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Review

Variation of plant species richness at different spatial scales

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Abstract

It is now realized that the variation in species richness is influenced by spatial and temporal scales. Pattern and scale are a central focus in ecology and biogeography. The species richness relationship depends on the scale of study and their correlated factors. The broad objective of this review is to elucidate how different scales are correlated with different explanatory variables to generate patterns of species richness. Addressing the problem of scale has both fundamental and applied importance in understanding variation in species richness along gradients. The understanding of pattern, its causes, and consequences is central to our understanding of processes such as succession, community development, and the spread and persistence of species. According to the hierarchical theory of species diversity there are mainly three categories of scales: local, landscape and regional. The local species richness or α-diversity is the diversity of individual stands. The β-diversity or species change is turnover between two elevational bands or between two plots or two sites. The regional or γ-diversity is the total richness of whole mountains or study systems and it has a combined influence from α- and β-diversity. The local species richness is affected by both local-scale processes (e.g., internal interactions) and broad-scale processes (e.g., evolutionary). Different explanatory variables according to the scales of study are necessary to explain variation at different spatial scales. Local factors (e.g., disturbance, grazing and tree cover) have been used to detect variation at a local scale. Generally, topographical factors are used to detect variation in species richness at a landscape scale; whereas climate, water-energy dynamics and historical processes are used to detect variation at a regional scale. However, it is not easy to separate strictly one scale from other because there is no clear boundary between them. The study of the whole elevation gradient from tropical to alpine zone or long latitude is a broad-scale study. The intermediate scale is a study on a local mountain, which covers the subtropical to warm temperate zones. To explain patterns of species richness, a pluralistic body of hypotheses, which incorporates historical, biological and climatic factors, is needed. This is depicted by the strong relationship between climate, biological interactions, and historical processes in influencing variation in species richness at different spatial scales.

Key-words: explanatory variables, hard boundaries, productivity, spatial scale, species richness, temporal scale.

Introduction

It has long been observed that species richness varies over a range of temporal and spatial scales (e.g., von Humboldt 1855; Wallace 1878; Simpson 1964; MacArthur and Wilson, 1967; Adams and Woodward 1989; Moore and Keddy 1989; Huston 1994; Brown and Lomolino 1998; Bhattarai 2003; Baniya *et al*. 2010; Gelashe 2017). These observations raise the obvious question in ecology and biogeography: Why are there many species in some places and few in others? These variations have been under intensive investigation by ecologists and biogeographers over the last two centuries (e.g., Dobzhansky 1950; Pianka 1966; Odland and Birks 1999; Whittaker *et al.* 2001; Qian *et al*. 2003; Bhattarai *et al*. 2004a; Pan *et al*. 2016). This is a complex subject of study and many hypotheses have been proposed and discussed to account for this variation. This complexity is reflected by more than 120 hypotheses compiled by Palmer (1994). Early explanations for the variation in species richness primarily considered as historical phenomena (Schluter and Ricklefs 1993). Such explanations were presented before ecology had emerged as a scientific discipline. The "origin of species" theory of Darwin (1859) revolutionized our understanding of the history of the earth and distributions of its organisms. The views of many naturalists changed and they directed their thinking towards ecological and evolutionary processes to explain the variation in species richness at different spatial and temporal scales.

The rise of community ecology in early 1960s further promoted our understanding and changed traditional thinking on the variation in species richness. Ecologists attempted to explain variation in species richness by ecological interactions (Schluter and Ricklefs 1993). Following the development of theories for population growth and interactions by Lotka (1932), Volterra (1926) and Gause (1934), it was realized that species that closely matched ecologically would compete strongly for resources and hence could not coexist. Hutchinson (1957) developed the concept of the multidimensional ecological niche to conceptualize how environmental conditions could limit the abundance and distribution of organisms. These predictions from community ecology were tested by field experiments to investigate the role of competition

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and other interactions in structuring natural populations (e.g., Connell 1961a, 1961b, 1983; Schoener 1983).

Three main fields of ecology – classical biogeography, community ecology, and population ecology – are all concerned in part with comparative species richness. Each of these three approaches has its own viewpoint and approach to interpreting the phenomenon of species richness (Schluter and Ricklefs 1993). Classical biogeographers are more concerned with the relationship of regional faunas and floras (e.g., Cain 1944; Udvardy 1969). Community ecologists emphasize the importance of dissimilarity or ecological distance between community samples (e.g., Goodall 1952). Theoretical population ecologists are more concerned with the role of species interactions (e.g., Hutchinson 1957, 1959). By 1967, MacArthur and Levins had formalized and strengthened the niche concept to explain the coexistence of species within a community. Through the development of community theory, MacArthur (1969) and other ecologists became aware about the importance of all the determinants emphasized in these approaches in influencing species richness along gradients in time and space. They recognized that at the local scale, species richness is likely to be constrained by ecological interactions, whereas species richness at a broad, regional scale may be influenced by historical process and events.

The work of Whittaker (1956, 1960, 1963, 1966, 1967, 1972, 1977) and Whittaker and Niering (1965, 1975) contributed important answers to several ecological issues concerning the distribution and composition of species along ecological gradients. Through the development of the theory of gradient analysis, interpretations of the observed patterns by ecologists and biogeographers were based on underlying biological, climatic, and historical factors. They observed patterns among many organisms in both the marine and the terrestrial realms (Huston 1994). Many explanatory variables, such as biomass (Grime 1973a; Gough *et al*. 1994), elevation (Terborgh 1977), precipitation (Brown and Davidson 1977), disturbance (Connell 1978), dispersal (Shmida and Wilson 1985), geographical range size (Stevens 1989, 1992), hard boundaries (Colwell and Hurtt 1994), species pool (Zobel 1992; Eriksson 1993; Päertel *et al*. 1996), and water-energy dynamics (O'Brien 1998; Bhattarai 2003) were tested for different groups of animals and plants to find causal relationships. From these studies a common consensus emerged among ecologists and biogeographers, namely that both latitudinal and elevational gradients are governed by the same underlying controls (Brown and Gibson 1983; Begon *et al*. 1990; Rohde 1992; Rahbek 1995). The elevational gradient in species richness is often claimed to mirror the latitudinal gradient (Stevens 1992). Although the elevational gradient in species richness has long been obvious to ecologists and biogeographers, it is not as well documented quantitatively as the latitudinal gradient (Brown and Lomolino 1998).

Elevational gradients can serve as experimental systems to investigate and test several ecological and biogeographical hypotheses (Körner 2000). Therefore, the elevation gradient is now receiving attention from ecologists and biogeographers in an attempt to document the patterns and to find underlying causes (e.g., Odland and Birks 1999; Heaney 2001; Grytnes 2003a). Ecologists and biogeographers have begun to re-evaluate the nature and generality of the elevational gradient in species richness, to clarify its conceptual framework, and to set the agenda for future research (Rahbek 1995, 1997; Lomolino 2001). We are now experiencing a resurgence in mountain research to find a more detailed understanding and to develop more effective strategies for conserving biological diversity. In order to gain a more comprehensive understanding about variation in species richness, Lomolino (2001) has called for a rigorous test of patterns for different groups of taxa and an analysis of climatic variables that are directly associated with a casual explanation for the observed patterns. Such tests and analyses can contribute to the development of a more general theory of species diversity. Consequently, such tests might reduce the many redundant, vague, or un-testable hypotheses and help focus on a reduced subset of hypotheses (Bhattarai 2003; Bhattarai *et al*. 2004a).

It is now realized that the variation in species richness is influenced by spatial and temporal scales (e.g., Palmer and White 1994; Rosenzweig 1995; Gaston 1996; Lomolino 2000). Despite this, there is still a weakness in the ecological literature to relate species to explanatory variables according to particular scales of analysis but all under the general heading of diversity (Whittaker *et al*. 2001). Unambiguous demonstrations of causality can only be attained by testing variables associated with different spatial scales along the gradient.

The Himalayas have the highest mountains with the longest bio-climatic gradient in the world (Bhattarai 2003). Within *ca.* 150-200 km in a north-south transect one can find a gradient from tropical or sub-tropical zones to permanent snow and ice (Dobremez 1976; Bhattarai *et al*. 2004a). Large environmental variation within small geographical areas makes the elevational gradient a unique situation to study species richness. Therefore, Himalayas have become one of the unique place to test many biogeographical hypotheses. The Himalayas have major hotspots of biodiversity with many endemic species (Singh 2001). The biodiversity is vulnerable because of the high human population density, increasing tourism, and global warming (Shrestha and Joshi 1996; Chaudhary 1999). If no conservation measures are undertaken, there is a serious risk of species extinction. Before developing conservation measures, it is essential to understand the processes creating and maintaining the patterns of species richness. If we can understand the factors controlling the spatial patterns, it would be possible to predict how patterns might change over time under the influence of these controlling factors. Therefore, the detection of patterns and understanding the underlying causal mechanisms behind the patterns are important for the future management and conservation of biodiversity.

Despite years of study at different spatial scales and intense theoretical interests, there are still many unanswered questions in ecology and biogeography. The mechanisms which connect climate and vegetation are poorly understood (Woodward 1987). The variation in species richness along environmental gradients may vary according to plant life-forms due to different eco-physiological processes and climatic tolerances (Bhattarai 2003; Bhattarai and Vetaas 2003). The literature dealing with this issue is sparse. Water-energy dynamics parsimoniously explains variation in woody species richness along the macro-scale climatic gradient, along the latitudinal gradient as well as along the altitudinal gradient (O'Brien 1993; Bhattarai *et al*. 2004a). The same climatic factors may control species richness differently at different ends. This has not, however, been demonstrated clearly. The well-studied hump-shaped relationship between herbaceous species richness and biomass is necessary to understand whether this relationship depends upon the environmental gradient or on internal interactions. Thus, the broad objective of this review is to elucidate how different scales are correlated with different explanatory variables to generate patterns of species richness.

Species Richness and Scale

Scale is the unit of space or time over which signals are integrated to convey a message (Allen and Starr 1982). It gives a rough indication rather than a precise figure (Blöschl and Sivapalan 1995). Pattern and scale are a central focus in ecology and biogeography (Levin 1992) and are closely inter-related (Hutchinson 1953). The species richness relationship depends on the scale of study (Whittaker *et al*. 2001). Addressing the problem of scale has both fundamental and applied importance in understanding variation in species richness along gradients. The understanding of pattern, its causes, and its consequences is central to our understanding of processes such as succession, community development, and the spread and persistence of species (Levin 1992). In the modern ecological literature, awareness of scale has greatly increased (e.g., Levin 1992; Palmer and White 1994; Weiher 1999; Mittelbach *et al*. 2001; Gering and Thomas 2002; Koleff and Gaston 2002; Grytnes 2002).

There are three aspects of scale in ecology: spatial, temporal, and organizational (Levin 1992). Species richness patterns, which are influenced by scale, are associated with the spatial extent and temporal duration (Figure 1). Different evolutionary forces act on these different scales (Levin 1992). In most ecological studies, the temporal scale is not generally taken into account directly (with the exception of paleoecology) when examining the distribution of species along gradient. In general, systems are organized into a hierarchy of spatial and temporal scales, and hierarchical theory predicts that the dynamics of a system at a lower scale affects the dynamics of systems at higher levels and vice versa (Allen and Starr 1982; O'Neill 1989).

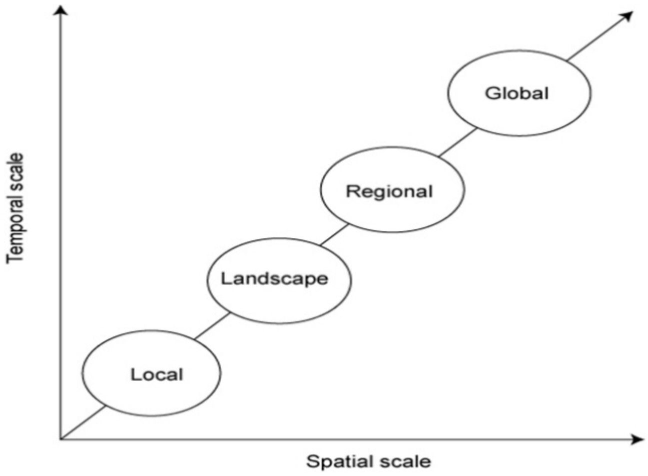

Figure 1. The relationship between spatial scale and temporal scale, and their corresponding patterns

The spatial scale is divided into three components: sample size (size of individual quadrats or grain, or focus), extent of study (geographical distance covered by the study area), and the number of sample units or intensity (Palmer and White 1994). Thus, when saying that patterns are scale-dependent means the degree to which the ecological phenomenon varies as a function of grain, extent, and number of samples. There is a strong relationship between grain size and study area. Small grain size is used to detect variation at a local scale and large grain size is used to detect that at a regional or coarse scale. Mittelbach *et al*. (2001) from a metanalysis of 171 published studies found a positive relationship ($r = 0.6$) between grain size and study area. Grain size is also related to the size of organisms (e.g., trees or herbs, Bhattarai 2003; for Lichens see Baniya *et al*. 2010). Palmer and White (1994) have demonstrated that variation of species richness in space is influenced by grain, extent, and number of samples. Therefore, it is argued that the selection of appropriate sample size, extent, and intensity is important to detect the relevant patterns along gradients (Bhattarai 2003).

The measurement of species diversity requires a clear and unambiguous term to represent diversity or richness. Different terms have been used to represent diversity (Whittaker *et al.* 2001). The oldest and most fundamental term is species number. As a term, species number proved unpopular, probably because it implies that the number of species in community can actually be determined. McIntosh (1967) suggested the alternative term of species richness to indicate the number of species in a community. Diversity, in general, has two components: species richness and evenness of the distribution of numbers among species. The term species richness indicates the number of species in a sample (Whittaker *et al.* 2001), and it is perhaps the least ambiguous of all the terms used in diversity research (Peet 1974). Some authors have adopted the term species density for the number of species sampled in a standardized sample unit (e.g., Lomolino 2001) but others have retained the term richness even in a standardized sample plot (e.g., Grytnes 2000). Different indices of diversity have been used by different authors creating considerable confusion in the ecological literature (Hurlbert 1971). However, the use of species richness is the most interpretable, fundamental measurement of community and regional diversity (Gotelli and Colwell 2001). It is a good surrogate as it acts as an integrator of many facets biodiversity patterns, it is applicable to both standardized and non-standardized plots, it is frequently measurable, and it is intuitive to all levels of readers. Gaston and Spicer (1998) called "species richness as a common currency". Species richness is defined as: the number of species present within smaller unit area at fine scale (e.g., 1 × 1 m plot, Bhattarai *et al*. 2004b), the number of species present in each 50 × 20 m plot or meso-scale (Bhattarai 2003) or the number of species present in each 100 m elevation band (Bhattarai *et al*. 2004a).

In addition to the various concepts of diversity, concepts of scale and space also vary. Whittaker (1960) proposed various scale descriptors represented by the Greek letters α, β, γ, δ and ε. The δ and ε components are not commonly discussed in the literature. According to the hierarchical theory of species diversity (Whittaker *et al.* 2001), there are mainly three categories of scales: local, landscape and regional. The local species richness or α-diversity is the diversity of individual stands, namely 1 × 1 m plots (Bhattarai *et al*. 2004b), 50 × 20 m plots (Bhattarai 2003), or in each 100-m elevation band (Bhattarai and Vetaas 2006). The β-diversity or species change is turnover between two elevational bands (e.g., Bhattarai *et al*. 2004a) or between two plots or two sites. The regional or γ-diversity is the total richness of whole mountains or study systems and it has a combined influence from α- and β-diversity (Brown and Lomolino 1998).

Some authors (e.g., Mittelbach *et al.* 2001) have categorized the scale according to geographical distance, local (0-20 km), landscape (20-200), regional (200-4000 km), and continental to global (>4000 km). The measurable spatial heterogeneity in climate can occur over distances of at least 100 km (cf. O'Brien 1998). However, along the elevation gradient, measurable environmental variation can be detected at the 100 m distance between upper and lower elevation band (Bhattarai *et al*. 2004a). Thus, elevated mountains can be considered as experimental site to various biogeographical hypothesis and principles.

The local species richness is affected by both local-scale processes (e.g., internal interactions) and broad-scale processes (e.g., evolutionary). Different explanatory variables according to the scales of study are necessary to explain variation at different spatial scales (Whittaker *et al.* 2001). Local factors (e.g., disturbance, grazing and tree cover) have been used to detect variation at a local scale (e.g., Vetaas 1997). Generally, topographical factors are used to detect variation in species richness at a landscape scale; whereas climate, water-energy dynamics and historical processes are used to detect variation at a regional scale (O'Brien 1998; Whittaker *et al*. 2001; Pan *et al*. 2016). Thus, if one moves from one scale to another, some information will be retained and some will be lost.

However, it is not easy to separate strictly one scale from other because there is no clear boundary between them. A broad-scale study by one investigator can be a meso-scale study to others and vice versa. The study of the whole elevation gradient from tropical to alpine zone or long latitude is a broad-scale study (Bhattarai 2003; O'Brien 1998). The intermediate scale is a study on a local mountain, which covers the subtropical to warm temperate zones (Bhattarai 2003). The study within a grassland community is a fine-scale study (Bhattarai *et al*. 2004b).

BROAD-SCALE STUDIES AND THEIR EXPLANATORY VARIABLES

Latitudinal and elevation gradients are well known broad-scale species richness patterns. These have been studied for several groups of plant and animals from a variety of habitats and regions (e.g., Richerson and Lum 1980; Currie and Paquin 1987; Wolda 1987; Adams and Woodward 1989; Stevens 1989; Tyron 1989; Currie 1991; Vazquez and Givnish 1998; Kessler 2000; Ohlemüller and Wilson 2000; Brown 2001; Heaney 2001; Md. Nor 2001; Vetaas and Grytnes 2002; Qian *et al.* 2003; Baniya *et al*. 2010). In general, broad-scale explanatory variables cannot detect richness patterns at the finer scales and vice versa.

Climate controls or exerts a strong controlling influence on the distribution of plants in all biomes (Woodward 1987). Climate generates and maintains the richness gradient at a broad-scale (Hawkins *et al.* 2003). Elevation only reflects species richness; climatic factors that co-vary with elevation influence species richness along the gradient. The climatic factors, which may vary with elevation, are temperature, potential evapotranspiration, length of growing season, humidity, air pressure, nutrient availability, ultraviolet radiation, moisture index, and rainfall (Funnell and Parish 2001). These various factors have been particularly emphasized as potentially important factors in explaining much of the variation in species richness at broad-scale studies (e.g., Pianka 1966; Richerson and Lum 1980; Currie and Paquin 1987; Currie 1991; O'Brien 1993, 1998; O'Brien *et al.* 1998; Grytnes *et al*. 1999; Odland and Birks 1999; Grytnes 2003a; Baniya *et al*. 2010, Pan *et al*. 2016).

The potential evapotranspiration, length of growing season, mean annual rainfall, number of rainy days, and moisture index are used as explanatory variables. The elevational range size of 100-1500 m is sufficient to encompass a range of climate (e.g., a temperature difference more than 8º C) over which species richness may vary. Along a latitudinal gradient this will be equivalent to more than 1000 km of horizontal distance (cf. Huston 1994). The whole elevation gradient has a temperature difference of more than 25ºC which may have different functional effects at the upper and lower ends of the gradient in influencing variation in species richness. Beside climatic factors, other factors that may explain variations in species richness over broad-scales considered are mass effects, hard boundaries, species-pool, species range-size and area.

FINE-SCALE STUDIES AND THEIR EXPLANATORY VARIABLES

One component of species richness patterns that has been the subject of much recent discussion by plant ecologists is the fine-scale patterns. The number of species occurring in plots of a fixed area of small to modest size is fine-scale variation. Ecologists have long been familiar with fine-scale patterns from the middle of the last century, mostly from small experimental plots (see Swingle 1946; Yount 1956). The development of the competitive exclusion principle led to an understanding of how species coexist in a community. One of the first comprehensive explanations for fine-scale species richness was presented by Grime (1973a, 1973b). These are seminal papers that created considerable interest on fine-scale variation in species richness. Fine-scale variations continue to attract the interest of community ecologists and to stimulate further study (e.g., Al-Mufti *et al.* 1977; Moore and Keddy 1989; Guo and Berry 1998; Mittelbach *et al*. 2001; Fox 2003).

Fine-scale pattern is influenced by different processes than in chance broad-scale patterns but productivity has been used to explain variation in richness at both scales (e.g., Mittelbach *et al.* 2001). But the measure of productivity differs between broad-scale and fine-scale studies. Fine-scale studies that have considered relationships with productivity include Grime (1973a, 1973b), Pacala (1993), Rosenzweig and Abramsky (1993), Tilman and Huston (1994), Grace (1999), Gross *et al.* (2000), and Mittelbach *et al.* (2001). Biomass is most often used as a surrogate measure for productivity (e.g., Grime 1973a, 1973b; Moore and Keddy 1989; Oba *et al.* 2001; Rajaniemi 2003). Other variables that are also frequently used to examine fine-scale species richness patterns include plant cover (Grytnes 2000), disturbance (Connell 1978; Huston 1979, 1994; Fox 1981; Vetaas 1997), fire (Auclair *et al.* 1976), mowing (Melman *et al.* 1988), plant size (Oksanen 1996), and species pool (Zobel 1997).

Variables and the Mechanisms Influencing Species Richness

PRODUCTIVITY

Productivity is the rate at which energy flows in an ecosystem (Kj/m^2/yr). Therefore, it is not surprising that productivity is correlated with species richness in many situations. Productivity was suggested as an important factor explaining variation in species richness from the mid-1960s (e.g., Connell and Orias 1964). The role of productivity as a determinant of species richness is of fundamental importance in understanding variation in species richness. It has thus been used as an explanatory variable at broad-scales (e.g., Pianka 1966; Currie and Paquin 1987; Currie 1991; Rosenzweig and Abramsky 1993; Huston 1994; Rosenzweig 1995; Hawkins *et al*. 2003; Bhattarai 2003), as well as at fine-scales (e.g., Grime 1973a, 1997; Gross *et al*. 2000; Rajaniemi 2003; Bhattarai *et al.* 2004b).

All ecologists and biogeographers have found a causal relationship between species richness and productivity (e.g., Connell and Orias 1964; Huston 1994; Rosenzweig 1995; Grytnes 2000; Mittelbach *et al.* 2001; Bhattarai 2003). But they have not reached a consensus about the mechanisms that underlie it (Oksanen 1997; Grime 1997). This discrepancy behind the mechanism is associated with different scales of study and the different formulation of productivity and taxonomic groups (e.g., Currie 1991; Wright *et al*. 1993; Rosenzweig 1995; Bhattarai 2003; Bhattarai *et al*. 2004a). The reviews of Grace (1999), Waide *et al.* (1999) and Mittelbach *et al.* (2001) are valuable contributions as they provide a very complete survey of productivity diversity literature. Terrestrial plants are the most commonly studied group (36 %), whereas studies of aquatic plants are relatively low (12 %) (Mittelbach *et al.* 2001). It is clear that patterns are emerging for both broad and fine-scales for trees, shrubs, woody climbers, ferns, lichens and herbs (e.g., Rosenzweig 1995; Bhattarai 2003; Baniya *et al*. 2010).

Although we define productivity as the rate of energy flow to a system, it is not easy to measure directly; this rate is rarely measured in nature. Instead, productivity is measured indirectly from surrogate variables (Mittelbach *et al.* 2001). Any estimate of productivity is related to scale. There are two common approaches in estimating productivity in natural systems: (i) climatic variables as a surrogate for productivity at broad-scales, and (ii) biomass accumulation as a surrogate for productivity at fine-scales.

(i) *Climatic variables as a surrogate for productivity* – Productivity can be estimated from climate indices (e.g., rainfall, temperature, potential evapotranspiration and actual evapotranspiration), which are surrogates and all correlate with productivity. At a global or continental scale, productivity is most commonly estimated from actual evapotranspiration or potential evapotranspiration (PET) using climatic data (e.g., Currie 1991). At scales smaller than the continent, productivity is estimated from rainfall. But this practice cannot be applied consistently along elevational gradients. Along the elevational gradient, within a small geographical distance, there is a large variation in temperature between the two ends of the gradient, which can influence the overall life-history attributes of plants. Therefore, even at a finer geographical scale, PET can explain a large proportion of the variation in richness data (e.g., Bhattarai 2003).

In early work, ecologists proposed that productivity would increase species richness but it has been found that this does not occur in all situations. It is well known that the productivity-richness relationship is scale dependent as well as being dependent on taxonomic groups (e.g., Bhattarai 2003). Ecologists have reached a new generalization for considering species richness-productivity relationships. Within a region (*ca.* small to medium-size areas), species richness is a unimodal function of productivity; whereas in biogeographical provinces or at a global scale, species richness is a monotonic function of productivity (e.g., Rosenzweig and Abramsky 1993; Mittelbach *et al.* 2001).

(ii) *Biomass as a surrogate of productivity* – The biomass-species richness relationship under the domain of "productivity diversity" is one of the well-studied subjects in ecology, but it is strongly debated (e.g., Rosenzweig 1995; Oksanen 1996; Grime 1997; Rapson *et al*. 1997; Waide *et al*. 1999; Grace 1999; Mittelbach *et al.* 2001). Most authors agree that biomass affects diversity (e.g., Brown 1973; Tilman and Pacala 1993; Grace and Jutila 1999; Mittelbach *et al.* 2001; Bhattarai *et al*. 2004b). However, no general consensus concerning the form of the pattern has emerged from either theoretical considerations or empirical findings (see the review by Waide *et al*. 1999).

Studies on biomass and species richness are especially common for terrestrial plants (e.g., Silvertown 1980; Tilman 1982; Huston 1994; Gough *et al*. 2000). Most studies that have experimentally manipulated productivity find that species richness decreases following an experimental increase in productivity (Gough and Grace 1998 and references therein). In herbaceous communities, the hump-shaped relationship between biomass and species richness is common (e.g., Waide *et al*. 1999). Other types of relationships found are positive linear, negative linear, and no relationship (e.g., Goldberg and Miller 1990; Mittelbach *et al*. 2001).

Grime (1979) proposed a hump-backed model to explain the species richness-biomass or-productivity relationship in herbaceous vegetation. It attempted to summarize the contribution of five different local processes: (i) dominance (competitive exclusion), (ii) environmental stress, (iii) disturbance, (iv) niche differentiation, and (v) colonization.

Huston (1979) proposed a dynamic equilibrium model to explain the species richness-productivity relationship. High productivity leads to high growth rates, which ultimately promote higher competitive displacement and low species richness. At the same time, a moderate frequency of disturbance lowers the rate of competitive displacement and promotes high species richness.

In a highly productive habitat, one or two species monopolies the available resources and exclude less competitive species, thereby creating low species richness. Huston (1994) elaborated this equilibrium theory to fit into a general framework, and proposed that, the population number of species remains constant as a result of a deterministic balance between the competitive abilities of the species. Tilman (1982) argued that equilibrium coexistence could occur when different resources control two competing species. The local heterogeneity in the ratios of resources can permit numerous species to coexist and this will favor a greater number of species at low supply rates of resources. Therefore, a lower equilibrium diversity will be expected under highly productive conditions.

From a meta-analysis, Mittelbach *et al.* (2001) found that when biomass is used as a measure of productivity, the unimodal relationship is dominant (65 %). Grace (1999) from a literature survey of biomass-species relationships came to a similar conclusion. Thus, the humped-shaped relationship between species richness and biomass is consistent with many other studies. In considering this relationship, various authors have gone as far as to state that the hump-shaped curve is "true" (e.g., Rosenzweig 1992) or "ubiquitous" (e.g., Huston and DeAngelis 1994).

Moore and Keddy (1989) have demonstrated that the species richness biomass relationship varies according to vegetation types. They found a hump-shaped relationship among vegetation types but no relationship within vegetation types. A number of other authors have reached similar conclusions, that the hump-shaped relationship is detected when studies are conducted over broad productivity ranges (e.g., Rosenzweig 1995; Guo and Berry 1998; Mittelbach *et al.* 2001).

Most of the fine-scale productivity-species richness relationships have been performed in wet and temperate regions (e.g., Gough and Grace 1998; Grace and Jutila 1999). It has been shown that the hump-shaped relationship depends upon internal interactions rather than external environmental factors. It is thought that environmental factors seem important than internal interactions in arid regions (Noy-Meir 1973). As far as I know, the hump-shaped relationship has not been tested in arid pasture-lands at high elevation.

Mechanisms underlying the hump-backed model

Despite the various studies, the productivity-diversity relationship has often been assumed to be unimodal (e.g., Al-Mufti *et al*. 1977; Rosenzweig and Abramsky 1993; Tilman and Pacala 1993). Rajaniemi (2003) grouped two categories of hypotheses to explain this unimodal relationship: (1) competition for any crucial resource leads to exclusion, and (2) competition for light leads to exclusion. The total competition intensity hypothesis (Grime 1977) and dynamic equilibrium hypothesis (Huston 1979) belong to the first category and argue that any resource leads to faster exclusion. The second set of hypotheses emphasizes higher productivity excluding poor light competitors [e.g., the habitat heterogeneity hypothesis of Tilman and Pacala (1993); the light competition intensity hypothesis of Newman (1973); light competition/random species loss hypothesis of Goldberg and Miller (1990)]. Oksanen (1996, 1997) proposed a no-interaction model, and argued that the hump-shaped relationship between plant species richness and biomass is apparent without considering any environmental variables and thus that it is an "artefact". He explained the humped-shaped curve as a result of a scaling "artefact" when small sample plots of fixed size are used for plants with variable dimensions. Therefore, important variables would not be the biomass as is assumed but the number of plants per unit quadrat. Since the publication of the no-interaction model, many debates have followed (e.g., Grime 1997; Marañón and García 1997; Rapson *et al*. 1997). There are three assumptions in Oksanen's (1996) hypothesis for the humped-back model: plants have a fixed size, bigger plants have more biomass, and there is a monotonic relationship between the number of plants and the number of species. Rapson *et al*. (1997) evaluated if the humped-back response is a result of fixed grain size. They found a similar hump-shaped curve with different quadrat sizes and the "no-interaction model" actually received limited support. Marañón and García (1997) discussed weak points in the "no-interaction model" on the grounds that a monoculture of plant density and fixed plant size are unrealistic situations for natural communities.

WATER-ENERGY DYNAMICS

Some authors have treated water-energy dynamics under the rubric of productivity (e.g., Hakwins *et al*. 2003) but it is argued that they are not exactly the same, and they are treated separately here. Water and energy are the basic categories needed to describe the dynamic variability in climate (Mather 1974). Precipitation acts as a measure of the amount of water actually available to meet the environmental demands of water. Potential evapotranspiration (PET; i.e., energy) is fundamental to water-budget analysis (Holdridge *et al.* 1971). O'Brien (1993, 1998) and O'Brien *et al.* (1998) demonstrated that spatial variation in woody species richness along the macro-scale gradient is explained by a linear function of water and a parabolic function of energy [i.e., species richness = water + $(\text{energy})^2$], which is the water-energy dynamics model (Figure. 2). This model parsimoniously explains variation in woody species richness along climatic gradients (Bhattarai 2003). It comprises a resource gradient (water) plus a regulatory gradient (energy), so it is a complex gradient model.

Water-energy dynamics predicts maximum species richness at sites where biological activity or photosynthesis is at a maximum and low species richness where biological activity is at a minimum. Such a relationship is consistent with earlier studies that found aspects of climate to be strongly related to various biological functions and factors, especially productivity, life-form diversity, and vegetation type (O'Brien *et al.* 1998).

This model is applicable to explain spatial patterns in woody species richness elsewhere in the world (O'Brien *et al.* 1998; Bhattarai 2003). Hawkins *et al.* (2003) found that water-energy dynamics could explain spatial variation in richness in 82 of a total 85 cases better than other climatic and non-climatic variables. In nature, optimum energy and maximum moist conditions always promote photosynthesis, which ultimately influences all ecophysiological processes and promotes species richness (Bhattarai 2003). The maximum species richness conditions in nature occur when water availability is high and the energy availability is optimum for plant physiological activities (Figure 2). The optimum function of energy and maximum function of water means that water is actively available to plants when energy conditions are not too high or too low. At very low energy conditions, i.e. high mountaintops or polar regions, water will freeze and occur as snow and ice, and is largely unavailable to plants. Their physiological activities and photosynthesis are at a minimum (Bhattarai 2003).

Similarly, tropical and sub-tropical deserts were characterized by a maximum heat/energy, where water will evaporate so that it is unavailable to plants, thus biological activity is at a minimum. The ambient energy regime determines the physical state of water. This means that water variables are not independent of energy variables. The maximum woody species richness at 600-800 m along the elevational gradient in Himalayas is associated with maximum moisture (mean annual rainfall *ca.* 2200 mm) and optimum energy (1200-1300 mm year^{-1}, Bhattarai 2003). Similarly, Bhattarai *et al*. (2004a) argues that maximum fern species richness at 2000 m along the Himalayan elevational gradient is associated with maximum moisture conditions

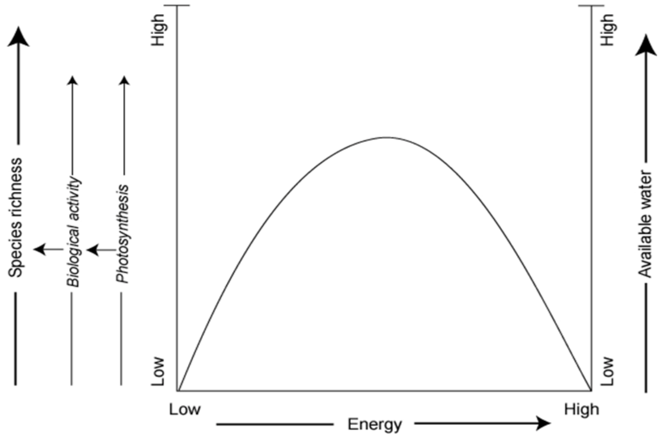

Figure 2. Water-energy dynamics model proposed by O'Brien (1993, 1998) to show the relationship between terrestrial plant species richness and water-energy. Species richness is a function of biological activity, which depends on photosynthesis, which in turn depends on water-energy dynamics (species richness = water + $(\text{energy})^2$). Species richness increases or decreases as a linear function of liquid water (right ordinate) and a parabolic function of energy (abscissa).

(having the highest number of rainy days and cloud zones) and optimum energy conditions. It is found that the optimum energy condition is different for ferns and woody (flowering plants) species. Ferns have low optimum energy requirements compared to flowering plants. This suggests that ferns require more moist conditions (cf. Odland 1993). The higher PET at lower elevations limits water availability, which creates harsh conditions for cool, moisture-loving ferns. Generally, fern richness is constrained by low energy and a short growing season (Bhattarai *et al*. 2004b). Odland (1993) studied phenology of frond development in ferns and found that more than one-month period is needed for its full development. This indicates that at higher elevation shorter growing season constraint for ferns to complete their life cycle, thus, ferns are found hardly up to 4800 m in the Himalayas (Bhattarai *et al*. 2004b). Flowering plants are reported up to 6500 m in Himalayas (Miehe 1989). This suggests that ferns are more sensitive to growing season compared to flowering plants as extensive fern growth does not occur until soil temperatures exceed 7°C.

MASS EFFECTS AND SPECIES POOL

Shmida and Wilson (1985) proposed the concept of mass effects in order to combine historical process, biological interactions, and climatic influences into a broad and potentially more complete understanding of variation in species richness along gradients. It is the establishment of species by propagules at sites where they cannot maintain viable populations. Ecologists have given different names for the phenomenon of mass effects. Brown and Kodric-Brown (1977) and Stevens (1992) called it the "rescue effect", and Pulliam (1988) called it the "source-sink effect". Whatever it is called, it is the same phenomenon and can influence variation in species richness along the environmental gradients.

Natural communities are never closed systems, exempt from the influences of adjacent areas. Therefore, every community may be influenced by mass effects (Shmida and Wilson 1985). Mass effects influence the spatial variation in species richness at both fine and broad-scales. The mass effects function to increase alpha or local species richness in general, but their influence depends upon the system. If surrounding habitats are highly heterogeneous, there is the probability of establishing new species from surrounding habitats and increasing beta diversity along the gradient (cf. Wilson and Shmida 1984; Shmida and Wilson 1985). If surrounding systems are homogeneous, mass effects will increase alpha-diversity through the expansion of species ranges. This is called neighborhood effects (Shmida and Wilson 1985).

The phenomena of mass effects argue that maximum species richness at mid-elevations along the elevational gradient may be associated with broad-scale mass effects where species have migrated from lower and higher elevations (Bhattarai 2003). Species migrations from the source will increase richness at the target site (mass effects), the source is a species pool, and the target is a sink. Therefore, mass effects and the species pool are linked concepts in ecology. But if we consider the temporal dimension, the two phenomena seem rather different. The species pool has a self-maintaining population in the target site but the mass effect produces temporary populations due to a failure in reproduction. This will be insufficient to balance local mortality (Pulliam 1988). Populations may persist in such habitats by continued immigration from more productive "source" areas nearby.

The mass effects along the elevational gradient may dilute the relationship between species richness and climatic variables. Generally, a weak pattern in herbaceous species richness along the elevational gradient is associated with mass effect (Bhattarai 2003). This may be caused by herbaceous attributes, like faster phase of growth, easier establishment and high dispersal ability (cf. Grime 1977; Bhattarai 2003). Many herbaceous species, particularly grasses, are wind dispersed and this may increase the mass effects and obscure the response to the climatic-elevational gradient (cf. Shmida and Wilson 1985). Therefore, non-significant patterns in herbaceous life-forms along the elevational gradient may be linked to active mass effects caused by attributes of herbaceous plants (Bhattarai 2003). Shmida and Wilson (1985) and Bhattarai (2003) argue that mass effects may explain unexplained patterns in species distributions along gradients. Several authors (e.g., van Horne 1983) have discussed the need to distinguish between sources and sink habitats in field studies for community analysis. The herbaceous species, particularly grasses, are more influenced by local factors compared to macro-scale climatic factors. Mass effects should be removed when one attempts to examine the casual relationship between species richness and climate variables (MacArthur 1965). Therefore, it can be argued that one should not lump herbaceous species particularly grasses and woody species together to examine the climatic relationships with species richness along climatic gradients.

HARD BOUNDARIES

In spite of the plethora of climatic, ecological, and evolutionary explanations proposed to explain variation in species richness along latitudinal or elevational gradients, the geometry of species ranges in relation to geographical boundaries has been ignored in most of the ecological literature (e.g., Pianka 1966; Terborgh 1977, 1985; Huston 1979; Shmida and Wilson 1985; Currie 1991). If geographical ranges for a group of species are placed at random within the area they jointly occupy, without regard to climate or history, more species will be found near the center of that area than near the edges; such process is called the hard boundary or mid-domain effect (Colwell and Hurtt 1994; Colwell and Lees 2000; Grytnes and Vetaas 2002; Grytnes 2003b). This random, one-dimensional placement of ranges between two boundaries or null model predicts a convex, symmetrical pattern of species richness. The pattern is either parabolic or quasi-parabolic depending upon alternative distributions of range size and midpoints (Colwell and Lees 2000).

Any natural biogeographical barriers that present some degree of resistance to species dispersal are called hard boundaries (Colwell and Hurtt 1994). Mountaintops in the elevational gradient and oceans, and arctic snowline in latitudinal gradients are hard boundaries because they limit the expansion of organisms beyond the boundaries (Colwell and Lees, 2000). Hard boundaries can be physical or climatic like the tree-line, snow-line and desert boundary. Thus, natural boundaries vary in their potential to limit species distributions. Lyons and Willig (1997) introduced the term soft boundaries, which provide some degree of resistance (e.g., orographic barriers) to the expansion of species ranges.

The mid-domain effect or hard boundary is a relatively new hypothesis and has been recently added to the list of species diversity hypotheses. Quantitatively, it explains a surprisingly high proportion of the geographical variation in species for diverse groups of organisms (Colwell and Lees 2000). Although the mid-domain effect can explain variation in species richness, it has been criticized as a theory of species diversity (e.g., Hawkins and Diniz-Filho 2002). They argued that such models ignore the fact that terrestrial species are distributed in two dimensions. The geometric models must explain longitudinal as well as latitudinal gradients (see Bokma and Mönkkönen 2000). The mid-domain effect has been tested by generating two-dimensional models in all cases but the fit of data to the models was poor (e.g., Bokma *et al.* 2001; Hawkins and Diniz-Filho 2002; Diniz-Filho *et al.* 2003).

Researchers (e.g., Bhattarai and Vetaas 2006) observed wider elevation ranges at mid-elevations and narrow elevation ranges at either end of the gradient and suggested that these may be caused by the presence of a mid-domain effect. When the gradient ends from both directions are discarded to avoid any hard-boundary effects, the hump-shaped pattern between species richness and elevation does not disappear. This suggests that the hump-shaped patterns might be primarily controlled by climate. If one considered the hard boundary as a primary factor in controlling variation in species along the elevation gradient it may underestimate the importance of climate variables (Hawkins *et al.* 2003). Hawkins and Diniz-Filho (2002) argued that the mid-domain effect cannot explain the species richness gradient, so it should therefore be eliminated from the theory of species diversity. But works based on simulations and on analytical null models by several authors (e.g., Colwell and Hurtt 1994; Willig and Lyons 1998; Colwell and Lees 2000; Grytnes and Vetaas 2002) have demonstrated that the mid-domain effect is often essential to explain variation in species richness in diverse groups of organisms. Therefore, it is argued that it needs to be verified further by future studies before making any final conclusions about the acceptance or rejection of the mid-domain hypothesis.

RAPAPORT'S RULE

Rapaport (1975, 1982) proposed that geographical ranges of species are larger at higher latitudes than at the equator. Stevens (1989) found a similar pattern from his observation on trees, mammals, birds, marine mollusks, fish, and reptiles in North America and named this pattern Rapaport's rule. He claimed that this rule can explain the variation in many different kinds of organisms at broad-scales. This rule became popular as "latitudinal Rapaport's rule". Stevens (1992) extended "latitudinal Rapaport's rule" to an "elevation Rapoport's rule", stating that species richness decreases with increasing elevation due to the increasing altitudinal range of species. Following its publication, it was used as potential theory to explain the variation of species along both altitudinal and latitudinal gradients. But this rule has been debated in many studies (e.g., Rohde *et al.* 1993; Colwell and Hurtt 1994; Rohde 1996) and has become a topic of intense debate and discussion within biogeography (e.g., Gaston *et al*., 1998; Fleishman, *et al.,* 1998). Bhattarai and Vetaas (2006) test how tree species richness along the elevational gradient is explained by Rapaport's elevation rule. They observed hump-shaped patterns between tree species richness and elevation and the elevation range sizes are larger at the middle of the gradient and decline at both ends, contrary to Steven's prediction.

AREA

The relationship between species richness and area has a long history in ecology (e.g., de Candolle 1855). Ecologists noticed it before any other diversity patterns. Indeed, it is one of the most general and best-documented patterns in nature for a wide variety of taxa and ecosystems (Brown and Lomolino 1998; Lomolino 2000). Regardless of the taxonomic group or type of ecosystem being considered, large areas have more species than small areas (Gleason 1922; Preston 1962; Williams 1964; Lomolino 2000). The species-area relationship truly deserves the status of a rule, and that we can confidently use it as a universal tool for understanding and conserving biological diversity. Rosenzweig (1995) comments that "you will find more species if you sample a larger area". The larger areas have more species due to the availability of more individuals, more habitats, and more biogeographical provinces (Williams 1964; Rosenzweig 1995, Bhattarai 2003). Therefore, area is an important variable in explaining variation in species richness at both broad and finer scales.

The influence of area on variation in species richness along the elevational gradient and latitudinal gradient has rarely been considered (e.g., Md. Nor 2001; Heaney 2001). Ecological studies that do not take into account the effect of area may detect spurious patterns (Rahbek 1997). It is very important to account the effect of area to find real patterns. One of the study where area is accounted is made by Bhattarai *et al*. (2004b) prior to considering variation in species richness along elevational gradients. Contrary to predictions from the species-area relationship, Bhattarai and Vetaas (2006) did not observe maximum species richness at the largest areas available along the elevation gradient. The areas often decrease with increasing elevation because of the generally steeper terrain towards the higher peaks (Körner 2000, 2002; Lomolino 2001). The reduction in area may influence species richness, which is well known from island biogeography, where small islands support fewer species than larger islands (Körner 2002 and references therein). This area-based explanation seems reasonable at first sight but only when applied to gamma diversity or total richness, not to species richness along the elevation gradients (Lomolino 2001).

Conclusions

To explain patterns of species richness, many hypotheses are proposed but most of them are complementary rather than exclusive. It is not possible to capture the many disparate phenomena of species richness at only one scale of analysis and or to express the patterns in few simple formulae. Therefore, a pluralistic body of hypotheses, which incorporates historical, biological and climatic factors, is needed to explain the observed variations in species richness. This is depicted by the strong relationship between climate, biological interactions, and historical processes in influencing variation in species richness at different spatial scales.

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