THE ROYAL SOCIETY

Extinction and the loss of functional diversity

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Although it is widely thought to influence ecosystem processes, there is little consensus on an appropriate measure of functional diversity. The two major perspectives, to date, are to assume that every species is functionally unique, or to assume that some species are functionally identical, such that functional groups exist. Using a continuous measure of functional diversity (FD) derived from the quantitative functional traits of species, we show that the loss of functional diversity from six natural assemblages was rapid compared with rates of loss from comparable simulated assemblages. Loss of FD occurred faster than loss of functional-group diversity in four of the six natural assemblages. Patterns of functional-group diversity loss depended on the number of functional groups and the number of species in an assemblage. Extinctions that occurred first for species with particular traits (e.g. low leaf nitrogen concentration, deep roots and large body size) caused greater loss of FD than expected by chance in four of the six natural assemblages. In two real assemblages, these trait-dependent extinctions had more severe effects on FD than our simulated worst-case extinction scenario. These data suggest that conserving a large proportion of the functional traits of species requires conserving a large proportion of all species.

Keywords: species richness; functional-group diversity; redundancy; trait-dependent extinction

1. INTRODUCTION

There is growing evidence of links between functional diversity and ecosystem processes (Chapin *et al.* 2000; Daily 1997; Díaz & Cabido 2001; Grime 2001; Huston 1997; Loreau *et al.* 2001; Tilman 2000, 2001). However, the possible effects of species extinctions on functional diversity remain constrained by the limited methods available for quantifying functional diversity. Either all species are considered to be functionally unique so that extinctions always reduce functional diversity (Ehrlich & Ehrlich 1983), or some species are considered to be functionally identical, such that functional groups can be identified. Within functional groups, such redundancy makes species richness irrelevant; all that matters is that the biomass within functional groups is maintained (Lawton & Brown 1993). Reality doubtless lies somewhere between these two extremes (Fonseca & Ganade 2001; Walker 1995); some species are more similar than others at coarse functional scales and all species differ at finer functional scales.

Here, we explore the impact of extinctions on functional diversity using both a recently developed continuous measure of functional diversity (FD) and functional-group diversity (Tilman 2001). The latter obviously requires that species are assigned to functional groups and, hence, an arbitrary decision about the scale at which differences between species are functionally insignificant (Fonseca & Ganade 2001; Hector *et al.* 1999; Hooper 1998; Naeem & Li 1997; Rastetter *et al.* 1999; Simberloff & Dayan 1991; Tilman *et al.* 2001; Vitousek & Hooper 1993). By contrast, FD does not require grouping and includes the large functional differences that might delineate functional groups, as well as smaller differences that would be ignored by assigning species to functional groups.

Using FD, we investigated both how the structure of trait complementarity among species and the order in which species go extinct affect functional diversity. Three particular comparisons highlight our results: (i) effects of randomly ordered extinctions from real assemblages of species compared with random extinctions from simulated assemblages; (ii) effects of extinction on FD compared with functional-group diversity; and (iii) effects of random extinctions from real assemblages compared with trait-dependent extinctions from real assemblages. Trait-dependent extinctions occurred when species with high or low values for a trait, such as body size or photosynthetic rate, suffered simulated extinction first.

2. METHODS

Calculating FD begins by measuring functionally important traits of species. In the six case studies that we selected from the primary literature, the authors used their expert biological knowledge to select these traits. They ranged from ecophysiological properties (e.g. leaf N, P uptake; Chapin *et al.* 1996), to prey consumed (e.g. percentage of all the prey consumed by a species; Muñoz & Ojeda 1997), to feeding behaviour (e.g. percentage of total time spent feeding; Holmes *et al.* 1979). The latter two types of trait should be particularly closely linked to ecosystem functioning because they concern resource use directly, which is important for ecosystem functioning (Loreau 1998). Ecophysiological traits, mostly used in plant studies, were the focus of the original studies because they determine many ecological processes with clear ecosystem-level consequences (e.g. Hobbie 1995). Three of the case study assemblages were of plants (Chapin *et al.* 1996; Díaz & Cabido 1997; Golluscio & Sala 1993) and three were of animals (Holmes *et al.* 1979; Jaksić & Medel 1990; Muñoz & Ojeda 1997). All relevant details of these assemblages are available in the original literature sources, including complete species lists.

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The s species by t traits matrix containing this information was transformed into an s by s distance matrix. This contains the distances between species in t-dimensional trait space. Hierarchical clustering of the distance matrix resulted in the functional dendrogram of which FD is the total branch length (PD, an accepted measure of phylogenetic diversity, is the total branch length of the evolutionary tree; Faith 1992; May 1990). This dendrogram is often used in assigning species to functional groups (Chapin *et al.* 1996; Díaz & Cabido 1997; Körner 1993; Lavorel *et al.* 1997) and guilds (Hawkins & MacMahon 1989; Simberloff & Dayan 1991; Terborgh & Robinson 1986). Extinctions result in the pruning of branches from the functional dendrogram, loss of the unique functional characters associated with those branches and decreased FD. For this paper, all traits were standardized to mean = 0 and variance = 1, distances were Euclidean and the clustering algorithm was the unweighted pair-group method using arithmetic averages (UPGMA). All simulations and analyses were performed in R (http://www.r-project.org).

We used the functional-group memberships reported in each of the case studies to examine how extinctions reduced functional-group diversity. Although some of the real assemblages were originally analysed for guild structure, there may be little distinction between functional groups and guilds (Allison *et al.* 1996; Simberloff & Dayan 1991; Vitousek & Hooper 1993).

Four extinction scenarios that differed in the order in which species extinctions occurred were simulated: (i) when species go extinct in random order (i.e. field of bullets; Raup 1991); (ii) when species go extinct in the order that minimizes the losses of FD caused by each extinction; (iii) when species go extinct in the order that maximizes the losses of FD caused by each extinction; and (iv) a trait-dependent order of species extinctions. Trait-dependent extinctions simulated the expected effects of nitrogen deposition in plant assemblages, and the loss of larger bodied species first in the animal studies. Nitrogen deposition can alleviate the stresses that favour large slow growing plant species in nutrient-poor environments, such as tundra, resulting in the loss of these slower growing species, dominance of faster growing species and reduced species richness (Chapin *et al.* 1995; Nilsson *et al.* 2002; Press *et al.* 1998; Theodose & Bowman 1997; Turkington *et al.* 1998; but see Jonasson 1992). Hence, trait-dependent extinctions in the plant assemblages were in the order of increasing leaf nitrogen concentration (Chapin *et al.* 1996) (the photosynthetic rate measurements were incomplete and also strongly correlated with leaf nitrogen; $r^2 = 0.81$) or rooting depth (Golluscio & Sala 1993) (because photosynthetic rate or a strongly correlated trait was unavailable). Extinctions from Díaz and Cabido's (1997) assemblage occurred first for larger species, although the matrix contained only ordinal trait values, with eight size classes of plant. The order of extinctions within these size classes was random. The extinction risk for animals can be correlated with body size, with larger bodied species suffering greater risk (Gaston & Blackburn 1995; Lawton 1995). Consequently, trait-dependent extinctions in the animal assemblages occurred in the order of decreasing body size. The body masses presented in Holmes *et al.* (1979) and Muñoz & Ojeda (1997) were used. Body masses for the assemblage studied by Jaksić & Medel (1990) were taken from Dunning (1993) (birds; mean of male and female mass), Wilson & Ruff (1999) (carnivores), and for snakes we converted total length (from the Colorado Herpetological Society web site, http://www.coloherp.org) to mass using the allometric relationship in Pough (1980).

We compared the effects of extinctions in real assemblages with the effects in simulated assemblages. One way to simulate the structure of the functional dendrogram is to vary the correlation structure of the trait matrix by altering the number of uncorrelated traits t by which s species differ. This effectively changes the dimensionality of the trait space that species occupy. Many uncorrelated traits (e.g. $t = 10$, $s = 20$) result in species that separate in high-dimensional trait space and allow all species to differ equally (all species can be equidistant in trait space; low redundancy). Few or no uncorrelated traits (e.g. $t = 0$, $s = 20$) result in species that separate in low-dimensional trait space and cause some species to be more similar than others (some species are closer in trait space; higher redundancy). We kept the total number of traits (correlated and uncorrelated) constant ($T = 10$) and varied the number of uncorrelated traits $t = 0$, $t = 1$ or $t = 10$. All trait values were normal [0,1]. The other method that we used to simulate the functional dendrogram was to make species clump in trait space. For simplicity, we clumped species ($s = 20$) along a single trait axis by assuming there were a number f of normal distributions of trait values along that axis, each with mean x_i. That is, the trait values of species i were normal $[x_i, 1]$; x_i took a limited number of values f that defines the number of functional clumps of species along the trait axis.

3. RESULTS

Randomly ordered species extinctions caused remarkably similar and rapid loss of FD among the six real assemblages (figure 1) compared with the initially slow losses that occurred in low-dimensional (few uncorrelated traits) simulated assemblages (figure 2). Low-dimensional trait space resulted in initially small losses of FD that accelerated as the number of species remaining in the assemblage decreased; such an effect is characteristic of assemblages that are functionally redundant. This redundancy occurs because species differ in their contribution to FD (redundancy can also result from differences in species' abundances and distributions), and it was more extreme in simulated assemblages with strong clumping of species in trait space (figure 2c). Here, initial extinctions had very little effect on FD because very similar species remained. Loss of all members of a clump of species, however, reduced FD greatly. Loss of FD in the real assemblages was more similar to the high-dimensional simulated assemblages where loss of FD was proportional to loss of species (i.e. the linear pattern in figure 2a). The order of extinctions was important in both real and simulated assemblages: loss of species that minimized sequential losses of FD caused a small initial but accelerating loss of FD (apparent redundancy in species' contributions to FD). Maximizing stepwise losses of FD sometimes caused relatively large initial and decelerating loss of FD (a keystone-like pattern; Sala *et al.* 1996).

The rate of loss of FD from real assemblages as a result of random species losses was rapid compared with the loss of functional group diversity in four of the real assemblages (figure 1a,d,e,f), although the losses were more similar in the other two (figure 1b,c). The difference or similarity between loss of FD and functional group diversity was associated with the average number of species per functional group and the evenness of the distribution of species among the functional groups. The four assemblages where functional group diversity was lost relatively
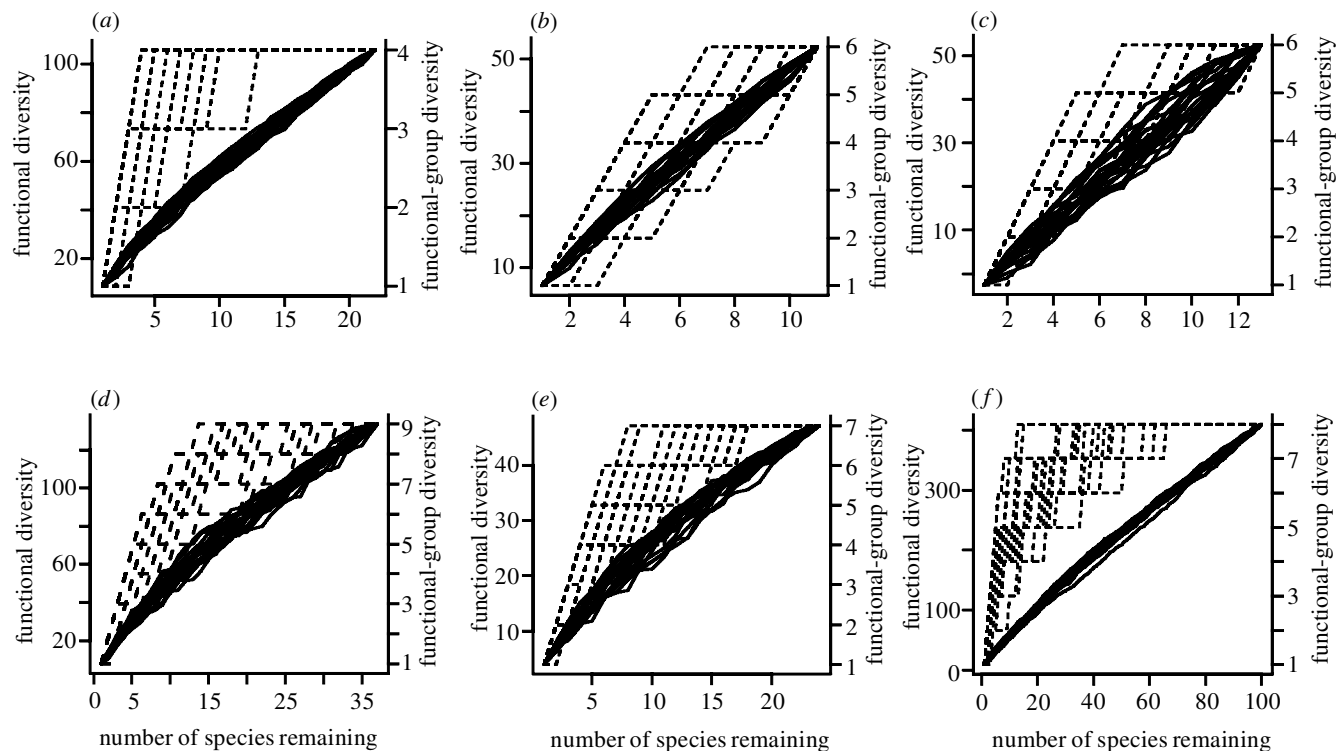
Figure 1. Effects of randomly ordered extinctions on functional diversity (FD) and functional-group diversity in real assemblages: (*a*) 22 species of insectivorous birds (Holmes *et al.* 1979); (*b*) 11 species of predatory vertebrates (Jaksić & Medel 1990); (*c*) 13 species of rocky intertidal fish (Muñoz & Ojeda 1997); (*d*) 37 species of arctic vegetation (Chapin *et al.* 1996); (*e*) 24 species of Patagonian forbs (Golluscio & Sala 1993); and (*f*) 100 species of Western-central Argentinean flora (Díaz & Cabido 1997). Solid lines show the loss of FD (left *y*-axis) for 10 random extinction trajectories. Dashed lines show the loss of functional group diversity (right *y*-axis) for 10 random extinction trajectories.

slowly had either or both a high average number of species per functional group (figure 1*a*, 5.5; *d*, 4.0; *e*, 3.4; *f*, 12.5) and/or even distributions of species among functional groups (figure 1, Simpson's equitability: *a*, 0.88; *d*, 0.88; *e*, 0.94; *f*, 0.68) compared with the two assemblages with similar rates of loss for both measures of functional diversity (figure 2, mean species per functional group: *b*, 1.8; *c*, 2.2; equitability: *b*, 0.61; *c*, 0.69).

Trait-dependent orders of species extinctions reduced FD to levels significantly (trajectories outside the 95% confidence interval) below those caused by randomly ordered species extinctions in four of the six natural assemblages (figure 3*a,d,e,f*). These lower than expected levels of FD occurred over differing ranges of species loss: for insectivorous birds, *ca.* 50–80% loss, arctic vegetation, *ca.* 50–100%, Patagonian forbs, *ca.* 10–75%, and Argentinean flora, *ca.* 20–60% and 70–80% loss. Hence, although maximum (all species remaining) and minimum (one species remaining) FD were identical for any assemblage (figure 3), there was little consistency in the range of species loss for which trait-dependent extinctions reduced FD below random levels. An especially severe reduction of FD occurred during trait-dependent extinctions in the assemblages of arctic vegetation and Argentinean flora. Here, FD dropped below the level of our worst-case extinction scenario, in which species were selected to maximize stepwise loss of FD (figure 3*d,f*). This also happened in some of the simulated assemblages (figure 2*b,c*).

4. DISCUSSION

A recent study suggested that extinctions may have little effect on functional diversity—a loss of 75% of species results in no loss of functional group diversity (Fonseca & Ganade 2001). Measuring the continuum of functional differences among species, from very large to very small, allows measurement of the contribution of every species to functional diversity. Such a measure (FD) applied to real assemblages of species shows rapid loss of functional diversity compared with both possible losses from simulated assemblages and loss of functional group diversity. The real assemblages showed little evidence of the redundancy of species' contributions to functional diversity that can occur in simulated assemblages. These results suggest that the functional traits of species are distributed such that species are relatively unique. Any complacency regarding the effects of extinction on the loss of functional diversity would be misplaced.

Small initial effects of extinctions on functional group diversity is an almost inevitable consequence of assuming that the species within these groups are functionally identical, so loss of a species may have no effect (Fonseca & Ganade 2001). The more species in the functional groups, the greater the apparent redundancy of species' contributions to functional diversity in the assemblage. Unfortunately, there is no objective way by which to decide how many species should be in how many functional groups (Simberloff & Dayan 1991). Even when the functional
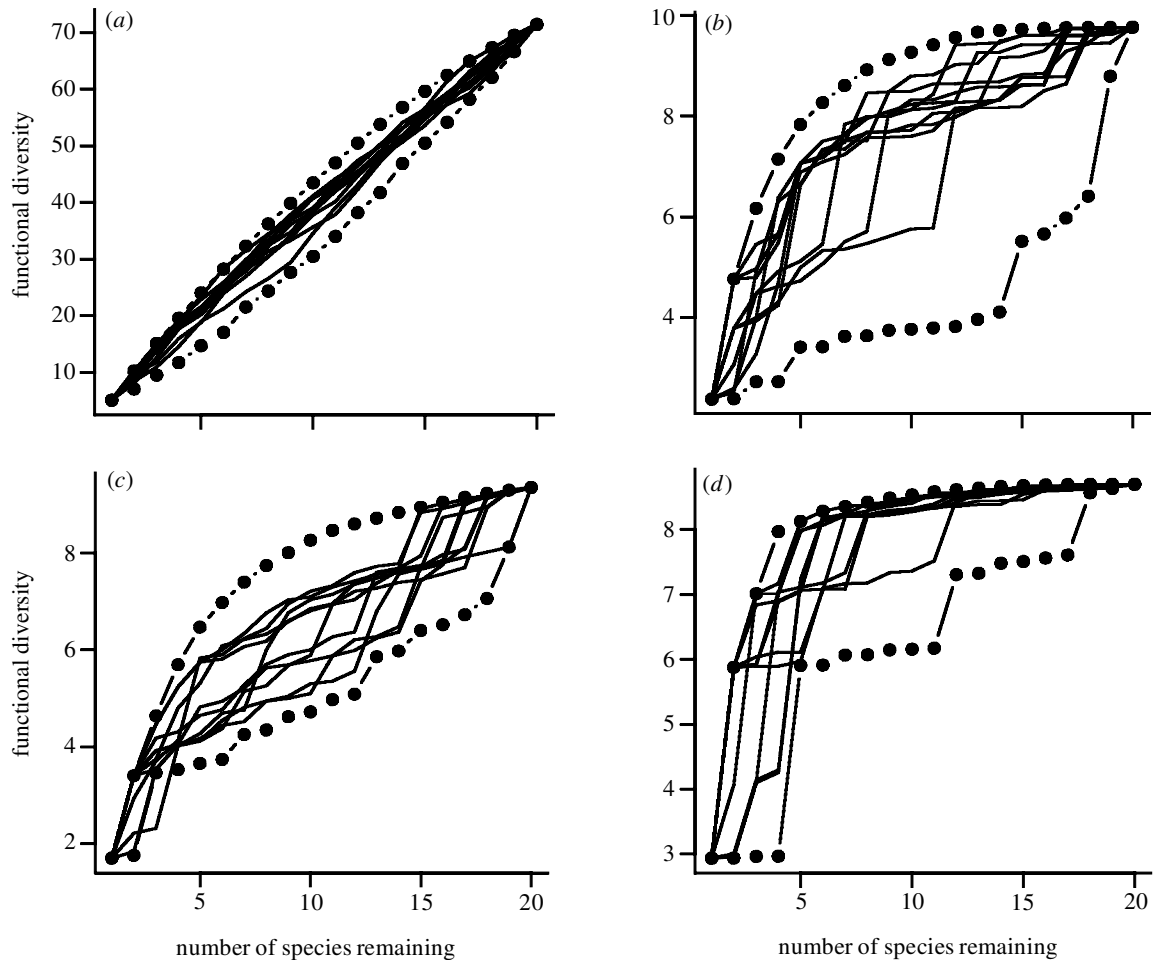
Figure 2. Effects of randomly ordered extinctions (solid lines) and best- or worst-case extinction scenarios (filled circles) on FD in 20 simulated species assemblages: (*a*) a simulated assemblage where species separate in high-dimensional trait space (number of uncorrelated traits $t = 10$); (*b,c*) simulated assemblages where species separate in lower-dimensional trait space: (*b*) $t = 1$, (*c*) $t = 0$; (*d*) a simulated assemblage where species occur in four functional clumps ($f = 4$) along one trait axis ($t = 0$).

groups are identified from a functional dendrogram, their number and composition depend on arbitrary decisions about the level of branching at which these groups occur. So the effects of species extinctions on functional group diversity are subjective underestimates of the effect of extinctions on functional diversity.

Why might there be little evidence of redundancy in species' contributions to functional diversity (FD) in the six real assemblages? These and unpublished analyses show that the number of uncorrelated functional traits is important—more traits result in more rapid initial loss of functional diversity. Between 6 and 27 traits were measured in the real assemblages, providing the potential for separation of species in high-dimensional trait space. Strongly correlated traits would, however, reduce the effective dimensionality of niche space, so that measuring many traits alone is not sufficient to create rapid effects of extinction. These results suggest that real species separate in trait space with sufficient dimensions for rapid loss of functional diversity. In thinking about the effects of extinctions on this diversity, we need to pay careful attention to the frequency with which sets of traits occur in combination rather than the representation of individual traits.

For evaluating the effects of extinction on FD, a critical question is which traits should be measured. Other authors have concluded that the measured traits should be those for which evidence exists of their functional importance (Chapin *et al.* 1996; Díaz & Cabido 1997; Leishman & Westoby 1992). This usually requires that a particular function is specified in advance, as is required to assign species to functional groups. For example, relative growth rate of a plant is probably important for primary production. Missing functionally significant traits from measures of FD will result in an underestimate of the effects of extinction on redundancy of species' contributions to functional diversity. This cautions that any empirical evidence of this redundancy will be overly optimistic.

It is easy to imagine that the number of such traits increases with the number of ecosystem functions considered to be important. Hence, measures of FD relevant to many aspects of ecosystem functioning may require high-dimensional trait space. This suggests the hypothesis that the functional diversity that is important for complete ecosystem functioning will be reduced by any number of extinctions. That is, there can be little redundancy of species' contributions to functional diversity in species assemblages unless one restricts the number of ecosystem processes that are considered important.
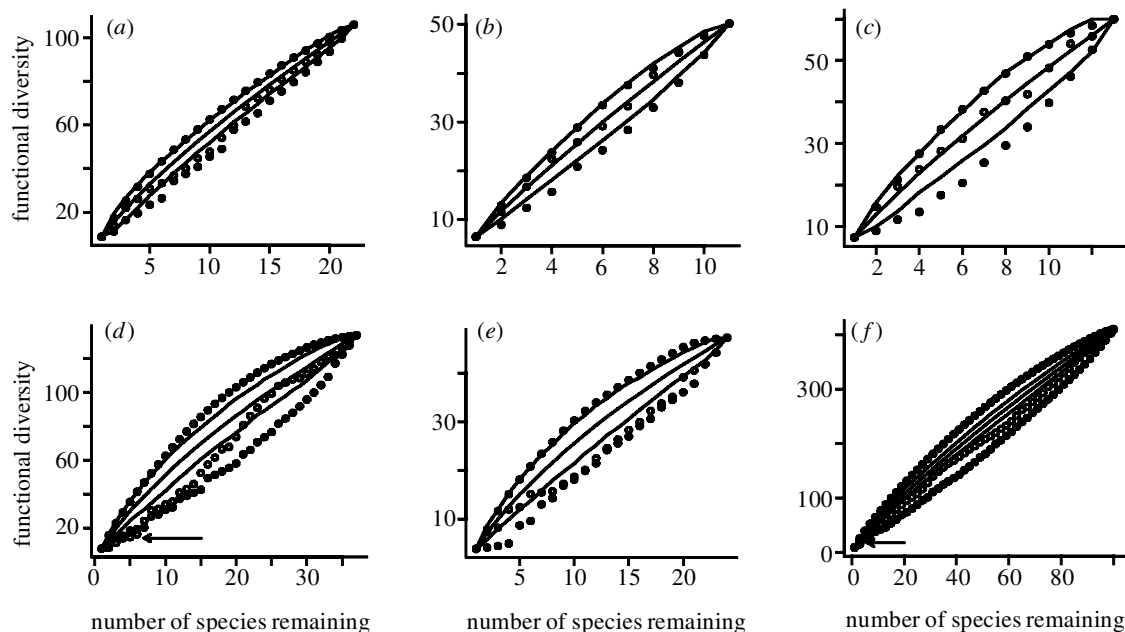
Figure 3. Effects of trait-dependent extinctions on FD in the six real assemblages (arranged as in figure 1). Solid lines show the mean and 95% confidence intervals of 100 random extinction trajectories. Open circles show the trait-dependent extinction trajectory. Filled circles show the trajectories of maximum or minimum stepwise loss of FD. In (*f*), points were plotted for one and even numbers of species only. The arrows in (*d*) and (*f*) show where trait-dependent extinctions reduced FD below a worst-case extinction scenario in which species loss maximized stepwise reductions of FD.

The order by which species disappear from an assemblage can alter importantly the rate of functional diversity loss in these real assemblages. When extinctions occurred in the order that minimized and maximized sequential losses of FD, there were redundant or keystone-like patterns of FD loss (Sala *et al.* 1996) within each assemblage, i.e. the effects of extinction will differ depending on whether a species that contributes greatly or not to diversity is lost. This differs from the observation that the order of species extinctions will be important when more or less abundant species suffer extinction first (Sala *et al.* 1996). Consequently, at least two hypotheses exist for how the order of species extinctions influences the loss of ecosystem functioning: interspecific differences in contributions to functional diversity and interspecific differences in abundance. The relative importance of these potential processes remains unclear.

Simulated trait-dependent extinction of species caused greater than random loss of functional diversity in four of the six assemblages. This mirrors the greater than random loss of phylogenetic diversity that can occur when extinctions are aggregated within particular taxa (Heard & Mooers 2000; Purvis *et al.* 2000; Von Euler 2001). Assuming random loss of species can produce conservative estimates of the rate of loss of both functional and phylogenetic diversity. We based the order of extinctions in the plant assemblages on the expected effects of nitrogen deposition, but did not assume a specific cause for the extinctions in the animal assemblages. Further studies of how other specific causes of extinction (e.g. habitat destruction, fragmentation and invasions) bias extinctions towards species with particular functional traits will help predict how particular types of disturbance will affect functional diversity.

It is especially worrying that trait-dependent extinctions

in the assemblage of arctic vegetation and Argentinean flora caused reductions of functional diversity that, with low numbers of species remaining, were more severe than our worst-case extinction scenario. In both cases, the trajectory of extinctions that maximized sequential loss of FD did not include the assemblage with minimum FD. This occurred because our worst-case scenario minimized the loss of FD caused by each extinction, as opposed to searching for the least diverse set of species at each diversity level. Hence, the initial extinctions (within any particular extinction trajectory) constrained the effects of subsequent extinctions such that a 'you can't get there from here' phenomenon occurred. It became impossible to reach the species set with minimum FD through loss of a single species (multiple species replacements/ substitutions were required). Other simulations suggest this phenomenon may not be uncommon in natural assemblages. Thus, not only may the trait-dependent patterns of species extinctions that are presently occurring result in unduly rapid loss of functional diversity, but they also have the potential to reduce this diversity faster than almost any other extinction scenario.

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