Regional and local patterns in plant species richness with respect to resource availability

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The hump-shaped relationship between plant species richness and productivity is a well-established and important paradigm. While plot-based species richness patterns on local scales have received much attention, little is currently known about species-based patterns on a regional scale. Using Ellenberg's indicator values for 1802 plant species in central Europe, we assess the patterns in regional species richness with respect to light, water, and mineral nutrient availability – three variables that strongly influence productivity. The results of this analysis are compared to those of published studies on smaller scales leading to the following conclusions:

1. On a regional scale in central Europe there is a hump-shaped relationship between soil nutrient supply and plant species richness within a given biome.
2. The peak in species richness for grasslands and wetlands occurs on nutrient-poor soils, while the peak for forests is on nutrient-rich soils.
3. Gradients in plant productivity controlled by different variables (i.e. water, nutrients, or disturbance) have dissimilar effects on plant species richness.

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Because of their broad implications for community ecology and conservation, the patterns in species richness across a productivity gradient have long been a subject of ecological inquiry (Connell and Orias 1964, Brown 1973, Whittaker and Niering 1975). Despite the lengthy history of this field, studies continue to emerge arguing for or against the generality of patterns, and the mechanisms driving these patterns (Waide et al. 1999, Mittelbach et al. 2001). If anything, the relevance of the debate has increased in recent years as it has become clear that the search for patterns in species richness has implications for the concurrent search for the ecosystem effects of biodiversity (Tilman and Downing 1994). Furthermore, regional and global anthropogenic changes continue to have widespread and significant effects on the productivity of terrestrial ecosystems (Sala et al. 2000). Predicting the effects of these changes on species-rich communities is an ongoing and important line of research that undoubtedly requires a comprehensive understanding of the patterns and mechanisms that connect resource availability, biomass, productivity, and species richness.

The most commonly reported pattern of biomass and species richness is the hump-shaped relationship (Grime 1973a, Mittelbach et al. 2001). Since Grime's work, many studies have argued that this relationship is unusually widespread for an ecological phenomenon (refs in Tilman and Pacala 1993). However, attempts to identify the mechanisms underlying the pattern have generated many competing hypotheses and debates (Oksanen 1996, Zobel and Liira 1997, Waide et al. 1999).

In those vegetation types that show the hump-shaped relationship, the location of the peak in species richness along a productivity gradient is crucial both for understanding species co-existence and for focusing conservation efforts. The consensus for most well-studied systems is that species richness peaks at relatively low

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biomass values and then declines above a threshold (see refs in Tilman and Pacala 1993). However, this threshold varies by as much as an order of magnitude across different community types (Marrs 1993). Moreover, forests may show a fundamentally different pattern with a species richness peak in the most productive systems (Grubb 1987, Peet and Christensen 1988).

One of the most striking points to emerge from recent work on species richness and biomass has been the prominence of scale in determining the type of pattern. Within a single community type (e.g. a *Typha* marsh or a particular type of semi-desert), there is often no significant relationship between biomass and species richness (Moore and Keddy 1989, Guo and Berry 1998). If plots are sampled across a range of community types, a hump-shaped relationship often, but not always, becomes evident (Waide et al. 1999). At a continental scale, a monotonically increasing relationship between productivity (usually inferred from actual evapo-transpiration) and species richness is the dominant trend (Pianka 1966).

Studies of observed patterns in species richness thus far have used one of two methods: plot-based counts or species lists. In plot-based studies, the species richness of a fixed-size area is assessed across some kind of abiotic or biotic gradient (Grime 1973a, b, Whittaker and Niering 1975). The scale of the sampled area may vary greatly from one community to whole continents. In flora- or fauna-based studies, species lists of different regions are compared (Pianka 1966, Latham and Ricklefs 1993). The patterns that then emerge within taxa or within a given growth form are compared with fossil evidence to deduce information about broad-scale climatic or historical controls on the richness of various taxa.

In the literature there exists a gap between these two approaches. At present, there is little information on species-based patterns in richness with regard to the resources that control productivity. The size of the regional species pools could affect local patterns (Taylor et al. 1990, Zobel 1997), and because most plant species have regional-scale distributions, that scale is of the uttermost importance for conservation of species richness. For the vast majority of species, any change (or combination of changes) that could cause the extinction of a given species would have to be at least regional in scale. In fact, many of the current and intensifying anthropogenic changes (e.g. nitrogen deposition, species invasions) are regional or even global in extent (Sala et al. 2000), suggesting that an understanding of regional-scale controls on species richness will become ever more vital.

This paper presents an analysis of the Ellenberg (1988) indicator values for central European vascular plant species. Ellenberg (1988) assessed the species distributions of 1802 plant species with regard to light, water, and nutrients. Each species has a value for each resource, and the number of species with a given combination of values is a measure of the number of species within central Europe that are found in any given habitat type. In our study, we examine the patterns in these values and compare them to the results of published studies.

Methods

The Ellenberg indicator values: advantages and limitations

In his seminal work, originally published in German in 1963, Ellenberg (1988) enumerated indicator values for moisture, soil N, light, soil reaction (pH), temperature, continentality, and soil salinity using decades of field experience (Table 1). The values, which generally follow a nine-point scale, exclude species that are distributed widely across a particular gradient. In addition, Ellenberg (1988) declined to rate a few plant species (eight percent for N, less for other values). Plant distributions are the result of many abiotic and biotic variables. The Ellenberg values should not be thought of as a physiological tolerance range for each species. Rather, each

Table 1. The ecological significance of Ellenberg indicator values for water, nitrogen, and light (Ellenberg 1988).

Ellenberg indicator value	Water value	Nitrogen value	Light value
1	Indicators of extreme dryness	Indicators of sites poor in available N	Plants in deep shade, may be less than 1% relative light intensity
3	Dry site indicators	More often on N-deficient soils than richer ones	Shade plants, mostly less than 5% relative light
5	Moist-site indicators	Average N availability	Plants in half shade, rarely in full light but generally more than 10% relative light
7	Damp-site indicators	More often in places rich in available N than in poor or average situations	Plants generally in well lit places but also occur in partial shade
9	Often in water-saturated, badly aerated soils	In extremely rich situations	Plants of full light
12	Submerged plants		

value represents the realized niche of a species, the results of environmental gradients, competition, and many other factors.

Because of their near-comprehensive nature, the Ellenberg indicator values offer a unique way to determine which habitat types are the most species rich on a regional scale. However, they differ greatly from the data used in most current ecological studies in that they were determined in a subjective fashion. This has prompted several tests of the quantitative validity of the Ellenberg values, which, on the whole, have shown that the Ellenberg values are remarkably consistent with quantitative assessments of environmental variables (Thompson et al. 1993, Wamelink et al. 1998, Schaffers and Sýkora 2000). The values have also been used in numerous ecological studies (Persson 1981, Hawkes et al. 1997, Hill and Carey 1997, Coomes and Grubb 2000, Dupré 2000, Hill et al. 2000, Prinzing et al. 2001).

While the reliability of the Ellenberg indicators has been well established, the quantitative interpretation of some of the indicators is not entirely straightforward (Table 1). For the Ellenberg water value, Schaffers and Sýkora (2000) found the strongest relationship ($r = 0.84–0.88$) with site-based average annual groundwater level and average lowest moisture content. The relationship is linear for most of the range but levels off at high soil water concentration. The interpretation of the Ellenberg N value is less clear. Schaffers and Sýkora (2000) noted that N values were not designed to index with a specific soil measurement but rather to represent a general index of nutrient status. Thompson et al. (1993) found that the values correlated well with leaf N for 45 British species ($r = 0.78$). In the Netherlands the nitrogen values correlated best with vegetation N-content and also with biomass ($r = 0.85–0.86$, Schaffers and Sýkora 2000). In our study, Ellenberg N values should not be interpreted strictly as a measure of nitrogen mineralization, but rather a conflation of the availability of all soil macronutrients.

In this study we analysed the association of Ellenberg light, water, and nutrient values. The patterns in the values were tested for independence using a G-test with William's correction. We also tested for trends in the pairs of values using Spearman's coefficient of rank correlation (Sokal and Rohlf 1995).

Patterns in published studies

There have been several recent reviews of aspects of the species-richness productivity relationship (Marrs 1993, Bedford et al. 1999, Grace 1999, Gross et al. 2000) and two comprehensive reviews across all scales and taxa (Waide et al. 1999, Mittelbach et al. 2001). In our study we focus on a much more limited scope than that discussed by either Waide et al. (1999) or Mittelbach et al. (2001). We will centre the following analysis on

studies of vascular plant species richness on a local to regional scale.

We began with the subset of the literature reviewed in Waide et al. (1999) that measured vascular plant species richness or all species in a major life form (e.g. perennials). We then added recently published studies. In order to search for generalities across biomes, we included only studies that examined single biomes and that could be categorized as forest, wetland, grassland, or semi-desert. We then eliminated studies on a continental scale and those with a sample size less than ten. For the purposes of this analysis grasslands were broadly defined as non-wetland, herb-dominated vegetation.

Waide et al. (1999) focused on the shape of published productivity–species richness relationships: negative, positive, hump-shaped, or none. To explore these relationships further we evaluated the hump-shaped relationships to determine where the species richness peak occurs in published studies relative to the range of values reported for the proxy for productivity that was used. For negative linear relationships, the maximum was considered to be zero percent of the range; for positive relationships it was considered to be 100 percent.

We used quadratic least squares regression to determine hump-shaped relationships (Waide et al. 1999). Although a generalized linear model (GLM) with Poisson errors may rest upon more realistic assumptions (Mittelbach et al. 2001), the vast majority of studies report least squares regression. Without all of the original data least squares regression was the only approach available to us. In four cases, we were able to compare the results from a GLM with Poisson errors to those from least squares regression. The choice of model changed the location of the species richness peak by only between 1.6 and 3.6 percent.

We used the maximum of the reported regression line as the species richness peak and determined where this peak lay relative to the range of sites sampled in the study. In cases where no statistics were reported we used data extracted from tables and figures. We then tested patterns in different biomes using a Kruskal-Wallis test (Sokal and Rohlf 1995).

In the absence of a consistent method to measure productivity, our analysis offers a way to test where the species richness peak lies across the sites sampled for a given study. Another advantage of this method is that it allows for comparisons across biomes (e.g. forests and wetlands) where the measured proxies for productivity consistently differ. However, peaks in different studies that occur at the same percentage of the total range do not necessarily represent the same absolute level of productivity or standing biomass. For previous work using the absolute levels of productivity proxies see Marrs (1993) and Mittelbach et al. (2001).

Results

Regional patterns in species richness

Our analysis showed a significant association between Ellenberg N and water values (G = 568.9, df = 88, p < 0.001; Fig. 1). The rank correlation was significant and positive (r_s = 0.362, p < 0.001). At low water values (1–4, Table 1), which correspond to dry habitats dominated by herbaceous or shrubby vegetation, the greatest concentration of species is at low N values (Fig. 1). In contrast, sites with intermediate water values (5–7, Table 1), consisting largely of forest vegetation, the greatest concentration of species is at high N values. At higher water values (8–10, Table 1), which correspond to saturated but only temporarily flooded soils, the peak in species richness again shifts to low N values.

To test whether the pattern is driven by differences between forest species and non-forest species, we compared Ellenberg's light values with his N values (Fig. 2). Ellenberg light and N values also showed a significant association (G = 267.3, df = 64, p < 0.001). The rank correlation was significant and negative (r_s = − 0.330, p < 0.001). Species with a light value of less than six can be thought of as primarily forest species, that is species of the understory (1–3) or canopy gaps of moderate size (4–5) (Ellenberg 1988). Consistent with the water analysis, the peak of forest species is at high N values and the peak for non-forest species is at a low N value.

For the forest vegetation, these patterns of species richness with respect to water and N values (Fig. 1 and 2) are driven primarily by herb richness. There are only 48 tree species in Ellenberg's analysis, and of those only 24 show a quantifiable distribution with respect to both nitrogen and water. Therefore of the 1416 species in Fig. 1a, 1392 will not be canopy dominants in a forest, suggesting that the pattern in Fig. 1 and 2 cannot be driven by patterns of tree species.

Patterns in published studies

There were significant differences in the location of the peak in species richness across biomes (Kruskal-Wallis chi-square = 11.46, df = 3, p = 0.0095; Table 2, Fig. 3). For wetlands the peak in species richness occurs at low to intermediate productivity. In forests and semi-desert vegetation, the peak lies at high productivity. For grassland vegetation no consistent pattern in the location of the peak was found.

Several studies have examined tree species richness across various biotic and abiotic gradients. However, these data showed conflicting patterns, perhaps because of methodological inconsistencies, differences in successional status, or the unclear connections between measured variables and productivity.
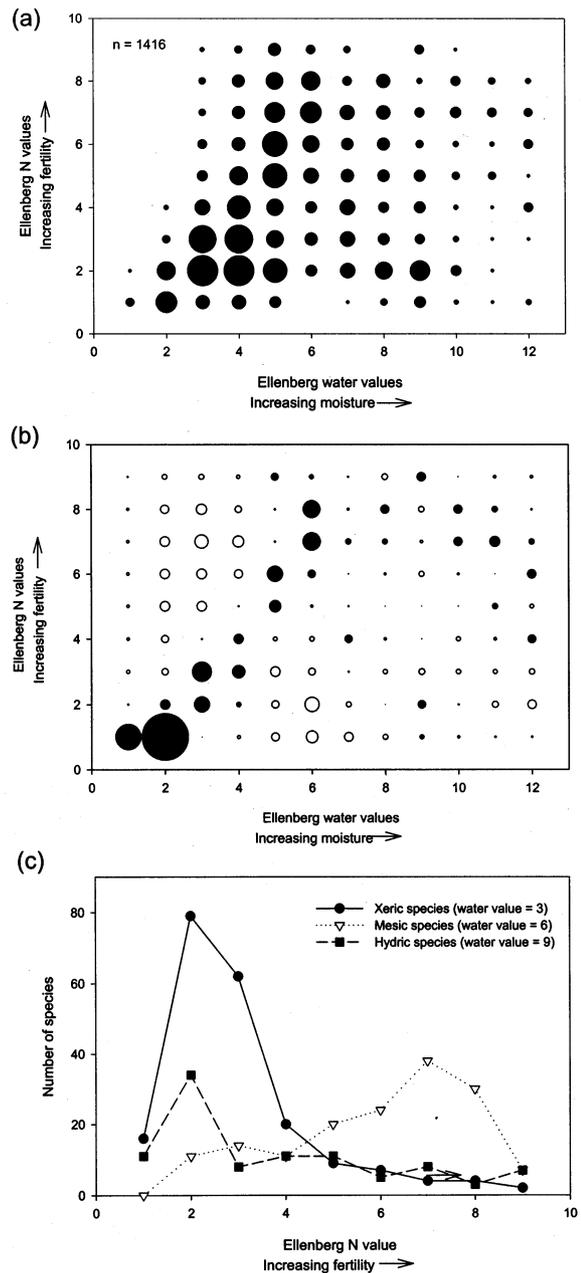

Fig. 1. Distribution of central European plant species with respect to Ellenberg water and N values. In (a) the area of the circle is proportional to the number of species with a certain pair of values. n = 1416. In Fig. (b) closed circles show Ellenberg value combinations with more species than expected based on a null hypothesis of independence. Open circles show value combinations with fewer than expected species. The area of the circle is proportional to the degree of the deviation as calculated in a chi-square test [(expected − observed)^2/expected]. Fig. (c) shows species distribution across Ellenberg N values for three Ellenberg water values (3, 6, and 9) corresponding to species found on xeric, mesic, and hydric soils. This figure shows three cross-sections of the data presented in Fig. 1a.
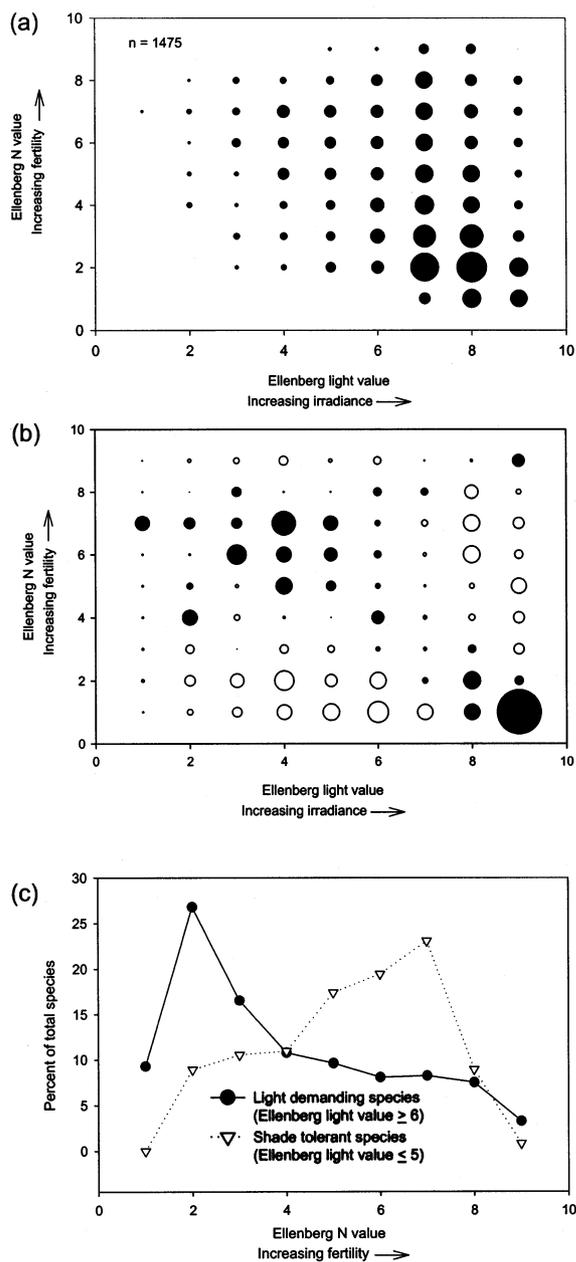
Fig. 2. The distribution of central European plant species with respect to Ellenberg light and N values. In (a) the area of the circle is proportional to the number of species with a certain pair of values. n = 1475. In Fig. (b) closed circles show Ellenberg value combinations with more species than expected based on a null hypothesis of independence. Open circles show value combinations with fewer than expected species. The area of the circle is proportional to the degree of the deviation as calculated in a chi-square test [(expected − observed)^2/expected]. Fig. (c) shows species distribution across Ellenberg N values for light-demanding species (Ellenberg light value ≥ 6) and shade-tolerant species (Ellenberg light value ≤ 5).

Discussion

On a regional scale, regardless of biome, the relationship between N values and species richness shows a humped shape (Fig. 1c, 2c). Importantly, some of the mechanisms driving the hump-shaped pattern in this study must differ from the mechanisms cited in the many previous plot-scale studies, e.g. that of Grime (1973a). On a regional scale there are few species specialized at the extremes with respect to soil nutrients and many more species either with broad ranges or with a peak at an intermediate value or both. This probably accounts for the humped shape of the curves (Fig. 1c, 2c). The mechanistic basis of the location of the peak in species richness is less clear and could be accounted for by either local- or regional-scale processes.

The similarity in species richness patterns at regional and local scales has lead to a recent interest in regional species pools as important determinants of local species richness (Taylor et al. 1990, Pärtel et al. 1996, Zobel 1997, Dupré 2000). Our results are consistent with the results of these studies – regional- and local-scale species richness show similar patterns for wetlands, grasslands, and forests. Wetlands are species rich on low-nutrient soils (Wheeler and Giller 1982), while forests are species rich on productive, high nutrient sites (Loucks 1962, Grubb 1987, Peet and Christensen 1988). Grasslands are most species rich on low-nutrient soils, consistent with experimental results (Lawes et al. 1882) and some observational studies (Inouye et al. 1987). However, this relationship is not found consistently for all grasslands and will be discussed further below. In any case, a correlation between a regional species pool and local richness does not imply causation in either direction (Herben 2000, Grace 2001a).

An additional complication is the species–area relationship (Gleason 1922). The most widespread environments may be expected to show a higher species richness than rare environments. However, it is difficult to conclude much about the relative strength of this relationship. As species currently found in central Europe represent a mix of speciation and immigration from other regions, with both processes operating over tens of millions of years, it may be historic (or non-European) habitats rather than current European habitat areas that are relevant, clouding the interpretation of any correlation between habitat area and species richness. In addition, historical disturbance, notably glaciations and associated drier periods, may have a significant effect on the extinction of European species and therefore the composition of the current regional species pool (Grubb 1987, Taylor et al. 1990, Gaston 2000).

Current theory posits that high biomass leads to competition for light, which then causes the hump-shaped richness–productivity relationship (Grime 1979). Clearly there are different classes of controls on

Table 2. Published studies that found a significant relationship between a proxy for productivity and plant species richness. Unless noted all studies counted species richness of all vascular plants. Peak species richness was calculated using the regression equation or directly from the data presented in each study. A significant quadratic term was used to identify hump-shaped relationships. List of studies modified from Waide et al. (1999); see text for details of inclusion criteria.

System type	Location	Productivity–species richness relationship		Sp. richness peak (percent of range in productivity)	Reference	Notes
		Proxy for productivity	Shape of relation			
Wetlands						
Fresh and salt marshes	Louisiana, USA	St. crop+litter biomass	Negative	0	Gough et al. 1994	
Fen	United Kingdom	St. crop biomass	Negative	0	Wheeler and Giller 1982	
Fen	United Kingdom	St. crop production	Negative	0	Wheeler and Shaw 1991	
Various wetland types	Canada	St. crop biomass	Negative	0	Moore and Keddy 1989	
Lakeshore, marsh	Canada	St. crop+litter biomass	Negative	0	Wisheu and Keddy 1989	
Shoreline	Canada	St. crop biomass	Humped	25.7	Shipley et al. 1991	
Salt marsh	Spain	St. crop biomass	Humped	40.0	Garcia et al. 1993	
Lakeshore	Canada	St. crop biomass	Humped	41.5	Wilson and Keddy 1988	
Riparian marshes	Alaska, USA	Productivity estimate	Humped	46.0	Pollock et al. 1998	
Lakeshore	Sweden	Growing days	Humped	54.0	Nilsson and Wilson 1991	
Lakeshore	Canada	St. crop+litter biomass	Humped	54.9	Wisheu and Keddy 1989	
Forests						
Deciduous forest	Canada	Soil nutrient index	Humped	82.5	Loucks 1962	
Mountainside	Sweden	Growing days	Positive	100	Nilsson and Wilson 1991	
Evergreen forest	SW USA	Annual rainfall	Positive	100	Harner and Harper 1976	
Rainforest	Australia	Phosphorus	Positive	100	Beadle 1966	
Semi-deserts						
Semi-desert	SW N. America	Biomass	Humped	38.2	Guo and Berry 1998	Small plots
Semi-desert	Israel	Annual rainfall	Positive	100	Vogel et al. 1986	Grasses only
Semi-desert	SW N. America	Annual rainfall	Positive	100	Brown 1973	Perennials only
Semi-desert	Arizona, USA	Annual rainfall	Positive	100	Barbour and Diaz 1973	Perennials only
Grasslands						
Sand plain	Minnesota, USA	Nitrogen	Negative	0	Inouye et al. 1987	
Mediterranean grassland	Spain	St. crop biomass	Humped	25.1	Puerto et al. 1990	
Sand dune	Israel	St. crop biomass	Humped	60.7	Kutiel and Danin 1987	
Grassland	The Netherlands	Nitrogen	Positive	100	Werger et al. 1983	
Tropical savanna	Venezuela	Annual rainfall	Positive	100	Sarmiento 1983	

biomass, of which the most prominent are productivity and disturbance. These two determinants of biomass must have different effects (Grime 1979, Huston 1979, Pollock et al. 1998), and their effects are often complicated by co-variance (Waide et al. 1999). The effects of different resource variables and non-resource variables, such as pH, flooding, and salinity, on productivity may also differ (Grace 2001b). The idea that these differences will have dissimilar effects on species richness is rarely considered, though Goldberg and Miller (1990) have tested this idea, adding nutrients and water to old-field vegetation. In the following analysis of published studies, we will further separate the potentially dissimilar effects on species richness of different controls on productivity.

Species richness patterns in wetland vegetation

Consistent with the model of Grime (1979) and the regional analysis presented in this paper (Fig. 1 and 2), the most species-rich wetlands are found at low to intermediate productivity (Fig. 3). In fact, the trends in both plot-based studies and in the analysis of the Ellenberg data toward greater species richness at lower N values would probably be even stronger if bryophyte
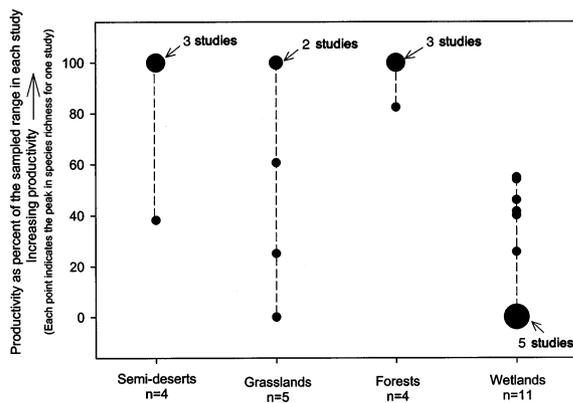
Fig. 3. The peaks in plant species richness for 24 studies in four different biomes. The peaks are graphed as a percent of the range in productivity (or productivity proxy) sampled in each study. The size of the bubble represents the number of studies. Studies that found no significant relationship between species richness and productivity are not shown. See Table 2 for details.

species were included. In a thorough analysis of fens across England and Wales, Wheeler and Shaw (1991) showed that although the most species-rich sites are found at low productivity, there are also many species-poor sites with low productivity. This variation can be due to pH, hydrology, or site history (Bedford et al. 1999).

In different types of wetland systems the controls on productivity can differ with important implications for the plant species richness. In fens, when the effects of anthropogenic disturbance are minor, productivity gradients are usually driven by nutrient availability (Bedford et al. 1999). In contrast, on the margins of lakes and rivers, variation in productivity can be driven by the substrate type, elevation relative to water level, and disturbance by floods or ice scour. In the nutrient-limited fens, there is a negative relationship between biomass and species richness (Wheeler and Giller 1982, Wheeler and Shaw 1991). In British fens (Wheeler and Giller 1982, Wheeler and Shaw 1991) and in a study that included a Canadian fen (Moore and Keddy 1989), there is a consistent species richness peak at the sites with the lowest biomass (Fig. 3, Table 2). In contrast, in four lakeshore studies, where the impact of disturbance on biomass is greater, there is often a hump-shaped relationship with a peak at between 0 and 55 percent of the range in biomass (Wilson and Keddy 1988, Wisheu and Keddy 1989, Nilsson and Wilson 1991, Shipley et al. 1991). These results are consistent both with the theoretical work of Grime (1979) and also with the empirical results of Pollock et al. (1998).

As noted by Wisheu and Keddy (1989) and Bedford et al. (1999), the peak in species richness at low productivity in wetlands is of considerable importance in the effort to conserve rare and species-rich communities. Species-rich communities also hold a disproportionate

number of rare species in both Britain and New York (Wheeler and Shaw 1991, Johnson and Leopold 1994). In the context of the landscape-scale eutrophication occurring in many regions (Morris 1991), our results portend a regional decline in species-rich communities and loss of rare species in wetlands.

Species richness patterns in forest vegetation

The processes that determine patterns of species richness in forests are complex. In an attempt to tease them out, we consider first the extent to which trends in different life-forms in temperate deciduous forests are consistent, then the extent to which the peaks in species richness concern gap-demanders as opposed to denizens of the understory, and finally the parallels and differences between temperate deciduous and tropical evergreen forests.

Our analysis of the Ellenberg values shows a peak in species richness at relatively high N values, and therefore at relatively high productivities, i.e. the opposite pattern to that found in grasslands and wetlands. This result arises overwhelmingly from richness in herbs as these are much more numerous in species than trees, shrubs or climbers. In general, the same trend was found for trees and climbers but not shrubs in an earlier analysis of European deciduous forests, based at the local scale (Grubb 1987). In temperate deciduous forest in eastern North America the trends in richness in different life-forms are not entirely coincident; Peet and Christensen (1988) found a positive relationship between soil nutrients and species richness for herbs and shrubs but not for trees.

Our result for herbs at the regional level agrees with the especially fine study made by Loucks (1962) at the local scale in eastern North America. He found a very strong correlation ($r = 0.94$) between total vascular plant species richness and soil nutrient factors after first controlling for moisture availability. Experimental additions of nutrients have yielded contradictory results. Ellenberg (1988) summarized the results of Grabherr who found that addition of various nutrients to the soil of beech forest increased the number of herb species markedly. In contrast, Fahey et al. (1998) found a decrease in species richness in deciduous forest, and Thomas et al. (1999) a similar decline in evergreen coniferous forest. Possibly the herbs concerned were so shaded that the effect of nutrient-addition was to reduce yield rather than increase it – a phenomenon documented for shrubs by Grubb et al. (1996).

An important feature of the numerous herb species found at high N values in European deciduous forest is that they are associated with treefall-gaps. Of the 262 forest species with N values of 5–9, 38 have shade-tolerance values of 1–3 (i.e. live in the understory) and 224 have values of 4–6 (i.e. flourish in gaps). Possibly

this pattern is to be explained in terms of heterogeneity in the gaps, not only in light-climate but also in extent of root competition and of soil disturbance associated with tree-fall (subsoil partly exposed, some soils raised up while hollows are made elsewhere). No one species will be favoured all over a gap, and therefore enabled to assume dominance by shading out other species as envisaged by Grime (1979) for grasslands. We suspect that the gradients in light regime are very important because it is not rare to find one species dominant in multiple-treefall gaps or clear-cut sites (Ellenberg 1988).

Heterogeneity of conditions in gaps is likely to be important for trees and shrubs in the forest too; the majority of these species are relatively light-demanding (Ellenberg 1988). Although most species become established in the understory, they need gaps for onward growth (Canham 1989). This emphasis on heterogeneity of conditions in gaps is complementary to the two partial explanations suggested by Grubb (1987) for the persistence of large numbers of tree species in the most productive forests in Europe: first, these forests are dominated by species which are not the most deeply shading, and secondly, trees – unlike herbs – rarely reproduce vegetatively so that it is easier for a given gap to be filled by a new dominant species.

In parallel with the effects in gaps, we see also effects in the understory. In European deciduous forests on the most infertile (highly acidic) soils there are typically no herbs in deep shade (less than two percent daylight). Many species of herbs are able to grow in much deeper shade on soils of higher pH and/or those which provide more nitrate (Ellenberg 1939, Peace 1984, Ellenberg 1988). Laboratory experiments show that relevant species can grow faster in deep shade when the nutrient supply is enhanced, mainly through a reduction in the allocation to roots (work by V. G. Karpov summarized in Walter and Breckle 1985, Peace and Grubb 1982, Peace 1984). Peace and Grubb (1982) suggested that faster growth enables these species to overcome various hazards in the field, and so persist in deeper shade on more fertile soils. Such a mechanism may be a significant partial explanation of the greater richness in herb species overall on higher-N soils insofar as it applies to the major shade-tolerant species in northern Europe which extend from the UK to Russia: *Oxalis acetosella*, *Galium odoratum*, *Lamiastrum galeobdolon* (Peace 1984, Ellenberg 1988).

Another partial explanation of the greater species richness of herbs on higher-N soils is the greater number of spring ephemerals found on fertile soils (Grubb and Marks 1989). This group of species is particularly favoured by deep shade because it enables them to avoid competition from taller-growing summer-green species which also leaf out early in the spring but which can tolerate only moderate shade (Grubb and Marks 1989). In the 'spring window', before the trees leaf out, the spring ephemerals have high rates of photosynthesis

which are made possible by high N concentrations in the leaves. In general, spring ephemerals can maintain these high foliar N-levels only on soils with at least a moderate nitrate supply; there are just a few widespread exceptions (Grubb and Marks 1989).

To summarize the position for herbs in European temperate deciduous forests, the majority of species on higher-N soils are gap-demanders. We hypothesize that heterogeneity in light regime and soil conditions is important in preventing competitive exclusion by one or a few of these species. The minority of herbs which live in the understory are composed of two types, evergreen or semi-evergreen species and spring ephemerals, and there are clear physiological explanations for both being able to flourish in deep shade only on fertile soils.

In tropical rain forests there is evidence that, after controlling for moisture, the greatest richness in species of trees, treelets and shrubs is found on soils richer in available nutrients (Beadle 1966, Gentry and Emmons 1987, Grubb 1987, Gentry 1988, Wright 1992, Tuomisto and Ruokolainen 1994). This may also be true for climbers and herbs (cf. Coomes and Grubb 1996). Tropical rain forests differ from temperate deciduous forests in that the great majority of species are highly shade-tolerant (Whitmore 1998). The forests on highly infertile soils let through just a little more daylight (Coomes and Grubb 2000), and therefore the greater numbers of species on higher-fertility soils must be extremely shade-tolerant. It has been shown experimentally that root competition can severely reduce the growth rate of saplings in tropical rain forest on highly infertile soil (Coomes and Grubb 1998), and the fragmentary evidence suggests that this is not the case on nutrient-rich soils (Coomes and Grubb 2000). We hypothesize that the reduction in intensity of root competition makes possible the greater number of strongly shade-tolerant species on soils higher in available nutrients.

Patterns in semi-desert vegetation

The trend in semi-desert studies is that species richness increases with rainfall, which is assumed to correlate with productivity (Fig. 3, Barbour and Diaz 1973, Brown 1973). Because semi-deserts, by definition, have well-spaced individuals of perennial species, it is unlikely that even at high biomass there is competition for light between them. Higher productivity in this range of biomass values leads to greater species richness, consistent with Grime's (1979) model. Comparing semi-deserts and deserts on a global scale, Waide et al. (1999) found a similar increase in species richness from the extremely low productivity deserts to semi-deserts. However, this pattern does not seem to hold on a more detailed comparison of the semi-deserts of southwestern

North America, perhaps because of complications of seasonality and temperature (Waide et al. 1999). The pattern is also dependent on scale. In a study of semi-desert micro-habitats using relatively small (0.25 m²) plots Guo and Berry (1998) found a species richness peak at an intermediate level of biomass.

Resource addition experiments in deserts and semi-deserts do not consistently show an effect of added resources on species richness, but when there is an effect, it is positive, consistent with observational studies. There is evidence that certain patterns of irrigation increase the species richness of annuals in the Chihuahuan semi-desert (Gutierrez and Whitford 1987, Gutierrez et al. 1988). However, a study in the Abu Dhabi emirate did not find an effect of added water on species richness (Oatham et al. 1995).

Patterns in grassland vegetation

Fertilization of grassland communities results in lowered species richness (Lawes et al. 1882, Tilman 1987), consistent with the results of our analysis of the Ellenberg values. As part of the model system for the development of the hump-shaped model, the mechanistic explanation has been thoroughly examined (Grime 1979, Huston 1979) as discussed above. However, the generality of this pattern across many natural gradients of different resources has not been tested previously.

The result of our review of natural productivity gradients neither supports the ubiquity of the hump-shaped relationship between productivity and species richness nor offers an alternative pattern (Fig. 3, Table 2). Limiting the survey to those studies that sampled exclusively grassland communities there were two positive relationships, two hump-shaped, and one negative (Fig. 3). This finding contrasts with the consistently low peak in species richness found in 11 studies of wetland vegetation (Fig. 3).

In wetlands there is a consistent peak in species richness at low productivity, perhaps because of the absence of water shortage. While nutrients and disturbance are the primary controls of species richness in herbaceous wetlands, in grasslands there is often the additional influence of drought, which exerts a strong control on the productivity of many sites. In fact, regional gradients in grassland productivity are much more likely to be caused by moisture than nutrient availability, though the factors do co-vary frequently. In a topographic sequence, water and nutrient availability often increase together along a soil catena (Werger et al. 1983, Puerto et al. 1990). However, on a larger scale the two factors can also co-vary negatively (Nye and Greenland 1960).

Increased water availability does not generally lead to a decline in species richness. High water availability usually leads to higher species richness, while high nutrient availability usually leads to lower species richness. Within arid grasslands in the United States, Venezuela, and Argentina, rainfall is positively correlated with an increase in the species richness of the system (Daubenmire 1970, Sarmiento 1983, Jobbágy et al. 1996). In the southern Kalahari, the habitat with the highest species richness has the highest moisture but the lowest nutrient supply (Leistner and Werger 1973). Across a rainfall gradient in central North America, the tall-grass prairie is much more species rich than the short-grass prairie (Wilson 2000). Along a topographical sequence in the Netherlands, the lower, wetter sites were more species-rich (Werger et al. 1983). In this study the lowest-lying and most species-rich sites were also the most nutrient-rich. In contrast, Inouye et al. (1987) found a negative relationship between soil nutrients and species richness for North American old fields.

There are, however, additional complications to this view. First, many of the species in moister grasslands are maintained by either low nutrient supply or disturbance. Also, at the extreme of water availability, grasslands become wetlands and species richness may sometimes decline (Dix and Smeins 1967, Grace et al. 2000), though this trend will depend on the type of wetland formed.

Experimental evidence also suggests that, in contrast to nutrient additions, biomass production stimulated by additional water will not lead to a decline in the species richness of the system. Goldberg and Miller (1990) added water and nutrients separately to plots of old-field annuals. While nitrogen and water alone increased the biomass of the plots to a similar level, only nitrogen led to a decline in species richness. The authors explain this in terms of the phenology of the system. Addition of either limiting resource stimulated production, but nitrogen addition caused higher biomass production and lower light levels earlier in the season than water addition, eliminating low-stature species.

A variant on this explanation seems more applicable to the observational studies cited above. Low nutrient concentrations are a chronic impediment to plant growth. However, water limitation is a periodic, acute limitation, and one that intermittently becomes severe enough to cause mortality. This idea that a more stochastic environment is more likely to cause the extinction of rare species is not new (Levinton 1979, Coomes and Grubb 2000). However, it has not previously been applied to the productivity–species richness relationship.

Based on this idea, sites in topographical positions or climates that suffer irregular and severe droughts could experience higher extinction rates and therefore develop lower species richness. After a severe drought in a Minnesota grassland, species richness fell 37 per-

cent, and did not recover significantly during the next two years (Tilman and Elhaddi 1992). Conversely, in some sites where water availability is relatively constant, notably tropical rainforests and some temperate ground-water-fed wetlands, there are often many plant species that persist at low levels of light, apparently dependent on the absence of drought.

Conclusion and implications for future research

The hump-shaped model of Grime (1973a, b, 1979) has been a valuable tool from the perspectives of both basic research and conservation (Marrs 1993, Verhoeven et al. 1993). However, it is now clear that the generality of the hump-shaped model should not be overstated (Waide et al. 1999). Even across community types, the scale at which the hump-shaped relationship is most common, a majority of published studies fail to find a hump-shaped relationship (Waide et al. 1999). Furthermore, productivity often limits species richness rather than controlling it tightly, creating a hump or triangle which may be 'filled in' to varying degrees (Grace 1999). There are also crucial differences in the location of the peak in species richness between forests and herbaceous vegetation.

From theoretical and conservation points of view, examining the causes of variation in the mechanistic links between productivity or disturbance and species richness offers a productive avenue for research. Ultimately, availability of resources varies naturally across sites and often as a result of anthropogenic change. Whether and to what degree increased resource availability will lead to increased productivity and a decline in species richness will depend on a wide variety of abiotic and biotic variables. Experimental work by Goldberg and Miller (1990) suggests that the addition of different resources, despite increasing biomass, does not necessarily have the same, negative effect on species richness. The observed patterns reviewed in this paper also suggest that this distinction between resources may also have important implications in unmanipulated systems.

As ecology is a science of 'contingent generalizations', studies in varied biomes must continue to refine where, at what scales, and for which taxa the hump-shaped model is applicable. Furthermore, the mechanisms driving this relationship remain unclear in important ways, and the extrapolation of much of this theory to tropical systems has only begun to be worked out. As the effects of anthropogenic change on species richness grow in intensity and scale, so does the importance of this area of research.

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