

Patterns of plant species richness in relation to different environments: An appraisal

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Abstract. We review patterns of plant species richness with respect to variables related to resource availability and variables that have direct physiological impact on plant growth or resource availability. This review suggests that there are a variety of patterns of species richness along environmental gradients reported in the literature. However, part of this diversity may be explained by the different types and lengths of gradients studied, and by the limited analysis applied to the data. To advance in understanding species richness patterns along environmental gradients, we emphasise the importance of: (1) using variables that are related to the growth of plants (latitudinal and altitudinal gradients have no direct process impact on plant growth); (2) using multivariate gradients, not single variables; (3) comparing patterns for different life forms; and (4) testing for different shapes in the species richness response (not only linear) and for interaction between variables.

Keywords: Diversity; Environmental gradient; Functional type; Life form; Nutrient gradient; Temperature.

Abbreviations: AET = Actual Evapotranspiration; PET = Potential Evapotranspiration.

Introduction

Biodiversity has recently emerged as an issue of both scientific and political concern primarily because of an increase in extinction rates caused by human activities (Ehrlich & Wilson 1991). Several very large experiments (Tilman & Downing 1994; Tilman 1996; Naeem et al. 1994, 1995; Kareiva 1994, 1996) have addressed the relationship between biodiversity, measured as species richness, and ecosystem function. However, they have failed to reveal a clear causal effect (Huston 1997). After a revision of some of the problems and hidden treatments in these experiments, Huston (1997) concluded that they do not provide evidence that increasing biodiversity improves ecosystem function and that “both local species diversity

and the rate of ecosystem processes such as productivity are determined by the amount and variability of the fundamental environmental resources that regulate plant growth and ecosystem processes”. Species richness patterns in relation to the environment need to be understood before drawing conclusions on the effect of biodiversity in ecosystem processes. Numerous problems regarding the study of species richness need to be clarified, including the role of disturbance (e.g. Grime 1979; Huston 1994), and the relative importance of biotic versus abiotic factors (Grime 1979; Cornell & Lawton 1992; Austin & Gaywood 1994). Many studies tend to have a zoological bias (Lawton 1999) though vegetation studies may have much to offer on general issues concerning biodiversity (Austin 1999). In this context, we review studies of plant species richness in relation to environmental gradients with emphasis on the potential differences in response to different types of gradients, differences between growth forms and the methodology necessary to investigate the observed patterns.

In general, plant community ecologists are concerned with patterns of species response to environmental gradients (e.g. Grime 1979; Tilman 1988; Wisheu & Keddy 1989; Moore & Keddy 1989) and tend to adopt (if only implicitly) a continuum approach to vegetation with its assumption of continuous change in composition with position in the multi-dimensional environmental space (Austin 1985, 1999). Huston (1979, 1994) reviewed species richness extensively, and regarded patterns of species richness as being determined by the interaction of disturbance with environmental gradients and competitive exclusion. Although over any large region the distribution of species richness is likely to be governed by two or more environmental gradients (Margules et al. 1987; Pausas 1994; Austin et al. 1996), species richness studies in relation to environmental gradients have been mainly single-factor studies.

Harrison et al. (1992) avoided the analysis of species/environment relationships as too problematic in their study of beta diversity gradients in Britain, prefer-

ring to concentrate on distance and dispersal. They examined the correlation between distance and the principal components of 16 climatic variables, concluding that “the strong correlation of distance with climate makes the interpretation in terms of dispersal versus habitat specificity ambiguous at best”. Richardson et al. (1995) tested several hypotheses based on biotic interactions to explain *Banksia* species richness in the south of Western Australia. They did not test for any relationship between species richness and environmental parameters; however they concluded that topographic and soil variability may be an explanation for the patterns of coexistence. They also commented that different regions (i.e. different environments) do show different patterns of coexistence. Nuñez-Olivera et al. (1995) studied different diversity indices in shrublands of central western Spain, and discussed the variation in richness as being due to competition and biogeographical patterns. A re-analysis of their data (Table 1) suggests that environmental parameters (especially rainfall) may also be involved in determining species richness. It is essential to consider the abiotic environmental (e.g. climatic) control over the niche dimensions of individual species and patterns of local species richness (alpha diversity) before attempting to develop general principles for diversity theory.

Cornell & Lawton (1992) have proposed that species richness is determined by local biotic interactions such as competition and predation, and regional or historical processes such as dispersal and speciation. Local communities may be saturated or unsaturated with respect to number of species depending on the relative importance of the two types of processes. It is implicitly assumed that occurrence of a species in a region is simply a function of dispersal and biotic processes. However, if species distribution is controlled by variations in climate or soils within a region, dispersal processes may have little relevance. Although part of the variation in local species richness may be related to the size of the species pool, high regional species richness in Cornell and Lawton's analysis could simply be a response to high environmental heterogeneity within a region. Any study on species pool should consider the filtering effect of the environment (Pärtel et al. 1996; Zobel 1997; Zobel et al. 1998).

In a recent experiment, Hector et al. (1999) found a consistent negative relationship between loss of plant richness and loss of above-ground productivity in eight European grasslands. However, they also found that sites with the lowest productivity were in both the north and the south of Europe, and presumably that low productivity values were caused by different mechanisms (e.g. low temperatures in the north and low water

Table 1. Mean number of woody species in the three groups of *Cistus ladanifer* shrublands (A, B and C with n = number of plots) proposed by Nuñez-Olivera et al. (1995), and mean values for annual rainfall (mm) and mean annual temperature (°C). Elaborated from the data in Nuñez-Olivera et al. (1995, Table 2 and Fig. 7). Significance: *** = $p < 0.0001$; ** = $p < 0.01$; ns = non-significant.

Group	n	Number of species	Rainfall mm	Temperature °C
A	14	8.86	681	16.4
B	14	5.57	583	16.2
C	17	5.35	607	15.9
Significance		***	**	ns

$\ln(\text{number of species}) = 1.024 + 0.01355 \times \text{rain}; n = 45; p < 0.05.$

availability in the south). The diversity-productivity relationship is important, especially for management and conservation purpose, but in order to understand the mechanisms controlling species richness there is a need to consider parameters that have direct impact on plant growth.

Below we review patterns of plant species richness found in different ecosystems in relation mainly to resources and direct environmental variables. We assume that environmental conditions act as a filter preventing species that belong to the regional flora but lack the traits required to survive in local conditions (Keddy 1992; Zobel 1997). We review the species richness pattern produced by this filtering effect, and emphasize the importance of multi-factor studies and the use of non-linear statistical techniques. The effect of disturbance is not reviewed extensively (see Huston 1994) and is only commented upon briefly.

Patterns of plant species richness

Nutrients

Many studies have found relationships between changes in species richness and a gradient of nutrient availability (e.g. Grime 1973; Huston 1980; Tilman 1982). The typical response observed has been a ‘humped-back curve’ (Grime 1979; Tilman 1982): species richness is low at low nutrient levels, increases to a peak at intermediate levels and declines more gradually at high nutrient levels. This pattern has been observed in a number of studies (e.g., Beadle 1966; Ashton 1977, 1989; Tilman 1982; Vermeer & Berendse 1983; Janssens et al. 1998; Lichter 1999). The humped pattern has been interpreted in different ways by different researchers (Grime 1979; Tilman 1982; Taylor et al. 1990; Huston & DeAngelis 1994). According to

Grime (1979), few species are able to tolerate extreme conditions of nutrient deficiency. As resources increase, more species can survive and hence species richness rises. At higher nutrient levels, a few highly competitive species become dominant, suppressing other species. This competitive exclusion causes a decline in species richness.

Calcium is often the most important exchangeable cation in the soil and can control the availability of other nutrients. Pausas (1994) found a humped response of species richness in relation to Ca-concentration in Pyrenean forests, while Peet & Christensen (1988) found a positive relationship in forests of the North Carolina Piedmont. However, Peet & Christensen (1988) studied a narrower range of soil calcium concentration than Pausas (1994). The different length of the gradient studied may explain the different pattern observed in many studies. For example, Tilman (1982) showed a decline in species richness in fertilized plots compared with control plots in the Park Grass experiment. We could assume that the study corresponds to the declining half of the nutrient gradient response. Decrease in species diversity following fertilization had earlier been reported for other plant communities (Milton 1947; Willis 1963; cited by Tilman 1983). Janssens et al. (1998) found that the highest number of species in European grasslands is found below the optimum soil phosphorus level for plant nutrition but at the optimum soil potassium level; beyond this optimum, species richness decreased. A less clear humped response is found for nitrogen for the same data set. The degree of correlation between the three soil nutrients is not mentioned nor is a statistical analysis presented. Huston (1980) found a decrease of tree species richness along a nutrient gradient in Costa Rican forests, while Tilman (1982) and Ashton (1989) showed a humped curve in tropical forests of Borneo. The different measures of nutrient availability used in the different studies make comparisons difficult; however, most grassland studies and most fertilization experiments showed a downward trend in species richness.

Many studies on species richness in relation to environment find a humped curve in relation to a productivity gradient where productivity is often imputed from the level of an environmental variable. Tilman & Pacala (1993) show eight humped curves along habitat productivity, three using soil nutrient measures, two using moisture measures and three based on biomass estimates. Only one from Beadle (1966) used a single soil nutrient. However, productivity is a biotic variable dependent on environment. Differential responses to different resource gradients (e.g. nutrient and moisture) can not be distinguished unless examined separately. Austin & Gaywood (1994) have pointed out that biom-

ass and productivity gradients carry the implicit assumption that a specific biomass level has the same effect, regardless of the environmental variable(s) determining the level. They suggest that experiments with two environmental gradients (e.g. Goldberg & Miller 1990) are required to test this assumption.

Austin & Smith (1989) proposed that there may be a second hump of high species richness and subsequent decline along the resource gradient as the nutrient concentration becomes toxic. Few studies have reported this bimodal response for plant communities (e.g. Meurk & Foggo 1988). The second potential hump may be confounded with the first if the data is plotted as a productivity gradient (Austin & Gaywood 1994), but supra-optimal levels are not usually reached in most studies. The lack of examples may be due to the lack of generality of this hypothesis, the lack of an appropriate statistical methodology to test it, or the lack of studies with sufficiently wide nutrient gradients; we cannot distinguish between these possibilities. pH is an environmental parameter related to nutrient and toxic element availability. Grime (1973) showed that the maximum number of species in an unmanaged grassland occurs at a soil pH of 6.1 - 6.5; species richness declined towards both acidic and alkaline soils. He concluded that few species are adapted nutritionally to exploit highly acidic or alkaline soils. Pausas (1994) showed a positive relationship between soil pH and moss species richness in the understory of *Pinus sylvestris* woodland; however, the range of pH studied was limited because the pine litter tends to be acidic, and so, the mosses in that study never grew on alkaline substrates. Pausas & Carreras (1995) found significantly more plant species in forests on bedrock with calcium carbonate (e.g., limestone) than in forests on non-carbonate bedrock (e.g., schists, granites, sandstone). Vetaas (1997) found that vascular plant richness, and also climber and herbaceous species richness, were positively related to pH in a study in the Himalayas. The length of the nutrient gradient, the correlation with other nutrients present and the influence of pH on nutrient availability may all influence the shape of the response of species richness to a nutrient. Gould & Walker (1999) found a unimodal relationship between species richness and pH for vascular species in arctic riverine communities – but not for lichens.

Braakhekke & Hooftman (1999), in an alternative approach while testing their 'resource balance hypothesis of plant species diversity', found maximum species richness at intermediate values of the nutrient ratios N/P, P/K and particularly K/N.

To summarize, there is a tendency for the response of species richness to a nutrient gradient to take a

humped shape or at least a unimodal envelope, but few examples show an unambiguous humped shape pattern (Oksanen 1996). In most fertilization treatments on grasslands, only a decrease in richness is observed.

Water

Different variables have been used as a surrogate for water availability (e.g., rainfall, topography, evapotranspiration, soil drainage index). As a resource, water, if appropriately measured, could generate a similar humped curve to that proposed for nutrients.

Richerson & Lum (1980) found a positive logarithmic relationship between Californian plant-species richness and rainfall, the environmental variable that accounted for the greatest variance in species richness in their study. Knight et al. (1982) and O'Brien (1993) found a positive correlation between mean annual rainfall and woody species richness in southern Africa. Gentry (1988) found an increase in neotropical plant species richness with precipitation up to about 4000 mm where species richness reaches an asymptote; however, he also noted that there were differences that could be explained by seasonality of rainfall and soil nutrients. He also reported very high richness for an aseasonal tropical system when approaching 1000 mm. Pausas (1994) used a moisture index based on soil and site parameters (topographic position, slope, soil texture, stoniness and soil depth) and found a humped curve of moss species richness. Margules et al. (1987) and Austin et al. (1996) found more *Eucalyptus* species at low annual rainfall levels in eastern Australia, but the pattern of variation in species richness also depended on the values of other variables like mean annual temperature and solar radiation. However, total tree species richness showed little relation to annual rainfall (Austin et al. 1996). Leathwick et al. (1998) used a water-balance model to estimate an annual root-zone moisture deficit and a minimum monthly mean humidity measure in a regression analysis of tree species richness patterns in New Zealand. They found humidity to be the second most important predictor after temperature.

In an extensive empirical analysis using several groups of plants and animals for the North American continent, Currie (1991) concluded that potential evapotranspiration (PET) is the best predictor of fauna species richness. For tree species, the only plant group considered, actual evapotranspiration (AET) was the best predictor of richness and showed a monotonically increasing relationship (Currie & Paquin 1987; Francis & Currie 1998). O'Brien (1993), using a similar approach in southern Africa, showed a quadratic response (humped curve) of woody species richness to minimum monthly PET.

However, in that study, the underlying factor could change from the effect of temperature (in the first part of the gradient) to the effect of water stress (in the second part of the gradient); a direct indicator of water availability would probably suggest a decrease in species richness with a decrease in water availability. The interpretation is further complicated by the fact that the simple linear correlation between species richness and precipitation is 0.776 and the correlation with minimum monthly actual evapotranspiration is 0.773; however, the role of actual evapotranspiration is not explored further in the paper (O'Brien 1993). Such correlations between variables are a consequence of physical relationships between the variables and the range of climatic conditions in the study region. O'Brien's relationship has recently been extrapolated world-wide (O'Brien 1998).

Similar problems of confounding variables have arisen in recent discussions of whether regional history or climatic differences between regions were more important in explaining species richness patterns (Latham & Ricklefs 1993; Francis & Currie 1998). The two hypotheses were equally plausible but could not be distinguished statistically because the predictors were correlated (Francis & Currie 1998). Several studies of tree species richness in relation to moisture components (Currie 1991; O'Brien 1993, 1998) have used geographical gridcell based counts of species richness. The large size of these grid cells (e.g. 2.5° lat. × 2.5° long, Currie 1991) ensures that internally many of the cells are highly environmentally heterogeneous.

Specht & Specht (1989, 1993) present evidence that the species richness of overstorey species (trees and shrubs taller than 2 - 3 m) is a function of an evaporative coefficient and of annual solar radiation, both of which are related to the shoot growth of the foliage canopy. These latter conclusions are based on various data sets from eastern Australia using simple linear regression.

There is a tendency towards increasing species richness with increasing water availability. However, as in the case of nutrient gradients, it is difficult to compare the species richness response to a moisture gradient in the different studies due to different measures of moisture availability, the different correlative analysis methods, and the different spatial scale used.

Light

Brown (1981), Wright (1983) and Currie (1991) have suggested that the capacity of the environment to support species is determined by the availability of energy. Knight et al. (1982) and Austin et al. (1996) found a negative relationship between tree species richness and annual incoming solar radiation in south-

ern Africa and south-eastern Australia, respectively (Fig. 1). However, in the Knight et al. (1982) study, the radiation is also negatively correlated with rainfall, and the decrease in richness could be explained by the decrease in rainfall. In New Zealand, total tree species richness increased with solar radiation, temperature, soil and atmospheric moisture (Leathwick et al. 1998). It is difficult to separate the effect of light from the other components in the water balance. Radiation has at least two effects on plants. It serves as a resource for photosynthesis, and shading (absorption) can reduce the availability of the resource to other plants. Light also supplies energy which results in evaporative demand and the potential for moisture stress. Various authors have combined radiation with precipitation to estimate evapotranspiration (see above; Currie & Paquin 1987; Currie 1991; O'Brien 1993; Specht & Specht 1989, 1993), or have used multiple regression techniques with several variables (Margules et al. 1987; Austin et al. 1996; Leathwick et al. 1998).

The energy hypothesis, where resources and heat are lumped together as a measure of available energy, has recently attracted attention (Wright 1983; Wylie & Currie 1993a,b). Species richness is expected to increase monotonically (if water is not limiting) with increasing available energy (e.g., potential evapotranspiration). In this context, the energy hypothesis has been considered an

extension of the species-area relationship (Wright 1983). However, this pattern is better fitted for animals (Wylie & Currie 1993a, b; Kerr & Currie 1998) than for plants (Currie & Paquin 1987; Currie 1991; Hoffman et al. 1994). The numbers of angiosperm species on 24 islands worldwide are better related to AET (related to water availability) times area than to PET (Wright 1983). Hoffman et al. (1994) found the opposite pattern to that of Currie and colleagues: plant species richness in a semi-arid ecosystem was negatively related to energy availability (PET), because the underlying factor was the reduction of water availability. Although some of these patterns are at larger scales than most of the studies reviewed here, they show the importance of considering both energy and water availability when studying patterns of plant richness.

Species richness tends to increase with radiation; however, many studies do not show this trend probably due to the interaction with other parameters. The increase in radiation is often associated with a reduction in water availability.

Temperature

Richerson & Lum (1980) found that plant species richness in California shows a negative response along a temperature gradient. Knight et al. (1982) found a positive linear relationship between South African tree species diversity and temperature. Austin et al. (1996) showed an increase in the richness of tree species, *Eucalyptus* species (see also Margules et al. 1987 and Austin 1987), and rainforest species with increasing temperature. However, they also showed that the pattern of increase depends on other environmental variables such as rainfall. Both Austin et al. (1996) and Leathwick et al. (1998) found that temperature was the environmental predictor that explained the most variance in total tree species, rainforest species (Austin et al. 1996), conifer species (Leathwick et al. 1998), and eucalypt species (Austin et al. 1996). The relative importance of the different environmental gradients and their interaction in determining the species richness of different growth forms needs to be examined further.

Several authors have used altitude (an indirect environmental variable) as a surrogate variable for temperature; however, this parameter is complex and may covary with other climatic factors (e.g., rainfall, cloud cover, wind) and with the degree of isolation on the top of mountains. A negative relationship between altitude and woody species richness has been reported in different ecosystems (e.g., in coniferous forests by Pausas 1994 and Rey Benayas 1995; in Alaska, Tennessee and Costa Rica reviewed by Stevens 1992).

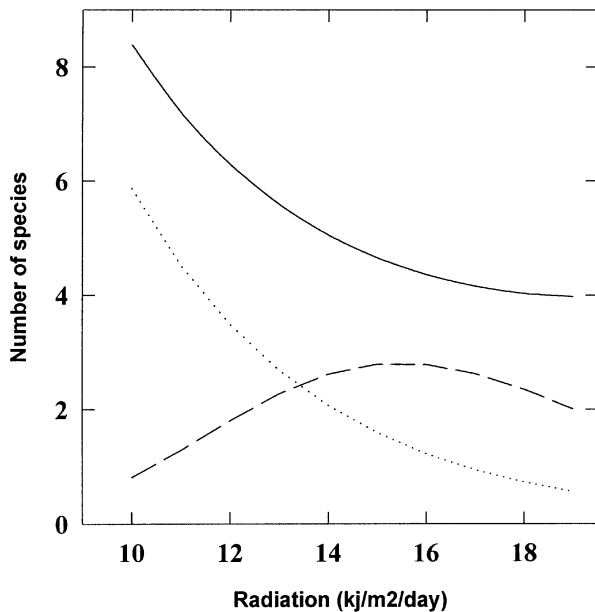


Fig. 1. Pattern of total tree species richness (solid line), eucalypt (sclerophyll) species richness (dashed line) and rainforest (broadleaf evergreen) species richness (dotted line) in relation to mean monthly solar radiation ($\text{kJ m}^{-2} \text{day}^{-1}$) in New South Wales, Australia. Statistical models elaborated by Austin et al. (1996).

Many studies have found a general increase in richness with temperature. However, the trend may be different when water is limiting; so both parameters need to be considered simultaneously.

Environmental heterogeneity

The effect of environmental heterogeneity is highly scale-dependent. The existence of environmental or resource heterogeneity may create high niche diversity and hence allow species to coexist at a large spatial scale. At the local scale, environmental and resource heterogeneity may explain part of the variability in species richness, but it may be secondary in importance to resource and direct variables. For example, in monospecific woodlands of the Pyrenees, understory shrub species richness showed a significant positive relationship with overstory heterogeneity (Pausas 1994). This heterogeneity gradient variable entered the model (using a forward stepwise procedure) after the environmental variables, suggesting that woody species richness is more related to the environment than to spatial heterogeneity. Richerson & Lum (1980) also showed a positive relationship between species richness in California and spatial (topographic) heterogeneity, and in that study, environmental variables were also more important than heterogeneity variables. The relation between species richness and within-gap heterogeneity has been reported elsewhere (Orians 1982; Brandani et al. 1987). At the large scale, Ricklefs (1977) suggested that the increase in plant diversity at low latitudes may be due to the greater heterogeneity of environmental conditions (latitudinal gradients in physical factors interacting with openings in the forest canopies). Analyses of environmental heterogeneity should include the actual environmental variables as well as an indicator of in-site variability in order to separate the two possibilities (Austin 1999), and the relative importance of each will depend on their range. Studies using arbitrary grid cells at a geographical scale (e.g. Harrison et al. 1992) should consider both within- and between-grid cell environmental heterogeneity (e.g. Palmer & Dixon 1990). Even for broad-scale regional studies, Latham & Ricklefs (1993) argue that small plot sizes should be used because it is only at that scale that species interactions contribute to determining species richness.

Climatic variability may be predictable (e.g. seasons) or unpredictable. Unpredictable (stochastic) climatic variation may be regarded as a form of disturbance. The presence of the seasons of the year enables different species with different physiological niches to coexist. A typical example can be found in hardwood

forests where vernal species flower before the tree canopy leaves appear. Another example is the different growing seasons of C3 (cool-season) and C4 (warm-season) grasses which permit these two types of species to coexist on the Colorado steppe (Monson et al. 1983). Scheiner & Rey Benayas (1994) suggested that climatic variability may be an important factor in explaining species diversity at the landscape level in their study. However, they did not test variations within landscapes (e.g., variations in altitude and topographic position). Landscape heterogeneity (microsite diversity) may well be a very important factor for explaining species diversity at the level reported by Scheiner & Rey Benayas (1994).

Environmental and resource parameters may determine species occurrence and their growth and competitive interactions, while parameters related to environmental heterogeneity (including disturbance, see below) tend to increase coexistence and maintain high richness. It is essential to consider both the level of the environmental variable and its heterogeneity simultaneously in order to distinguish between the two types of parameters.

Disturbance

Disturbance-, resource- and direct environmental gradients constitute three types of gradients that determine plant growth and survival. The intermediate disturbance hypothesis (Loucks 1970; Grime 1973; Connell 1978; Huston 1979, 1994; Tilman, 1983) suggests that species richness reaches a maximum at some 'intermediate' level of disturbance. Zeevalking & Fresco (1979) and Lubchenco (1978), studying grazing intensity gradients produced by rabbits and periwinkles, respectively, and Wilson & Keddy (1988), studying a wave-exposure gradient on a shoreline, provide classical examples that support the intermediate disturbance hypothesis. During & Willems (1984) provide experimental support on chalk grasslands. Huston (1994) gives details of this hypothesis and its consequences, and demonstrates its applicability with numerous different examples. On the other hand, Hubbell et al. (1999) recently found little evidence of the intermediate disturbance hypothesis when studying a large data set in a tropical rainforest. Hiura (1995) found a humped disturbance response in Japanese beech forests, but he also found that temperature was a more important factor in predicting forest species diversity. Vetaas (1997) examined the impact of canopy disturbance on species richness in an oak forest and the results provide support for the intermediate disturbance hypothesis while controlling for other environmental variables.

Without a definition of intermediate disturbance that is independent of its effects, the argument is circular. Currently, any peak on richness is assumed to be in the intermediate level of the gradient; thus, the intermediate hypothesis fits well. Furthermore, the increase in species richness after a disturbance is related to a transient increase in the availability of resources (e.g. Grace & Pugsek 1997), but different mechanisms may produce the observed pattern. Collins et al. (1995) found a significant monotonic decline in species diversity with increasing frequency in experimental disturbance. However, they also reported that richness reached a maximum at an intermediate time interval since the last disturbance. They suggested that a discrete disturbance may be an extinction-causing event whereas recovery following disturbance is a balance between immigration and extinction (Loreau & Mouquet 1999). Glenn & Collins (1992) showed the importance of the scale of disturbance in the differential effect on immigration and extinction rates.

The important point is that different processes are often confounded under the concept of disturbance (frequency, intensity, season and extent), and thus generalizations are difficult. Different disturbance regimes or different moments after disturbance may underlie different processes, with different resource limitations. For instance, the humped response could be due to the switch from the limitation of one resource (e.g. light) to the limitation of another (e.g. water) at different stages of the vegetation dynamics. The richness peak may occur when no resource is limiting (Lichter 1999). To better understand the species richness patterns, the different processes associated with disturbance should be disaggregated.

Potential approaches

Brown (1981) suggested that “a general equilibrium theory of diversity must contain two kinds of constraints, capacity rules and allocation rules”. He proposed that capacity rules define the ability of sites to support life, and are related to the environmental characteristics of the sites. Allocation rules determine how available energy is apportioned among species. Such rules will depend on biotic processes such as competition and predation, and on the physiological and morphological properties that allow the species to exist in particular environmental conditions. Differences in the environmental adaptability of different species groups may explain the differential patterns of richness in relation to environment (Cody 1991; Currie 1991). A comprehensive analysis incorporating different environmental gradients, growth forms and biotic processes has yet to be done.

We argue that there is a need to emphasise the following approaches when studying the species richness-environment relationship: (a) choose the appropriate variables incorporating parameters related to resources availability and to direct environmental factors; (b) study multidimensional gradients using non-linear regression techniques; and (c) separate species richness into the richness of the different functional types. Below, some examples are reviewed to show the importance of these aspects in studying plant species richness.

Appropriate variables

We assume that resource availability plus the response to direct environmental variables (i.e., parameters that have a direct physiological impact on plant growth or on resource availability but are not consumed, e.g. temperature; Austin 1980) are the primary causes of the observed patterns on plant species richness at local scale, and that disturbance and dispersal are secondarily important. Another group of variables that has often been used to explain plant species richness include the indirect environmental variables (i.e., variables that, in themselves, do not have any impact on plants or resource availability but may be correlated with one or more direct variables). Examples of this type that have been applied to studies on plant species richness are altitude, latitude or distance from the coast (e.g. Glenn-Lewin 1977; Brown & Gipson 1983; Silvertown 1985; Currie 1991; Stevens 1989, 1992; Pausas & Sáez 2000). Patterns of species richness along these gradients do not have any direct causal relationship to plant growth.

Numerous different potential causal variables may be correlated with the same indirect gradient, completely precluding any mechanistic interpretation, and therefore, little advance in ecological understanding can be made by studying such variables. Similar arguments can be applied to productivity gradients. Several studies have concentrated on species richness patterns along productivity gradients (Moore & Keddy 1989; Grime 1979; Tilman & Pacala 1993; Hector et al. 1999). However, different combinations of environmental parameters may lead to similar productivity values (Austin & Gaywood 1994). Furthermore, inappropriate data analysis is producing misinterpretations in the diversity-productivity experiments (Garnier et al. 1997). Productivity depends on the environment (as we hypothesise for species richness), and so it should not be used as an independent variable for predicting vegetation attributes (such as species richness) if primary factors are the main interest.

Multidimensional gradients

In many of the studies only single environmental gradients have been considered or, where multiple regression techniques have been used, only linear additive models with no interaction terms have been fitted. No strong ecological conclusion can be drawn from testing linear regressions only; non-linear relationships are too common in ecology to be ignored. Few studies (e.g. Margules et al. 1987; Currie 1991; Pausas 1994; Austin et al. 1996) have considered how species richness varies in an environmental space defined by more than one axis of environmental variation and tested for different possible response shapes. Species that seem to coexist (overlap) when examining one or two gradients (eg. climatic gradients) may be segregated by a third gradient (e.g. soil nutrients). Austin et al. (1996) explained tree species richness in NSW by a multi-factor model of seven environmental variables (temperature, topography, rainfall, radiation, seasonality of rainfall, soil nutrients and bedrock type) plus plot size. They found that both eucalypt species richness and rainforest species richness were higher at high temperatures and at high or intermediate rainfalls. However, although these species appeared overlapping in the environmental space defined by temperature and rainfall, they were in fact clearly segregated by topography. Similar conclusions were reached by Leathwick et al. (1998) using six environmental parameters to predict tree species richness in New Zealand.

Most fertilization experiments or nutrient gradient studies do not take into account the availability of water or light, and at intermediate nutrient levels the limiting factor may switch from nutrient to water or light; as one resource limitation is reduced, another resource may become limiting. This change in resource stress may produce the humped response. Eek & Zobel (1997) found that additional illumination in an enrichment experiment mitigates the effect of fertilization, indicating that observed changes in biomass were due to increased light competition (and not root competition). Goldberg & Miller (1990) added water and/or one of three nutrients (nitrogen, phosphorus, and potassium) to a first-year old-field community dominated by annuals. Watering increased productivity (total above-ground biomass), but had no effect on species richness. Nitrogen produced a smaller increase in biomass, but reduced species richness considerably compared to the controls. Other nutrient additions had little effect. Annuals accounted for more than 90% of the above-ground biomass in the community, and one annual species *Ambrosia artemisiifolia*, was responsible for the watering response. Experiments of this kind with a greater range of functional types including perennials are needed.

Margules et al. (1987) and Austin et al. (1996) found that tree species richness showed a complex dependency on temperature, rainfall, and radiation (due to aspect) requiring the use of an interaction term between rainfall and temperature. For a given aspect, the shape of the *Eucalyptus* species richness curve against the mean annual temperature depended on the mean annual rainfall. At low rainfall levels, the peak of species richness was at high temperatures giving a skewed curve, whereas at intermediate levels of rainfall the peak of richness was at an intermediate temperature.

Functional types

Several interpretations of species richness patterns are based on competitive interactions. For example, the humped curve of species richness along a resource gradient is based on competitive exclusion at high resource levels (Grime 1979). In a similar way, the intermediate disturbance hypothesis is based on competitive interactions because disturbance reduces competitive exclusion by reducing the dominant competitor and allowing the growth of inferior competitors.

Because functional types are defined as groups of species that use the same resources and respond to the environment in a similar way, competition would be expected to be more intense within the same functional type than between different functional types. Although exceptions to this assumption have been observed (tree/grass interactions), patterns of species richness might be more interpretable by considering both the species richness of the different functional types and total species richness. Different functional types are adapted to different environmental conditions in such a way that competitive interactions are minimized. Spatial heterogeneity may well be related to the number of functional types because of the increase in microsite diversity. The factors influencing the number of functional types may be very different from those influencing the number of species within a functional type (Moore & Keddy 1989; Nilsson et al. 1989; Cody 1991; Huston 1994). Few data are available to test this hypothesis. At 'equilibrium', species should differ sufficiently in order to coexist (by niche, life form or phenology differentiation, Bengtsson et al. 1994); however, the magnitude of this difference is unknown.

Environment can be interpreted as a filter removing species that lack traits for persisting under a particular set of conditions (Keddy 1992). In this context, Díaz et al. (1998) provide an example of a significant relation between climatic factors and several plant traits across a wide spectra of plant growth forms in a climatic gradient in central-western Argentina. This relation

between the environment and the key functional traits is the basis of the environment-based functional types. Disturbance can be considered a second filter, and several traits have been recognized to be of great importance for prevailing under a particular disturbance regime (Noble & Slatyer 1980; Pausas 1999 a, b).

Pausas & Carreras (1995) found that of all the variables studied, only bedrock type was significantly related to species richness in Pyrenean forests. However, when they studied the species richness of different life forms, temperature and moisture also became significant (i.e., woody species richness showed a positive relationship with increasing temperature whereas non-graminoid herbs showed a negative relationship). The increase in predictability achieved by subdividing total species richness into different life forms has also been observed by Nilsson et al. (1989), Pausas (1994), Austin et al. (1996) and Leathwick et al. (1998). Although life forms are often a crude division of functional types, it has often been suggested as a first approximation for functional-type subdivision (Lavorel et al. 1997).

Grubb (1987) and Goodland (1971) found a positive relationship between tree species richness and soil fertility, and a negative relationship between herb species richness and soil fertility. Grubb (1987) proposed that these relationships could be explained by the fact that herbs have more potential for competitive exclusion and establishment in gaps than trees. Wright (1992) found a positive relationship between soil fertility and herbs or understory shrubs richness but did not find a robust relationship with tree species richness. He suggested that differences in the rooting depths of herbs, shrubs and trees could explain the different patterns of species richness between life forms in relation to drought. Moore & Keddy (1989) also found different patterns of species richness with different species types while studying the species richness-biomass relationship.

Austin et al. (1996) found that tree species richness is only slightly (positively) related to soil nutrients (Fig. 2a). However, when the total tree species is split into species groups, each of these groups presents a different and strong pattern (Fig. 2). The humped pattern appears only for the eucalypt *Monocalyptus* subgenus. The different patterns of the different subgenera of *Eucalyptus* suggest that they may be related to two functional types. This suggestion agrees with the experimental evidence reviewed by Noble (1989), showing different behaviour patterns for different eucalypt subgenera. Different patterns of species richness depending on species group were also observed for other variables such as incoming solar radiation (Fig. 1; for details see Austin et al. 1996). Leathwick et al. (1998)

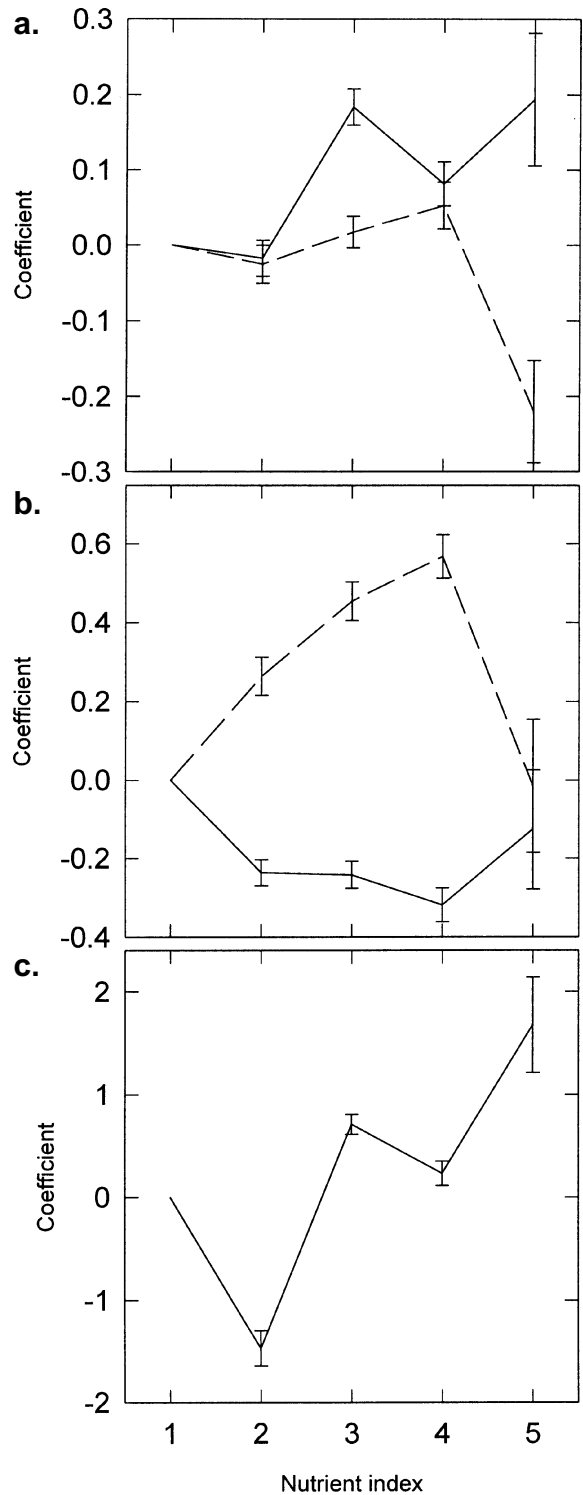


Fig. 2. Pattern of tree species richness along a nutrient gradient for different functional groups in New South Wales, Australia. a) Total tree species (solid line) and eucalypt (sclerophyll) species (dotted line); b) eucalypt *Monocalyptus* (solid line) and *Symphyomyrtus* (dotted line) subgenera; and c) rainforest (broad-leaved evergreen) species. The pattern is expressed by the coefficients in the regression (derived from Austin et al. 1996). Vertical lines refer to the standard error.

also found distinctly different responses for different types of trees in New Zealand. Richness of broad-leaved angiosperm trees increased with solar radiation, temperature and moisture, while conifer species occurred maximally with low insolation, low moisture deficit and high humidity, intermediate temperatures and impeded drainage. Maximum *Nothofagus* species richness occurred on sites with high insolation, low temperatures, high soil moisture but low atmospheric moisture.

Pausas et al. (1999) showed that species-area curves in Mediterranean post-fire shrublands follow the classic power function (linear log-log relationship) for nested plots (Preston 1962; Rosenzweig 1995). However, when different growth forms were considered, different patterns were elucidated: woody species more aptly followed a semi-log relationship, while herbaceous species fitted well in a log-log relationship. That is, herbaceous species showed a higher rate of species addition at the large scale than woody species.

Recently, open-top chamber and FACE experiments in natural pastures have suggested different responses to CO₂ enrichment between grasses (monocots) and forbs (Lüscher 1996; Poorter et al. 1996; Potvin & Vasseur 1997); that is, grasses were reduced and forbs were favoured. Other studies showed different behaviour between C3 and C4 grasses (Owensby 1996; Poorter et al. 1996). In contrast to nutrient enrichment, CO₂ enrichment increased diversity and decreased dominance in Quebec grasslands (Potvin & Vasseur 1997).

Concluding remarks

There are a variety of patterns of species richness along environmental gradients reported in the literature. Part of this variety may be explained by the different types and lengths of gradients studied, particularly when using variables with no direct biological meaning, and by the fact that most studies search for the pattern of one environmental parameter at a time without considering other parameters simultaneously. In general, most studies show a tendency towards an increase in species richness with temperature and water availability, as well as with increased environmental heterogeneity. Also, most nutrient enrichment studies suggest a decrease in species richness. However, different responses may be observed due to interactions between parameters, including disturbance factors, and to switches in resource limitation along the gradient. Single gradients may reflect limitations on different resources at each end of the gradient, and hump-shaped responses may arise as a consequence of these shifts.

To advance in the understanding of species richness patterns along environmental gradients, we emphasize

the importance of the following points:

1. It is important to choose appropriate variables, that is, variables reflecting the amount of resources or resource availability, and environmental variables that have direct physiological impact on plant growth.

2. We suggest studying multidimensional gradients of resource and environmental parameters, and using non-linear regression techniques and interactions. Single-gradient analyses can easily be confused with other variables, and non-linear patterns are too common in nature to be omitted in the analysis of species richness. It is also important to study long environmental gradients in order to define the response shape of species richness unambiguously.

3. When studies are carried out using arbitrary sampling units (e.g., geographical grid systems), variables incorporating environmental heterogeneity should be considered.

4. Patterns of species richness may be clarified if disaggregated into different functional types. We suggest studying the pattern of species richness for each functional type independently but on the same sites.

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