

Is the productivity of vegetation plots higher or lower when there are more species? Variable predictions from interaction of the 'sampling effect' and 'competitive dominance effect' on the habitat templet

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Using a habitat templet model, we predict that the productivity (total biomass) of plots within a plant community may be positively, negatively or not at all related to variation in the number of species per plot, depending on successional stage (time since major disturbance) and habitat carrying capacity (reflecting the total resource supplying power of the habitat). For plots of a given size, a positive relationship between productivity and species richness is predicted in recently disturbed habitats because local neighbourhoods here will have been assembled largely stochastically, usually from a pool of available species with a right-skewed size frequency distribution. Hence, in the earliest stages of succession, plots will have relatively high total biomass only if they contain at least some of the relatively uncommon larger species which will, in turn, be more likely in those neighbourhoods that contain more species (the sampling effect). Among these will also be some of the more common smaller species; hence, these high biomass, species-rich plots should have relatively low species evenness, in contrast to what is predicted under effects involving species complementarity. In late succession, the plots with high total biomass will still be those that contain relatively large species but these plots will now contain relatively few species owing to increased competitive exclusion over time (the competitive dominance effect). In intermediate stages of succession, no relationship between plot productivity and species richness is predicted because the opposing sampling and competitive dominance effects cancel each other out. We predict that the intensity of both the sampling and competitive dominance effects on the productivity/species richness relationship will decrease with decreasing habitat carrying capacity (e.g. decreasing substrate fertility) owing to the inherently lower variance in between-plot productivity that is predicted for more resource-impooverished habitats.

Variation in the productivity of vegetation plots within a plant community may have several causes. There may be variation between plots in soil fertility, or variation in the proximity of plot yields to the carrying capacities of their component species, e.g. because of local variation in density and/or time available for growth between impacts from herbivores (Aarssen 2001). Recent research has focussed particular attention, however, on

the role of variation in species richness and species composition. The way in which species richness affects plot productivity (usually estimated by standing crop biomass) has become one of the most hotly debated subjects in terrestrial ecology (Aarssen 1997, 2001, Garnier et al. 1997, Grime 1997, Huston 1997, Naeem and Li 1997, 1998, Tilman 1997, Tilman et al. 1997, Chapin et al. 1998, Hector 1998, Loreau 1998a, b, 2000, Wardle 1998, 1999, 2001, van der Heijden 1999, Waide et al. 1999, Huston et al. 2000, Schwartz et al. 2000). Exactly what form the relationship should take, if any, and what approach(es) should be adopted to reveal its mechanisms are at the heart of the debate. Results from previous studies are varied, with some finding significant positive relationships (Naeem et al. 1994, 1996, Tilman et al. 1996, Hector et al. 1999, Troumbis and Memtsas 2000, Loreau and Hector 2001a, b) and others finding negative (Rusch and Oesterheld 1997, Wardle et al. 1997b, Grime 1998) or inconsistent relationships (Hooper and Vitousek 1997, Wardle et al. 1997a, Hooper 1998, Kenkel et al. 2000). Studies demonstrating a positive relationship have received the most attention (Wardle 1999), perhaps because of their implications for conservation efforts (Hector et al. 2001), and the appealing notion that the potential benefits of high biodiversity (e.g. high productivity) might be easily quantified. Most of these same studies, however, have been strongly criticized for (among other reasons see Garnier et al. 1997, Huston 1997, Wardle 2001) failing to sufficiently control or account for the 'sampling effect' (Aarssen 1997, Huston 1997, Wardle 1999, Huston et al. 2000).

The sampling effect occurs when the higher biomass of higher diversity planting treatments is due to their increased likelihood of including particular, relatively

large species, rather than due to any direct effects of higher diversity involving increased complementarity of resource use or facilitative interactions. The statistical consequences of randomly sampling species that differ in productivity (i.e. size) make it very difficult to attribute a positive productivity/species richness relationship to deterministic ecological processes (Aarssen 1997, Huston 1997), such as inter-specific complementarity or facilitation (Loreau 1998a), especially in studies on natural vegetation where monocultures and hence, relative yield total methods (Hector 1998, Loreau 1998b, Loreau and Hector 2001a, b) are unavailable. While it might seem obvious (according to a survey of experts by Schlapfer et al. 1999) that plots or communities with higher species richness have the potential for higher productivity through increased complementarity or facilitation, establishing the degree to which these effects actually contribute to a positive relationship over and above the sampling effect has, thus far, escaped the efforts represented by most studies (Huston 1997, Waide et al. 1999, Wardle 1999; but see Loreau and Hector 2001a, b, Špačková and Lepš 2001). We argue here that the enormous and ubiquitous variation in maximum potential size that exists between plant species presents a simple premise for predicting a prominent and widespread sampling effect within natural vegetation. By contrast, in the relatively few cases where complementarity has been detected in plant species mixtures, the yield advantage of the mixture compared with component monocultures is relatively small, and unless legumes are present, complementarity is rarely seen at all (reviewed by Jolliffe 1997). This general paucity of evidence for niche differentiation (i.e. complementarity) in both planted mixtures and natural vegetation (Willson 1973, Silvertown and Law 1987, Bengtsson et al. 1994, Hubbell 2001), despite numerous attempts to detect it, presents very little if any premise for predicting any significant ‘sampling effect’ in natural vegetation that might be associated with an increased chance, in higher diversity assemblages, of having sets of species with complementary resource use (Loreau et al. 2001).

Why have empirical studies failed to show a consistent relationship between the productivity and species richness of plant assemblages? Aside from failure in some cases to control for other plot-level sources of variation in productivity, recent studies have suggested that the productivity/species richness relationship will depend on the larger-scale environmental context, e.g. resource availability of the habitat (Fridley 2002), or variation in the interaction of spatial heterogeneity and disturbance (Cardinale et al. 2000). Based on a similar argument, we propose here that for vegetation plots of a given size, the within-habitat relationship between the productivity and species richness of these plots can be expected to display wide variation in direction from positive to neutral to negative depending on the posi-

tion of the habitat along major environmental gradients. We combine variation in time since disturbance with variation in habitat carrying capacity in a two-way continuum model in the style of the ‘habitat templet’ (Southwood 1977, Taylor et al. 1990) for predicting variation in the within-habitat (between-plot) relationship between productivity (y-axis) and species richness (x-axis) along habitat gradients (Fig. 1. See Huston 1994 for a parallel approach for predicting variation between habitats in the relationship between species richness (y-axis) and productivity (x-axis)). The model assumes that there is negligible between-plot variation in both soil fertility and in the proximity of component species’ yields to their respective carrying capacities. Variation in productivity then is predicted simply as a consequence of between-plot variation in the relative abundance of large (productive) species. This variation is generated by two independent effects that interact on a successional gradient and which produce only incidental correlations with species richness.

The habitat templet model: the ‘time since disturbance’ axis

In the earliest stages of succession, i.e. on land laid bare but left to accumulate biomass naturally following a major disturbance (e.g. soil cultivation), initial species composition at the local neighbourhood scale (e.g. within plots or quadrats) will have been affected relatively little by species interactions. Hence, large, productive species may commonly coexist, at least temporarily, with several smaller species. Over time, however, larger species commonly dominate the vegetation and competitively exclude many of the less productive, smaller species from several local neighbourhoods or even from the entire community (Grime 1979). Most of the available empirical data on dominance and supe-

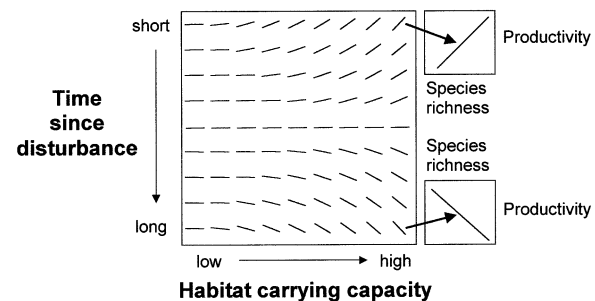


Fig. 1. A ‘habitat templet’ model for predicting effects of time since disturbance and habitat carrying capacity on the productivity/species richness relationship across plots (e.g. quadrats) within a plant community. Line segments indicate the direction (positive, neutral, or negative) of the relationship between productivity and species richness (small graphs at right) predicted for habitats with different combinations of time since disturbance and habitat carrying capacity. See text for details.

rior competitive ability in plant competition (leading to competitive exclusion and hence, reduced diversity) identify a general advantage for large plant size (Keddy 1989, Aarssen and Keogh 2002). Hence, according to the model proposed here, variation across habitats in time since disturbance represents a continuum of two interacting effects: with decreasing time since disturbance, neighbourhood composition within a community is more stochastically determined (i.e. with relatively weak effects of species interactions), thus representing an increasing 'sampling effect'. In contrast, increasing time since disturbance increases competition intensity (Taylor et al. 1990) thus increasing the effect of competitive exclusion on species assemblage composition, which we refer to here as the 'competitive dominance' effect.

(a) Early stages in succession

A strong sampling effect, resulting from a relatively short time since disturbance, promotes a positive productivity/species richness relationship, as depicted toward the top side of the habitat templet in Fig. 1. This effect, we argue, is an inevitable product of the ubiquitous right-skewed frequency distribution of potential species sizes typical of natural communities; i.e. with many relatively small species but relatively few species capable of very large size (Brown 1995). The same right-skewed species size distribution also occurs across regional floras (Aarssen and Schamp 2002). Accordingly, when neighbourhood assembly is relatively stochastic, as in early successional stages that precede the noticeable influence of competitive interactions, most of the neighbourhoods with relatively low species richness will contain only the relatively common, smaller species. Hence, total plot biomass will, on average, be constrained by the relatively low values defined by the limited biomass potential of these small species. Variance in total biomass among these low diversity plots could be high, however, because a few of these plots will, by chance, contain very large species. This prediction of relatively high variance in plot productivity at low diversity has also been reported for randomly planted mixtures (Loreau et al. 2001). We suggest that these experimental mixtures are analogous to natural stochastically assembled neighbourhoods (plots) in early successional vegetation. Both, therefore, can be expected to exhibit a positive relationship between total plot productivity and species richness owing to the sampling effect.

In contrast, only the most species-rich neighbourhoods in early succession have a high probability of containing some of the relatively uncommon, very large species (in addition to smaller ones) – again, a result of stochastic assembly from a right-skewed frequency distribution of species sizes. Accordingly, these species-

rich plots will have relatively high total biomass but at the same time, because of their assemblage size structure, will exhibit relatively low species evenness, measured in terms of per-species contributions to total plot biomass. This negative relationship between plot biomass and species evenness represents an additional 'signature' prediction of the sampling effect in early successional communities (Drobner et al. 1998). This contrasts with the effects of species complementarity, where productivity is expected to be positively related to species richness but also, we predict, positively (or neutrally but not negatively) related to species evenness. Hence, under the sampling effect, a positive relationship between productivity and species richness is only an incidental consequence of the fact that species evenness has a negative relationship with both productivity and species richness.

(b) Late stages in succession

Our model predicts that the sampling effect in natural vegetation will impact strongly only in early succession. As time since disturbance increases, an increasing competitive dominance effect is predicted, promoting eventually a negative relationship between productivity and species richness for plots within the community, as depicted toward the bottom side of the habitat templet in Fig. 1. Later in succession, therefore, the relatively low diversity that occurs in some local neighbourhoods will be less a product of stochastic assembly (the sampling effect) and more a product of local (plot-level) exclusion that has occurred over time by large species, which, by virtue of their large potential size, confer a relatively high total plot biomass (plus possibly high evenness if they are all large). Moreover, the intensity of this competitive dominance effect can be expected to increase over time because mean species size, especially in resource-rich habitats, generally increases in later succession as larger and larger species colonize and get established. Species-rich plots can, however, occur in late succession. These plots either do not happen to contain larger species, or they could belong to neighbourhoods in which the local outcome of competition over time since the last disturbance has favoured relatively small species. These persistent species here may be able to avoid exclusion across generations, despite intense competition, because the strength of their competitive abilities, rather than conferred by large size, is more a product of relatively high survival (longevity) under competition and/or relatively high fecundity allocation (i.e. fecundity per unit plant size per unit time) under competition (Aarssen and Keogh 2002). Hence, because the component species under this scenario all have relatively small size potential, these plots have relatively low total biomass with relatively high species richness (plus possibly high evenness). The high species

richness here arises either because many smaller species are able to coexist when there is no threat of local exclusion by larger species, or simply because more individuals and hence, more species can physically fit within a given plot size if they are all small than if they are all large.

Unlike the sampling effect in early succession, therefore, there is no basis under the competitive dominance effect for predicting that species evenness within plots in later succession will have any generally significant (positive or negative) relationship with either plot productivity or species richness.

(c) Intermediate stages in succession

In intermediate successional stages, some low-diversity plots will still show relatively low total biomass because some of the early successional sampling effect still remains, whereas other low-diversity plots will have relatively high total biomass because of the emerging competitive dominance effect by large species. Low-diversity plots in intermediate successional stages can be expected, therefore, to have even higher variance in total plot biomass compared with low-diversity plots in early succession. The residual sampling effect and developing competitive dominance effect are expected to cancel each other out here, leaving no significant relationship between productivity and species richness in communities where time since last disturbance is of intermediate duration (Fig. 1). Moreover, any positive effect of species diversity on productivity that may result from some degree of complementarity or facilitation between certain species may also be diluted or overshadowed by the opposing competitive dominance effect as it develops with increasing time since the last major disturbance.

The habitat templet model: the 'habitat carrying capacity' axis

The above interplay between the positive influence of the sampling effect and the negative influence of the competitive dominance effect will be modulated, we predict, by variation in habitat carrying capacity, defined on the second axis of the habitat templet (Fig. 1). Habitat carrying capacity represents the maximum potential biomass that the habitat is capable of supporting, which reflects the total resource-supplying power (e.g. including soil fertility) of the habitat (Taylor et al. 1990). We predict that decreasing habitat carrying capacity will cause a decreasing intensity (i.e. shallower slope) of the relationship between plot productivity and species richness (Fig. 1; Fridley 2002). With increasing resource-impoverishment (i.e. in habi-

tats with lower carrying capacity), the mean plot productivity will decrease. This lower upper limit to plot productivity necessarily restricts between-plot variance to low values compared to what is possible in habitats with higher carrying capacity. This lower variance in plot productivity (on the y-axis), in turn, reduces the steepness of the relationship and indeed, we predict, reduces the likelihood of detecting any statistically significant relationship between plot productivity and species richness, regardless of the time since disturbance (as depicted along the left side of the habitat templet; Fig. 1). Hence, in habitats that have remained largely undisturbed for a great length of time, the predicted negative relationship between plot productivity and species richness (resulting from the competitive dominance effect) becomes less negative with decreasing habitat carrying capacity (from right to left along the bottom side of the habitat templet; Fig. 1). Similarly, in recently disturbed habitats, the predicted positive relationship between plot productivity and species richness (resulting from the sampling effect) decreases with decreasing habitat carrying capacity (from right to left along the top side of the habitat templet; Fig. 1). Note again that there is no predicted relationship between plot productivity and species richness when time since disturbance is intermediate in duration because the sampling effect and competitive dominance effect cancel each other out and this is predicted regardless of habitat carrying capacity (Fig. 1).

A minor variation on the above model may be proposed based on some research (Brooker and Callaghan 1998) suggesting that positive (facilitative) interactions between plants might be expected to increase in frequency with decreasing habitat fertility. If such facilitation effects are stronger than competition effects in impoverished, late successional habitats (i.e. bottom left corner of Fig. 1), then plots that have greater species richness may generally have greater opportunity for facilitation and hence, greater productivity (i.e. with a positive rather than neutral relationship).

Conclusions

The above model argues that a wide variety of productivity/species richness relationships might be expected for plots within natural vegetation ranging from positive to neutral to negative depending on the successional stage (time since the last major disturbance) and the resource-supplying power (e.g. soil fertility) of the habitat. Testing the above predictions across a variety of natural habitat types will require large data sets, e.g. from a collaborative effort similar to the ones undertaken by the experimental approaches of the ECOTRON (Naeem et al. 1994) and BIODEPTH (Hector et al. 1999). A number of researchers may

already be in possession of appropriate data sets that can be analysed for this purpose. This could provide the basis for a much-needed comprehensive evaluation of the productivity/species richness relationship as it exists for plots within natural vegetation.

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