Successional diversity and forest ecosystem function

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Forest inventory data was used to examine the relationship between successional diversity and forest ecosytem function. The inventory data show that stands composed of early successional species are more productive than stands composed of late successional species, whereas stands composed of late successsional species have lower turnover than stands composed of early successional species. Taken alone, these results would suggest that forests should be managed in a way that favors the most productive early successional species or longest-lived late successional species, depending on whether the goal is to maximize productivity or maximize carbon storage. However, the inventory data also show that stands with low successional diversity fix and store less carbon than stands with high successional diversity. This result suggests that forests should be managed in such a way as to retain species diversity while also favoring species that maximize the ecosystem function of interest.

Key words: carbon storage; diversity; forest; productivity; succession.

INTRODUCTION

Over the past decade numerous experiments have been conducted to examine the relationship between species diversity and ecosystem function. In most ecosystems, the relationship between diversity and productivity has been shown to be positive (Tilman *et al.* 1997). In a few ecosystems, however, no significant relationship has been observed, while in others increasing species diversity has been shown to decrease productivity (Hooper & Vitousek 1997). These divergent results have stimulated a vociferous debate that revolves around a single question: what factors determine whether the relationship between diversity and productivity is positive?

Recent syntheses of the experimental results suggest that a positive relationship between diversity and productivity depends on a positive relationship between productivity and competitive ability (Kinzig *et al.* In press). If a species' ability to maximize carbon gain in a particular environment also confers a competitive advantage in that environment, competition will maximize productivity by favoring the most productive species. Thus, a polyculture will be more productive than a monoculture because the most productive species will prevail in each environment within the ecosystem. However, there may be exceptions in which a species' ability to maximize carbon gain does not confer competitive dominance.

In forests, for example, fast-growing early successional species are replaced by slower growing late successional species (Horn 1974). Thus, productivity is not maximized by competition because stands dominated by slow-growing late successional species fix less carbon than forests dominated by fast-growing early successional species. Nor is productivity necessarily enhanced by successional diversity; stands containing a mix of early and late successional species may fix less carbon than stands dominated by a single fast-growing early successional species.

Forests have scarcely been mentioned in the biodiversity debate due to the difficulty of conducting experiments in ecosystems with slow dynamics. Yet, there is a vast store of observational data on forests that can be used to examine whether forest ecosystems differ in some fundamental way from other kinds of ecosystems. While

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observational data cannot be used to establish causality, they can be used to document whether the relationship between diversity and productivity is positive, negative, or neutral.

In this paper, we use inventory data to examine relationships between successional diversity, productivity, and carbon storage in forests. To motivate the analysis, we first present a simple null model that is similar to previous Markov models of forest succession (Horn 1975; Van Hulst 1979; Binkley 1980). The null model predicts that productivity is highest in low diversity stands of early successional species, and that carbon storage is highest in low diversity stands of late successional species. We then analyze the forest inventory data to evaluate the predictions of the null model. Contrary to the predictions of the null model, analyses showed that stands with low successional diversity fix and store less carbon than stands with high successional diversity.

NULL MODEL

Consider a forest that consists of a mosaic of patches at different stages of succession, each patch being dominated by a single tree belonging to one of n species. To model the successional dynamics of this mosaic, we assume that there is a simple competitive hierarchy among the n species. Upon death, an individual of species 1 is replaced by an individual of species 2, which is replaced by species 3, and so on up to species n, which is replaced by species 1. Thus, if X_1 is the fraction of patches occupied by species 1, the rate of change for species 1 is:

$$dX_1/dt = -M_1X_1 + M_nX_{(n)} \tag{1}$$

where M_1 is the mortality rate for species 1 and M_n is the mortality rate for species n, the last species in the successional sequence. Similarly, the rate of change for any of the remaining species is:

$$dX_i/dt = -M_iX_i + M_{(i-1)}X_{(i-1)} \tag{2}$$

where X_i is the fraction of patches occupied by species i, $X_{(i-1)}$ is the fraction of patches occupied by the preceding species in the successional sequence, and $M_{(i-1)}$ is the mortality rate for the preceding species in the successional sequence.

Equations 1 and 2 can be expressed in matrix form as follows:

$$
\begin{bmatrix}
dX_1/dt \\
dX_2/dt \\
dX_3/dt \\
\bullet \\
\bullet \\
\bullet \\
dX_n/dt
\end{bmatrix}
=
$$

$$
\begin{bmatrix}
-M_1 & 0 & 0 & \bullet & \bullet & \bullet & M_n \\
M_1 & -M_2 & 0 & \bullet & \bullet & \bullet & 0 \\
0 & M_2 & -M_3 & \bullet & \bullet & \bullet & 0 \\
\bullet & \bullet & \bullet & \bullet & & & \bullet \\
\bullet & \bullet & \bullet & & \bullet & & \bullet \\
\bullet & \bullet & \bullet & & & \bullet & \bullet \\
0 & 0 & 0 & \bullet & \bullet & \bullet & -M_n
\end{bmatrix}
\begin{bmatrix}
X_1 \\
X_2 \\
X_3 \\
\bullet \\
\bullet \\
\bullet \\
X_x
\end{bmatrix}
\tag{3}
$$

This system of equations can then be solved to obtain the equilibrium abundance of each species, expressed here in terms of species longevity. First, we express the average lifespan of each species as the reciprocal of its mortality rate: $L_i = 1/M_i$. Then, replacing the left-hand side of equation 3 with zero, it is easy to show that the area occupied by species i is proportional to its longevity:

$$X_i^* = L_i/\Sigma_L \tag{4}$$

where Σ_L is the total length of the successional sequence.

We can also solve for the equilibrium productivity, mortality and storage, provided we make two simplifying assumptions about the age-dependence of productivity and mortality. First, if we assume that production is constant with respect to tree age, then the productivity of the successional mosaic is calculated as a simple area-weighted average:

$$\overline{P} \equiv \sum_{i=1}^{n} \frac{L_i}{\Sigma_L} P_i \tag{5}$$

where P_i is the productivity of species i, and the productivity of species i is weighted by the fraction of area occupied by species i; that is, L_i/Σ_L.
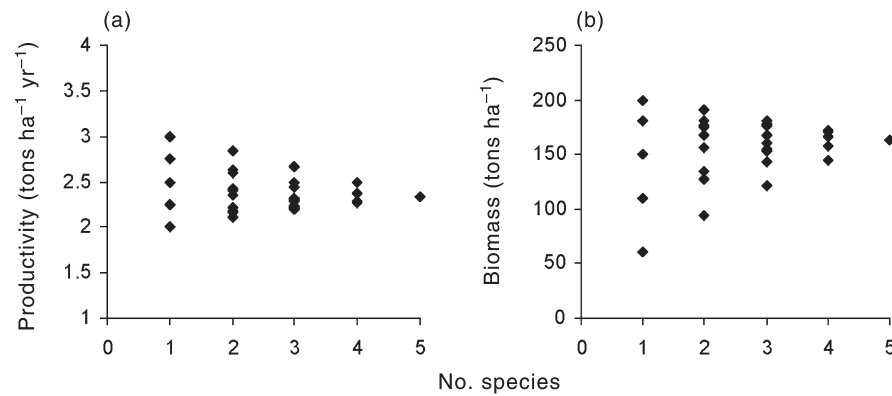
Fig. 1. (a) Equilibrium productivity $\overline{P}$ for each of the 31 successional mosaics. The highest value in the upper left-hand corner represents the species 1 monoculture. The lowest value in the lower left-hand corner represents the species 5 monoculture. (b) Equilibrium biomass $\overline{PL}$ for each of the 31 successional mosaics. The highest value in the upper left-hand corner represents the species 5 monoculture. The lowest value in the lower left-hand corner represents the species 1 monoculture.

Second, if we assume that mortality is random with respect to age, the age distribution of tree species i is:

$$q_i(a) = \frac{1}{L_i} e^{-\frac{a}{L_i}} \qquad (6)$$

the total biomass stored in trees of species i is:

$$\int_0^\infty q_i(a)(P_i a)da = P_i L_i \qquad (7)$$

the total biomass stored in the mosaic is:

$$\overline{PL} \equiv \sum_{i=1}^n \frac{L_i}{\Sigma_L} P_i L_i \qquad (8)$$

and the fraction of biomass lost to mortality is:

$$\overline{M} \equiv \frac{\overline{P}}{\overline{PL}} \qquad (9)$$

because the mortality rate is equal to productivity P at equilibrium.

To illustrate the predictions of this model, we use a five-species system and assume an inverse relationship between longevity and productivity. From species 1–5, longevity increases from 20 to 100 years and productivity decreases from 3 to 2 tons ha^{-1} year^{-1}. Later we show that these assumptions are qualitatively consistent with the inventory data. Here we simply note that by assuming longevity increases from the bottom to

the top of the competitive hierarchy, we are also assuming that competitive ability is correlated with longevity.

In a five-species system, there are 31 possible combinations of species, including five different monocultures, one five-species polyculture, five four-species polycultures, 10 three-species polycultures, and 10 two-species polycultures. Figure 1 shows the productivity $\overline{P}$ and total biomass $\overline{PL}$ for each of the 31 possible mosaics. The common pattern in both of these graphs is that the 31 mosaics form a triangle of points in which the upper boundary decreases with increasing diversity. The reason is that $\overline{P}$ and $\overline{PL}$ are averaged community values calculated by weighting the contribution of each species by its equilibrium abundance. Thus, the average community values for polycultures are necessarily intermediate between the extreme values for monocultures. For example, the species 1 monoculture is more productive than any of the polycultures simply because species 1 is the most productive species. Conversely, the species 5 monoculture is less productive than any of the polycultures because species 5 is the least productive species. The triangular pattern observed in Fig. 1 holds true no matter how the P and L values vary among the species.

To facilitate comparison with the inventory data, we now divide the 31 mosaics into early and late successional categories based on the average lifespan L of the species in each mosaic:
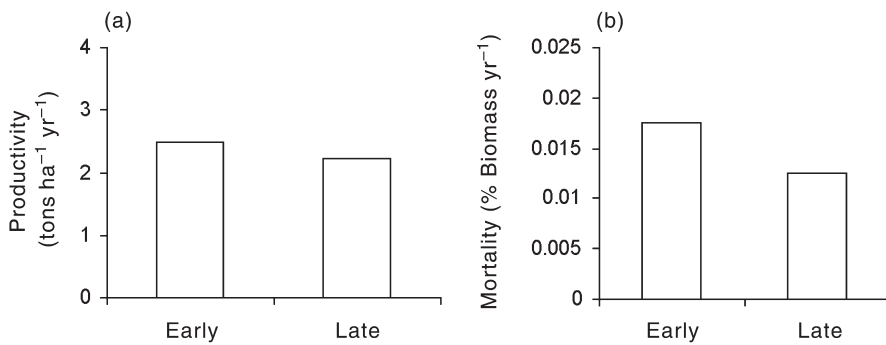
Fig. 2. (a) Average productivity of early and late successional mosaics. (b) Average mortality of early and late successional mosaics.
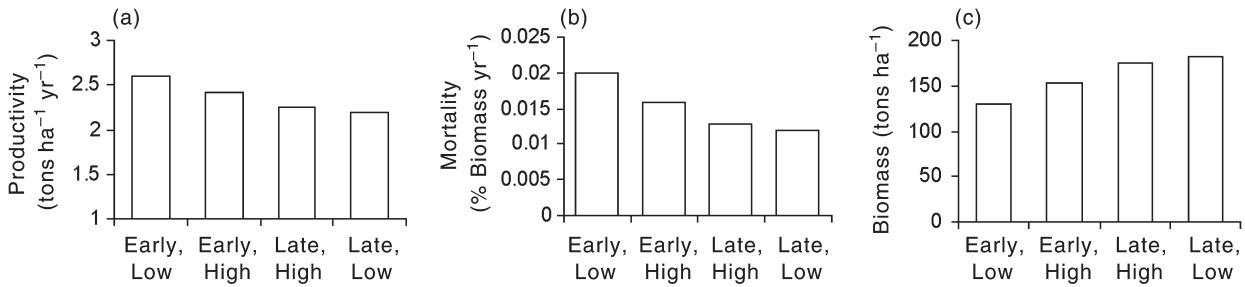
Fig. 3. (a) Average productivity, (b) mortality, and (c) biomass of successional mosaics in each of four categories: (i) early successional with low diversity; (ii) early successional with high diversity; (iii) late successional with low diversity; and (iv) late successional with high diversity.

$$\overline{L} = \frac{\sum_{i=1}^{N} L_i}{N} \qquad (10)$$

where ΣL_i is the total timespan of the successional sequence and N is the number of species in the successional sequence. The average lifespan is longest in mosaics composed of long-lived late successional species. Thus, the late successional category includes mosaics in which the average lifespan is > 60, and the early successional category includes mosaics in which the average lifespan is ≤ 60.

To illustrate how productivity and mortality vary with successional composition, we calculate the average $\overline{P}$ and $\overline{M}$ for both of these categories. Early successional mosaics are more productive than late successional mosaics (Fig. 2a); however, early successional mosaics also have a higher turnover than late successional mosaics (Fig. 2b). Later we show that these patterns are qualitatively consistent with the inventory data.

To illustrate how productivity and mortality vary with successional diversity, we further divide these two categories into four categories: (i) early successional with low diversity; (ii) early successional with

high diversity; (iii) late successional with low diversity; and (iv) late successional with high diversity. The low diversity category includes mosaics with one or two species and the high diversity category includes mosaics with more than two species.

Figure 3a,b shows the average productivity $\overline{P}$ and mortality $\overline{M}$ for each of these four categories. The low-diversity early successional mosaics are more productive than either of the high diversity mosaics (Fig. 3a). Similarly, the low-diversity late successional mosaics have a lower turnover than either of the high diversity mosaics (Fig. 3b). The net result of these differences in productivity and mortality is that the low-diversity late successional mosaics store more carbon than either of the high diversity mosaics (Fig. 3c).

If correct, the null model would have important implications for the biodiversity debate and the management of forests as carbon sinks. First, the null model suggests that forest productivity would be maximized by planting monocultures of the most productive early successional species. Second, the null model suggests that carbon storage would be maximized by planting monocultures of the longest-lived late successional species.

METHODS

To test the predictions of the null model, we analyzed inventory data obtained from the Forest Inventory and Analysis (FIA) database. The FIA data are collected by the United States Forest Service using a standardized methodology described by Hansen *et al.* (1992) and Birdsey and Schreuder (1992). We will now give a brief description of the FIA sampling methods and a more detailed description of the methods we used to analyze the data.

Sampling methods

Inventories are performed separately for each state and follow a two-phase sampling procedure known as double sampling for stratification. In the first phase, a random sample of points is located on aerial photographs and classified by land cover and forest type. In the second phase, a subsample is selected from each of the classes or strata in the first-phase sample. This stratified subsample serves as the second-phase sample of plots that are visited in the field.

For each plot, the classification is verified in the field and a number of additional plot classification variables are recorded if the plot is forested, including stand age and stand origin (plantation *vs* natural). Trees are sampled at a cluster of points covering an area of approximately 1 acre (2.47 ha). Trees between 2.5 cm and 12.7 cm in diameter at breast height (d.b.h.) are sampled in a circular subplot centered on each of the points. Trees wider than 12.7 cm d.b.h. are sampled at each point using horizontal point sampling. For each tree sampled, a number of observations are recorded, including species, status (live, cut, or dead from natural causes), current d.b.h., and previous d.b.h. (if the tree was measured in the previous inventory). The data can be downloaded directly from FIA database (http://www.srsfia.usfs.msstate.edu).

Indices

We analyzed data from 24 670 natural forest plots in 11 states, including Indiana, Michigan, Illinois, Wisconsin, Minnesota, Iowa, Missouri, Kansas, Nebraska, South Dakota, and North Dakota. For each of the species occurring in this sample, we calculated a successional niche index:

$$NI_i = \frac{\sum_{j=1}^{J} K_{ji} Age_i}{N_i} \qquad (11)$$

where NI_i is the niche index for species i, J is the number of plots in the sample, K_{ji} is the number of trees of species i with a crown in the canopy of plot j, N_i is the total number of trees of species i in the sample, and Age_j is the age of the stand in plot j. The niche index is a measure of a species' position in the competitive hierarchy of species.

For each plot in this sample, we then calculated the mean niche index of the trees occurring in that plot:

$$\overline{NI}_j = \frac{\sum_{i=1}^{S} NI_i K_{ji}}{\sum_{i=1}^{S} K_{ji}} \qquad (12)$$

where $\overline{NI}_j$ is the mean niche index for plot j and S is the total number of species, NI_j is a measure of the successional composition of a plot and is analogous to the average lifespan L calculated above.

Finally, for each plot we calculated the standard deviation from the mean niche index:

$$S_{NI} = \sqrt{\frac{\sum_{i=1}^{S} \left(NI_i - \overline{NI}_j\right)^2 K_{ji}}{\sum_{i=1}^{S} K_{ji} - 1}} \qquad (13)$$

where S_{NI} is a measure of the successional diversity of a plot; that is, the farther the species in a plot deviates from the mean niche index, the greater the successional diversity of the plot. In other words, the S_{NI} of a plot that contains a mix of early and late successional species will be greater than the S_{NI} of a plot that is dominated by early successional species or a plot that is dominated by late successional species.

Growth, mortality and biomass

From the 24 670 plots analyzed earlier, we selected stands > 30 years in age that had no evidence of harvesting in the recent past. We excluded stands < 30 years old because they do not have closed
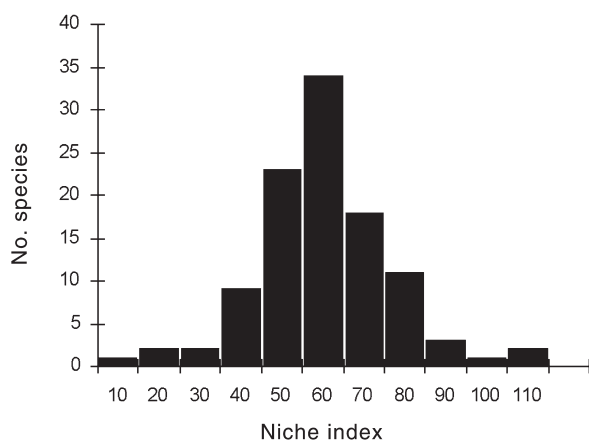
Fig. 4. Niche index of each of the species in the sample, which contains 11 states.
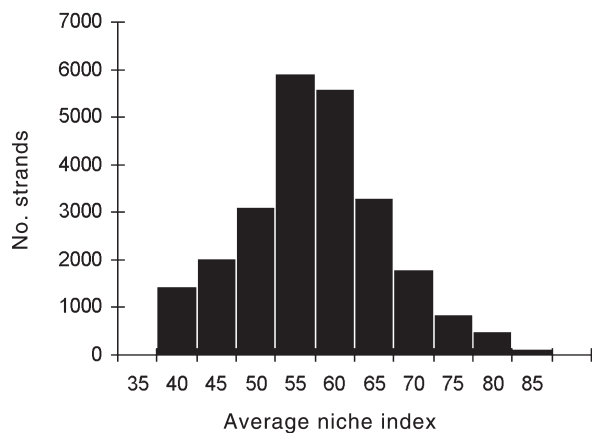

Fig. 5. Average niche index of each of the stands in the sample containing 11 states.

canopies and would therefore introduce undue variation in growth unrelated to the variables of interest. Stands with evidence of harvesting were excluded for the same reason.

For each tree in each of these plots, we calculated aboveground dry biomass. The aboveground biomass was calculated using allometric equations relating tree mass to d.b.h. (Schroeder *et al.* 1997). The aboveground biomass of each living tree was then summed to obtain the aboveground biomass of each plot, following the methods of Caspersen *et al.* (2000).

We also used the methods of Caspersen *et al.* (2000) to calculate growth and mortality for each of the remeasured plots. Growth is the change in biomass density of living trees measured in the

first inventory that survived to the second inventory. Mortality is the biomass density of living trees measured in the first inventory that died by the second inventory. Mortality is expressed on a percentage basis by dividing by the biomass of the plot at the time of the first inventory.

Data–model comparison

To facilitate comparison between the model predictions, we divided the plots into the same categories used earlier. First, we divided the plots into two successional categories: (i) plots composed of early successional species; and (ii) plots composed of late successional species. The late successional category included plots with a mean niche index $NI_j > 60$, and the early successional category included plots with a mean niche index $NI_j \leq 60$. These categories are comparable to the categories used in Fig. 3a,b. We then further divided these two categories into four categories: (i) early successional with low diversity; (ii) early successional with high diversity; (iii) late successional with low diversity; and (iv) late successional with high diversity. The high diversity categories included plots in which the standard deviation S_{NI} was > 7.0, and the low diversity categories included plots in which the standard deviation S_{NI} was ≤ 7.0. For each of these four categories, we calculated the average biomass, the average growth, and the average mortality. These averages can be compared to the averages presented in Fig. 4.

RESULTS

Indices

The species included exhibit an approximately normal distribution along the successional niche axis (Fig. 4). For most species, the niche index NI_i falls between 30 and 90, indicating that these species are most commonly found in stands between the age of 30 and 90 years. The plots included show an approximately normal distribution along the successional niche axis (Fig. 5). For most plots, the average niche index NI_j falls between 40 and 80, indicating that the species found in the plot are most commonly found in stands between the age of 40 and 80 years.
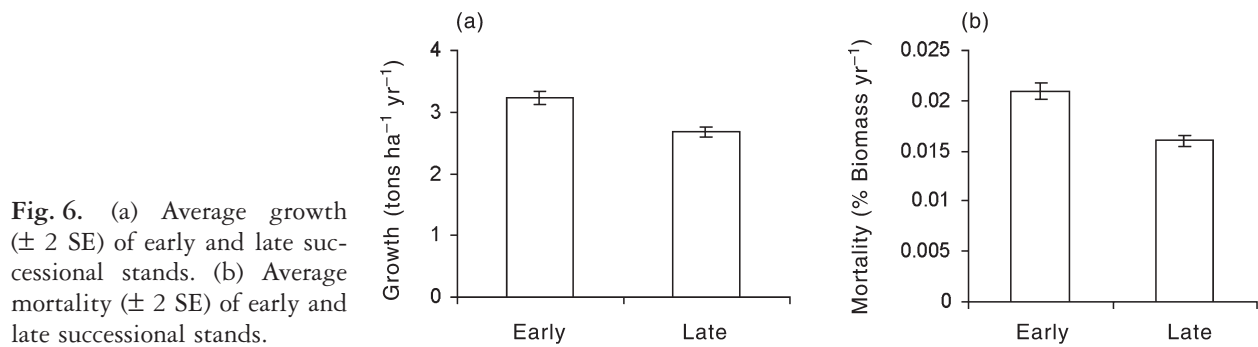
Fig. 6. (a) Average growth (± 2 SE) of early and late successional stands. (b) Average mortality (± 2 SE) of early and late successional stands.
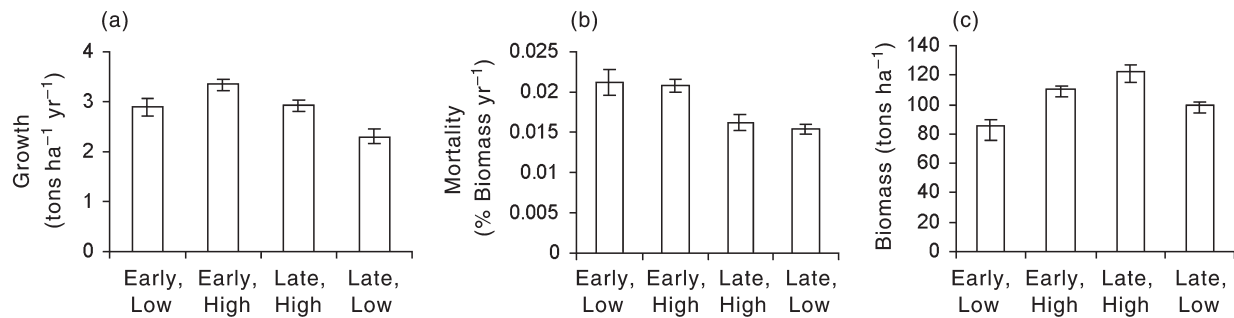
Fig. 7. (a) Average growth, (b) mortality, and (c) biomass of forest stands in each of four categories: (i) early successional with low diversity; (ii) early successional with high diversity; (iii) late successional with low diversity; and (iv) late successional with high diversity.

Successional composition

Figure 6 shows the average growth and mortality of early and late-successional stands. Early successional stands are more productive than late successional stands (Fig. 6a), whereas late-successional stands have lower turnover than early successional stands (Fig. 6b). These results are qualitatively consistent with the null model (Fig. 2).

Successional diversity

Figure 7 shows the average growth, mortality, and biomass for each of the four categories used in Fig. 3. These results contradict the null model in two ways. First, growth is highest in high-diversity early successional stands (Fig. 7a), not in low-diversity early successional stands (Fig. 3a). Second, biomass is highest in high-diversity late successional stands (Fig. 7c), not in low-diversity late successional stands (Fig. 3c). Otherwise, Figs 3 and 7 exhibit the same qualitative patterns.

Considered together, the growth and biomass data suggest that species diversity enhances pro-ductivity and carbon storage. Yet, there may be alternative reasons that inventory data are inconsistent with the predictions of the null model. For example, low diversity plots may have experienced more selective harvesting prior to the first census interval. However, it is unlikely that correlations between stand age and successional composition are responsible for the discrepancies between Figs 3 and 7. Transient solutions of the null model give the same qualitative patterns seen in Fig. 7. Furthermore, restricting the data analysis to include only plots within 10 year age classes gives the same qualitative patterns as those seen in Fig. 7.

DISCUSSION

One of the dominant paradigms in forest ecology is that the principal axis of functional variation among tree species is a successional axis. Thus, it is commonly assumed that functional diversity is synonymous with successional diversity. Indeed, this assumption underlies many gap models as well
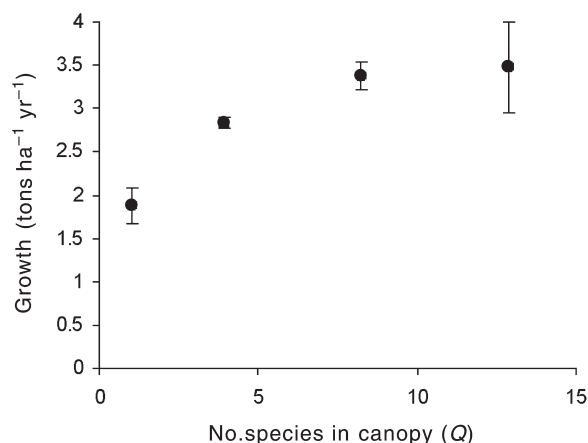
Fig. 8. Relationship between stand growth and species diversity *per se*.

as the null model presented in this paper. If this assumption were true, then productivity would be highest in monocultures of the most productive early successional species, not in stands with high successional diversity. However, the inventory data show that stands with high successional diversity fix and store more carbon than stands with low successional diversity, regardless of successional composition.

Why, then, are productivity and storage positively correlated with successional diversity? The most likely explanation is that there is another axis of functional variation among tree species that is correlated with the successional axis. Indeed, the index of successional diversity S_{NI} presented in this paper is positively correlated with other indices that measure species diversity *per se*. For example, S_{NI} is positively correlated with the number of tree species Q with at least one tree in the canopy of the plot ($r = 0.23$, $P < 0.05$). Thus, it is possible that stands with high successional diversity are more productive because there is additional functional variation among species that enhances the productivity of high diversity stands.

To examine this possibility, we assessed whether productivity is positively correlated with diversity *per se*. Figure 8 shows the relationship between growth and Q, a simple index of species diversity. Growth increases almost twofold from monocultures to the highest diversity polycultures. These data suggest that there is in fact additional functional variation among species that enhances the productivity of high diversity stands. Of course, it

is also possible that causality runs in the opposite direction; that is, more productive stands may simply permit the coexistence of more species. Unfortunately, cause and effect cannot be disentangled from observational data. Nonetheless, the data do demonstrate a strong positive relationship between productivity and diversity *per se*.

There are two primary conclusions that can be drawn from the data analysis. First, successional composition has a significant effect on forest ecosystem function; that is, early successional stands are more productive than late successional stands, whereas late successional stands have a lower turnover than early successional stands. This result has clear implications for the management of forests as carbon sinks. If the goal is to sequester carbon in forest products, then forests should be managed in such a way as to favor fast-growing early successional species over slow-growing late successional species. On the other hand, if the goal is to sequester carbon in living trees, then forests should be managed to favor long-lived late successional species over short-lived early successional species.

Second, successional diversity is positively correlated with productivity, as is species diversity *per se*. If increased diversity does in fact enhance productivity, then this result also has important implications for the management of forests as carbon sinks. In particular, this result would suggest that forests should be managed in such a way as to maintain species diversity, while also favoring species that maximize the function of interest. Conversely, if the correlation reflects the fact that more productive stands permit the coexistence of more species, then this result challenges our understanding of the mechanisms that maintain species diversity. Clearly, disentangling cause and effect presents a considerable challenge to forest ecologists interested in the biodiversity debate.

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