

# More diverse plant communities have higher functioning over time due to turnover in complementary dominant species

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**More diverse communities have been shown to have higher and more temporally stable ecosystem functioning than less diverse ones, suggesting they should also have a consistently higher level of functioning over time. Diverse communities could maintain consistently high function because the species driving function change over time (functional turnover) or because they are more likely to contain key species with temporally stable functioning. Across 7 y in a large biodiversity experiment, we show that more diverse plant communities had consistently higher productivity, that is, a higher level of functioning over time. We identify the mechanism for this as turnover in the species driving biomass production; this was substantial, and species that were rare in some years became dominant and drove function in other years. Such high turnover allowed functionally more diverse communities to maintain high biomass over time and was associated with higher levels of complementarity effects in these communities. In contrast, turnover in communities composed of functionally similar species did not promote high biomass production over time. Thus, turnover in species promotes consistently high ecosystem function when it sustains functionally complementary interactions between species. Our results strongly reinforce the argument for conservation of high biodiversity.**

Jena Experiment | redundancy | grassland | species richness | evenness

The current global decline in biodiversity has prompted many studies to test the importance of species richness for maintaining ecosystem functioning. These studies show that species loss has negative effects on a range of ecosystem functions and services (1, 2) but that relatively few species are needed to sustain many functions (2), suggesting high redundancy (3). However, such redundancy is reduced if more than one ecosystem function is considered (4–6) or if species that do not contribute to a particular ecosystem function in one year are needed to maintain that function over time (7). Coexistence between species can be promoted if they have different responses to a temporally changing environment (8), and diverse communities have been shown to be more temporally stable in ecosystem function than less diverse ones (9, 10). These lines of evidence would suggest that a temporal change in the species driving function could allow diverse communities to maintain consistently high functioning over time. However, so far no study has quantified the importance of turnover in species for sustaining ecosystem function.

Asynchronous species fluctuations, driven by intra- and inter-specific density dependence, demographic stochasticity, or different responses to the temporally changing environment, can all stabilize community biomass (11). Both uncorrelated species fluctuations (12, 13) and compensatory dynamics can have this effect (14, 15). Fluctuations in species abundances are generally higher in more species-rich and more even communities, and can allow such diverse communities to maintain a more stable bio-

mass over time (16). Thus, maintenance of functioning over time might be promoted by turnover between functionally complementary species, with different species needed for function in different years. In some cases, however, production among dominant species alone can stabilize community biomass, meaning greater stability in less even communities (17, 18). In this case, the presence of a species in the community with temporally stable high productivity might be sufficient to guarantee function over time, in which case species turnover would not promote high functioning. The relative importance of these two processes might depend on functional diversity: There will be little complementarity between functionally similar species (19), so turnover between species could be important in sustaining consistently high biomass production only in functionally diverse communities.

Here we investigate these questions in a long-term biodiversity experiment, the Jena Experiment, that has plots with 1, 2, 4, 8, 16, and 60 species chosen from a pool of 60. Species belong to one of four functional groups, and functional group richness is manipulated to be as orthogonal as possible to species richness to determine the relative importance of species versus functional diversity in driving ecosystem function (20). We use 7 y of data to first calculate how well communities of different diversities function over time. We do this by calculating the number of years in which each community reaches a threshold of a certain percentage of the maximum biomass production in a year (5, 6). In this study, we focus on biomass production as the function of interest, and in the following, “functioning” refers to consistently high biomass production, because focusing on aboveground biomass production allows us to easily calculate individual species contributions to function. In principle, our method could be extended to consider all other functions for which species-specific contributions are known.

For each community, we then calculate the turnover in the number of species needed for function (biomass production in this case) across multiple years, which we refer to as functional turnover (FTO) (21). Usually, only a small proportion of the species contributes a large fraction of the community biomass production, and we can consider these dominant species as those principally driving function (22). First, we calculate each species’ proportional contribution to function. Then we define the number of species necessary to maintain function within a community ( $S_{\min}$ ) as the minimum set of species whose contributions to function exceed an assumed threshold level of function for that

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community. The use of a threshold to define the species that sustain function is similar to the approach in Gamfeldt et al. (5), who argued that the use of a 50% threshold was analogous to the use of the  $EC_{50}$  threshold in ecotoxicology as the concentration of a substance giving 50% of maximum effect. Note that the 50% threshold is conservative, as it assumes that a large loss of function is acceptable; however, we do not imply that such a loss of function would be desirable in natural communities. This approach allows us to estimate  $S_{min}$  across multiple years, because all of the species needed for function in individual years must be present to guarantee function across all years. FTO is the percentage increase in the number of species needed for function across multiple years. This method allows us to estimate functional turnover within communities, unlike other approaches that consider multiple communities to identify the species contributing to function (4, 7). Therefore, we can identify the drivers of high functional turnover and the effect of this turnover within communities.

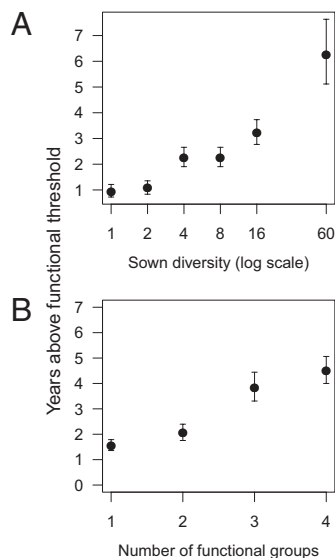
In a neutral community (23), biodiversity would not increase ecosystem functioning because all species are functionally equivalent. Nevertheless, species abundances would fluctuate over time (11), leading to the appearance of functional turnover. However, if all species are ecologically equivalent, each one should have an equal chance to contribute to function and  $S_{min}$  should be a random sample of the species in the community. By contrast, in a niche-structured community, certain species with particular traits would be more likely to contribute to function than others. To test whether our communities follow neutral dynamics, we compared the number of times each species contributed to function across a range of experimental communities.

## Results and Discussion

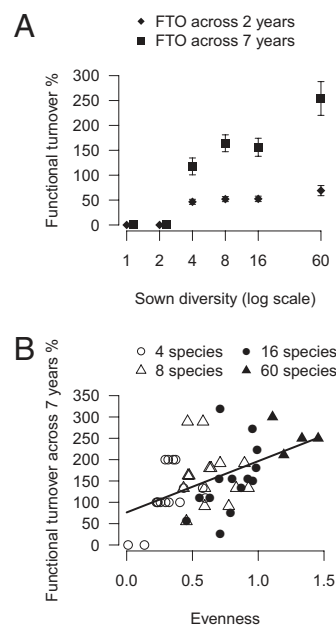
We found that more diverse plots had high biomass production for longer time spans (see Fig. 1*A* for 50% biomass threshold). Using thresholds other than 50%, or analyzing average biomass

across years rather than using thresholds, confirmed this result (*SI Text* and Figs. S1 and S2). Communities with three or four functional groups present also had higher functioning over time than those with only one or two functional groups (Fig. 1*B*). Species richness within functional groups was important because higher species richness increased functioning over time within plots with four functional groups ( $P < 0.01$ ) and within plots with three functional groups ( $P = 0.05$ ). Thus, both high functional and high species diversity are needed to maintain function over time. High biomass production in diverse communities can arise through complementary interactions between species, niche partitioning or facilitation, (complementarity effects), or the selection of particular highly productive species (selection effects) (24). We found that both processes were important: Communities with higher mean complementarity effects ( $P < 0.001$ ) and those with higher selection effects ( $P < 0.001$ ) had higher functioning over time. Selection effects, however, were only significant when fitted in a model along with complementarity effects. This result is similar to the observation that overyielding is associated with greater stability of biomass over time (25). Diverse communities are known to maintain a more temporally stable biomass (9), and it has often been suggested that they should be more resilient to environmental change (26). We show that both species-rich and functionally diverse communities maintain a consistently higher functioning over time than less diverse communities and examine the mechanisms behind this.

The species driving biomass production changed over time (Fig. 2). Functional turnover was significantly above 0 for all diversity levels with four or more species (FTO was only meaningful and calculated for plots with four or more species) and only 2 out



**Fig. 1.** Effect of biodiversity on maintenance of biomass production over time. (A) Species-rich communities exceeded a threshold level of function in a larger number of years than species-poor communities did (GLM main effect of species richness,  $P < 0.001$ ). (B) Communities with a larger number of functional groups present had higher functioning for more years than those with only one or two functional groups (GLM main effect of number of functional groups,  $P < 0.01$ ). Error bars are always  $\pm 1$  SE and are calculated by back-transforming SEs from GLMs; error bars can therefore exceed 7 (the maximum number of years).

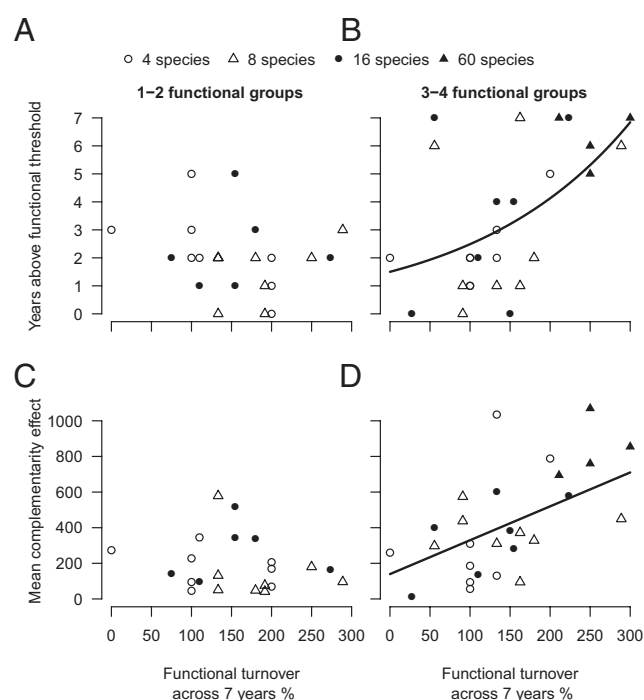


**Fig. 2.** Functional turnover in communities of different diversities. (A) FTO across 2 or 7 y in plots of different species richness. FTO was higher in more species-rich communities, when calculated across 2 y (ANOVA main effect of species richness,  $P = 0.02$ ) and across 7 y (ANOVA main effect of species richness,  $P < 0.01$ ). Error bars are  $\pm 1$  SE and are calculated from linear models. We show FTO as 0 for communities with only one or two species because it cannot be calculated for monocultures and is not meaningful for two-species plots. (B) FTO across 7 y in communities of different evenness; communities with different numbers of species are shown with different symbols. FTO across 7 y was higher in more even plots (ANOVA main effect of evenness,  $P < 0.001$ ); evenness remained significant after correcting for species richness.

of 16 four-species communities showed no turnover at all over 7 y. Our use of a 50% threshold to measure FTO is relatively conservative because only abundant (mostly dominant) species were included in the minimum set needed to exceed a threshold level of biomass (Fig. S3). Thus, using a lower threshold, and therefore including subordinate species in this set, resulted in higher values of FTO without, however, changing our conclusions (Fig. S2C). The turnover that we observed across 2 y was similar to the turnover between species contributing to different functions calculated by Hector and Bagchi (4). Our FTO values were very closely related to the inverse of their overlap values (*Methods*), so the overlap between pairs of functions that they calculated as ranging from 0.49 to 0.19 would correspond to FTO values of 0.51–0.81. These values were close to the FTO values of 0.46–0.69 that we calculated across 2 y. Our FTO values are also very similar to the mean overlap value of 0.45 (equal to FTO of 0.55) between species contributing to function across pairs of years calculated by Isbell et al. (7) in their study looking at how many species are required for function across different functions, times, and places. We found even higher FTO across longer time spans: More than twice as many species were needed to sustain function across all 7 y compared with just 1 y (Fig. 2A). In many cases, species went from being subordinate, or even absent from a biomass sample, in some years to becoming dominant and providing function in other years (Fig. S3). This shows that redundancy was much lower when considering maintenance of function over time and, importantly, that species that might be dismissed as functionally unimportant in some years can in fact be needed for function at other times (also see *SI Text* and Fig. S4). The recent results of Isbell et al. (7) (who estimated how many species were needed for function over time using a different method) agree with ours in showing functional turnover. In addition to this, our approach allows us to estimate functional turnover within communities to address whether diversity promotes consistently high functioning over time via high levels of functional turnover.

Functional turnover was higher in more diverse plots: Both higher species richness and higher evenness increased FTO (Fig. 2A and B). The effect of evenness was independent of species richness, as higher evenness significantly promoted functional turnover even after correcting for species richness (Fig. 2B). Diverse communities may have higher turnover for several reasons: Dominant species may have more stable populations than subordinates (27), leading to low turnover in uneven communities. Species-rich communities might have higher turnover because population stability is generally lower in these communities (9), although not necessarily for all of the species in the community (27). Additionally, species-rich communities could contain a wider range of species that can respond to changing conditions (28, 29) and more even communities may be better able to respond to environmental fluctuations via changed biomass contributions per species than those strongly dominated by one or few species (30, 31). Thus, turnover may well have been higher in diverse communities because they contain different species able to provide function under different environmental conditions, and this higher turnover may have allowed diverse communities to maintain a consistently high level of function.

The turnover in the functionally important species within communities was correlated with higher biomass production over time, particularly where functional group diversity was higher (Fig. 3A and B and Fig. S5). Fitting the number of functional groups as a two-level factor (levels 2≤ and >2 functional groups) in the model rather than as a continuous variable resulted in a lower value of the Akaike Information Criterion (AIC) (from 193.1 to 191.7). In communities with three or four functional groups, higher levels of functional turnover increased functioning over time, but FTO had no effect in communities with only one or two functional groups (Fig. 3A and B). During model



**Fig. 3.** The relationship of FTO with functioning over time and complementarity effects. (A) In plots with one or two functional groups, there was no significant relation between FTO and functioning over time (main effect from GLM,  $P = 0.38$ ; from major axis regression,  $P = 0.15$ ). (B) In plots with three or four functional groups, there was a significant positive relation between FTO and functioning over time (main effect from GLM,  $P < 0.01$ ; major axis regression,  $P < 0.001$ ). The fitted line is the prediction from the GLM with Poisson errors, back-transformed, and therefore a curve on the original scale. (C) There was no relationship between mean complementarity effects and FTO in plots with one or two functional groups (main effect from ANOVA,  $P = 0.27$ ; major axis regression,  $P = 0.14$ ). (D) In plots with three or four functional groups, there was a significant relationship between FTO and mean complementarity effects (main effect from ANOVA,  $P = 0.02$ ; major axis regression,  $P < 0.001$ ). In all plots, different numbers of species are shown with different symbols; we corrected for species-richness effects on FTO by also fitting sown diversity in the models.

simplification, species richness was dropped from the model, suggesting that the significant effect of species richness on functioning over time was due to higher FTO in more species-rich plots. This suggests that, in general, diverse plots do not simply maintain function over time because they are more likely to contain species with temporally stable high productivity (a “temporal selection effect”), but that in fact the identity of the species sustaining biomass production changes through time, allowing diverse communities to maintain high levels of functioning. This was not the case in communities composed of functionally similar species, where high functional turnover did not maintain high levels of biomass production. Therefore, only complementary interactions between functionally dissimilar species seemed to maintain high levels of functioning over longer timescales, which is in line with the recent finding that species belonging to different functional groups fluctuate more asynchronously with each other than do species of the same functional group (27). It therefore seems unlikely that neutral fluctuations in species abundances could maintain high levels of functioning, because under neutrality all species should be functionally equivalent.

We found some evidence for a temporal selection effect. Evenness also affected functioning over time ( $P < 0.01$ ), but the slope of the relationship was negative if species richness and



functional turnover were fitted in the same model. Three plots strongly dominated by a productive legume (*Onobrychis viciifolia* Scop.) exceeded 50% biomass production in 6 or 7 y despite having FTO <200% (Fig. 3). These plots are responsible for the negative effect of evenness on functioning over time, and when they were excluded, evenness no longer had a significant effect ( $P = 0.11$ ). Together with the observation of positive selection effects on biomass production over time, this suggests that some communities maintain high functioning through time because they are dominated by productive species with temporally stable abundance. However, these communities are very much the exception, and most of them maintain high function through complementary turnover in abundant species.

Further evidence for the importance of functional complementarity in driving FTO comes from the fact that high levels of turnover occurred in communities with high mean complementarity effects; as for functioning over time, an interaction between number of functional groups and FTO was significant ( $P < 0.01$ ; Fig. 3 C and D). In this case, fitting a continuous variable for the number of functional groups resulted in a more parsimonious model (AIC = 312) than fitting a two-level factor (AIC = 315), because the relationship between FTO and complementarity effects was stronger in communities with four functional groups present. There was no significant relationship between selection effects and FTO ( $P = 0.13$ ). Therefore, although both complementarity and selection effects promoted functioning over time, high levels of FTO only occurred when species had complementary interactions with each other. This agrees with results showing that the dominant species within our communities differ in their trait combinations (32). Turnover of dominants in more functionally diverse communities could in fact maintain high levels of complementarity in these communities with the species identity of the interacting partners changing over time.

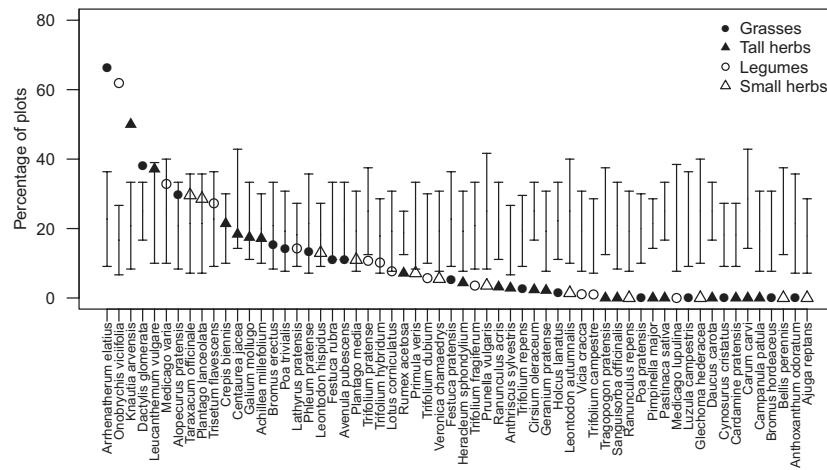
Fluctuations in species over time, and therefore the functional turnover we observe, may be driven by competitive interactions, demographic stochasticity, or changes in the abiotic or biotic environment (11, 33). We analyzed the effect of interspecific competition on FTO by simulating FTO in the absence of interspecific competitive interactions (SI Text). Simulated FTO without interspecific competition was lower than the observed FTO (Fig. S6). This suggests that dominant species vary less in abundance when they experience only intra- rather than interspecific com-

petition, and is in line with the observation that increasing species richness has overall negative effects on temporal stability at the population level (9). Thus, competitive interactions between species are important for driving the functional turnover that maintains high functioning over time. It is further possible that compensatory interactions are important in driving functional turnover.

Neutral dynamics, however, seem not to drive functional turnover, because the species contributing to function within communities tended to be the same across communities; that is, a small number of species contributed to function much more often than expected by chance and a large number contributed less often (Fig. 4). In neutral communities sensu Hubbell (23), the species contributing to function should be a random sample of the species in the community.

No species contributed to function (i.e., belonged to the minimum set of dominant species needed for 50% biomass production) in all years and in all plots, and several species that were subordinate in some years went on to become dominant and provide function in other years (Fig. S3). However, 18 out of 60 species remained subordinate in all years and never contributed to function in any plot at any time (Fig. 4). Normally, it would be desirable to sustain a higher level of function than 50% and in this case not only the dominant species would be considered functionally important, although it is unlikely that subordinate species (<5% biomass) would make significant contributions to function. The species that contributed to function most often across years were largely the same as those that have been shown to be highly productive across communities in a single year (32). This suggests that turnover within a set of potentially dominant species maintains function over time, although it would not be possible to predict the identity of these species by looking at an individual community in a single year. Species that never contributed to biomass production might become important under more extreme environmental conditions, and many of them are likely to contribute to functions other than biomass production (4, 5, 7, 34). In addition, some species may have effects on functioning that are disproportionate to their abundance if they facilitate other species.

Transient dynamics might be important in communities establishing from seed. We find no evidence for a change in the magnitude of FTO over time in Jena Experiment communities



**Fig. 4.** Average percentage of plots in which each species contributed to function. Points show the average percentage of plots in which each species contributed to 50% of the biomass production out of the total number of plots into which it was sown. These are average percentage numbers of plots per year and are calculated across 7 y. Species are ranked according to the percentage of plots in which they contributed to function. The error bars show the 95% confidence intervals for the percentage number of plots in which each species would be expected to contribute to function by chance (Methods). Points outside this range denote species that contributed to function more or less frequently than expected by chance.

(*SI Text*), suggesting that FTO is not principally driven by transient dynamics or successional change in species abundances. Some individual species' abundances may have shown a directional trend over time (*SI Text*); however, if species-rich communities are able to sustain higher levels of functioning during successional changes this would also be an important effect of diversity, particularly as compositional change is likely to occur in communities in response to global change or restoration (35).

This analysis examining how diverse communities maintain consistently high functioning shows that the most important mechanism is turnover in functionally complementary species, rather than the presence of dominant species with consistently high biomass. Turnover was high and species that appeared to be redundant and unimportant with respect to maintaining function in a single year became dominant and were required to maintain function in other years. Turnover in functionally diverse communities may sustain complementary interactions between species over time and therefore ensure a consistently high level of function in these communities. Therefore, we highlight that protecting biodiversity is essential to preserve the ability of ecosystems to sustain functioning across time, and is likely to be of particular importance in the light of global change.

## Methods

**Jena Experiment.** The Jena Experiment is a grassland biodiversity experiment in Germany (for a description of the experimental design, see refs. 20 and 36). The experiment contains 82 plots of 20 × 20 m with 1, 2, 4, 8, 16, or 60 plant species. Plant species belonged to four functional groups (FGs): grasses, legumes, small herbs, and tall herbs (20). The number and presence of FGs were varied systematically; for example, plots with four or more species could have one, two, three, or four FGs. The data used here were individual species and total biomass data from 2003 to 2009. The experiment was harvested twice yearly, during peak standing biomass in late May and again in late August. We only use data from May because species-specific biomass data were not available for August 2004, and because annual peak biomass is achieved in late May; however, analyses using August data instead give the same result (*SI Text* and *Figs. S7–S9*). Biomass harvesting was done by clipping the vegetation at 3 cm; harvested biomass was sorted into target species (species sown in the particular plot) and dried at 70 °C for at least 48 h (for more details, see ref. 36).

For each plot, we also calculated its mean evenness, based on average biomasses for each species across all years. We calculated this as Rényi evenness with  $\alpha = \infty$ , which is the logarithm of the proportional abundance of the most abundant species (37). This estimates evenness, giving highest weight to the most abundant species, and is the measure of evenness least related to species number. We could therefore use this measure alongside species richness to calculate the relative importance of species number and evenness in affecting functional turnover.

We also calculated mean complementarity and mean selection effects for each community over time, using the additive partitioning method of Loreau and Hector (24). Following Marquard et al. (38), we excluded three outlier values of both the complementarity and selection effects, two from 2005 and one from 2006.

**Calculation of Functioning over Time.** To calculate the functioning of a community over time, we calculated the number of years in which it reached a threshold of 50% of the maximum biomass across communities in a given year (for analyses with other thresholds, see *SI Text*). Maximum biomass was calculated as the mean of the five most productive plots, following ref. 6. The number of years was analyzed in general linear models (GLMs) with Poisson errors. Explanatory variables were species richness (log-transformed), number of functional groups (continuous), and the presence of legumes, grasses, and tall herbs. We also analyzed number of years as a function of the average complementarity and average selection effects for each plot. In these models, we also fitted species richness (log-transformed), number of functional groups (continuous), and the presence of legumes, grasses, and tall herbs. For all GLMs, we simplified full models by removing nonsignificant terms and comparing models with  $\chi^2$  tests.

**Calculation of FTO in the Jena Experiment.** To calculate functional turnover within communities, for each plot we calculated the number of species needed to sustain function ( $S_{\min}$ ) for all individual years, for all combinations of 2 y, and across all 7 y.  $S_{\min}$  was calculated as the minimum number of

species in a community needed to achieve a threshold of 50% of the total biomass of that community. For analyses with other thresholds, see *SI Text*.  $S_{\min}$  across multiple years was calculated as all of the species that contributed to function during those years. We then calculated mean  $S_{\min}$  for each number (1, 2, 7) of years for each plot. For each plot, FTO was calculated comparing mean ( $S_{\min,1}$ ) for 1 y with mean ( $S_{\min,2}$ ) across 2 y or  $S_{\min,7}$  across all 7 y, according to Eq. 1:

$$\text{FTO} = \frac{\text{mean}(S_{\min,n}) - \text{mean}(S_{\min,1})}{\text{mean}(S_{\min,1})}, \quad [1]$$

where  $n = 2$  or 7.

We compared our method of calculating turnover with that used by Hector and Bagchi (4), who calculated overlap between species contributing to different functions using Sørensen's index. This measure is inversely related to our FTO because it measures the proportion of species that contribute to both functions, whereas we calculate the proportion of extra species needed for function across multiple years. Using our data, we calculated overlap between species contributing to function between pairs of years and compared the average overlap values per plot with FTO across 2 y. The two measures are very closely negatively correlated ( $R^2 = 0.99$ , slope =  $-0.98$ ). We use FTO because it is easier to extend this measure to consider turnover across multiple years.

FTO values across 2 or across 7 y were analyzed separately in ANOVA models. Explanatory variables were species richness (log-transformed), evenness, number of functional groups (continuous), and the presence of legumes, grasses, and tall herbs. Evenness was fitted after species richness in these ANOVA models, and we used type I sums of squares to assess the significance of the evenness effect. This means that evenness is corrected for species richness and a significant effect of evenness is not due to more species-rich plots being more even. Model validation showed that errors were normal and variance was homogeneous.

We also analyzed the effect of FTO across 7 y on functioning over time. As before, we used GLMs with Poisson errors to model functioning over time, and explanatory variables were species richness (log-transformed), number of functional groups (continuous), presence of legumes, grasses, and tall herbs, FTO across 7 y, and interactions between FTO and all other variables. We also repeated this analysis including evenness as well. Again, we simplified full models by removing nonsignificant terms and comparing models with  $\chi^2$  tests. We further analyzed the effect of FTO on the mean complementarity effects and mean selection effects over time. We used ANOVA models for these analyses, with the same terms as for the analysis of functioning over time; fitting species richness first in these models meant that we corrected for differences in FTO between plots with different numbers of species. To improve normality of errors, complementarity and selection effects were square root-transformed and the result was multiplied by  $-1$  if the original value was negative (38).

We also analyzed the relationship between FTO and functioning over time and between FTO and mean complementarity effects, using major axis regression. This corrects for the fact that there is error in both  $x$  and  $y$  variables. Analyses were carried out separately for communities with three or four functional groups and for those with one or two functional groups, to test the interaction between FTO and number of functional groups. Analyses were conducted using the lmodel2 package (39) in R 2.12 (40).

**Number of Times Individual Species Contributed to Function.** For each species, we determined the number of times it occurred among the minimal group of species contributing 50% of biomass, across all years and all plots in which it occurred. We then estimated the number of plots in which it would be expected to contribute to function by chance. To do this, for each plot we randomly selected a number of species equal to the average  $S_{\min}$  in 1 y for that plot from the list of species originally sown into the plot. Using these random sets, we then calculated the number of plots in which each species contributed to function. We repeated this process 1,000 times to generate 1,000 random sets of species for each plot and 1,000 estimates of the number of times each species would be expected to contribute to function by chance. We then calculated 95% confidence intervals for the number of plots in which each species contributed to function and could therefore determine for each species whether they contributed to function significantly more or less often than expected.

In each community, we also calculated the relative abundances of all of the species that were needed for function across 7 y (i.e., were part of  $S_{\min,7}$ ). We calculated abundances for these species in the years in which they did contribute to function and also in the years in which they did not. Species were then classified into dominants (relative abundance >25%), intermediates (5–25%), and subordinates (<5%). We could then estimate the number of times species that were subordinate in a community at some point contributed to function at another time point.

