Resource quantity, not resource heterogeneity, maintains plant diversity

M. Henry H. Stevens* and Walter P. Carson
Program in Ecology and Evolution, Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, U.S.A.
*Correspondence and present address: Department of Botany, 316 Pearson Hall, Miami University, Oxford, OH 45056 USA. E-mail: HStevens@muohio.edu

Abstract
Resource heterogeneity has often been proposed to explain the maintenance of plant species diversity and patterns of species diversity along productivity gradients. Resource heterogeneity should maintain biodiversity by preventing competitive exclusion because different species are superior competitors in different parts of a heterogeneous environment. In natural systems, however, resource heterogeneity covaries with average resource supply rate, making the effect of heterogeneity difficult to isolate. Using a novel experimental approach, we tested the independent effects of resource heterogeneity and average supply rate on plant species diversity. We show that the average supply rate of the most limiting resource controlled species diversity, whereas heterogeneity of this resource had virtually no effect. These findings also suggest that biodiversity declines with increasing productivity because at high enough levels of productivity one resource may always be driven to sufficiently short supply to exclude many species.

Keywords
Assemblage level thinning, enemy free space, heterogeneity, productivity gradient, resource ratio, species diversity, species richness.

INTRODUCTION
Spatial heterogeneity of one or more limiting resources should prevent competitive exclusion and maintain high species richness (Hardin 1960; MacArthur 1970; Grubb 1977; Ricklefs 1977; Tilman 1982; Palmer 1994; Crawley 1997; Nicotra et al. 1999; Kassen et al. 2000). Several general theoretical models of local species interactions (MacArthur 1970; Levin 1976; Tilman 1982; Abrams 1988; Pacala & Tilman 1994) make at least two robust predictions: (1) spatial heterogeneity of limiting resources governs the number of co-occurring species (i.e. species richness), and (2) species habitat requirements and the relative abundance of different microhabitat types determine species relative abundances. In contrast, a wide variety of other hypotheses suggest that species richness is determined by the average supply rates of the most limiting resources (Preston 1962; MacArthur & Wilson 1963; Wright 1983; Rosenzweig & Abramsky 1993; Abrams 1995; Hurtt & Pacala 1995; Srivastava & Lawton 1998; Grace 1999; Stevens & Carson 1999b; Morin 2000; Hubbell 2001). Although critical differences exist within this group of hypotheses, each predicts that: (1) species richness will increase with increasing resource and energy availability, and (2) the most abundant species in the species pool may dominate any particular site by chance alone. For the remainder of this paper, we will refer to these two sets of predictions as the heterogeneity hypothesis and the energy hypothesis.

Here we test the heterogeneity hypothesis and the energy hypothesis by measuring the relative importance of spatial heterogeneity and the average supply rate of light in governing a widespread but paradoxical pattern: plant species richness falls as soil resource availability and productivity rise (Grime 1973; Tilman 1982; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993; Waide et al. 1999; Gough et al. 2000; Gross et al. 2000; Mittelbach et al. 2001). The resolution to this paradox appears to lie with how light availability covaries with productivity (Tilman & Pacala 1993; Huston & DeAngelis 1994). As soil resources rise, and plant communities become more productive, light availability in the understorey declines. Understorey light availability probably governs species richness because all individuals of both canopy species and understorey specialists must survive and grow in the understorey at some point in their ontogenies (Grubb 1977; Harper 1977). Heterogeneity-related hypotheses assume that species specialize in different light levels (e.g. Ricklefs 1977; Pacala et al. 1996; Kobe 1999) or different ratios of light and soil resources (Tilman 1982;

We used a novel experimental approach to test the independent contribution of light heterogeneity to plant species richness (Stevens 1999). After establishing an experimental productivity gradient in an herbaceous plant community, we used shade frames to manipulate independently understorey light heterogeneity, and the average supply rate of understorey light. This allowed us, for the first time, to test whether light heterogeneity governs species richness along productivity gradients. This also allowed us to test the key underlying assumption of whether species specialize in low-light environments.

METHODS

In 1995, we sprayed with herbicide and ploughed an abandoned agricultural field in north-western Pennsylvania, USA. We fertilized 192 plots (4 x 4 m, each separated by 1 m) at four different rates for 3 years (1996–8) (Osmocote™ slow release fertilizer, 18–6–12 NPK, at rates of 0, 8, 16 and 32 g N m⁻² year⁻¹). By 1997, the field was dominated by several Solidago spp., Agropyron repens and Milium effusum (Stevens 1999). In free-standing vegetation without shade frames, our soil resource gradient created patterns widely observed in other studies of herbaceous plant productivity gradients: as soil resources rise, above-ground biomass increases, and species richness, average understorey light supply rate, and understorey light spatial heterogeneity fall (e.g. Grime 1973; Al-Mufti et al. 1977; Tilman 1987; Stevens & Carson 1999b; Stevens 1999).

Six designs of shade frames (Fig. 1) (1 m W x 0.75 m H x 3 m L) provided three levels of spatial heterogeneity at each of two average supply rates when placed over growing vegetation (“heterogeneity” and “average supply rate” are the standard deviation and mean of a spatial array of point light measurements) (Table 1). We selected the levels of supply rate and heterogeneity to represent the range of each observed in free-standing vegetation at the above levels of fertilizer (Table 1). Over a two-year period (1997, 1998), the shade frames took the place of the canopies formed by the tallest plants (e.g. Euthemia graminifolia, Solidago altissima). As plants grew taller throughout the growing season, they were guided around the opaque outside walls of the shade frames, so that tall plants did not cast shade in the 30 x 150 cm sample plots (Fig. 1) and confound the shade treatments. At the beginning of the 1997 growing season, one shade frame was placed in each of the 192 plots fertilized with one of four levels of soil fertilizer (above) resulting in 24 unique treatment combinations (n = 8). The shade frames did not

Figure 1 The six shade frame types created three levels of light heterogeneity at each of two levels of average light supply rate (see Table 1). In this schematic, the degree of shading indicates shade cloth opacity (density) with black areas transmitting < 1% of ambient light and white (no shade cloth) transmitting 100% ambient light. Shade frames were oriented north–south and placed over growing vegetation. Ramets over 50 cm tall were guided around the outside, plastic-sheet walls of the frames. Plants were sampled in three contiguous 30 x 50 cm subplots, and light was sampled at 150 1.0 cm intervals along the dashed transect.
substantially affect other environmental variables, and they
took controlled light heterogeneity independently of average
supply rate of light and soil resources (Stevens 1999). The
size of the sample plots and the scale of the spatial
heterogeneity was proportional to the size of individuals
(Fig. 1), so that many small individuals or a fraction of the
largest clonal individuals could occupy a patch of a given
light availability. Thus, the spatial scale of the heterogeneity
was proportionally similar to most canopy gaps found in
forest and old-fields (Goldberg & Gross 1988; Canham
et al. 1990; Kelly & Canham 1992). The spatial patterns of the
spectrum neutral shade cloth (PAK Unlimited, Inc.,
Cornelia, Georgia, USA) mimicked levels of light hetero-
genesis observed in free-standing vegetation at the same
levels of fertilizer addition (Stevens 1999). Even though the
vast majority of these species spread clonally, we removed
the shade frames at the end of the 1997 growing season to
allow natural colonization by seed. Frames were replaced at
the beginning of the following growing season.

We measured percentage PAR (photosynthetically active
radiation, \( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)) at 150 points spread out
at 1 cm intervals along the length of a 30 \( \times \) 150 cm sample
plot centred under each frame (Fig. 1). We used two
Quantum point sensors (LiCorr, Inc., Lincoln, NE), one
15 cm above the soil surface, the other above the
vegetation, and converted PAR readings to percentage
transmittance by the canopy (percentage PAR transmitted).
We used the mean and standard deviation (Tilman 1982;
p. 103) to quantify average supply rate and heterogeneity of
light in each sample plot. We derived species richness and
relative abundance from estimates of percentage cover of
each species in each sample plot. We recorded all light and
cover data so that, within each 30 \( \times \) 150 cm sample plot,
three contiguous 30 \( \times \) 50 cm subplots could be analysed
separately, resulting in 576 subplots used for analyses where
specifically indicated below.

To test the direct effects of light heterogeneity, average
light supply rate, and average supply rate of soil resources,
we regressed ln(species richness) on the ln(SD[percent-
age PAR]), ln(mean[percentage PAR], and ln(g N m
\( ^{-2} + 2 \)), each measured directly for each 30 \( \times \) 150 cm sample plot.

To test whether species were common in low-light plots
because they were regionally common, or because they
preferred low-light conditions, we regressed species’ fre-
quencies of occurrence in low-light plots on (1) species’
frequencies of occurrence in moderate-light plots and
(2) their observed resource ratios in the moderate-light
plots (all variables log transformed). Unlike other measures
of abundance (e.g. density, biomass), each species’ frequency
of occurrence (i.e. the number of plots in which a species is
present/total number of plots) is precisely the contribution
of each species to overall mean species richness, and the
sum of all species frequencies equals mean species richness
(Palmer & van der Maarel 1995; Stevens & Carson 1999a).
We calculated each species’ resource ratio as the mean of
(subplot percentage PAR)/(g N applied m
\( ^{-2} + 2 \)), using
only data from the moderate-light shade frames. Thus, the
resource ratio used for each species in this study should be
considered a “realized resource ratio”.

To test the assumption that species had different
resource requirements, we used ECOSIM software (Gotelli
& Entsminger 2001) to test whether mean electivity
overlap was smaller than expected by chance, using the 15
species that occurred in at least 50 of the 576 30 \( \times \) 50 cm
subplots. Electivity overlap takes resource abundance into
account, and is preferred to niche overlap (cf. Silvertown
et al. 1999) when resources vary in abundance (Lawlor
1980; Gotelli & Graves 1996). This analysis retained each
species’ niche breadth and reshuffled zero abundance
values (randomization algorithm 3, Gotelli & Graves
1996). We calculated the mean percentage PAR transmitted
in each subplot, and pooled each of these means into one

\[
\begin{array}{|c|c|c|}
\hline
\text{Frame type} & \text{Av. Supply rate (mean)} & \text{Heterogeneity (SD)} \\
\hline
\text{High – Gap} & 0.34 (0.013) & 0.306 (0.021) \\
\text{High – Cont.} & 0.36 (0.015) & 0.151 (0.012) \\
\text{High – Unif.} & 0.38 (0.011) & 0.060 (0.0072) \\
\text{Low – Gap} & 0.021 (0.00062) & 0.072 (0.0095) \\
\text{Low – Cont.} & 0.025 (0.0014) & 0.059 (0.0054) \\
\text{Low – Unif.} & 0.018 (0.0023) & 0.005 (0.00058) \\
\hline
\text{Free-standing vegetation (g N m}^{-2} \text{ year}^{-1}) & & \\
0 & 0.23 (0.022) & 0.130 (0.014) \\
8 & 0.092 (0.019) & 0.056 (0.014) \\
16 & 0.031 (0.011) & 0.029 (0.012) \\
32 & 0.010 (0.0030) & 0.006 (0.0012) \\
\hline
\end{array}
\]
of seven categories of light levels (0–5%, 5–15%, 15–25%, 25–35%, 35–45%, 45–55%, and > 55%; higher light levels were exceedingly rare). The seven light categories and four soil fertility categories resulted in 28 different resource combinations. Other combinations, including fewer resource combinations (moderate vs. low light) and more combinations (10 light levels × 4 soil fertilizer levels) achieved the same qualitative result.

**RESULTS AND DISCUSSION**

Average supply rate of light, and not light heterogeneity, governed species richness. The decline in average supply rate of light caused a substantial decline in plant species richness that was independent of the effects of soil resource availability and light heterogeneity (Fig. 2a; partial \( R^2 = 0.402^{***} \)). In contrast, the increase in soil resources (partial \( R^2 = 0.056^* \)) and the decline in light heterogeneity (partial \( R^2 = 0.004 \) NS) caused much smaller declines in richness (Figs 2b.c). The results agree with results obtained in previous years (Stevens 1999), and they provide no support for a role of light heterogeneity in influencing species richness.

Species composition in the species-poor, low-light plots was best predicted by species’ relative abundances in the moderate-light plots and not by species’ habitat preferences. Specifically, species’ frequencies of occurrence in moderate-light plots explained 37% of the variability in species’ frequencies in low-light plots (Fig. 3a), whereas species’ light : nitrogen ratios explained only 6% of the variability (Fig. 3b). These results favour the energy hypothesis, where random assembly from the species pool generates local neighbourhoods, and total density in each local community determines local species richness (Hurtt & Pacala 1995; Stevens & Carson 1999a; Hubbell 2001). In addition, most species occurred most often in similar light : nitrogen conditions, and this also is consistent with the energy hypothesis. Specifically, mean pairwise electivity overlap (similar to niche overlap, Lawlor 1980; Gotelli & Graves 1996) was substantially greater than expected by chance (observed mean electivity overlap = 0.516, bootstrapped mean = 0.441, \( P < 0.001 \)), and this broad overlap was consistent among several levels of habitat resolution (see Methods). These findings provide no support for the assumptions that underlie the heterogeneity hypothesis.

The above support for the energy hypothesis is consistent with a variety of possible mechanisms. First and foremost, decreasing understorey light availability generally causes a large decrease in stem density (Stevens & Carson 1999b), and consequently richness should decrease by chance alone (“More Individuals” hypothesis, Preston 1962; Rosenzweig & Abramsky 1993; Srivastava & Lawton 1998). Assuming that not all species exist in every plot, different species will disappear from different plots, and many species will “win by default” because the best low-light specialists are not present everywhere (Hurt & Pacala 1995). The effect of increasing productivity is to exacerbate this “winning by default”, and is not related directly to specialization in any particular light level. Further, any strict interspecific hierarchy can be weakened by positive indirect effects (Miller 1994), by large within-population variability in resource requirements (Clements 1929; Linhart & Grant 1996), or by equally strong intraspecific effects (Brokaw & Busing 2000; Hubbell 2001).

Our conclusions may apply to other light-limited plant communities because the plant community used in this experiment shares many characteristics with other

![Figure 2](https://example.com/figure2.png)

**Figure 2** Effects of (a) average light supply rate (units = log(mean PAR)), (b) fertilizer (units = log[g N m\(^{-2}\) + 1]) and (c) light heterogeneity (units = log[SD PAR]) on species richness (log[no. of spp. 0.45 m\(^{-2}\) + 1]) (multiple \( R^2 = 0.824^{**} \); Type III sums of squares on all factors, * \( P < 0.05 \), ** \( P < 0.005 \), *** \( P < 0.001 \)). The above partial regression plots plotted all variables as residuals of the labelled variable, given the two factors not shown in the plot (Neter et al. 1996). As a result, these partial regression plots obscure the clustering of light supply rate treatments (low, high) and heterogeneity treatments (uniform, continuum, gap) that would be apparent in a simple scatter plot.

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light-limited plant communities. As in virtually all other communities, the community used here had already undergone a sorting process, where some potential community members (e.g. annuals) had been largely excluded. As in other plant communities (e.g. Bazzaz 1996; Pacala et al. 1996), this community exhibited no stable equilibrium prior to experimental treatments. As with species in other communities, the herbaceous species in this community undoubtedly differed significantly in many ways (Grime et al. 1988) including physiological responses to variation in light levels (Latham 1992; Kobe et al. 1995; Larcher 1995; Kobe 1999). Herbaceous perennials also commonly exhibit a large degree of genetic variation within populations (Thomas & Bazzaz 1993; Geber & Dawson 1997) and local adaptation (Linhart & Grant 1996). Thus it is not clear that the community used in this experiment differs from other communities in ways that would prevent generalization to other communities where light is limiting (Bazzaz 1996).

Lastly, our results and those of other studies along productivity gradients (Leibold 1996; Bohannan & Lenski 2000) suggest that the average abundance of a single resource that limits most species in a community also controls species richness. Favoured explanations for why species diversity declines with increasing productivity appear to depend on the system where the pattern occurs (Waide et al. 1999; Mittelbach et al. 2001). In terrestrial plant assemblages, increasing soil resource supply rates increase above-ground biomass, which causes declines in another key resource, light. In our study, it was the decline in average light supply rate that drove down species richness along our soil fertility gradient. In aquatic systems, increasing the inorganic nutrients increases predation rates, and this increase in predation can drive down prey species richness (Leibold 1996; Bohannan & Lenski 2000). If we envision a set of conditions that reduces the effects of predation, this set of conditions could constitute a resource that we call predator-free space (Holt 1977; Jeffries & Lawton 1984; Holt & Lawton 1994). One species may be a superior competitor for predator-free space when it “consumes” this resource by supporting higher predator abundances than other species, and reduces remaining predator-free space to such an extent that other species fail to persist (Holt & Lawton 1994). The decline in species richness observed along productivity gradients in both terrestrial and aquatic systems thus results from a decline in the average supply rate of the most limiting resource, whether that resource is light or predator-free space. The symmetry of the effect of predators and competitors on a population is an old idea (MacArthur 1970), and it now promises to unify explanations for the loss of diversity along productivity gradients in different ecological systems. We suggest that reducing the resource that limits most species, not the resource most limiting to total ecosystem productivity, will cause species richness to decrease as well. We propose that such a relatively simple idea, analogous to Liebig’s law of the minimum, has been overlooked in previous explanations for the complexity of ecological systems.

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