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.

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, preferring 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(number of species) = 1.024 + 0.01355 × 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.

Introduction

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 biomass 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 humpshaped 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 rootzone 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.