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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

On similarity among local communities in biodiversity experiments

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As a potential mechanism to explain how biodiversity loss may influence variability in ecosystem functioning, we examine the hypothesis that biodiversity loss lowers similarity in species composition among local communities and that this decreased similarity in turn lowers ecosystem reliability. Ecosystem reliability refers to the probability that a system will provide a consistent level of performance over a given unit of time. This hypothesis is compared with other hypotheses that make similar predictions, including the sampling effect, insurance, and resource use complementarity hypotheses. We provide evidence for the similarity hypothesis through a reanalysis of a recent experiment and show that a key assumption of the hypothesis may be robust through computer simulations. We also address problems and possible solutions regarding how to separately test the similarity and other hypotheses in biodiversity experiments.

Recently, an increasing number of experiments have sought to uncover a causal relationship between biodiversity and ecosystem functioning. These studies have often been unable to distinguish between alternative mechanisms to explain possible biodiversity effects identified in the experiment. This problem has created a lively discussion among ecologists on what constitutes a biodiversity effect, what mechanisms may be responsible for such effects if they exist, and what experimental design can adequately detect these mechanisms (e.g., André et al. 1994, Givnish 1994, Aarssen 1997, Garnier et al. 1997, Grime 1997, Huston 1997, Wardle et al. 1997, 2000, Doak et al. 1998, Hector 1998, Hodgson et al. 1998, Lawton et al. 1998, Loreau 1998, 2000a, Tilman et al. 1998, Wardle 1998, 1999, Allison 1999, Naeem 1999, 2000, Schläpfer and Schmid 1999, Van der Heijden et al. 1999, Hector et al. 2000, Hulot et al. 2000, Huston et al. 2000, Petchey 2000, Tilman 2000).

As one such mechanism, we focus on the degree of similarity in species composition among local communities (hereafter "similarity" unless otherwise specified; conceptually the inverse of Whittaker's [1972] beta diversity; see also Loreau 2000b). The potential effect of similarity on ecosystem functioning has only recently begun to be recognized (Huston 1997 ["variance reduction effect"], Tilman et al. 1997, Wardle 1998, Tilman 1999) and has not been well investigated conceptually. We attempt to show that similarity has important implications for understanding the relationship between biodiversity and ecosystem functioning. We first introduce what we call the similarity hypothesis and contrast it with other hypotheses that make similar predictions. We then present experimental evidence for the similarity hypothesis. This evidence is derived from a reanalysis of a recent experiment (Naeem and Li 1997), as a supportive device. Finally, we describe simulations that investigate how biodiversity loss alters similarity under several scenarios of local community assembly and local species extinctions.

Similarity hypothesis

The similarity hypothesis (Fig. 1a) assumes that the degree of similarity in species composition among local communities increases as biodiversity increases, with an asymptote at the maximum diversity possible as determined by the regional species pool. The hypothesis then predicts that this increased similarity in species composition in turn increases similarity among local communities in the routes and rates of energy and material flows through the functional groups present in the system. Thus, local ecosystems will function more similarly to one another. Consequently, spatial variability in ecosystem functioning will be reduced, or ecosystem reliability – defined as the probability that a system will provide a consistent level of performance over a given unit of time (Naeem 1998) – will be improved in a spatial dimension.

Two characteristics of the similarity hypothesis further clarify what the hypothesis is and is not about. First, while ecosystem reliability may refer to a local community or a set of local communities, the similarity hypothesis concerns the latter only. Second, the similarity hypothesis predicts how biodiversity influences the variability of ecosystem functioning, but not the magnitude of increase or decrease in ecosystem functioning. Other hypotheses described below predict both magnitude and variability.

The similarity hypothesis contrasts with other hypotheses that make similar predictions but invoke different mechanisms (Fig. 1). The sampling effect hypothesis (Fig. 1b; Aarssen 1997, Huston 1997, Tilman et al. 1997) predicts that productivity or other ecosystem processes increase with biodiversity because higher diversity communities have a higher probability of containing key species with strong impacts on the properties being measured (e.g., a highly productive species). This hypothesis can be extended to predict that, as the probability of containing the key species increases, ecosystem functioning becomes predominantly determined by the key species in a greater number of local communities. As a result, variability in ecosystem functioning among local communities decreases, leading to greater ecosystem reliability. The sampling effect hypothesis differs from the similarity hypothesis in some important ways. The sampling effect hypothesis, usually applied to magnitudes of ecosystem functioning, is attributable to individual species. On the other hand, the similarity effect, most often relevant when considering variation in ecosystem functioning, concerns species composition, not individual species and their relative impacts on ecosystem processes. Moreover, unlike the sampling effect, the similarity effect could occur even when all the species in a functional group were contributing equally to energy and material flows. It should also be noted that some ecologists regard the sampling effect to be an artifact of certain experimental designs (e.g., Aarssen 1997, Huston 1997, Wardle 1999), while others consider it a mechanism by which biodiversity affects ecosystem functioning (e.g., Tilman 1997, Tilman et al. 1997, Van der Heijden et al. 1999). This difference in the interpretation of the sampling effect remains unresolved.

The insurance hypothesis (Fig. 1c; Lawton and Brown 1993, Naeem and Li 1997, Naeem 1998, Yachi and Loreau 1999; see also Andrén et al. 1995, Doak et al. 1998, Tilman et al. 1998, Hughes and Roughgarden 2000) predicts that ecosystem reliability increases when species redundancy, defined as the number of species (S) per functional group (F), or S/F, increases. Ecosystem reliability increases with increased S/F because a larger S/F should increase the probability that compensatory growth – in which one species within a functional group increases in response to the reduction or loss of another in the same functional group – will occur. The insurance hypothesis has been applied in both spatial (Naeem and Li 1997) and temporal (Naeem 1998, Yachi and Loreau 1999; see also Doak et al. 1998, Tilman et al. 1998, Hughes and Roughgarden 2000) dimensions. The insurance and similarity hy-

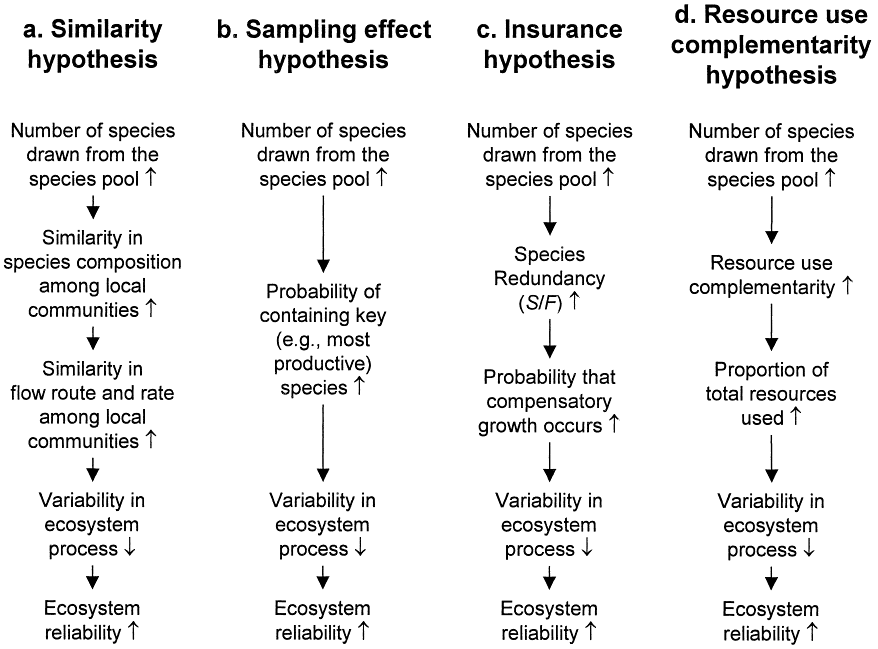

Fig. 1. Schematic representation of hypotheses on how biodiversity may regulate ecosystem reliability. Downward and upward arrows following phrases represent decrease and increase in the factor specified by the phrase.

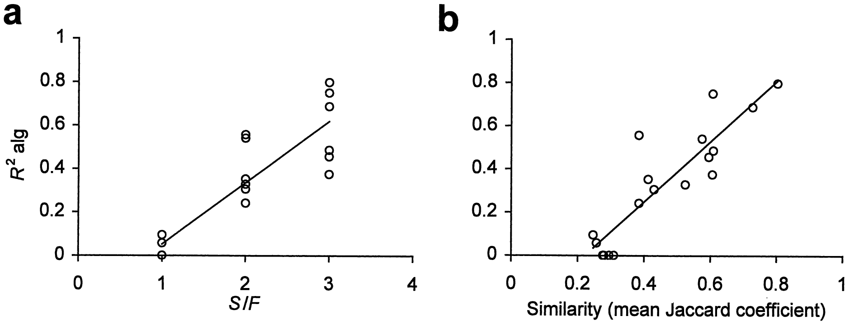

Fig. 2. (a) S/F (i.e., species per functional group) and ecosystem reliability as represented by R^2alg. (b) Similarity and ecosystem reliability as represented by R^2alg. R^2alg is the R^2 of a linear regression fitted to the natural log of the algal biomass as a function of number of functional groups in a microcosm. See Naeem and Li (1997) for a detailed description of how they measured the R^2alg.

potheses differ in that species redundancy and compensatory growth are necessary assumptions in the former, while they are not in the latter.

The resource use complementarity hypothesis (Fig. 1d; Trenbath 1974, Hooper 1998) predicts that as biodiversity increases, partial non-overlap of niches of species within functional groups will lead to more complete utilization of the total resources available. This hypothesis can be extended to predict that if the total resource level is held constant across local communities, then inter-community variance in the proportion of total resources utilized converges to zero as this proportion increases to one (cf. Petchey's [2000] model of resource use complementarity, which does not explicitly assume resource limitation and predicts that the biodiversity-ecosystem variability relationship depends on the extent of resource use overlap among species). This will in turn lead to greater ecosystem reliability. The resource use complementarity and similarity hypotheses differ in that the former requires making assumptions about resource use and resource requirements while the latter does not. The similarity, sampling effect, insurance, and resource use complementary hypotheses are not mutually exclusive; they can operate simultaneously.

Naeem and Li's (1997) experiment reconsidered

Can the similarity hypothesis actually operate to affect ecosystem functioning? We show that the experiment by Naeem and Li (1997) provides at least circumstantial evidence for the hypothesis. Naeem and Li (1997, 1998) and Wardle (1998) recently discussed the interpretation of the results from Naeem and Li's (1997) microcosm experiment originally designed to test the insurance hypothesis. Naeem and Li varied S/F in their microcosms, measured ecosystem reliability, and concluded that their results supported the insurance hypothesis. Wardle (1998) criticized this conclusion, arguing that the increased ecosystem reliability might not have resulted from increased S/F per se, but from increased similarity in species composition among replicates of more diverse communities. This problem arises because there was a positive correlation between S/F and similarity in Naeem and Li's design. Owing to the correlation, the presented results cannot distinguish between the two alternatives, S/F or similarity, in terms of which factor was responsible for the observed increase in ecosystem reliability. Wardle (1998) did not specify any mechanisms linking similarity and ecosystem reliability, but one possibility is the one proposed by our similarity hypothesis.

We reanalyzed the results of the experiment in an attempt to test the two competing hypotheses separately. We calculated similarity by first computing the Jaccard similarity coefficients (Jaccard 1901) of each functional group for all possible pairs of replicates in the treatment (there were six treatments corresponding to different environmental conditions, i.e., two light intensities × three nutrient levels) and then taking the mean of those coefficients. The Jaccard coefficient uses binary data, i.e., presence or absence of species. An index using quantitative data such as Lande's (1996) similarity index based on Simpson diversity would have reflected actual similarity more accurately. Such data were not collected by Naeem and Li, so an index using binary data was the best index that could be used for this experiment. Many other similarity indices have been proposed (Krebs 1999), which tend to be correlated. In calculating the similarity index, we used species compositions at the end rather than at the start of the experiment (cf. Wardle 1998) for two reasons: (1) a substantial number of local extinctions occurred in the experiment and (2) the results from a similar microcosm study (McGrady-Steed et al. 1997) suggest that most of the extinctions occurred soon after the experiment began, and that throughout most of the duration of the experiment, the microcosms held essentially the same species compositions as those at the end of the experiment. Using the similarity data computed, we examined how ecosystem reliability was related to similarity. We also conducted multiple regressions with S/F and similarity as independent variables and ecosystem reliability as the dependent variable.

We found that the relationship between autotrophic biomass and the number of functional groups (R^2alg) – one of the two measures of ecosystem reliability used by Naeem and Li (1997) – becomes more predictable not only as S/F increases ($R^2 = 0.695$, $P < 0.001$, Fig. 2a), as Naeem and Li originally reported, but also as similarity increases ($R^2 = 0.799$, $P < 0.001$, Fig. 2b), as Wardle (1998) suggested. Similarly, standard deviation in bacterial densities (SDbac) – the other measure of ecosystem reliability – decreases as both S/F ($R^2 = 0.353$, $P = 0.009$, Fig. 3a) and similarity ($R^2 = 0.270$, $P = 0.027$, Fig. 3b) increase. These results suggest that not only S/F but also similarity may have indeed been affecting ecosystem reliability. However, when S/F and similarity were treated simultaneously as two independent variables in multiple regressions, the regressions could not separate the effect of S/F and similarity ($P > 0.05$, Table 1). This occurred because the high correlation between S/F and similarity persisted until the end of the experiment despite the frequent local extinctions during the experiment ($R^2 = 0.807$, $P < 0.05$, Fig. 4). Furthermore, the correlation coefficients were not significantly different between S/F and similarity in either R^2alg or SDbac ($P > 0.2$, Fisher r-to-z transformation). Finally, these results did not qualitatively change when similarity was expressed by beta diversity (calculated as gamma diversity divided by mean alpha diversity) instead of the Jaccard coefficient. Hence, the multiple regression analyses could not distinguish which of the two hypothesized causes was really responsible for the increased ecosystem reliability.

Our reanalysis thus leaves the insurance and similarity hypotheses equally possible. A key assumption of the insurance hypothesis is compensatory growth among species within each functional group (Naeem 1998). Naeem and Li did not collect data on abundance of each species, so the necessary information to examine compensatory growth is lacking for this study (cf. McGrady-Steed and Morin 2000). The lack of abundance data also prevents us from testing the sampling effect and resource use complementarity hypotheses. Future experiments should obtain abundance information to provide more rigorous evidence for or against the hypotheses. Additionally, the use of a larger (but still overlapping [sensu Naeem and Li 1998, cf. Wardle 1998]) species pool than that used by Naeem and Li will help minimize the problem of the correlation between S/F and similarity. A larger species pool would presumably create a lower similarity among high-diversity replicates, reducing the strength of the correlation and thus making multiple regressions more effective at separating possible effects of S/F and similarity. A larger species pool may also mimic nature more closely (Ricklefs and Schluter 1993). In any case, the possibility remains that both the insurance hypothesis and the similarity hypothesis were true in Naeem and Li's experiment. It is worth noting, however, that in addition to the trends in ecosystem reliability, Naeem and Li also observed an average increase in algal biomass with increased S/F. As mentioned above, the similarity hypothesis does not predict such changes in magnitudes of ecosystem functioning. Mechanisms other than the similarity hypothesis, potentially including insurance effect (i.e., a performance-enhancing effect, sensu Yachi and Loreau 1999), sampling effect, and resource use complementarity, must have been responsible for the increase in algal biomass.

How are biodiversity and similarity related?

The strong positive correlation between biodiversity and similarity in Naeem and Li's experiment (Fig. 4) was in this case due to the design of the experiment. Is this relationship general? Does biodiversity loss always lead to a decline in similarity in species composition in the real world? Or does the relationship depend on, for example, the pattern of species occurrence and extinction in local communities? These questions are important to the similarity hypothesis because the answers partly determine its generality. The conventional experimental approach employed by Naeem and Li models biodiversity loss by creating increasingly depauperate communities consisting of decreasing numbers of species drawn at random from a species pool. This design assumes that every species in the species pool has the same probability of occurrence in a local community and that local extinctions occur randomly with regard

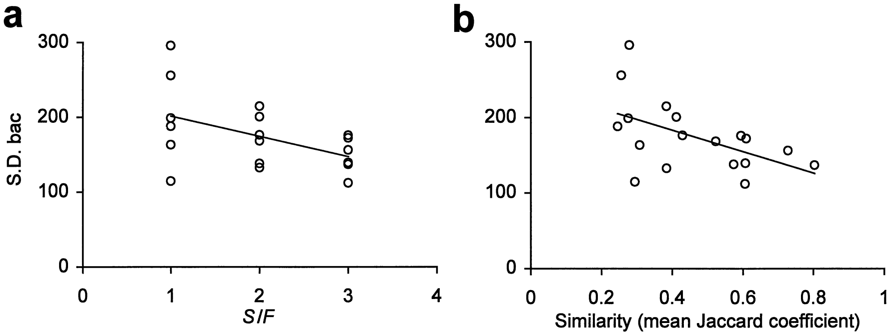

Fig. 3. (a) S/F (i.e., species per functional group) and ecosystem reliability as represented by SDbac. (b) Similarity and ecosystem reliability as represented by SDbac. SDbac is the standard deviation of bacterial densities among replicate microcosms. See Naeem and Li (1997) for a detailed description of how they measured SDbac.

Table 1. Summary of multiple regression analyses relating ecosystem reliability (R^2alg and SDbac) to S/F and similarity.

	Intercept		S/F		Similarity	
	Parameter	P	Parameter	P	Parameter	P
R^2alg	240.16	<0.0001	0.51	0.9878	-144.46	0.3802
SDbac	-0.30	<0.0001	0.12	0.1981	0.83	0.0844

Notes: R^2alg and SDbac are as in Figs 2 and 3. Multiple regressions were not significant ($P = 0.0951$) for R^2alg and significant ($P<0.0001$) for SDbac.

to species. However, these assumptions rarely hold in nature: some species occur in more communities than other species, and species with certain sets of functional and other characteristics are more prone to extinction than are other species (e.g., Duncan and Young 2000). Since it was not intuitively clear what relationship would be expected between biodiversity and similarity in such more realistic cases, we conducted a set of computer simulations to explore the relationship.

Our simulations first constructed ten initial local communities each consisting of 50 species. These 50 species were chosen randomly from a common species pool of 100 species, based on either a uniform or canonical lognormal distribution of the probability of occurrence in the local communities. The uniform distribution mimicked the conventional experimental design. The canonical lognormal distribution (Preston 1962) was used as a representative example of the species distribution observed in nature (e.g., Whittaker 1975, Grime 1998). Once the initial communities were assembled, the simulations allowed sequential local extinctions of species. For each extinction event, the community from which a species goes extinct was chosen randomly, and the species to go extinct from that community was chosen randomly based on, again, either a uniform or canonical lognormal distribution of the probability of extinction. Again, the uniform distribution mimicked the experimental design and the canonical lognormal distribution more closely approximated natural systems. We assumed a complete inverse relationship between the probability of initial occurrence and that of local extinction. As local extinctions proceeded, mean Jaccard coefficient was measured, averaged over all the 45 ($= {}_{10}C_2$) pairwise Jaccard coefficients between the ten local communities. The simulations were terminated when mean local species richness reached five or when every species in the community went extinct in one of the communities. The two distributions of initial occurrence and of local extinction created four ($= 2 \times 2$) sets of simulations, each of which was replicated four times.

We also conducted an additional set of simulations to examine the effect of difference in initial species richness among the local communities on the biodiversity-similarity relationship. Species richness often varies among natural local communities as seen, for example, in the species-area relationship (MacArthur and Wilson 1967; see also studies on nestedness of species assemblages [e.g., Patterson and Atmar 1986, Simberloff and Martin 1991, Wright and Reeves 1992, Lomolino 1996, Boecklen 1997, Wright et al. 1998]). Thus, we used the same simulation algorithm as above, except that we constructed the ten initial communities each consisting of either 5, 15, 25, 35, 45, 55, 65, 75, 85, or 95 species, instead of 50 species for each community. These simulations served as an example of high variation in initial species richness.

When all communities initially held 50 species (Fig. 5a, b), similarity generally decreased as mean local species richness decreased under all the scenarios examined. The rate of this similarity decline, however, depended on the distribution of the probability of initial species occurrence and of local species extinction. Within the same initial occurrence scenario, the rate was higher under the uniform distribution of the probability of extinction than under the lognormal distribution. When communities started with unequal species richness (Fig. 5c, d), similarity stayed at about the same level with a slight increase over a wide range of mean local richness (from 50 to 20 species) under one scenario (i.e., the scenario with the lognormal distribution for both initial occurrence and extinction; open circle in Fig. 5d). However, similarity showed the same trend of

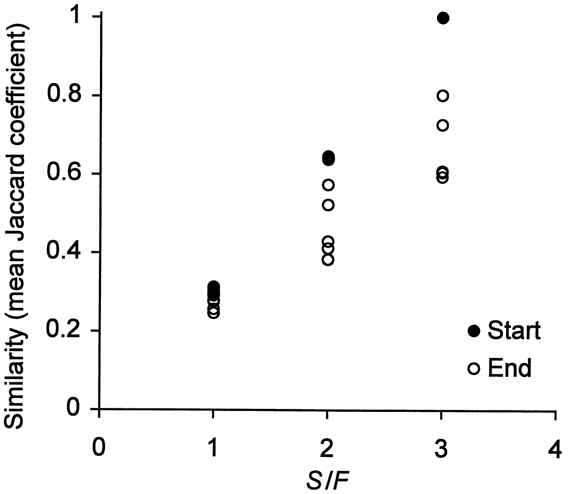

Fig. 4. S/F (i.e., species per functional group) and similarity of species composition at the start and end of Naeem and Li's (1997) experiment.

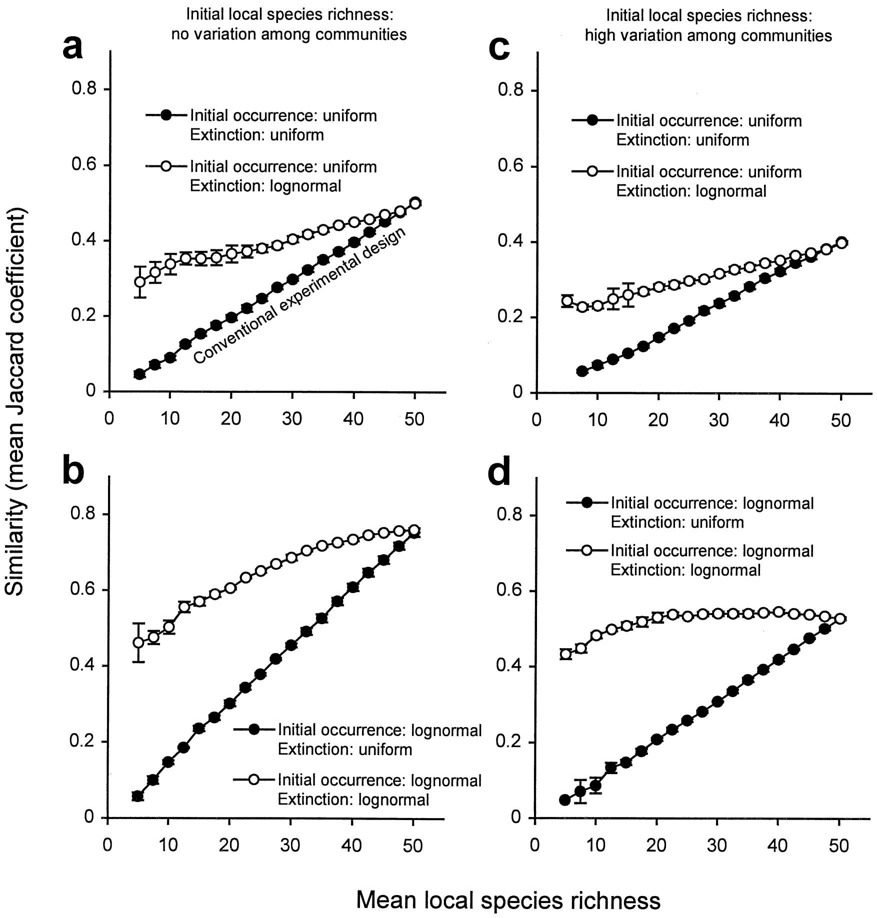

Fig. 5. Results of the computer simulations, showing how local extinctions, which result in reduction in mean local species richness, change the degree of similarity among local communities (mean Jaccard coefficient ± 1 standard error). Initial communities consisted of 50 species each (a and b) or of either 5, 15, 25, 35, 45, 55, 65, 75, 85, or 95 species (c and d; see text) chosen randomly from a common source pool of 100 species with either a uniform (a and c) or canonical lognormal (b and d) distribution of the probability of species occurrence. Species were allowed to go extinct sequentially according to either a uniform (closed circle) or canonical lognormal (open circle) distribution of the probability of local extinction.

general decline as in the previous simulations. The initial similarity and the rate of similarity decline, however, were generally lower than in the previous simulations.

These results have two important implications. First, for testing the similarity hypothesis, the conventional experimental design of manipulating biodiversity using the uniform distribution of the probabilities does not adequately model biodiversity loss in natural communities (Wardle 1999). The conventional design is often justified as a general, exploratory tool (e.g., Hector et al. 2000). In our simulations, however, similarity declined at a considerably higher and more consistent rate under the conventional experimental design involving the uniform distribution than under more realistic scenarios involving the lognormal distributions. Therefore, the conventional design may overemphasize the importance of similarity. A design with a more realistic distribution of species occurrence and extinction, such as a lognormal distribution, may more accurately assess the importance of the change in similarity associated with biodiversity loss occurring in nature.

With regard to this first implication, the similarity hypothesis is similar to the sampling effect and insurance hypotheses. The same type of overemphasis occurs with the sampling effect hypothesis; random community assembly maximizes the importance of the sampling effect (Wardle 1999). Some (e.g., Wardle 1999) have used this as a basis to argue for interpreting the sampling effect as an artifact of the conventional experimental design. This argument, if valid, would apply to the similarity hypothesis as well. But the validity of the argument is ultimately an empirical question. It partly depends on the degree to which the structure of real communities deviates from randomness (Wardle 1999), which can differ greatly from ecosystem to ecosystem (Loreau 2000a). A similar phenomenon also occurs with the insurance hypothesis; its importance is maximized when communities are assembled randomly with respect to functional groups (i.e., when the mean probability of species occurrence is the same across functional groups), though the importance is not affected by the assembly pattern within functional groups. The resource use complementarity hypothesis is the only one of the four hypotheses discussed here that is not necessarily maximized by random community assembly.

Second, despite the difference in the rate of similarity under different scenarios, the overall trend of the similarity decline with local extinctions was observed under almost all of the scenarios examined, regardless of the initial occurrence and extinction patterns. This indicates that the assumption of the similarity hypothesis that similarity is coupled with biodiversity (the first link in Fig. 1a) may prove robust, even though the importance of the hypothesis depends on the patterns of community assembly and species extinction. A thorough evaluation of the hypothesis' generality would require empirical data, not just theoretical simulations. Nonetheless, with regard to the relationship between biodiversity and similarity, our simulations suggest that the similarity hypothesis holds true for a variety of situations and is potentially very general. The exceptional case in which similarity did not significantly change over a wide range of biodiversity (open circle in Fig. 5d) merits further consideration; however, as the scenario involved – the canonical lognormal distribution both for initial occurrence and for subsequent extinction applied to communities having high variation in species richness – may be closest to the situations encountered most often in nature.

There are several caveats concerning the simulation results. First, the simulations did not explicitly allow the species to disperse among local communities or re-colonize local communities from the source pool. When dispersal or re-colonization or both occur, it could either increase or decrease similarity (Loreau and Mouquet 1999). Second, in the simulations, both initial species occurrence and subsequent local extinctions were independent of what other species were present or absent in the community. In nature, both are in some circumstances affected by the presence or absence of other species through species interactions including antagonistic and facilitative interactions (Drake 1990, Leibold et al. 1997), possibly changing the diversity-similarity relationship. Third, our simulations did not take into account external factors that can cause variation in species composition in nature, such as environmental gradients and successional stages. Fourth, as in our reanalysis of Naeem and Li's experiment, Jaccard coefficients are only a coarse index of similarity. When not only species composition but also their relative abundances are an important aspect of similarity, different results may be obtained if a quantitative index of similarity is used.

Finally and most importantly, the simulations only examined how sensitive the relationship between biodiversity and similarity is to the scenario of initial species distributions and local species extinctions. This relationship is only part of the mechanism proposed by the similarity hypothesis (i.e., the first link in Fig. 1a). Although it seems to make intuitive sense to expect a causal relationship between similarity and ecosystem reliability (from the second to last links in Fig. 1a), further quantitative analysis is needed to examine whether and how they are related, before a firm judgment can be made about the likelihood and importance of the similarity hypothesis. Related theoretical studies that deal with variation in ecosystem functioning in uni-trophic (especially plants) systems (Tilman et al. 1997, Petchey 2000) do predict mechanisms similar to those that the similarity hypothesis predicts. However, the effect of similarity in more general, multi-trophic systems like that of Naeem and Li's needs further theoretical considerations.

Conclusions

The similarity hypothesis may explain how biodiversity loss influences variability in ecosystem functioning. This hypothesis appears general. Its key assumption that similarity decreases with biodiversity loss did not depend on the pattern of species occurrence or extinction in most cases in our simulations. However, the simulations also suggest that the conventional design of biodiversity experiments – in which replicate communities are constructed by random draws of species from a species pool, based on the uniform distribution of the probability of species occurrence and extinction – may overemphasize the importance of similarity. Furthermore, the experimental reanalysis shows that the conventional design sometimes makes it difficult to separately test the similarity hypothesis and other hypotheses. To avoid these problems, future experiments will benefit from using a large species pool relative to local communities, constructing local communities based on a more realistic pattern of species occurrence and extinction than the random draws of species, and obtaining data on the abundance of each species. Designing experiments that can distinguish between possible mechanisms on ecosystem responses to biodiversity loss will be critical to resolving current issues concerning the proper interpretation of experiments and providing better means for assessing the possible role (or lack thereof) of biodiversity in contributing to ecosystem functioning.

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