Reply to Wardle et al.

Issues in Ecology, Number 4, on biodiversity and ecosystem functioning, provides a brief overview of basic principles concerning biotic influences on ecosystem processes and a conservative summary of current evidence that directly addresses the role of biodiversity in these processes. The report is a distillation of a longer document that more fully detailed the views of the panel members (Shahid Naeem [chair], T. Chapin, Robert Costanza, Paul Ehrlich, Frank B. Golley, David Hooper, J. H. Lawton, Robert O'Neill, Harold Mooney, O. Sala, Amy Symstad, and David Tilman). This longer document was condensed to produce a report that was deemed by the editors and science writers to be accessible to a broad, nonscientific audience, including high school students, while remaining true to its content. In this issue of the *ESA Bulletin,* Wardle et al. express concern that their opinion did not receive a strong enough voice, and therefore call into question the validity of the document, the process of its production, and motivation of its authors. I regret their dissatisfaction, but am frankly puzzled by all three aspects of their response.

Although the production process could have benefited from more extensive input in its final stages, especially if time and resources had permitted, the main message and the bulk of the report's content would not have been altered. The report is both accurate and fairly represents the diversity of opinion surrounding the issues. This *Issues in Ecology* brochure will serve the public by providing an introduction to this topic and motivating deeper appreciation of the potential roles of the earth's extraordinary, but rapidly declining, biodiversity.

This *Issues in Ecology* volume reflects the viewpoints of the panel and contains much information, of which Wardle et al. disagree only with a portion. There are three parts to the report: (1) its overview of fundamentals, (2) its summary of evidence, and (3) its suggestion for future research to address uncertainties. Wardle et al. are concerned primarily with the second part, expressing consternation that their interpretation of the experiments of others were not discussed. Here, I suggest that their dichotomization of the issues is misplaced and masks the true balance found within the report and the discipline. I will also show that a wide breadth of opinions is reflected in the report's cautionary tone and throughout the body of the report. In total, the concerns of Wardle et al. are unwarranted.

"Debate" in new disciplines

The hallmark of a new and active science is a dynamic exchange of ideas and information among scientists. This exchange is frequently mistaken as evidence that a particular discipline lacks useful scientific insight. For example, exchange of ideas among evolutionary biologists over constantly emerging new ideas is frequently misinterpreted as a lack of evidence for evolution (Futyuma 1983), when nothing could be more solidly documented in biology than evolution itself.

Study of the ecosystem consequences of biodiversity decline is a relatively new focus in ecological research, so, not surprisingly, there is an active exchange of ideas. The recent explosion of research in biodiversity can be traced to a conference in 1992 (Schulze and Mooney 1993), although its intellectual roots can be traced to Darwin and possibly further (McNaughton 1993). Experimental research on the relationship between biodiversity and ecosystem functioning is less than a decade old, and publications of experimental results appeared only in 1994 (Naeem et al. 1994, Tilman and Downing 1994). Wardle et al. are concerned primarily with recent exchanges among authors (André et al. 1994, Givnish 1994, Aarssen 1997, Garnier et al. 1997, Grime 1997, Huston 1997, Wardle et al. 1997*b*, Hodgson et al. 1998, Wardle 1998, Naeem 1999, Wardle 1999). Although known to Wardle et al., their response did not reference replies to these opinions and other related issues (Naeem et al. 1995, Allison et al. 1996, Tilman 1997, Tilman et al. 1997*b*,*c*, 1998, Doak et al. 1998, Hector 1998, Lawton et al. 1998, Loreau 1998, Naeem and Li 1998, Allison 1999). There is an ongoing, active exchange of opinions and ideas that is typical of an emerging discipline.

Wardle et al. feel that this exchange is not reflected in the *Issues in Ecology* brochure on biodiversity–ecosystem functioning (henceforth, the BD–EF *Issues*). The majority of articles Wardle et al. refer to (André et al. 1994, Givnish 1994, Aarssen 1997, Grime 1997, Wardle et al. 1997*b*, Wardle 1998, 1999, Naeem 1999) are commentaries. Most of these are short (1–4 pages) opinion pieces that express concerns over interpretations of findings. Some of these reports are longer reevaluations of the experiments themselves (Garnier et al. 1997, Huston 1997, Hodgson et al. 1998), and these papers have stimulated new approaches to analyzing, modeling, and conducting empirical research. Similar commentaries (Naeem et al. 1995, Tilman 1997, Tilman et al. 1997*c*, Naeem and Li 1998) and longer studies (Allison et al. 1996, Tilman et al. 1997*b*, 1998, Doak et al. 1998, Hector 1998, Lawton et al. 1998, Loreau 1998, Allison 1999) have addressed these and other issues. *Issues in Ecology* does not document such technical exchanges concerning experimental design, statistical issues, and theory, although its coverage of topics balances ideas and evidence according to their relative weights. For the part that focused on evidence, the report summarized important, well-replicated findings. Wherever necessary, however, coverage was cautious, generally reflecting the variation in opinions expressed in published exchanges.

Is our report biased?

The biggest question raised by Wardle et al. is this: Does our report truly reflect majority opinion, or is it slanted? Certainly we feel that the report is balanced and objective. Indeed, if anything, the report possibly understates the magnitude of biodiversity's role in ecosystem functioning. Two studies support this conclusion. Schläpfer and colleagues (Schläpfer and Schmid 1999, Schläpfer et al. 1999) have written literature reviews on this issue, and their conclusions agree with that of the BD–EF *Issues*. Over 56 different hypotheses stemming from seven core biodiversity hypotheses were identified in their review, 20 of which have been addressed scientifically (Schläpfer and Schmid 1999). In spite of this overwhelming richness of ideas, their conclusion was, "While some of the studies found negligible effects of biodiversity, effects that are beneficial to humans were found in a wide range of ecosystem contexts, even at the limited time scale of ecological experiments." In a survey of expert opinion concerning the discipline (Schläpfer et al. 1999), the majority opinion was that ". . . (1) ecosystem process rates are strongly correlated with biological diversity, and (2) these same processes are (although to a varying extent) important for the delivery of humanly defined 'ecosystem services' by natural systems." Thus, an independent recent scientific literature review and results of a recent survey and summary of expert opinions both lead to conclusions that are congruent with, but stronger, than our *Issues in Ecology* report.

One school of thought, not two

The "diversity debate," as Wardle et al. have chosen to call it, is not described correctly. Wardle et al. describe a debate in which one party subscribes to a "population biology" perspective, while another subscribes to an "ecosystem property" perspective, suggesting that such perspectives are mutually exclusive. This description is incorrect. The panel members represent, in much the same way Wardle et al. do, a group of scientists who combine population and ecosystem perspectives in their own research and writings. The "debate" Wardle et al. refers to more accurately reflects issues concerning the disentanglement of the functional and taxonomic components of biodiversity. Some studies (Naeem and Li 1997, Tilman et al. 1997*a*, Symstad et al. 1998, Naeem et al. 1999) have simultaneously manipulated both functional and taxonomic diversity, and have argued that variation in functional diversity or functional identity of species can be a dominant factor in ecosystem functioning. Studies that have manipulated only functional groups (Hooper and Vitousek 1997, 1998, Hooper 1998) suggest that the strongest biotic influences of ecosystem functioning concern functional properties of species. Many studies have shown an asymptotic relationship between species richness and ecosystem functioning, but not all (Schläpfer and Schmid 1999). All of these points are raised in the report (see below). Functional and taxonomic diversity are, however, inextricably linked. As one randomly increases species, invariably functional group representation will increase.

The importance of functional diversity is not a new idea, and has been examined and discussed by many researchers (Raunkier 1934, Root 1967, Körner 1993, Smith et al. 1993, Chapin et al. 1996, Mooney et al. 1996, Hooper and Vitousek 1997, Smith et al. 1997, Hooper and Vitousek 1998), and has important bearing on many issues in ecology, not just biodiversity and ecosystem functioning (Barbault et al. 1991, Walker 1992, Lawton and Brown 1993, Cowling et al. 1994, Andren et al. 1995, Beare et al. 1995, Walker 1995, Gitay et al. 1996, Jaksic et al. 1996, Ehrlich and Walker 1998, Mikola and Setälä 1998, Naeem 1998). The studies by Grime, Wardle, Berendse, Mikola, Hooper, Setälä, and their colleagues cited by Wardle et al. also make important contributions to this literature. These studies, however, are often not related to the issues surrounding the ecosystem consequences of declining biodiversity, nor are they in conflict with the report. As defined by the report, biodiversity refers to the "genetic and functional diversity across population, community, ecosystem, landscape, and global scales." The majority of studies have shown that change in biodiversity, whether it be functional or taxonomically defined, can affect ecosystem functioning, and the report summary claims no more than this.

Creating dichotomies, although a useful heuristic device, generally misrepresents scientific exchange. Labels such as "population" vs. "ecosystem" or "functional diversity" vs. "species diversity" reflect endpoints of a continuum, not discrete schools of thought. There is only one school of thought, and that is that composition and nature of the earth's biota, or biodiversity, contributes to ecosystem functioning.

Correlational studies and other evidence

Evidence by which fundamental principles in ecology are derived consists of a blend of theory, simulation, experiment, and observation. The trade-offs, known as internal vs. external validity (Manly 1992), prevent either pure theory or pure observation from providing reliable insights into the mechanisms that govern and permit us to predict community and ecosystem properties (Naeem, *in press*). These issues are well known, and several volumes review and discuss them (Hairston 1989, Peters 1991, Manly 1992, Scheiner and Gurevitch 1993, Hilborn and Mangel 1997, Underwood 1997, Resetarits and Bernardo 1998). The need for experiments in ecology is well known, and panel members, as well as Wardle et al., have contributed to theory, simulation, experimental, and observational studies.

In the section entitled, "Observational studies," we explicitly acknowledged that correlations between biodiversity and ecosystem functioning can show a variety of relationships. We state, however, that it is difficult to control statistically for confounding effects; therefore we turn our attention to experimental results for further insight. Interestingly, a figure presenting results from six studies, three observational and three experimental, was included in the original document, but the science writers, editors, and peer reviewers all strongly advocated removal of this figure. We regret Wardle et al.'s dissatisfaction with the collective decision of many individuals not to discuss the classic arguments concerning the relative merits of descriptive vs. experimental, but perhaps they may appreciate that this small brochure simply cannot accommodate extensive coverage of such a complex issue.

Curiously, Wardle et al. claim that decomposers were inadequately covered. Both the panel members and Wardle et al. have examined decomposers and the rates of decomposition in experimental studies and recognize the importance of these organisms and associated ecosystem functions. Fig. 5, for example, shows decomposers to be as important as producers, and the lead text (page 4) clearly indicates that plant production, decomposition, and other processes are the primary functions of interest. Furthermore, in "Future Research," the brochure expressly lists decomposers along with consumers as important areas for further development to address uncertainties.

A few recent studies (Van der Heijden et al. 1998, Naeem et al. 2000) have suggested that decomposer diversity, or perhaps more importantly, detritivore identity and composition (Mikola and Setälä 1998), are quite important to ecosystem studies. Studies of rates of decomposition in which biodiversity was manipulated have reported negative (Naeem et al. 1994) or weak trends (Knops et al., *submitted*, Hector et al., *in press*). One study manipulated diversity of plant litter and found little evidence for effects of plant litter diversity on decomposition processes (Wardle et al. 1997*a*), which is largely in agreement with other findings. In comparison to plant studies, however, this research, although well known to the panel members, is not as well developed.

Agro-ecological studies were not discussed in the report because their findings are mixed and the diversity of manipulated plants is seldom more than two or three species, although many studies show greater production with greater diversity (Swift and Anderson 1993). Of larger concern is that agricultural research is biased toward looking for overyielding and conducts its research on heavily managed soils, all of which makes the interpretation of this literature difficult. Finally, although the agricultural literature is well known to the panel, the report was clearly concerned with the loss of diversity from unmanaged ecosystems. The cover and Figs. 2 and 3, for example, clearly show that the report considers agro-ecosystems as the lower boundary for diversity. Thus, agricultural research is not readily adaptable to the needs for this report.

Wardle et al.'s sense that decomposers or agro-ecological research were not treated sufficiently is a matter of opinion, but we suggest that inspection of the report will reveal otherwise and should allay their concern. The report defines a strong and important role for decomposers and calls for further work in this important area. The report considers agroecosystems and associated literature to be quite distinct from biodiversity research.

Conclusions and a look to the future

The production of a report such as the *Issues in Ecology* report on biodiversity and ecosystem functioning is most likely unfamiliar to many researchers. Scientists are more familiar with agency, inter-agency, or governmental panel reports reflecting symposia, many iterations of report writing, and the production of longer volumes or reviews that contain executive summaries. *Issues in Ecology* is clearly quite different. An *Issues in Ecology* report does not permit lengthy discussions of technical issues or extensive coverage of exchanges among scientists, even though these are central to the scientific process. Contrary to Wardle et al.'s opinion, this report is very much in line with others in the series (Daily et al. 1997, Vitousek et al. 1997, Carpenter et al. 1998).

Expert opinion is provided by many scientific panels when urgency dictates the need for a summary of current evidence and a clear statement of majority opinion. As in most reports of this nature, the full richness of individual opinions is seldom found in such documents. Reports for the Intergovernmental Panel on Climate Change, for example, are frequently controversial. The Sustainable Biosphere Initiative (Lubchenco et al. 1991), though the product of an extensive process by the ESA, was also controversial, as Wardle et al. note.

Finally, we must note that our report reflects the concerns that Wardle et al. raise. Not only does the report explicitly address observational studies, decomposers, and the issues surrounding functional vs. taxonomic diversity; the tone of the report also reflects the need for caution, given differences in opinions on some issues. First, each bulleted point concerning current research uses the word "may" to acknowledge that the verdict is still out on many issues. Second, the fourth bulleted point states, "the identity and abundance of species in an ecosystem can be as important as changes in biodiversity in influencing ecosystem processes." Third, in the *Summary*, the report states, "although these three points have been repeatedly observed . . . there is still debate about the mechanisms behind them." Fourth, the *Conclusions* state, "although a number of uncertainties remain, the importance of ecosystem services to human welfare requires that we adopt a prudent strategy of preserving biodiversity in order to safeguard ecosystem processes vital to society." Finally, five uncertainties are discussed (pages 9–10) that reflect issues raised by Wardle et al. and others.

I hope that the comments in this paper clear up the "curiosity" expressed by Wardle et al. about the production of such a document. Certainly it should inform others who engage in such a process that providing accessible summaries of contemporary issues in the ecological sciences is difficult. The accumulation of additional experimental data and the development of effective theory will provide us with the tools necessary to better explain and predict the ecosystem consequences of declining biodiversity. The panel members, Wardle et al., and many others will continue to work toward a clearer understanding of this potential role of biodiversity, and hopefully a rich and lively exchange will continue.

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To Bonferroni or Not to Bonferroni: When and How Are the Questions

Statistical tables (e.g., ANOVA, regression, correlation coefficients, and chi-square values) are commonly reported in *Ecology* and similar journals. Rice (1989) pointed out that tests for the statistical significance of individual components of such tables are often biased, so that too many of these components are considered "significant" (i.e., the null hypothesis is rejected when it is actually true, or a Type I error). As an example, he noted that in a hypothetical table of 10 correlation coefficients, there is a 40% probability of observing at least one significant ($P < 0.05$) individual correlation by chance alone. Rice detailed a sequential Bonferroni correction procedure (originally developed by Holm 1979) to control this problem while simultaneously maintaining adequate power to correctly reject one or more false component null hypotheses within a given statistical table.

However, Rice (1989) noted that, as pointed out by Miller (1981), there is no clear criterion for deciding exactly what constitutes a family of statistical tests, nor is it clear when a simultaneous-inference test such as the sequential Bonferroni correction is required. He argued that such choices depend upon the desired group-wide Type I error rate, and suggested that simultaneous inference be employed whenever:

1) a group of two or more tests is scanned, and the P values of component tests are used to determine where significant differences occur (i.e., a posteriori testing), or

2) two or more tests (that cannot be pooled) address a common null hypothesis, and rejection of the null hypothesis is possible when only some of the tests are found to be individually significant.

Our goals in this note are to (1) assess the extent to which the use of Bonferroni corrections has increased following Rice's (1989) widely cited paper; (2) examine the level of agreement on when and how to employ Bonferroni corrections; and (3) offer some recommendations for dealing with multiple tests of significance. We will focus on the more conceptual/philosophical side of these issues, and will not attempt to evaluate the various methodologies available for performing Bonferroni significance corrections. (For an examination of these more technical aspects, see discussion and references in Holm 1979, Miller 1981, Simes 1986, Hotchberg 1988, Wright 1992, and Scheiner and Gurevitch 1993.)

To assess the extent to which Rice's (1989) paper affected the subsequent use of Bonferroni corrections, we used the JSTOR database to perform full-text searches for the word "Bonferroni" in all *Ecology* papers published between 1920 and 1999. We then manually examined each flagged paper to determine if and how Bonferroni corrections were performed. Since there were no papers containing the word "Bonferroni" prior to 1982, we divided the remaining years into two time periods to examine the change in usage of Bonferroni corrections before and after Rice's (1989) sequential Bonferroni correction procedure. Between 1982 and 1989, we found a mean of 2% of