

Biological diversity and probability of local extinction of ecosystems

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Summary

1. With a mathematical model, we demonstrate that two principle components of biological diversity have antagonistic effects on the probability of ecosystem functioning (i.e. on ecosystem reliability, *sensu* Naeem 1998). Increasing the number of functionally analogous species in the system is shown to enhance reliability, while increasing the number of functions or processes which these species support (functional diversity) has a negative influence.
2. Probability of functioning was calculated from the likelihood that essential ecosystem functions are lost, which was based on the probability of local extinction of the species that support these functions.
3. A third component of diversity, heterogeneity among extinction probabilities of different species, enhanced probability of ecosystem functioning for species belonging to the same functional group, but only in species-poor systems. In contrast, heterogeneity among species of different functional groups drastically reduced probability of ecosystem functioning and this reduction was more pronounced when more groups were present.
4. The model further predicts an asymptotic relationship between number of functionally analogous species and probability of functioning, rather than a linear or complex one. In case the species are very prone to extinction, saturation occurs at higher species numbers, which indicates there is less species redundancy in vulnerable systems.

Key-words: Functional groups, interspecific differences, mathematical model, species richness

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Introduction

Globally various types of anthropogenic disturbance threaten the diversity of biological systems (Soulé 1991; Barbier, Burgess & Folke 1994; Heywood 1995; Swanson 1995). The question of whether this degrades the functioning of these systems has become acute (Naeem *et al.* 1994, 1996; Schulze & Mooney 1994; Bolker *et al.* 1995; Hooper & Vitousek 1997; Tilman, Knops *et al.* 1997) and new perturbations like climate change may aggravate current losses of diversity (Peters & Lovejoy 1992; Gates 1993; Kareiva, Kingsolver & Huey 1993; Boyle & Boyle 1994). Particular features of ecosystems will become more critical as human pressure continues to increase and stability is probably the one most studied. Historically, lower diversity has been associated both with reduced (Hairston *et al.* 1968; Leffler 1977; McNaughton 1977; King & Pimm 1983; Frank & McNaughton 1991; Tilman 1996) and with enhanced (Hairston *et al.* 1968; May 1973; Leffler 1977; Pimm 1979) stability, mostly in theoretical studies that were focused on dynamic stability of populations.

In this paper, we do not concentrate on population dynamics, but on the influence of diversity on an ecosystem property that is also critical to performance, but which has received less attention: the susceptibility to losing ecosystem functions following local extinction of species.

Elton (1927) was the first to link diversity to ecosystem features, in this case to resistance to invasion. MacArthur (1955) suggested that a multitude of pathways for energy to reach a consumer would make a system less sensitive to the loss of one of these pathways. This raises the question of whether diversity also protects against *complete* loss of an ecosystem function and, by extension, against disappearance of the ecosystem itself if that function was essential. Such a protective role of diversity might ensue from a lower probability of losing all the supporting species to a given function, when more species are present. Direct evidence for this conjecture, however, is scanty. In aquatic microbial communities, McGrady-Steed, Harris & Morin (1997) measured less variable ecosystem respiration rates when biodiversity was enhanced.

Lower variability in functional properties may imply a reduced probability of ecosystem loss but one does not *per se* ensue from the other. Also using bacterial microcosms, Naeem & Li (1997) confirmed that ecosystems perform more consistently and fluctuations in population densities are dampened when multiple species represent each functional group. This was ascribed to compensatory growth of functionally equivalent organisms after an extinction. Contrastingly, extinction itself was higher in microcosms with more functional groups, indicating that functional diversity has an adverse influence. Mathematically, these results can be explained from the perspective of reliability engineering (Naeem 1998), which suggests that species redundancy indeed provides insurance against ecosystem 'breakdown'.

In this paper, we further analyse the influence of diversity on loss of ecosystem function. Two main components of diversity are assessed: one is the number of functionally analogous species in the system and the other the number of different functions which these species support (diversity within and between functional groups, respectively). In addition we introduce a third component of diversity, the degree to which species differ, and its influence on probability of functioning (reliability) is analysed for species belonging to the same or to different functional groups. Finally, we investigate how diversity affects the persistence of systems of which the functioning requires given minimum numbers of species. Our objective is to demonstrate that the relationships between components of diversity (species or functions) and probability of functioning can take a wide range of shapes, depending on the extinction probabilities (and their distribution) of individuals species.

Model development and results

IMPORTANCE OF THE NUMBER OF SPECIES WITHIN A FUNCTIONAL GROUP

Species which support the same function within an ecosystem can be considered as functionally analogous, thus constituting a 'functional group' (Huston 1994; Smith, Shugart & Woodward 1997). For example, symbiotically N-fixing plants support the biogeochemical function of atmospheric N input, deep-rooting species stabilize the soil and protect against erosion, etc. The probability that a particular function is lost not only depends on the probability of extinction of the species but also on their number or species richness. Given n is the number of species supporting a function F , p is the probability that a species disappears (for example owing to disturbance, competitive exclusion, gradual changes in growth conditions, etc.), I is a function indicator (1 if the function is preserved, 0 if it is lost, with $I = 1$ if $n \geq 1$ and $I = 0$ only if $n = 0$), then the probability of $I = 0$ equals p^n (probability that all n species which support

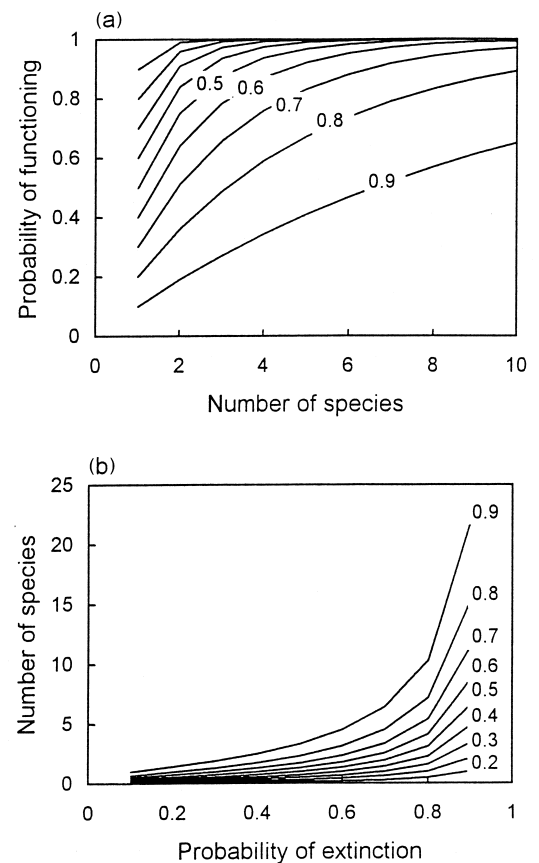


Fig. 1. (a) Relationship between probability (P) of ecosystem functioning and number of species. Simplified case where all the species are functionally equivalent and support one and the same function. The relationships are given for different extinction probabilities (p) of the species (curve labels); (b) number of species required to obtain a given P (curve labels), expressed as a function of p .

F , disappear). The probability that F is preserved ($I = 1$), is therefore:

$$P = 1 - p^n. \quad \text{eqn 1}$$

In this concept, P can assume all values from 0 to 1. Equation 1 requires that all the species which support F are substitutable, such that when part of them is lost, the remaining ones take over their role because they are functionally equivalent. Also, in a first approach, the extinction probabilities of the species were assumed similar and independent.

Figure 1 plots how, in a system with one functional group, probability of functioning changes with species richness and with extinction probability of the species. Although biological systems involve more functions supported by different groups of species, this simple case is modelled first and will then be extended to more complicated ones. From Fig. 1a, two conclusions can be drawn that automatically follow from equation 1: (1) P increases with n , so systems with more functionally analogous species are more robust, and (2) the P – n relationship is asymptotic, which confirms one of the general models proposed for diversity-functioning curves (Vitousek & Hooper

1994). The major change in P therefore occurs with transitions at low n , which is compatible with the intuitive appreciation that adding extra species to an already large pool will change relatively little. However, if the species are susceptible to extinction (high p), then the P – n curve saturates less rapidly, such that addition of species continues to enhance the probability of functioning up to higher n -values (less ‘effective functional redundancy’, cf. Lawton & Brown 1994). Therefore, systems can still be maintained under these conditions provided they contain many functionally equivalent species. This is demonstrated in Fig. 1b, showing the value of n required to obtain different target levels of P , expressed as a function of p :

$$n = \log(1 - P)/\log p. \quad \text{eqn 2}$$

At low to moderate p , the n – p relationship approximates linearity, hence the increase in species richness required to neutralize an increase in extinction probability, is almost constant. At higher p , this demand in terms of number of species becomes much higher.

IMPORTANCE OF THE NUMBER OF FUNCTIONAL GROUPS WITHIN A SYSTEM

The concept can be readily extended to a series of functions F_1, F_2, \dots, F_q , under the assumption that the whole system will fail in case at least one function is no longer maintained ($I = 0$ for a particular F_i , owing to extinction of all the species which support it). This implies that all F_i represent essential processes and that any ‘redundant’ functions, those of which the loss does not affect the performance of the whole, are not included in the analysis. An example of an essential function is stabilizing the soil, which relies on deep-rooting species. Loss of these species will make the system collapse under erosion, even if other species, which support different functions, are not directly affected by the event or process which made the deep-rooting species disappear. Following equation 1, the probability that a particular F_i does *not* disappear over a given time frame, is given by

$$P_i = 1 - p_i^n. \quad \text{eqn 3}$$

As a consequence, the probability that none of the F_i are lost equals:

$$P_{\text{total}} = \prod_{i=1}^q (1 - p_i^n) \quad \text{eqn 4}$$

and the probability that at least one F_i is lost is therefore $1 - P_{\text{total}}$. Only in this last case the whole is affected, because all F_i are essential. P_{total} thus represents the probability of maintaining the entire ecosystem, defined similarly to P in equation 1. In case one of the functions is supported by a single species only, the latter could be attributed the status of ‘keystone species’ (Paine 1966; Bond 1994), as it would then have a disproportionately large influence.

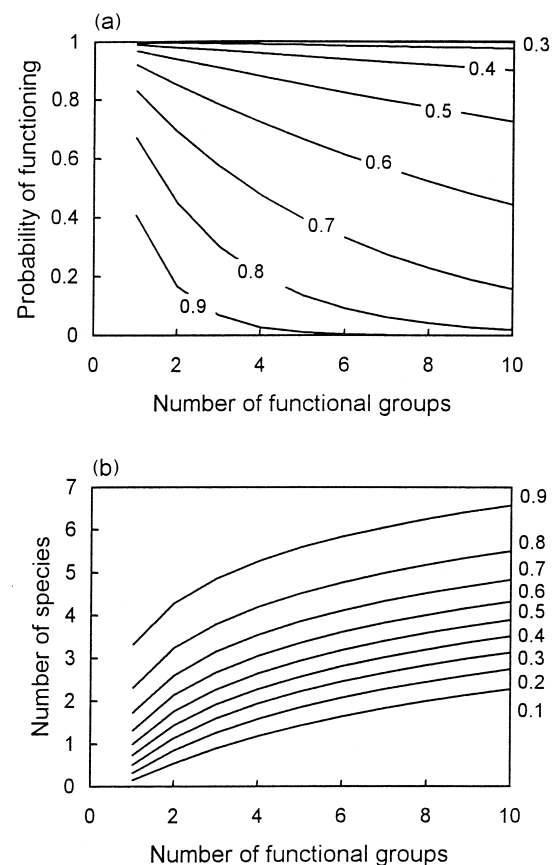


Fig. 2. (a) Probability (P_{total}) of functioning in ecosystems with several functional groups, which all support essential functions. Relationships between P_{total} and number of functional groups are given for different extinction probabilities (p) of the species (curve labels), but only for the case of five species supporting each function; (b) number of species for each function, required to obtain a given P_{total} (curve labels), expressed as a function of the number of functional groups in the system. The value of p was set at 0.5.

Figure 2a demonstrates that an increase in the number of essential functions (functional diversity or q) has an opposite effect on the probability of functioning compared to an increase in the number of species per functional group. The analysis is presented for the case that all n_i and all p_i are the same, so that $P_{\text{total}} = (1 - p^n)^q$, with $n = 5$ as an example. For a given p and n , an increase in q reduces P_{total} , which is evident because more functions can potentially be affected. This increases the risk of one particular function being totally lost. As a consequence, the required number of species to obtain a target value of P_{total} , calculated from equation 4 as

$$n = \log[1 - 10^{(\log P_{\text{total}})/q}]/\log p, \quad \text{eqn 5}$$

increases with q (Fig. 2b, shown for $P = 0.5$). Contrary to Fig. 1b, however, this increase saturates. The n – q curves in Fig. 2b constitute a contour diagram with isoclines of equal P_{total} , which demonstrates that varying n and q independently within the same system has opposite effects: n enhances P_{total} while q reduces it. Similar to P , the change of P_{total} with q also varies with p (Fig. 2a; the same is true for n , not shown).

Overall, the ranges of species richness, functional diversity and extinction probability of the species determine the shape of the curve.

INTERSPECIFIC DIFFERENCES WITHIN FUNCTIONAL GROUPS

Thus far it was assumed that species have identical p -values. Although extinction probabilities are probably more uniform within than between functional groups, total equality of p among species is unrealistic. For this reason, interspecific dissimilarities were introduced by varying p around a constant mean, first among species that support the same ecosystem function. The degree of interspecific difference can be considered as a third component of diversity. Figure 3 shows that more heterogeneous extinction probabilities among the species enhance the likelihood that ecosystem functioning is maintained in all cases, but more strongly in species-poor systems (compare Fig. 3a,b,c). That interspecific differences in extinction probability promote ecosystem reliability is not surprising, but its quantitative impact is less straightforward to appraise, and we demonstrate this with a simple example: in a two-species system with $p_1 = p_2 = 0.5$, $P = 1 - (0.5)^2 = 0.75$, while in a two-species system with the same mean p of 0.5 but $p_1 = 0.1$ and $p_2 = 0.9$, $P = 1 - (0.1 \times 0.9) = 0.91$. This higher P is clearly owing to the insensitive species with a p of 0.1, which is unlikely to become extinct, hence the probability that at least one of both species is maintained is higher. In quantitative terms, however, the probability distribution of the p -values has a much smaller impact on P than its average value (compare changes along the x -axis with changes between curves in Fig. 3). It is therefore concluded that interspecific differences within functional groups are of secondary importance.

INTERSPECIFIC DIFFERENCES BETWEEN FUNCTIONAL GROUPS

Dissimilarity between functional groups was introduced by the same procedure (varying p around a constant mean). Contrary to within-group differences in extinction probability between species, between-group differences have a considerable, negative influence on the probability of ecosystem functioning, especially at higher mean p -values (Fig. 4). This response pattern was independent of the number of species per function (not shown) but the decline in P_{total} with more heterogeneous p -values was considerably faster when more functional groups were present (Fig. 4a vs d). Why interspecific differences in extinction probability between groups deteriorate ecosystem reliability may be intuitive and its quantitative impact can be understood best with a similar example as in the previous paragraph: in a system with two functions and one species per function, with $p_1 = p_2 = 0.5$, $P_{\text{total}} = (1 - 0.5) \times (1 - 0.5) = 0.25$, while in a corresponding system with the same mean p of 0.5 but $p_1 = 0.1$ and $p_2 = 0.9$,

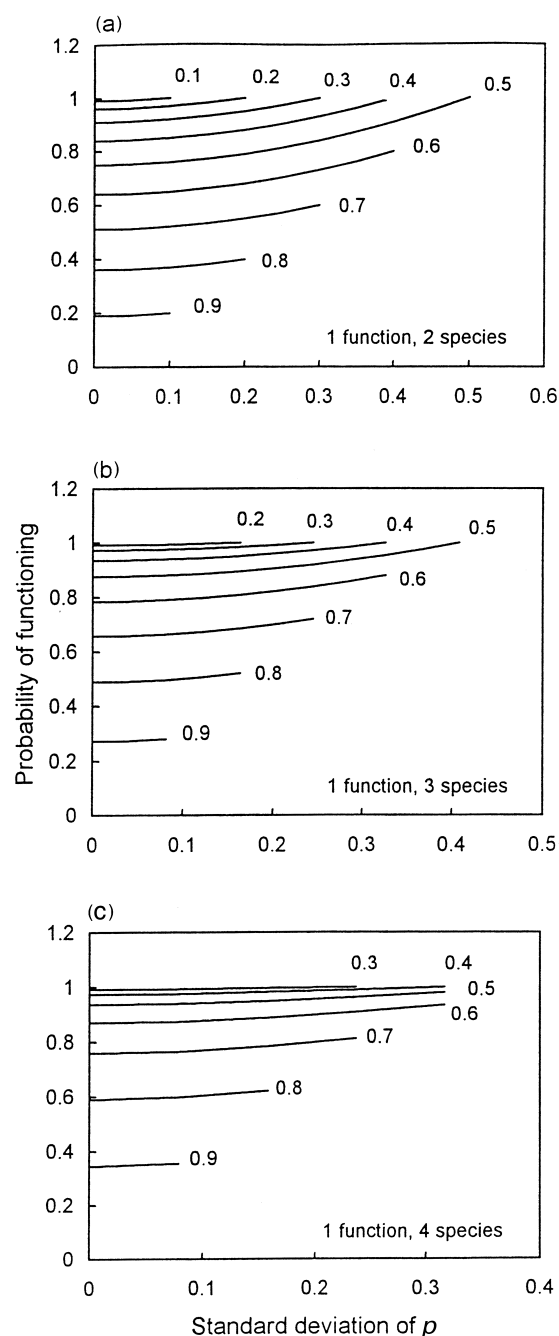


Fig. 3. Influence of heterogeneity in extinction probability among the species within a functional group on probability (P) of ecosystem functioning. Heterogeneity was introduced by varying the extinction probabilities (p) of the species, with steps of 0.05 around the mean. The degree of heterogeneity or interspecific dissimilarity was expressed as one standard deviation of p . Simulations are for systems with one essential function, supported by two, three or four species (a, b and c, respectively). Curve labels are the mean p -values.

$P_{\text{total}} = (1 - 0.1) \times (1 - 0.9) = 0.09$. In this case it is clearly the species prone to going extinct with a p of 0.9 which enhances the risk that at least one of the essential functions is lost. It is concluded that interspecific differences between functional groups can have an equally large (negative) effect on ecosystem reliability than the number of groups itself.

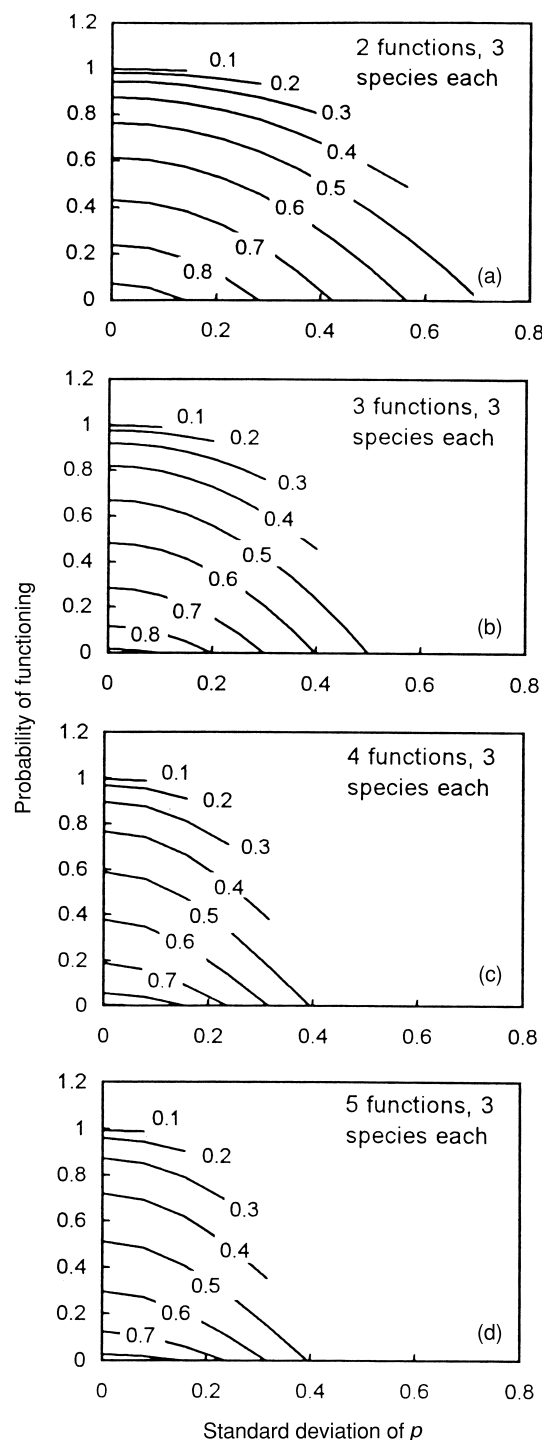


Fig. 4. Influence of heterogeneity in extinction probability among the species of different essential functional groups on probability (P_{total}) of ecosystem functioning. Heterogeneity was introduced and expressed similarly as in Fig. 3. Simulations are for systems with two to five essential functions (a–d) and three species per function in all cases. The p -values were varied between groups and kept the same within groups. Curve labels are the mean p -values.

FUNCTIONS THAT REQUIRE MORE THAN ONE SPECIES

Up to this point, an ecosystem function was lost only if all its supporting species become extinct, hence the

perpetuation of one species sufficed to maintain it. This assumes full compensatory growth, which may not always occur. To sustain some functions will require minimum number of species, other than just one (without necessarily assuming interactions between these species), and the probability of maintaining such thresholds can readily be calculated. Assume a system with one function, supported by n species with extinction probability p . The likelihood that exactly x species out of n persist, equals

$$P(x, n) = \binom{n}{x} \times (1-p)^x \times p^{n-x}, \quad \text{eqn 6}$$

with $\binom{n}{x}$ the number of different combinations of x species that can be drawn from n . The probability that *at least* x species out of n persist, is then given by

$$P(x, n)^* = \sum_{i=x}^n p(i, n). \quad \text{eqn 7}$$

Equation 1 was actually a special case of equation 7, because it expressed $P(1, n)^*$, or the probability that at least one species out of n is maintained (Fig. 1a).

In Fig. 5, we have plotted $P(x, n)^*$ as a function of n . Irrespective of the extinction probability of the species, the likelihood that a given minimum number of them is maintained invariably increases with the original species richness of the system. Similar to $P(1, n)^*$, $P(x, n)^*$ saturates at higher n if the species become more prone to extinction. A notable difference with the case in Fig. 1a, however, is the near impossibility of maintaining a function that requires more than just a few species, if the latter have high extinction probabilities (Fig. 5c). For example, given a system of 10 species with $P = 0.9$, and a threshold of three species for maintaining a function, then the probability of success is only 0.07. Only more complete compensatory growth or extremely high species richness can prevent system failure under these conditions. In most cases, however, the influence of species richness followed a similar pattern in systems that rely on either few or many equivalent species.

Discussion

The model demonstrates that different components of diversity have opposite effects on the likelihood to maintain ecosystem functioning. Functional diversity makes the system less reliable, while functionally equivalent species make it more robust. This is a consequence of the two main principles of the model, namely (1) that a function benefits from more supporting species and (2) that the presence of more critical functions increases the risk. In many natural species-rich communities, both components of diversity are high at the same time, so their probability of functioning, for example, after perturbation, will not *per se* be different from species-poor communities

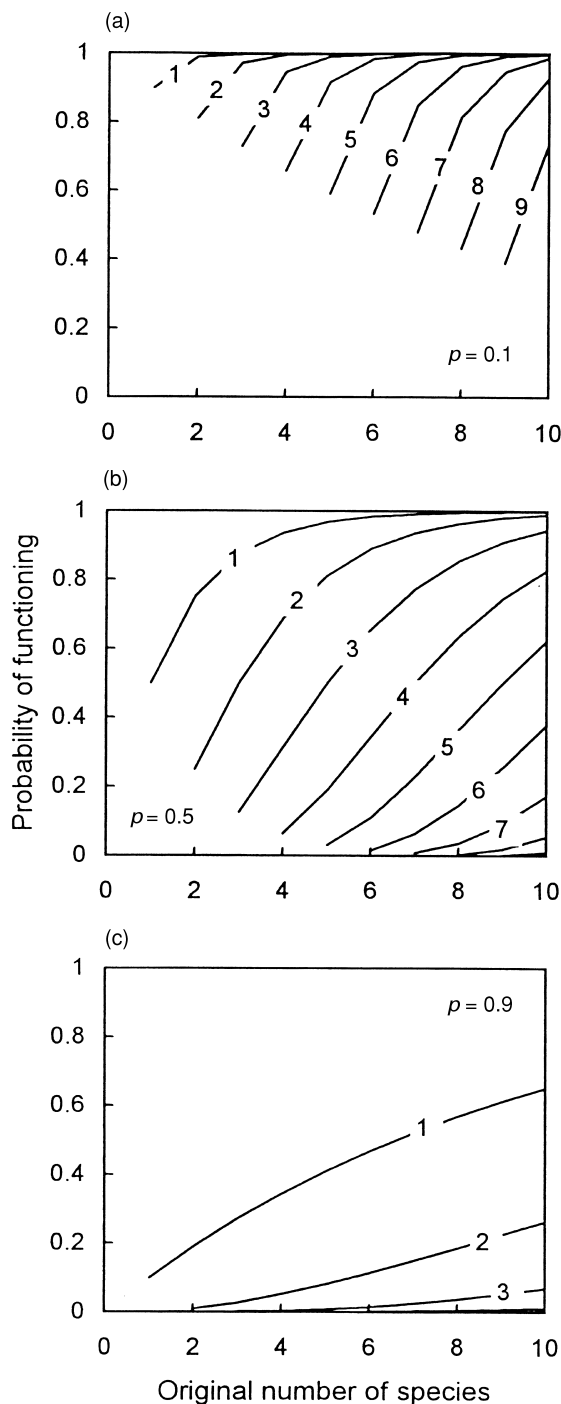


Fig. 5. Probability (P) of maintaining an ecosystem function that relies on more than one species, expressed as a function of the number of species that was present prior to extinction. Simplified case with only one functional group. Curve labels indicate how many species the function requires. Extinction probability of the species was set at $P = 0.1$, 0.5 or 0.9 (a, b and c, respectively).

(high n and high q cancel out). In calcareous grassland, for example, mycorrhizal symbiosis is critical to ecosystem functioning and these root–fungal associations are sensitive to environmental stress (e.g. eutrophication, acid immissions, heavy metals, Larcher 1995). The presence of this essential function therefore enhances

the risk of ecosystem failure, counterbalancing the insurance provided by a high species-richness. Such antagonistic effects, together with the fact that $P_{\text{total}} - q$ and $P_{\text{total}} - n$ curves can differ in shape as shown above, can provide a basis to explain conflicting empirical trends. Another reason is confounding of species richness and species identity. Species-rich communities typically contain other species than species-poor ones, so differences in reliability can arise from the fact that the species are different, just as well as from the fact that richness or functional group number is different (Givnish 1994). A recent experiment with microbial microcosms has eliminated this bias by artificially composing many different species assemblages, randomly selected from a total pool (Naeem & Li 1997). The outcome, enhanced ecosystem reliability with increasing species number per functional group, is consistent with our model results. Similarly, their finding of higher extinction if more functional groups are present, is compatible with the increased probability of whole ecosystem loss in our simulations. McGrady-Steed *et al.* (1997) reached a similar conclusion in – although not randomly assembled – aquatic microbial communities: respiration became less variable as diversity increased. Some authors have questioned the technique of random assembly in diversity studies (Huston 1997; Aarssen 1997; Wardle 1999) but the ‘artefacts’ that the method is supposed to produce could also represent the statistical component of diversity. Irrespective of the outcome of this debate, the problem can be avoided in models like the current one because species number and extinction probability can be varied independently.

In accounting for the low reliability of some species-rich systems (low P_{total} in spite of high n in our model terminology), we did not yet discuss the possibility that the species could be particularly susceptible to extinction. Returning to the case of calcareous grassland, high probabilities of extinction (high p) might ensue from the incapacity of many species to withstand the competitive pressure by fast-growing invaders, for example, upon eutrophication. In a broader context, it would be useful for generalization of our model results if p -values could be predicted from known species characteristics or properties, for example, rarity, but this is currently problematic. Stochastic extinction probability theory (Soulé 1987; Simberloff 1988) predicts that a minimum population size is required to prevent extinction, which is in turn coupled to a minimum area. On statistical grounds, rare species would therefore *per se* have higher extinction probabilities. However, extinction can also be deterministic, if the disappearance of one keystone species prompts an outburst of secondary extinctions in highly connected species within the food web. In that regard, common species could also be susceptible to extinction. Bond (1994) devised a protocol to identify such species, but concluded that criteria to distinguish the vulnerable ones (high p) are lacking. Without rules

to predict extinction probability in individual species, ecosystem reliability cannot be assessed on a wider scale. In addition, broad-scale classification of ecosystems is also required with respect to functional diversity (cf. Smith *et al.* 1997) and with respect to diversity within functional groups. Here lies another major impediment to making generalizations about extinction probability, because delimitation of functional groups is currently far from unambiguous. Recently, Gitay & Noble (1997) reviewed about 20 related concepts since the 1960s, e.g. guilds, leagues, modules, syndromes, functional analogues, ecological species groups, etc., and finally proposed the definition of groups of organisms with a similar behaviour in response to a particular perturbation, where the response is mediated through the same mechanism. Although practical techniques and criteria are being developed to delimit functional groups (e.g. Woodward & Kelly 1997), rigorous circumscription in experiments is rare, which hinders the application of models based upon them. We propose that, when linking such models to experimental data, the adequacy of the functional grouping be tested by comparing the extinction probabilities of the species: if these are similar between and within groups, it is unlikely that the groups are accurately defined.

As experimental evidence on the importance of numbers of species and functional groups to ecological communities accumulates, the significance of interspecific differences has remained largely unexplored. In some ecosystem processes, this 'hidden' component of diversity was shown to explain much more variance than species numbers (62.8 vs 37.2% in productivity, Tilman, Lehman & Thomson 1997). Our model suggests that the degree of interspecific difference (in this case in extinction probability) also has drastic effects on the chances to maintain ecosystem functioning (see Fig. 4), especially if the species belong to different functional groups. Particularly worrying about this result is that the relationship between heterogeneity among extinction probabilities of different species and likelihood of ecosystem failure does not saturate, contrary to most observed relationships between diversity and ecosystem processes (e.g. Naeem *et al.* 1996; Hooper & Vitousek 1997; Tilman, Knops *et al.* 1997). This suggests that interspecific differences are an underestimated element of diversity with a potentially overriding influence. We therefore propose that future experimental and modelling studies assess its effect, preferably by manipulating it directly and independently.

Traditionally, ecologists have modelled ecosystem behaviour by relating food web components. Especially the diversity–stability relationship has been addressed in this way (e.g. Pimm 1982; DeAngelis, Bartell & Brenkert 1989; Berryman *et al.* 1995). Although we did not model stability, some of these studies are relevant to our analysis. For example, with an increasing species richness, and a constant level of

connectance, simple food web models become less prone to further species loss following the deletion of one species (Pimm 1982). From this, one can similarly infer a higher resistance to subsequent deletions and, ultimately, to the loss of all the species that support a particular process or function, which is equivalent to a lower probability of complete ecosystem failure in the concept of this study. In our approach, we disregarded the food web nature of ecosystems, by focusing exclusively on elements of the system that are susceptible to loss, namely species and functions. Because this approach is general – functions nor species are specified – the predicted behaviour does not depend on the type of ecosystem or organisms. However, some of the assumptions that we made suggest that the model may not be valid in all cases. In particular, in real ecosystems, p could be lognormally distributed rather than normally, because most communities are characterized by few abundant and many rare species (Ugland & Gray 1982; we assume that extinction probability is coupled to rarity). However, irrespective of whether vulnerable species or robust ones are added to such skewed p -distributions, it follows from equation 1 that every addition with $p < 1$ increases P , only the magnitude of the increase varies. So the pattern that functionally equivalent species insure against loss is not altered. Similarly, the increased likelihood of system failure when more essential functions are present is not affected by a different p -distribution either, nor is the mechanism altered which enhances P when the range of p -values becomes wider (the decrease of the lowest p still governs the outcome, see 'Interspecific differences within functional groups'). The principles of the model are therefore fairly robust with respect to p -distribution. A second assumption in most simulations was that persistence of at least one supporting species was sufficient to maintain a function. Substitution of species that are lost requires sufficiently high propagation rates in the survivors and this density compensation within the same functional group can theoretically be complete or totally absent (Walker 1991). Reality will usually lie somewhere between these extremes but Fig. 5 demonstrates that, again, the general response pattern to diversity remains the same, regardless of the extent of compensatory growth. One option that we deliberately did not investigate, is partial loss of ecosystem function, which could result from losing part of the species. The reason for this is straightforward: the model was constructed to predict probabilities of ecosystem functioning and not to relate numbers of (surviving) species to ecosystem processes. The latter constitutes a different field of investigation, with important recent theoretical advances (Tilman, Lehman & Thomson 1997; Loreau 1998), although it would definitely be of interest to link the two.

Finally, in this paper, diversity was considered from a statistical point of view, by considering aggregative properties of ecosystems. The analysis was concerned

with numbers of species and numbers of functions. Statistical phenomena have been identified before with respect to the influence of diversity on ecosystem function, for example, on reliability (Naeem 1998), on stability (Doak *et al.* 1998; Tilman *et al.* 1998) and on productivity (e.g. the selection probability effect, Huston 1997; or the influence of species differences along niche axes defined by resources, Tilman, Lehman & Thomson 1997). All these studies considered variables of diverse nature in which species could differ. This does not preclude, however, that a different class of mechanisms, in particular physiological ones, may also influence ecosystem processes and their dynamics as diversity increases. In Mediterranean grasslands, for example, plant diversity determined soil microbial biomass, hyphal length and enzyme activity (Chapin *et al.* 1998), while the below-ground diversity of arbuscular mycorrhizal fungi in European calcareous grasslands contributed to nutrient capture and productivity (van der Heijden *et al.* 1998). Similarly, we also consider it unlikely that the relationship between diversity and extinction probability can be fully explained on the basis of either class of arguments alone but the theoretical evidence presented here confirms that at least the statistical component cannot be neglected.

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References

- Aarssen, L.W. (1997) High productivity in grassland ecosystems: effected by species diversity or by productive species? *Oikos* **80**, 183–184.
- Barbier, E.B., Burgess, J.C. & Folke, C. (1994) *Paradise Lost?* Earthscan Publications, London.
- Berryman, A.A., Michalski, J., Gutierrez, A.P. & Arditi, R. (1995) Logistic theory of food web dynamics. *Ecology* **76**, 336–343.
- Bolker, B.M., Pacala, S.W., Bazzaz, F.A., Canham, C.D. & Levin, S.A. (1995) Species diversity and ecosystem response to carbon dioxide fertilization: conclusions from a temperate forest model. *Global Change Biology* **1**, 373–381.
- Bond, W.J. (1994) Keystone species. *Biodiversity and Ecosystem Function* (eds E.-D. Schulze & H. A. Mooney), pp. 237–253. Springer-Verlag, Berlin.
- Boyle, T.J.B. & Boyle, E.B. (1994) *Biodiversity, Temperate Ecosystems and Global Change*. Springer, Berlin.
- Chapin III, F.S., Sala, O.E., Burke, I.C., Grime, J.P., Hooper, D.U., Lauenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A.R., Naeem, S., Pacala, S., Roy, J., Steffen, W.L. & Tilman, D. (1998) Ecosystem consequences of declining biodiversity. Experimental evidence and a research agenda for the future. *Bioscience* **48**, 45–52.
- DeAngelis, D.L., Bartell, S.M. & Brenkert, A.L. (1989) Effect of nutrient recycling and food-chain length on resilience. *The American Naturalist* **134**, 778–805.
- Doak, D.F., Bigger, D., Harding-Smith, E., Marvier, M.A., O'Malley, R. & Thomson, D. (1998) The statistical inevitability of stability–diversity relationships in community ecology. *The American Naturalist* **151**, 264–276.
- Elton, C. (1927) *Animal Ecology*. Sidgwick and Jackson, London.
- Frank, D.A. & McNaughton, S.J. (1991) Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos* **62**, 360–362.
- Gates, D.M. (1993) *Climate Change and its Biological Consequences*. Sinauer Associates, Sunderland, MA, USA.
- Gitay, H. & Noble, I.R. (1997) What are functional types and why should we seek them? *Plant Functional Types. Their Relevance to Ecosystem Properties and Global Change* (eds T. M. Smith, H. H. Shugart & F. I. Woodward), pp. 3–19. Cambridge University Press, Cambridge.
- Givnish, T.J. (1994) Does diversity beget stability? *Nature* **371**, 113–114.
- Hairton, N.G., Allan, J.D., Colwell, R.K., Futuyma, D.J., Howell, J., Lubin, M.D., Mathias, J. & Vandermeer, J.H. (1968) The relationship between species diversity and stability: an experimental approach with bacteria and protozoa. *Ecology* **49**, 1091–1101.
- Heywood, V.H. (1995) *Global Biodiversity Assessment*. Cambridge University Press, Cambridge.
- Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302–1305.
- Huston, J. (1994) *Biological Diversity. The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Huston, J. (1997) Hidden treatments in biological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460.
- Kareiva, S.P., Kingsolver, J.G. & Huey, R.B. (1993) *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, MA, USA.
- King, A.W. & Pimm, S.L. (1983) Complexity, diversity and stability: a reconciliation of theoretical and empirical results. *The American Naturalist* **122**, 229–239.
- Larcher, W. (1995) *Physiological Plant Ecology. Ecophysiology and Stress Physiology of Functional Groups*. Springer-Verlag, Berlin.
- Lawton, J.H. & Brown, V.K. (1994) Redundancy in ecosystems. *Biodiversity and Ecosystem Function* (eds E.-D. Schulze & H. A. Mooney), pp. 255–270. Springer-Verlag, Berlin.
- Leffler, J.W. (1977) *A microcosm approach to an evaluation of the diversity-stability hypothesis*. PhD thesis, University of Georgia, Athens, GA, USA.
- Loreau, M. (1998) Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of the National Academy of Sciences USA* **95**, 5632–5636.
- May, R.M. (1973) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ, USA.
- MacArthur, R.H. (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536.
- McGrady-Steed, J., Harris, P.M. & Morin, P. (1997) Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165.
- McNaughton, S.J. (1977) Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *The American Naturalist* **111**, 515–525.
- Naeem, S. (1998) Species redundancy and ecosystem reliability. *Conservation Biology* **12**, 39–45.
- Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–737.
- Naeem, S., Hakansson, K., Lawton, J., Crawley, M.J. & Thompson, L.J. (1996) Biodiversity and plant productivity in a model assemblage of plant species. *Oikos* **76**, 259–264.

- Paine, R.T. (1966) Food web complexity and species diversity. *The American Naturalist* **100**, 65–75.
- Peters, R.L. & Lovejoy, T.E. (1992) *Global Warming and Biological Diversity*. Yale University Press, New Haven, USA.
- Pimm, S.L. (1979) Complexity and stability: another look at McArthur's original hypothesis. *Oikos* **33**, 351–357.
- Pimm, S.L. (1982) *Food Webs*. Chapman & Hall, London.
- Schulze, E.-D. & Mooney, H.A. (1994) *Biodiversity and Ecosystem Function*. Springer, Berlin.
- Simberloff, D. (1988) The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* **19**, 473–511.
- Smith, T.M., Shugart, H.H. & Woodward, F.I. (1997) *Plant Functional Types. Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, Cambridge.
- Soulé, M.E. (1991) Conservation: tactics for a constant crisis. *Science* **253**, 744–750.
- Soulé, M.E. (ed.) (1987) *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Swanson, T.M. (1995) *The Economics and Ecology of Biodiversity Decline: the Forces Driving Global Change*. Cambridge University Press, Cambridge.
- Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Sieman, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences U.S.A.* **94**, 1857–1861.
- Tilman, D., Lehman, L. & Bristow, C.E. (1998) Diversity–stability relationships: statistical inevitability or ecological consequence? *The American Naturalist* **151**, 277–282.
- Ugland, K.I. & Gray, J.S. (1982) Lognormal distributions and the concept of community equilibrium. *Oikos* **39**, 171–178.
- van der Heijden, H.G.A., Klironomos, J.N., Ursic, M., Moutoglou, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.R. (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **369**, 69–72.
- Vitousek, P.M. & Hooper, D.U. (1994) Biological diversity and terrestrial ecosystem biogeochemistry. *Biodiversity and Ecosystem Function* (eds E.-D. Schulze & H. A. Mooney), pp. 3–13. Springer-Verlag, Berlin.
- Walker, B.H. (1991) Biodiversity and ecological redundancy. *Conservation Biology* **6**, 18–23.
- Wardle, D. (1999) Is 'sampling effect' a problem for experiments investigating biodiversity – ecosystem function relationships? *Oikos* **87**, 403–407.
- Woodward, F.I. & Kelly, C.K. (1997) Plant functional types: towards a definition by environmental constraints. *Plant Functional Types. Their Relevance to Ecosystem Properties and Global Change* (eds T. M. Smith, H. H. Shugart & F. I. Woodward), pp. 47–65. Cambridge University Press, Cambridge.

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