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Unifying the relationships of species richness to productivity and disturbance

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Although species richness has been hypothesized to be highest at 'intermediate' levels of disturbance, empirical studies have demonstrated that the disturbance–diversity relationship can be either negative or positive depending on productivity. On the other hand, hypothesized productivity–diversity relationships can be positive, negative or unimodal, as confirmed by empirical studies. However, it has remained unclear under what conditions each pattern is realized, and there is little agreement about the mechanisms that generate these diverse patterns. In this study, I present a model that synthesizes these separately developed hypotheses and shows that the interactive effects of disturbance and productivity on the competitive outcome of multispecies dynamics can result in these diverse relationships of species richness to disturbance and productivity. The predicted productivity–diversity relationship is unimodal but the productivity level that maximizes species richness increases with increasing disturbance. Similarly, the predicted disturbance–diversity relationship is unimodal but the peak moves to higher disturbance levels with increasing productivity. Further, these patterns are well explained by the opposite effects of productivity and disturbance on competitive outcome that are suggested by the change in community composition along these two environmental gradients: higher productivity favours superior competitors while higher disturbance levels favour inferior competitors.

Keywords: biodiversity; species richness; productivity–diversity relationship; disturbance–diversity relationship; intermediate-disturbance hypothesis

1. INTRODUCTION

Species richness, the number of biological species in a particular community, is predicted to be highest at 'intermediate' levels of disturbance (intermediate-disturbance hypothesis; Levin & Paine 1974; Connell 1978; Hastings 1980; Pacala & Crawley 1992). However, empirical work suggests that the disturbance–diversity relationship can be either negative or positive depending on the productivity of the ecosystem (reviewed in Proulx & Mazmuder 1998). Proulx & Mazmuder (1998) demonstrated that plant species richness increases with increasing grazing pressure in a nutrient-rich environment but decreases in a nutrient-poor environment, over a variety of ecosystems. This implies that the disturbance level that maximizes species richness is influenced by the level of productivity (Huston 1994; Proulx & Mazmuder 1998).

Similarly, hypothesized productivity–diversity relationships can be positive (Abrams 1995), negative (Rosenzweig 1971) or unimodal (Grime 1973; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993). Indeed, empirical work (reviewed in Rosenzweig & Abramsky 1993; Huston 1994) has demonstrated the existence of these diverse patterns but there is little agreement as to the underlying mechanisms (Rosenzweig & Abramsky 1993; Abrams 1995). Moreover, it is unclear under what conditions each pattern is realized.

It was Huston (1994) who pointed out the importance of the disturbance–productivity interaction as a determinant of species richness. By making a simple extension to the Lotka–Volterra competition model, he hypothesized that the diverse patterns of productivity–diversity and disturbance–diversity relationships are a result of the disturbance–productivity interaction (Huston 1994). However, his model did not incorporate these two factors explicitly. In addition, since multispecies coexistence is realized under non-equilibrium states in his model, it cannot give a constant level of species richness or community composition for a given condition, making its conclusions concerning the trends of species richness less clear.

Here, to develop a more comprehensive picture of how disturbance and productivity shape the structure of a competing-species community, I examine a simple, tractable model in which these two factors are explicitly incorporated and the competitive outcome is obtained as an equilibrium state.

2. MODEL

The model that I employ here is a modification of the n-species patch-occupancy model with one-sided competition (Hastings 1980; Tilman 1994), in which the environment consists of a large number of discrete patches each of which is empty or occupied by one of the n species, and the proportion of patches occupied by each species changes over time due to inter-patch colonization by dispersal and within-patch extinction of the species. Each species i ($1 \leqslant i \leqslant n$) is characterized by colonization rate (c_i), extinction rate (m_i) and its ability to survive within-patch competition. It is assumed that species i always competitively excludes species j if $i < j$. These parameters are assumed to be constant for simplicity. For the coexistence of multispecies, such a system generally requires that a superior competitor has a lower colonization rate or a higher extinction rate (Hastings 1980; Tilman 1994). Here, I assume this trade-off. Such a mechanism has been used to explain the coexistence of multispecies in many animal and plant communities (e.g. Levin & Paine 1974; Hastings 1980; Tilman 1994; for other references, see Tilman *et al.* 1994).

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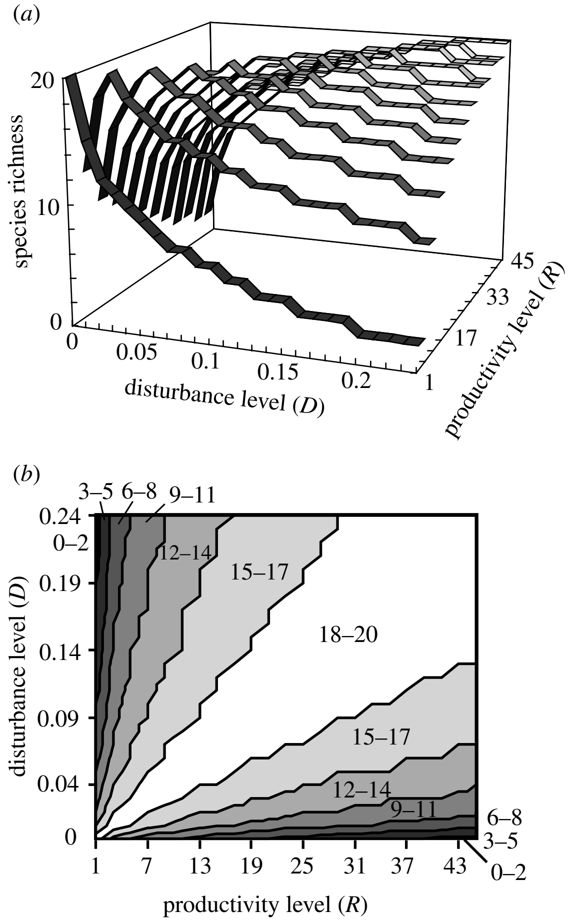

Figure 1. Effects of disturbance and productivity on species richness (*a*) and (*b*). In (*b*), the numbers of coexisting species are indicated in the parameter space of disturbance and productivity levels. Parameters are $c_i = 0.1/0.9^i$, $m_i = 0.05$ and $n = 20$.

To explore the impacts of productivity and disturbance on the community structure, I make two simple modifications to this model: an increase in productivity enhances the colonization rate of all species by a constant, *R*, and an increase in disturbance increases the extinction rate of all species by a constant, *D*.

Thus, the dynamics of the proportion, p_i, of patches occupied by species *i* is represented as

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = c_i R p_i \left(1 - \sum_{k=1}^{i} p_k\right) - (m_i + D)p_i - \sum_{k=1}^{i-1} c_k R p_k p_i, \quad (i = 1, 2, \ldots, n), \qquad (1)$$

where the first term represents colonization, the second term is the loss by local extinction and the last term is the loss by competitive exclusion.

3. RESULTS

The system governed by equation (1) converges to a unique equilibrium point (Hastings 1980; Tilman 1994), which is obtained by setting the right-hand side of the equation equal to zero with $p_i > 0$ for $i = 1, 2, \ldots, n$.

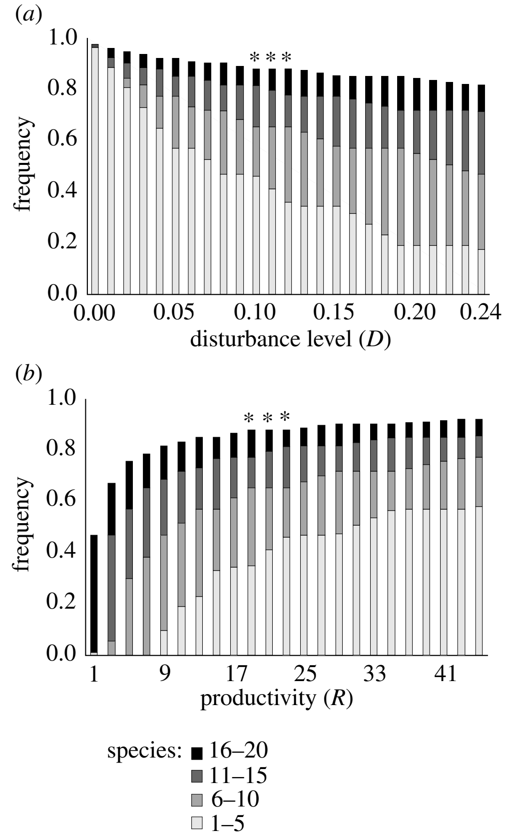

Figure 2. Effects of (*a*) disturbance and (*b*) productivity on community composition. The bars with asterisks represent the conditions under which species richness is maximized. The parameters (c_i, m_i, n) are the same as in figure 1, the other constant parameter in each panel is $R = 23$ (*a*) and $D = 0.1$ (*b*).

Figure 1 represents the effects of an increase in productivity, *R*, and in disturbance, *D*, on the number of coexisting species. As is clear from figure 1*b*, species richness is highest along the diagonal ridge where productivity and disturbance are well balanced, and lowest at the two extremes: where either the productivity level is high and the disturbance level is low or the productivity level is low and the disturbance level is high.

With increasing disturbance level, the species number increases until it reaches a plateau and then decreases, indicating the existence of a disturbance level that maximizes species number (figure 1*a*). The position of this peak shifts towards a higher disturbance level as productivity increases. At the extremes, species number only increases with disturbance level when productivity is extremely high, and only decreases when productivity is extremely low. Similarly, the species number is maximized at a certain level of productivity (figure 1*a*). This productivity level increases with increasing disturbance. At the extremes, productivity is positively correlated with species richness when disturbance is high, whereas it is negatively correlated when disturbance is low.

Figure 2 illustrates the effects of changes in productivity and disturbance on the species composition at equilibrium. Productivity and disturbance, respectively, have positive and negative effects on the total coverage ($\sum_{i=1}^{n} p_i$) as is easily understood. Also, with increased productivity or reduced disturbance, the proportion of poorer competitors always decreases while that of superior competitors increases.

4. DISCUSSION

In this paper, I have demonstrated how disturbance and productivity interactively determine species richness. Not surprisingly, the species richness of the equilibrium community is influenced by both productivity and disturbance. Yet, their impacts on species richness are not as straightforward as previously proposed by authors considering only one factor (Hastings 1980; Rosenzweig & Abramsky 1993; Abrams 1995). In general, the relationships of species richness to productivity and to disturbance are both unimodal. However, the level of one factor that maximizes species richness depends on the level of the other factor, leading to the diverse patterns seen in these relationships.

This model predicts that a positive disturbance–diversity correlation is observed only when productivity is high, a negative correlation only when productivity is low and a unimodal pattern when productivity is moderate (figure 1*a*). This theoretical prediction is consistent with the patterns observed by Proulx & Mazmuder (1998), which revealed the reversal of the effect of grazing on plant species richness in nutrient-rich and nutrient-poor environments. For the productivity–diversity relationship, the model predicts a similar trend (figure 1*a*). The prediction of opposing impacts of productivity on species richness under high- and low-disturbance environments remains to be tested.

The community composition along the two environmental gradients (figure 2) suggests that increased productivity and reduced disturbance favour superior competitors. This trend can be explained as follows: disturbance, which produces empty patches, encourages superior colonizers (i.e. inferior competitors) while it disfavours superior competitors by reducing competitive exclusion. In contrast, higher productivity, which increases the colonization rate, encourages inferior colonizers (superior competitors) while it disfavours inferior competitors by increasing the risk of competitive exclusion.

These results allow us to explore the mechanisms by which productivity and disturbance determine species richness. If disturbance and productivity are balanced, the trade-off between the species allows the coexistence of more species, and species richness is maximized (figure 1*b*). However, if disturbance is higher and productivity is lower, then species richness decreases since poorer colonizers (superior competitors) cannot survive. If disturbance is low and productivity is high, species richness decreases because poor competitors (superior colonizers) are outcompeted by superior competitors (Grime 1973). Thus, these separately developed hypotheses describing the relationships of species richness to disturbance and productivity can be unified.

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REFERENCES

Abrams, P. A. 1995 Monotonic or unimodal diversity–productivity gradients: what does competition theory predict? *Ecology* **76**, 2019–2027.

Connell, J. H. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310.

Grime, J. P. 1973 Control of species diversity in herbaceous vegetation. *J. Environ. Mgmt* **1**, 151–167.

Hastings, A. 1980 Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* **18**, 363–373.

Huston, M. A. 1994 *Biological diversity: the coexistence of species on changing landscapes.* Cambridge University Press.

Levin, S. A. & Paine, R. T. 1974 Disturbance, patch formation, and community structure. *Proc. Natl Acad. Sci. USA* **71**, 2744–2747.

Pacala, S. W. & Crawley, M. J. 1992 Herbivores and plant diversity. *Am. Nat.* **140**, 243–260.

Proulx, M. & Mazmuder, A. 1998 Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**, 2581–2592.

Rosenzweig, M. L. 1971 Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**, 385–387.

Rosenzweig, M. L. & Abramsky, Z. 1993 How are diversity and productivity related? In *Species diversity in ecological communities* (ed. R. E. Ricklefs & D. Schluter), pp. 52–65. University of Chicago Press.

Tilman, D. 1994 Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2–16.

Tilman, D. & Pacala, S. 1993 The maintenance of species richness in plant communities. In *Species diversity in ecological communities* (ed. R. E. Ricklefs & D. Schluter), pp. 13–25. University of Chicago Press.

Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994 Habitat destruction and the extinction debt. *Nature* **371**, 65–66.