studies, to separate and measure the effects of these two non-exclusive mechanisms, complementarity and selection effects. In addition, it was recognized that the biological relevance of the sampling effect turns in part on whether species extinctions are random, and research had to be conducted to address this question [Loreau *et al.*, 2001]. It was also agreed that a greater number of species may be needed to maintain stability in ecosystems

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(the "insurance hypothesis") and that further experiments were needed to test this hypothesis specifically controlling diversity and the environmental variation.

Another important question addressed in the conference was how to reconcile the observational and experimental data on diversity-productivity relationships. Recall that observational studies had repeatedly shown a hump-backed relationship, where productivity peaks at intermediate levels of diversity but declines at higher levels. By contrast, the biodiversity-ecosystem function experiments showed a positive relationship of increasing productivity with diversity. These results were reconciled by realizing that the observational studies were plotting diversity not against productivity in a fixed environment, but against productivity across a range of environmental gradients, such as soil fertility and disturbance regime. Consequently, decreasing productivity at higher diversity levels may be due (for example) to decreases in soil fertility in those environments, but if soil fertility was held constant, productivity may be observed to increase with diversity, as was observed in the controlled biodiversity-ecosystem function experiments. Thus, rather than being interpreted as contradictory results, the observational and experimental results are interpreted as revealing different mechanisms operating under different conditions. It was concluded that much further work needed to be done to investigate feedbacks between diversity, ecosystem functioning and environmental factors [Loreau *et al.*, 2001].

In addition, it was acknowledged that most of the experimental evidence came from grasslands ecosystems, where only plant diversity was manipulated. Therefore, before making generalizations to other ecosystems (*e.g.*, aquatic) and other trophic levels (*e.g.*, consumers, decomposers) further research was needed in these areas.

Finally, it was agreed that it is *functional traits* of species and their interactions that predominately affect ecosystem functioning. Consequently there was a call for more research on the relationship between species diversity and functional diversity, and in defining functional groups or types relevant for ecosystem functioning [Loreau *et al.*, 2001].

4.6 More Recent Work

The "synthesis conference" helped to frame a research agenda that has shaped more recent work on biodiversity-ecosystem function relationships. This work has helped to refine our understanding of the mechanisms relating diversity to ecosystem functioning, including the role of selection effects, such as interspecific competition that can cause one species to dominate a community (selection effects can be positive or negative depending whether the dominant species is positively or negatively associated with ecosystem functioning). The synthesis framework also helped initiate a second generation of biodiversity experiments, such as the Jena Project in Germany [Roscher *et al.*, 2007; Temperton *et al.*, 2007], and the forest biodiversity mega-project in Sabah, Malaysia [Scherer-Lorenzen *et al.*, 2005]. These experiments usually have some subset of the following characteristics: i) the

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treatments include as many monocultures as possible, in order to make comparisons of overyielding, complementarity, and selection, ii) the design is balanced to allow contrasts for plots with and without certain species or groups of species, iii) they are designed with the objective of testing specific mechanisms directly beyond the general overyielding in a specific function, iv) they extend for longer time periods, and larger spatial scales, v) experimental design includes replications and local environmental control, and vi) they consider biodiversity and ecosystem function effects across more trophic levels (producers, consumers, predators).

As a follow up to the synthesis conference, in 2005 a committee of scientists from the Ecological Society of America published a review in *Ecological Monographs* titled 'Effects of biodiversity on ecosystem functioning: a consensus of current knowledge' [Hooper *et al.*, 2005]. Like most papers in the literature this report starts by describing the threats that biodiversity loss and environmental degradation pose to society, and finishes by recommending to policy makers to set biodiversity as a priority for action. But the tone of the 2005 report is moderate and balanced, discussing uncertainties and contradictions present in the literature, avoiding generalizations and describing the many factors other than diversity that can influence ecosystem functioning.

The main points stressed in the report are: i) functional composition is more important than species richness in affecting ecosystem functioning; ii) abiotic controls (climate, resources, disturbance) interact with biodiversity to influence ecosystem properties, and the feedbacks between biotic and abiotic controls are central to understanding ecosystem functioning; and iii) diversity effects and the underlying mechanisms can differ among ecosystem properties and ecosystem types. The report notes that diversity may have no effect on some ecosystem processes (*e.g.*, when multiple species carry out similar functional roles or abiotic conditions primarily control the process) but as larger spatial and temporal scales are considered, greater diversity is needed to maximize functioning.

With less certainty, the authors assert that i) complementarity of resource use by certain combinations of species can increase productivity; ii) species richness decreases exotic species invasion under similar environmental conditions (though not across all environments); and iii) species diversity can stabilize ecosystem process in response to disturbances and variation in abiotic conditions. The authors note areas of uncertainty that need further research, including i) the relationships between taxonomic diversity, functional diversity, and community structure; ii) ecosystem response across multiple trophic levels to varying composition and diversity of consumer organisms; and iii) the need for long-term experiments to assess temporal stability and perturbations to assess response to and recovery from disturbances. Finally, meta-analyses of the more than 150 biodiversity experiments conducted in terrestrial and marine ecosystems conducted recently [Balvanera *et al.*, 2006; Cardinale *et al.*, 2006; Cardinale *et al.*, 2007; Stachowicz *et al.*, 2007] reported that on average the effect of biodiversity on ecosystem processes was positive, although effects varied with scale and hierarchical level (population, community, ecosystem). In most studies diverse communities performed better

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than the average of monocultures although in very few cases diverse communities were better than the best monoculture (*i.e.*, transgressive overyielding was infrequent). Other issues considered recently involve looking at the effect of measures of biodiversity other than richness, like evenness and diversity indices on ecosystem function [Wilsey *et al.*, 2005; Losure *et al.*, 2007; Kirwan *et al.*, 2007].

4.7 Discussion

The aim of section 4 was to provide an overview of research and debate over the relationship between biological diversity and ecosystem functioning. Here we pause to reflect on attributes of this debate that are illuminated by the discussion of the diversity-stability debate in section 2 and the discussion of biodiversity and ecosystem function concepts in section 3.

One of the lessons learned from the earlier diversity-stability debate was that apparently conflicting experimental and theoretical results may be in fact be compatible, because the arguments actually employ different concepts or measures of diversity or stability. We see this pattern in the biodiversity-ecosystem function debate as well. It shows up in several places, but in the review above we see it explicitly with respect to measures of productivity. In observational studies, ecosystem productivity is confounded with effects due to environmental variation, while in the biodiversity experiments environmental variation is controlled. These different measures of productivity resulted in different diversity-productivity curves, but the curves were really measuring different effects, and so were not genuinely incompatible.

We also saw that the earlier stability-diversity debate was subject to biases arising from ideological commitments relating to environmental policy and concern over biodiversity loss. The worry was that a desire to promote conservation policies would bias researchers to look for confirming evidence for positive diversity-stability relationships and downplay or ignore contrary evidence. This was precisely the charge made by the critics of the 1999 ESA report, that the authors of the report were driven by a desire to influence public policy in favor of conservation, and that this lead them to give a biased review of the biodiversity-ecosystem function literature and to make hasty generalizations about the implications of the research for conservation policy.

In sections 2 and 3 we also noted that philosophical attitudes toward holism and reductionism in ecology can predispose ecologists toward or away from positive diversity-stability relationships, because such relationships have an historical association with holistic views of ecological dynamics. And we noted that such views are likely to be aggravated by the language of ecosystem "functions", insofar as these are taken to imply that ecosystem behaviors are goal-directed in some sense, or that ecosystems have behaviors that may be judged against certain idealized ecosystem "types". It is difficult to judge the degree of influence that these sorts of philosophical biases have on biodiversity-ecosystem function research, since ecologists are unlikely to comment on such issues in their research activity. But there

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is anecdotal evidence that reductionistically-oriented, neo-Gleasonian plant ecologists are inclined to be more cautious about this research program and the general conclusions for environmental policy that many want to draw from it.

The public disagreement surrounding the 1999 ESA report was embarrassing for the institution and the participating ecologists, but as we described above, it resulted in a productive dialogue among scientists that helped to address misunderstandings and build a consensus framework for a research program that would work to resolve remaining uncertainties. Post-synthesis research has been much more conciliatory in tone and more cautious in its declarations, but also more productive in illuminating the various mechanisms at work, and in articulating a more unified vision of ecological science that spans the historical schism between population/community and ecosystem ecology.

5 CONCLUSION

In this paper we presented a survey of the debate over the relationship of biodiversity to ecosystem functioning. Our goal was to provide an overview that would help researchers and commentators to understand the various different sources of conflict that have played a role in structuring the debate. Some of these sources of conflict have roots in earlier debates in ecology over diversity-stability relationships, the relationship of ecology to environmental policy, and in the long-standing schism between reductionistic and holistic research traditions. Consequently, our review has focused on situating the biodiversity-ecosystem function debate within this broader intellectual history.

It is our conviction that members of any scientific field can benefit from instruction in the history and philosophy of their field. Such instruction can help researchers, teachers and students to better understand the conceptual issues they confront in their on-going research projects, and to appreciate the broader social and humanistic significance of their work. We hope that this overview of the historical and philosophical foundations of the biodiversity-ecosystem function debate will prove similarly helpful as a guide to the issues and controversies surrounding this exciting area of ecological research.

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