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Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function

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Abstract

I examine a number of problems that need to be identified and accounted for when examining the relationships between diversity and ecosystem function. Among these are measures of diversity and complexity in ecosystems: species richness, diversity indices, functional groups, keystone species, connectance, etc, all of which may be difficult to relate to ecosystem function. Several important distinctions, when testing diversity–function relationships empirically, are discussed: Diversity of functional groups, diversity within functional groups vs. total diversity; manipulating variables such as body-size distributions vs. manipulating diversity per se; effects of diversity vs. effects of biomass; and diversity–function relations under stable vs. changing conditions or perturbations. It is argued that for the management and development of sustainable ecosystems, it is probably more important to understand the linkages between key species or functional groups and ecosystem function, rather than focusing on species diversity. This is because there are possible mechanistic relations between what species do in ecosystems and ecosystem function. Diversity, being an abstract and aggregated property of the species in the context of communities and ecosystems, lacks such direct relations to ecosystem functions. © 1998 Elsevier Science B.V.

1. Introduction

The relationships between diversity, complexity, stability and ecosystem function have, in various disguises, been some of the fundamental questions in the history of ecology. They are central to both community and ecosystems ecology and need to be understood to predict, for example, how communities and ecosystems respond to environmental change. In recent years, the recognition that species may play important roles in ecosystems and the rapidly emerging interest in the preservation of biodiversity have prompted ecologists to ask new questions on the relationships between 'diversity' and 'ecosystem function' (whatever these mean) (for example, Walker, 1992; Schultze and Mooney, 1993; Jones and Lawton, 1995; Johnson et al., 1996). One reason for the interest in the functional role of biodiversity (rather than species) in ecosystems is that society might be more likely to take action to preserve biodiversity if it could be shown that there was some direct economic gain by doing it.

Although there are cases of clearly stated and experimental tests of hypotheses about the relationships between diversity and ecosystem function (e.g.

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Naeem et al., 1994a; Tilman et al., 1996), several authors have pointed out that the development of operational concepts, testable hypotheses and clearly defined variables remains a problem in this field of research (Gaston, 1996a, b; Martinez, 1996). In this paper, I will discuss some of the problems that need to be addressed in examining diversity–function relationships. Many of my points have also been discussed by others, e.g. Lawton (1994), Lamont (1995), and Martinez (1996). For the purpose of this paper, ecosystem functions are loosely defined as ecosystem processes and ecosystem stability. Thus, for a soil ecologist the important issues concern (i) whether the diversity of species or functional groups of decomposers and soil animals affects the rates of processes such as decompostion and nutrient cycling and (ii) if diversity affects how process rates or community composition of soil organisms respond to perturbations such as climatic change or introduced species (see Martinez (1996) for a detailed discussion about defining function in ecosystems).

Scientific examinations of a phenomenon have (at least) two goals: one is to make predictions about the phenomenon into the future and under new circumstances, the second is to understand *why* such predictions can (or cannot) be made. These goals are often intertwined and cannot be separated. I will argue that examinations of the relationships between diversity and ecosystem function are made more difficult and conceptually problematic because there is no direct mechanistic relationship between diversity and ecosystem function. Most previous studies of diversity–ecosystem function relations have not examined the crucial component for mechanistic explanations of these relationships (the '*why*' component), namely, species and the effects that species (not diversity) have on ecosystems (although possible mechanisms were discussed by, e.g., Naeem et al., 1994a and Tilman et al., 1996). As a first step, quantifying relationships between diversity and a number of ecosystem functions is of interest. However, for the long-term goal of managing and developing sustainable ecosystems, it is probably more important to understand the linkages between key species or functional groups and ecosystem function, rather than focusing on the species' diversity as such. Chapin et al. (1996) emphasized that ecosystem sustainability may depend on a fairly small number of interactive controls. In soils, some examples are earthworms, bacterivorous nematodes or mycorrhizal fungi, all of which have been shown to affect ecosystem processes.

2. What measure of diversity should be related to ecosystem function?

There are several different aspects of diversity and ecosystem complexity that can be used to explore the relations between ecosystem function and diversity: species richness, a variety of diversity indices, the presence of particular keystone species, the number of functional groups, food web connectance, etc. In this section, I will discuss the pros and cons of these measures, with emphasis on a number of problems that need to be understood when examining diversity–function relations.

2.1. Species richness

Species richness is, in principle, a well defined and frequently useful measure of diversity that is often thought to capture much of the essence of biodiversity (Gaston, 1996b), even though it is unlikely that all species in even a single ecosystem will ever be identified and counted. The possible forms of the relationship between species richness and ecosystem function have been much discussed (in my view too much) in the recent literature (e.g. Vitousek and Hooper, 1993; Lawton, 1994; Johnson et al., 1996; Martinez, 1996). The problem is that attempts to quantify these relationships at first glance seem scientific and valuable, but at closer scrutiny they may, in fact, not be very interesting.

These attempts can be questioned from different perspectives. First, the use of species number as an indicator of an ecosystem's diversity suggests that all species are potentially equal with respect to function. Is one earthworm species equal to 0.5, 1, 10 or 100 species of mites or fungi? One of the reasons that interest in island biogeography declined rapidly a decade ago was that the theory did not take into account the identities of species, when community ecologists had repeatedly shown that, for example, species of predators and plants could not be treated as equivalent. Assuming all species are equal with respect to function is repeating the same mistake.

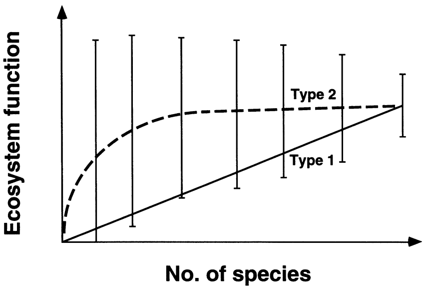

Fig. 1. A hypothetical example of an attempt to quantify the form of the relationship between an ecosystem function and diversity. The Type 1 curve represents the hypothesis that all species are important for ecosystem function, while Type 2 is the species redundancy hypothesis. The bars indicate the range of responses as different numbers of species are randomly drawn from a source pool of species, given that species effects on ecosystem function are mainly species-specific (idiosyncratic) and not related to diversity. Note that although an average response may be observed, it neither allows a distinction between the two different hypotheses (Type 1 and Type 2), nor does this average response allow any useful prediction of what will happen in individual cases of species deletions.

Second, too much focus on the forms of the relationship may easily degenerate into a sterile debate without much scientific substance. There are more important questions for ecology than determining whether the relation between species richness and particular function is of Type 1, or Type 2 (Fig. 1), or Type 3, 4, . . . n. Unless we know more about what species actually *do* in ecosystems, such exercises are of doubtful value.

Third, the forms of the relationship may be different for different functions such as decomposition, nitrogen mineralization or primary production. We may not even agree on what the important functions are. Consider, for example, the intimately coupled processes of decomposition and nutrient mineralization, both of which are components of ecosystem productivity and turnover of organic matter and nutrients. Many soil ecologists would probably agree intuitively that high decomposition and nutrient mineralization rates are desirable for ecosystem productivity, and that high diversity may be positively related to nutrient mineralization rates (e.g. Setäla and Huhta, 1991). However, if we consider it desirable that soils store carbon to negate the consequences of global warming, or that nutrients are not mineralized because of risks of leaching to surface and ground water, the situation is reversed. Discussions on the forms of the relationships can easily become muddled and mixed with social issues that have wider connotations than the purely scientific ecological questions we are addressing.

Fourth, the species concept as such may be problematic (e.g. Gaston, 1996b). For soil microorganisms, this is well known, but defining species may be difficult also in many soil animal groups. Some examples are mites and collembola, where a number of species are parthenogenetic (Siepel, 1994). Counts of the ‘number’ of ‘species’ is difficult when there are ‘species’ consisting of asexual clones.

Finally, and most important, what do we do if the effects of species diversity on ecosystem function is idiosyncratic (Lawton, 1994), that is, if species’ identities rather than diversity matters? Quantifying the form of the relationship would in this case be possible, but hardly meaningful in the sense that we would be able to predict anything useful from measuring species richness. For example, if there is a particular species or group of species that have a large effect on a particular ecosystem function, their position on the diversity axis will determine the form of the relationship. As pointed out by Lawton (1994), it may be possible to estimate the average effects on a function of a certain number of randomly drawn species, but if the variability around these averages is large because of the idiosyncratic effects of some of the species, this average will not be very informative. Furthermore, as illustrated in Fig. 1, it may be difficult to distinguish between the different hypothesized forms of the average relationship.

Martinez (1996) suggested that a generally acceptable convention for arranging species along the x-axis of Fig. 1 would ameliorate the situation. For example, a ranking of species according to the likelihood that they will disappear from the ecosystem (defined at a particular spatial scale) in response to perturbations, i.e. ranking by extinction probabilities, is a possibility, although I find it unlikely that we will be able to estimate local extinction rates for the majority of the species in diverse ecosystems. On the other hand, it may be possible to use some other variables for describing extinction risk, such as body size, local abundance or population variability, to rank species along the x-axis. This may ultimately allow more accurate quantification of diversity–function relationships, and the degree to which species have species-specific idiosyncratic effects on ecosystem function (see also the discussion of keystone species below).

Measures of diversity using diversity indices (e.g. McNaughton, 1993) have the same problems as species richness measures. However, here there is also the problem of interpreting what the indices actually indicate. For example, does the evenness or richness component, or both, relate to function? And why should we expect a community's evenness as such to be related to ecosystem function?

2.2. *Keystone species*

Keystone species can be defined in different ways. Some have suggested that they are species whose effects on their communities or ecosystems are much larger than expected from their abundance or biomass (Power and Mills, 1995). However, this definition does not necessarily include species that are dominant in ecosystems, for example, beech in beech forests. Thus, it is probably better to define keystone species as species which have large effects on communities or ecosystems. Focusing on keystone species in relation to ecosystem function makes it possible to account for the idiosyncratic effects of individual species. However, I cannot see any obvious relations between the number of keystone species and ecosystem function, apart from those associated with idiosyncratic species (see above) or functional groups (see below).

According to Folke et al. (1996), a limited number of organisms and groups of organisms seem to control the critical processes necessary for ecosystem functioning. They termed these species 'keystone process species', the set of which may be changing over time or space. Among such species are the 'ecosystem engineers' (e.g. Lawton, 1994; Jones and Lawton, 1995), classical keystone species (Power and Mills, 1995), species such as earthworms acting as interactive controls (Chapin et al., 1996), or those involved in what is popularly termed trophic cascades (e.g., certain fish and *Daphnia* species in lakes; Carpenter and Kitchell, 1993). Identifying keystone process species and quantifying their effects is urgently needed for linking species and ecosystems, and for managing ecosystems sustainably, but does not necessarily have any bearing on the diversity–function question.

2.3. *Functional groups*

Functional groups are usually defined with respect to some ecosystem function (e.g. Moore and DeRuiter, 1991; Bengtsson et al., 1995). This imposes some degree of circularity when ecosystem function is explained by the diversity or presence of certain functional groups. Nonetheless, using the diversity of functional groups (i.e. the number of functional groups) in an ecosystem provides a link between a measure of diversity and function, although the tests for the effects of functional group diversity may actually test our ability to properly define functional groups, rather than the effects of diversity. I personally believe that using some measure of functional diversity in the ecosystem will be the most efficient and useful way to relate diversity to ecosystem function.

There are however drawbacks. Functional groups are aggregated units, and their definition has a degree of arbitrariness, no matter how careful we are. How detailed can we be when we define functional groups? In reality, no species (or individuals) are identical and each may be regarded to have a different function, if we really want them to. The aggregation problem is common to most areas of ecology, and there is no simple solution. Furthermore, as with species, the functional groups defined with respect to one particular function may not be the same as those defined with respect to another function.

There is no definition of functional groups that is generally agreed upon. Nonetheless, some kind of food web is probably a good starting point for defining functional groups. Feeding is a most important ecological process, being an essential component in both the consumer–resource interactions of population–community ecology and in the energy and nutrient transfers of ecosystems ecology. In grassland and agricultural soils, the food web models developed by e.g. Hunt et al. (1987), Moore and DeRuiter (1991), and DeRuiter et al. (1993, 1995) were used for defining functional groups. With some modifications, these models are also useful in forest soils (Persson et al., 1980; Bengtsson et al., 1995). The functional groups thus defined are based on fairly accurate information on many species, but still most such groups are very aggregated. Many ecologists are not satisfied with such webs containing 10–20 very aggregated functional groups. It would be very useful if functional groups could be defined more stringently.

Functional groups can be defined in other ways than in terms of feeding relations. Ecosystem engineers such as termites and earthworms have effects on carbon and nutrient distributions and soil structure that cannot be solely attributed to feeding interactions (Anderson, 1995). These non-trophic effects need to be included in the concept of functional groups to make it more useful. Furthermore, it would be desirable to include some measure of the strengths of the consumer–resource and non-trophic interactions when defining functional groups. Additional factors that may be useful are microhabitat distributions (Faber, 1991), life history traits (Hunt et al., 1987; Moore and DeRuiter, 1991), and physiology. Among plants, the pros and cons of different classifications have been discussed by, e.g. Woodward and Cramer (1996).

Using the food web approach, Martinez (1996) suggested that species may be assigned to functional groups by using standard quantitative statistical methods to examine similarities and differences in feeding relations or substrate utilization. It should be possible to incorporate non-trophic effects, interaction strengths, microhabitat distributions, and other relevant variables, provided such knowledge exists for many of the species in the system. If this could be done even for a small number of food webs in soils, the usefulness of the functional group concept to examine diversity–function relations would be substantially enhanced. However, as Martinez points out, such assignments still have some degree of arbitrariness. Choosing how similar two species should be to be placed in the same functional group is one example.

All this shows that it would be desirable if soil ecologists were able to provide the information needed to define functional groups in consistent ways, and then proceed to examine the relations between the diversity of functional groups and ecosystem function for whole communities and food webs. However, the construction of interaction webs for soil systems based on consistent definitions of functional groups, not only in terms of feeding but also on other activities, is an immense task. Collaborations between a large number of soil ecologists will be required, and can lead to important advances.

2.4. *Food web complexity*

Some time ago, it was believed that food web theory could shed light on the relationship between complexity (in terms of feeding relations) and stability in ecosystems, using species richness and food web connectance as measures of complexity (e.g. May, 1973; Pimm, 1982). If this was the case, it would also be relevant for the diversity–function issue. In soils, this issue has been examined by Moore and Hunt (1988) and DeRuiter et al. (1993; this issue), who argued that real soil food webs are stable because of compartmentation and variation in interaction strength across trophic levels. In recent years, food web theory has been severely criticized (e.g. Hall and Raffaelli, 1996), and it is at present doubtful whether it is useful for examining these questions. However, better knowledge of patterns of interaction strength in food webs may provide new insights in the future.

3. Ecosystem functions may be related to diversity in different ways

I have until now avoided defining ecosystem function rigorously and explicitly – a good example of most discussions about functional implications of diversity being too general. When asking scientific questions about diversity and function, we should always ask: 'Which function?'. Many functions or 'ecosystem services' are provided by the various components of ecosystems, and there is no reason to expect that individual species or diversity have the same relation to different functions. For example, why should the effects of a species or functional group be the same on rates of ecosystem processes (productivity, decomposition, nutrient cycling, transfers between trophic positions), on ecosystem stability (resistance, resilience), on community composition and on community stability? Yet all are interesting scientific questions in their own right. Defining the particular function we are relating to diversity means that we acknowledge that effects may differ depending on what we are interested in. Also, it makes it easier to delineate the domains of what we are studying. The problem in studying these relationships is not that there are many functions and measures of diversity, but to avoid confounding them and making or rejecting generalizations too early (see also Martinez, 1996).

4. Some important distinctions when testing diversity–function relationships empirically

When we examine questions about diversity and ecosystem function, it is important to understand and define what we are actually testing for. We require good experimental designs and appropriate statistical tests (Lamont, 1995). It should be possible to explain the observed results by underlying processes at lower levels of organization, i.e. we should address the '*why*' component, not only correlate diversity and ecosystem function. To be able to do this, some important distinctions need to be understood.

4.1. Diversity of functional groups, diversity within functional groups vs. total diversity

Does it matter for a function if we have one or ten nitrogen-fixing plant species? Or one or ten species of fungivorous Collembola? Does it matter if there are one or ten functional groups of bacteria? Or one or several functional groups of insect predators? Or do we just need many species, without explicit regard to which functional groups they belong?

Questions such as these address some points that, up to now, have not been given enough attention. For example, interpretation of the innovative Ecotron experiment (Naeem et al., 1994a) is made more difficult because some functional groups of plants appear to have been absent in the low-diversity treatment (André et al., 1994, but see Naeem et al., 1994b). Separation of the effects of low vs. high diversity within functional groups and the effects of the diversity of functional groups is needed in future studies.

Provided we have an idea as to which species should be assigned to which functional groups, these questions may appear to be obvious candidates for a good factorial experiment. Unfortunately, the number of possible treatments is so large that such experiments will rapidly run amok. Nonetheless, experiments separating the effects of species richness and the presence of functional groups are urgently needed. A number of laboratory microcosm experiments with similar protocols but with different organism groups could in a short time shed light on these issues.

4.2. Manipulating variables such as body-size distributions vs. manipulating diversity per se

Litterbag studies have a long tradition in soil ecology, and have sometimes been used in examinations of the relationships between diversity and ecosystem function (e.g., Andrén et al., 1995). However, a major problem with such 'exclosure experiments' is that manipulations of diversity and of other components of community composition are likely to be confounded. Litterbags mainly manipulate body-size distributions of soil animals, and any diversity manipulation is a by-product. Body-size distributions in ecosystems are of substantial interest (Holling, 1992), and body-size has long been recognized as a key feature of organisms in soils (e.g. Swift et al., 1979). However, body-size distributions and diversity are clearly not the same thing. In fact, body-size distributions may have mechanistic relations to ecosystem functions, such as energy flow, nutrient cycling and decomposition, because feeding and physiological rates vary predictably with body size (e.g. Peters, 1983). Diversity lacks such direct mechanistic relations to function.

4.3. Effects of diversity vs. effects of biomass

Experimental tests of diversity-process rate relations need to separate effects of diversity (keeping biomass constant) and biomass (keeping diversity constant). This is because most rates of ecosystem processes are mechanistically related to biomass - through uptake, feeding and physiology. There are no such clear relations between measures of diversity and process rates. Thus, an essential ingredient in this kind of experiment is having treatments with similar initial biomass distributed over different numbers of species or functional groups. If differences in process rates with diversity are found despite similar initial biomass, this would indicate that diversity is of importance, i.e. the species are not similar and complementary with respect to function.

4.4. *Diversity-function relations under 'stable' vs. under changing conditions or perturbations*

Examining diversity–function relationships under stable or equilibrium conditions will not tell us very much. Under such conditions it is likely that a small number of key species have considerable effects on ecosystem functions. The crucial question is whether more diverse ecosystems are more resistant or resilient when environmental conditions change (Folke et al., 1996). Hence Tilman and Downing (1994) asked the right question, although they did not use a good system to test it (as is evident when reading Tilman et al., 1996). In the context of a changing global climate and other large-scale environmental perturbations, the important questions pertain to whether the resistance or resilience of ecosystem processes, or other aspects of ecosystem function, depend on diversity. However, this imposes some difficulties for the whole enterprise of relating diversity to ecosystem function. It is impossible to know what changes in climate or what large-scale perturbations that natural and managed ecosystems will experience in the future. Hence it is difficult to predict which species will be of importance in the future. This was elegantly shown in a 10-year experiment on lake acidification (Frost et al., 1995). Secondary production remained fairly constant as pH dropped from 6.1 to 4.7, but zooplankton species composition changed dramatically. It was not possible to predict the few dominant species under acidified conditions from knowledge about the initial conditions when these species were rare.

This crucial question of resilience and diversity should be given the highest priority. Field experiments are highly desirable whenever they are possible to carry out, but in many cases controlled manipulations of diversity and perturbations of the system will have to be performed in the laboratory. Both soil microcosms and larger climate chambers such as the Ecotron (Naeem et al., 1994a) would be appropriate. Problems with manipulating diversity have been discussed above, and can be avoided. Choosing perturbation is probably a matter of taste, although it is likely that different perturbations, such as freezing (Allen-Morley and Coleman, 1989), drying, heating, or application of pesticides or heavy metals, will yield different results when measuring resistance and resilience. The ideal experiment would be using the same soil system, crossing functional diversity and species richness with several perturbation treatments, and examining the effects at both the community and ecosystem levels.

5. Concluding remarks: are we asking the right questions?

Many of the above considerations lead me to a conclusion that may, at least at first sight, be slightly worrying and politically incorrect: When we ask if diversity plays a role for ecosystem function we are in fact asking the wrong question.

Diversity does *not* play a role for ecosystem function, and there is no reason to expect that it does. Species may be important for ecosystem function, but diversity is an abstract aggregated property of species in the context of communities or ecosystems – there is no mechanistic relationship between diversity and ecosystem function. It is naive to contemplate that one single number – species richness, a diversity index, the number of functional groups, or connection – can capture the complex relationships and interactions between many species and the functions performed by these interactions. In fact, it negates most ecological research since the 1960s. Correlations between diversity and ecosystem functions – which may very well exist – will be mainly non-causal correlations only. This is because diversity and ecosystem function are not linked directly, but through the species and functional groups whose interactions provide most of the mechanisms for ecosystem functions (Fig. 2). It is, therefore, the effects of different key species or groups of species we should be looking for. A focus on functional groups and species such as keystone species or ecosystem engineers is probably the most efficient way of providing more mechanistic explanations (at the community, population and individual levels) of ecosystem processes and stability. I strongly believe that the most important scientific issue in research on biodiversity and ecosystem function is to provide such mechanistic explanations.

One practical reason for focusing more on functional groups and individual species is the recently raised questions on sustainability of managed and natural ecosystems (e.g. Goodland, 1995; Vandermeer, 1995; Chapin et al., 1996). A sustainable manage-

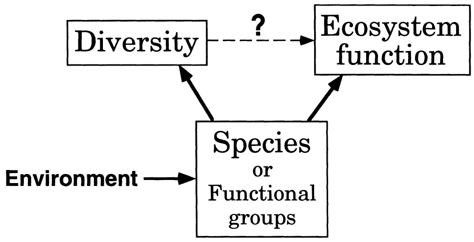

Fig. 2. Diversity and ecosystem function has no direct relationship to each other, but both are functions of the presence and activities of species and functional groups, and their interactions. The environment affects species and functional groups, and the outcomes of their interactions, but not diversity or ecosystem function directly. The question mark indicates the question whether diversity and function are related. The effects of species and functional groups on the environment (apart from their effects on ecosystem functions) have been omitted for clarity. The omission does certainly not imply that these effects are less important.

ment of ecosystems will require knowledge of the effects that key species have in ecosystems, i.e. mechanistic explanations of ecosystem processes, not non-mechanistic correlations between diversity and ecosystem processes. In soil ecology, there is a long tradition examining the linkages between the composition of the soil organism community and the functioning of the ecosystem (e.g. Persson et al., 1980; Coleman et al., 1983; Moore and DeRuiter, 1991). Therefore, rather than excessive focus on the effects of diversity on ecosystem function, we should concentrate on continuing and expanding the studies of species and functional groups in soils.

Another reason for focusing on the effects of species and functional groups on ecosystem function is that a theory on these issues is emerging, albeit slowly. It appears that analyses of ecosystem processes in soils can be based on consumer–resource interactions derived from population ecology, provided that recycling of carbon and nutrients are incorporated (DeAngelis, 1992; DeRuiter et al., 1995; Zheng et al., 1997). Thus, theoretical predictions concerning the effects of species or functional groups on process rates may be possible, and can be tested empirically. This seems unlikely in the case of diversity.

Does all this imply that diversity is of less importance? Certainly not. However, the main importance of diversity is not that it in itself has a function in ecosystems, but that high diversity implies that there is a source of new species performing functions or ecosystem services as human needs or environmental conditions change (Frost et al., 1995; Folke et al., 1996). Although it is possible to regard this provision of 'natural insurance capital' (Folke et al., 1996) as a functional role of diversity, such an argument lacks scientific content unless diversity is linked to what species do in ecosystems.

It has already been pointed out that it is difficult to predict which species will be important for ecosystem functions as environmental conditions change, even in fairly well-studied types of ecosystems. But even if we could predict this, it would be arrogant to expect that we can predict all future environmental conditions. Hence, preserving biodiversity as an insurance is a matter of caring for the future, in addition to the present.

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