Scale and species richness: towards a general, hierarchical theory of species diversity

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Abstract

Aim Current weaknesses of diversity theory include: a failure to distinguish different biogeographical response variables under the general heading of diversity; and a general failure of ecological theory to deal adequately with geographical scale. Our aim is to articulate the case for a top-down approach to theory building, in which scale is addressed explicitly and in which different response variables are clearly distinguished.

Location The article draws upon both theoretical contributions and empirical analyses from all latitudes, focusing on terrestrial ecosystems and with some bias towards (woody) plants.

Methods We review current diversity theory and terminology in relation to scale of applicability. As a starting point in developing a general theory, we take the issue of geographical gradients in species richness as a main theme and evaluate the extent to which commonly cited theories are likely to operate at scales from the macro down to the local.

Results A degree of confusion surrounds the use of the terms alpha, beta and gamma diversity, and the terms local, landscape and macro-scale are preferred here as a more intuitive framework. The distinction between inventory and differentiation diversity is highlighted as important as, in terms of scale of analysis, are the concepts of focus and extent. The importance of holding area constant in analysis is stressed, as is the notion that different environmental factors exhibit measurable heterogeneity at different scales. Evaluation of several of the most common diversity theories put forward for the grand clines in species richness, indicates that they can be collapsed to dynamic hypotheses based on climate or historical explanations. The importance of the many ecological/ biological mechanisms that have been proposed is evident mainly at local scales of analysis, whilst at the macro-scale they are dependent largely upon climatic controls for their operation. Local communities have often been found not to be saturated, i.e. to be non-equilibrial. This is argued, perhaps counter-intuitively, to be entirely compatible with the persistence through time of macro-scale patterns of richness that are climatically determined. The review also incorporates recent developments in macroecology, Rapoport's rule, trade-offs, and the importance of isolation, landscape impedance and geometric constraints on richness (the mid-domain effect) in generating richness patterns; highlighting those phenomena that are contributory to the first-order climatic pattern, and those, such as the geometric constraints, that may confound or obscure these patterns.

Main conclusions A general theory of diversity must necessarily cover many disparate phenomena, at various scales of analysis, and cannot therefore be expressed in a simple formula, but individual elements of this general theory may be. In particular, it appears possible to capture in a dynamic climate-based model and 'capacity rule', the form of the

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grand cline in richness of woody plants at the macro-scale. This provides a starting point for a top-down, global-to-local, macro-to-micro scale approach to modelling richness variations in a variety of taxa. Patterns in differentiation/endemicity, on the other hand, require more immediate attention to historical events, and to features of geography such as isolation. Thus, whilst we argue that there are basic physical principles and laws underlying certain diversity phenomena (e.g. macro-scale richness gradients), a pluralistic body of theory is required that incorporates dynamic and historical explanation, and which bridges equilibrial and nonequilibrial concepts and ideas.

INTRODUCTION

The grand cline in diversity from low at the poles to high at the equator has long been recognized as one of the most general biogeographical patterns, and although there are exceptions within particular taxa (e.g. grasses), it is the general nature of this trend that suggests the existence of some fundamental underlying control. However, ecologists have failed to agree on what that control might be: indeed it is typically described as 'unexplained' (e.g. Taylor & Gaines, 1999), which appears to us as an unduly negative assessment. This peculiar lack of consensus stems in part from: (1) a failure to distinguish different biogeographical response variables under the general heading of diversity, and (2) a general failure of ecological theory to deal adequately with geographical scale.

Considering these two problems in turn, the simplest dichotomy amongst response variables is that between biogeographical aspects of diversity and ecological aspects (Table 1). The former centres on taxonomic distinctiveness or endemism, and the latter, at its simplest, involves counts of the number of species in a given geographical area. Areas rich in endemics are often also species rich, which is one reason why thinking about these topics often gets conflated, but patterns in richness and endemism are not necessarily positively related (Ceballos & Brown, 1995), e.g. remote oceanic islands are rich in endemics but impoverished in species (Whittaker, 1998; Brown & Lomolino, 2000; Heaney, 2000). As a first order generalization, the explanation for biogeographical patterns of distinctiveness requires theories focusing on evolution and historical contingencies (e.g. Brown, 1988; Bush, 1994; Bennett, 1997; Qian & Ricklefs, 2000; Willis & Whittaker, 2000), whilst species richness patterns can often be related to contemporary ecological processes and controls (e.g. Brown, 1988; Wilson, 1990; Currie, 1991; O'Brien, 1998).

The second general weakness in the ecological literature is the failure to distinguish factors relevant to particular scales of analysis (but see: Brown, 1988; Currie, 1991; O'Brien et al., 1998; Lyons & Willig, 1999; Brändle & Brandl, 2001; Crawley & Harral, 2001). In part, this failing can be laid at the door of Island Biogeography, in which a recurrent theme of the last 35 years has been the search for an understanding of species-area relationships, and which of several factors (isolation, island elevation, energy, etc.) control the variation in their form (review in Whittaker, 1998). The scale-dependency of these relationships has only recently become generally appreciated (e.g. Palmer & White, 1994; Rosenzweig, 1995; Gaston, 1996; Lomolino, 2000a), but has long been evident (e.g. see Whitehead & Jones, 1969). The relative significance of such key factors as area and isolation will depend on how great a range the sample islands (or other sample units) encompass for each variable. However, it is not just the range, but what the upper and lower limits of the variables are relative to the ecology of the taxon under consideration, e.g. an island may be considered isolated for terrestrial mammals but not for most birds, large for snails but not for ungulates. In respect of island area, Lomolino (2000b) and Lomolino & Weiser (2001) demonstrate that the conventional approach of simplifying and linearizing species–area relationships by log-transformation has served to obscure scale-dependent features, including a threshold separating small islands influenced by episodic disturbances – among which richness tends to be independent of area – from larger islands. This serves to illustrate that environmental factors of ecological importance vary differentially (often nonlinearly) with area (Innes, 1998). Arguably, by confounding variation in area with variation in other environmental factors, the search for a general understanding of diversity patterns by this means is fatally weakened (Whittaker, 1998, 2000).

We contend therefore, that an important starting point in analysing spatial patterns in richness is to control area: a step that is very often ignored or fudged in analysis, especially at coarser scales. Moreover, by the above line of reasoning, statistical means of controlling area involve the danger of smuggling in artefacts or of hiding real patterns. This would occur when other factors of ecological importance happen to co-vary with area across the samples. The simplest means of controlling area is to use sample units of equal dimensions: it is also by far the most satisfactory means. Thus, in order to evaluate the merits of different diversity theories and hypotheses, it is necessary to collect and analyse data at prescribed spatial scales, repeating the process at a variety of

Table 1 Key diversity and scale concepts

	Meaning
Diversity concepts	
Species diversity	Varied meaning: e.g. number of species, or indices weighted by abundance distributions of species (equitability); implying of itself no standardization of sampling
Species richness	Number of species, implying of itself no standardization of sampling
Species density	Number of species in a standardized sample, e.g. per unit area; more precise than the above but less widely adopted
Species turnover, i.e. differentiation diversity	In the present context meaning compositional turnover in space between two inventory (typically alpha-scale) samples, expressed by a variety of indices or multivariate analyses, and thus qualitatively different from species richness or density
Endemism	An endemic is simply a species confined to a particular geographical area; a focus on areas of high numbers of endemics implies an interest in biogeographical distinctiveness (whether at species or other taxonomic level)
Scale concepts	
Spatial scale	Should refer to the size of the base unit used in sampling and analysis, but in practice usage of this term varies, such that either or both of 'extent' and 'focus' may be meant; moreover, size of sample unit is very often not held a constant but is allowed to vary within a study
(Geographical) extent	The geographical space (distance) over which comparisons are made, whether they be using 1 m^2 or 10,000 km^2 sample units, i.e. of itself implying nothing about spatial scale in the strict sense
Focus	The spatial scale at which data are collected (also called the 'grain') or, in cases, at which data are aggregated for analysis (e.g. local or field scale to regional scale); this concept, unlike 'extent' can be synonymous with spatial scale

Whilst the table refers to species as the unit of analysis, the terms can of course be applied at other taxonomic levels. Most of these terms are well established, although 'extent' and 'focus' may be less familiar (but, see, e.g. Peterson & Parker, 1998; Nekola & White, 1999; Gross *et al.*, 2000).

different scales to reveal where on the continuum particular factors have greatest relevance (see e.g. Crawley & Harral, 2001). As a general case, no matter how important we know an environmental factor to be to the ecology of a group of organisms, if that factor happens to exhibit no measurable variation across a series of fixed-area sites, it clearly cannot be causing any non-random pattern of richness that might be found across those sites.

Whilst it should not be anticipated that any single environmental variable, model or hypothesis should have explanatory power across all scales of analysis, as recent macroecological analyses indicate (Brown, 1999; Enquist *et al.*, 1999; West *et al.*, 1999), some relationships may be so fundamental that they operate across all scales without being easily detectable at all scales. Thus, a general theory of diversity must address the question of scale (Auerbach & Shmida, 1987; Currie, 1991; Lyons & Willig, 1999) and it must do so explicitly. With regard to evolutionary change and temporal scale, Bennett (1991) has put forward a framework of four tiers of change and how they may relate to different categories of forcing factor (Table 2a). A matching framework with respect to spatial scale and richness is presented in Table 2b. This is elucidated by an examination of some of the more commonly cited ideas in explanation of diversity variations in space, focused on the scale at which their effects are most likely to be manifested, i.e. how they might fit into the theoretical hierarchy. We favour a top-down, broad-to-fine (macro-to-micro) scale approach to this spatial analysis, while recognizing that signal can be detected in both directions through the hierarchy, top-down and bottom-up (Allen & Starr, 1982; Brown, 1995; Huston, 1999). The argument presented herein is written with a plant-bias. This is for two reasons

(1) it is where our own first interests lie, and (2) plants are the base of the food chain and whilst plants depend on other organisms, they are the logical place to begin building towards a general model.

DIVERSITY TERMINOLOGY AND SCALE DELIMITERS

In developing these arguments, it is necessary to ensure that the terms used have clear and discrete meanings. In practice, this is not the case (Table 1). The term species richness is used for the number of species in a sample. Species diversity is commonly used interchangeably for richness, but at local scales of analysis it is often expressed as indices that weight both the richness and equitability (evenness of abundance across species) of a sample. As noted, one of the problems in this literature is the common failure to distinguish spatial scale, or to hold area constant. Accordingly, some authors have adopted the term species density for the number of species sampled in a standardized sample unit, e.g. per unit area (e.g. Whittaker, 1975; Lomolino, 2001). Others have used this protocol, i.e. holding area constant, but retain the terms diversity or richness rather than density (e.g. O'Brien, 1993; Fraser, 1998). In addition to the various concepts of diversity, concepts of scale and space also vary (Table 1): indeed some authors appear to make no distinction between the very different concepts of (1) spatial scale in the sense of the base-unit or focus of analysis (2) geographical extent of the study, and (3) the geographical distance between sample points (relevant when using point data). Labelling these rather different properties 'spatial scale' provides considerable scope for confusion, particularly in meta-analyses and reviews.

Table 2 Hierarchical schema of diversity and scale factors. (a) Temporal hierarchy of dominant processes controlling evolutionary patterns seen in the geological record (modified from Bennett's (1991) Table 8.2). A number of qualifiers could be added to this table, for instance: *in certain contexts, the dominant trend from orbital forcing might be gain rather than loss; †speciation can of course occur sympatrically, i.e. it does not depend upon isolation, and it can be very swift. (b) Spatial signatures in species richness at differing spatial scales and relationship to Cody's (1975) and R.H. Whittaker's (1975) spatial tiers, and Bennett's (1997) evolutionary tiers. Spatial and temporal scales are related, but imperfectly. R.H. Whittaker's delta-scale differentiation diversity falls between his gamma and epsilon scales. Differentiation contrasts between entire (large) regions or continents (final row of table) appear not to have been given a Greek letter code

(a)

Bennett's tiers	Periodicity	Evolutionary outcomes	Explanatory variables
First		Microevolutionary change within species	Natural selection
Second	20–100 kyr	Disruption of communities, loss of accumulated change	Orbital forcing*
Third		Speciation	Isolation†
Fourth	c. 26 Myr	Sorting of species/spread of innovation	Mass extinctions

(b)

Spatial scale	Cody tiers	R H W tiers	Phenomena	Explanatory variables	Bennett's tiers
Local	Alpha	Alpha	Species richness within local communities/patches	Microenvironmental and biotic interactions, e.g. grazing	First
Landscape	Beta	Beta-gamma	Turnover of species between communities (beta), or inventory of whole landscape (RHW's gamma)	Topography, catena effects, soils, disturbance (e.g. fire)	First
Regional	Gamma	Epsilon	Differential overlap of species, ranges, e.g. latitudinal gradients	Water-energy dynamics, climate and physiographic modification of same; residual historic patterns	First, second and third
Inter-regional/continental			Replacement of higher taxa, e.g. placental mammals by marsupials	Plate tectonics, major environmental change – catastrophic or otherwise	Second, third and fourth

The first two columns of Table 2b provide alternative scale descriptors, each employing the greek lettering scheme (α β γ, etc.), initially put forward by R. H. Whittaker (1960). There is general agreement over his terms alpha and beta. However, his gamma scale was intended to apply to the inventory diversity (species richness) of a whole landscape, such as a mountain. Others adopted his scheme, but generally took gamma diversity to refer to greater areas, i.e. to regional diversity (see, e.g. Tramer, 1974; Cody, 1975), perhaps because Whittaker initially set no upper bound to the term. This version of the scheme we term Cody's tiers. Whittaker (1977) then set out a more detailed framework that we only partly reproduce within column 2 of Table 2b. This encapsulated first what he termed inventory diversity, or simply richness, assessed at four scales: (1) point scale (2) alpha (3) gamma (landscape), and (4) epsilon (regional). Secondly, it encapsulated a separate phenomenon, compositional turnover. This he termed differentiation diversity, and he identified three scales: (1) internal beta or pattern diversity, lying between the inventory scales of point and alpha; (2) beta diversity, between alpha and gamma scales, and (3) geographical differentiation or delta diversity, between gamma and epsilon scales. He thus subdivided diversity into seven categories in total. Whatever the merits of this 'clarification', it has not been widely adopted and most authors referring to the framework in practice follow Cody's version, as we do immediately below.

What actual spatial scales do the terms alpha, beta, gamma translate to? Shmida & M. V. Wilson (1985) suggest for terrestrial plants that 10^2–10^4 m^2 is appropriate for alpha diversity, and 10^6–10^8 m^2 for gamma diversity, with beta diversity constituting the turnover between patches at the alpha scale. Given that different taxa of terrestrial and aquatic plants and animals differ by many orders of magnitude in body size it is evident that the spatial scales at which alpha, beta and gamma should be operationalized can vary between taxa. For instance, J. B. Wilson (1990) adopts 10^3 m^2 (0.1 ha) as an appropriate upper limit for within-community or alpha diversity (a lower limit than Shmida & Wilson, 1985), but argues (Wilson, 1994) that for phytoplankton this would translate to something closer to 10×10 cm. Shmida & Wilson (1985) in their floristic analyses, suggest that gamma diversity corresponds to 10^6–10^8 m^2, although many of the recent macro-scale analyses typically use larger grid cells, of the order 1000 km^2 (Linder, 1991; c. 750 km^2) to 10,000 km^2 (10^{10} m^2) or larger (e.g. Currie & Paquin, 1987; O'Brien, 1993). The precise scale chosen is often a matter of convenience relating to the scale at which species have been mapped (e.g. Linder, 1991). O'Brien (1993) argued that because distances of at least 100 km allow for significant variation in climate from cell to cell within a continent, the grid cell size adopted in her study, 25,000 km^2, was therefore an appropriate scale, commensurate with measurable variation in climate and a satisfactory level of accuracy and precision in the species range data available.

Thus, empirical studies of higher plant subsets corresponding to Cody's gamma scale span at least four orders of magnitude of area. Similarly, the scale at which the differentiation diversity tiers apply is also variable, commensurate with variation in the application of the inventory tiers. Outwith the Whittaker/Cody tiers, comparisons are sometimes made between large regions or between continents, in which if area is controlled at all, it is by statistical means (e.g. regression), and most interest focuses on differentiation diversity and historical biogeographical explanations (e.g. Qian & Ricklefs, 2000). Thus, there is no set spatial scale that corresponds to the Cody or Whittaker tiers, and indeed, many authors, including several of those cited above, do not use this terminology. We favour the use of the more intuitive (and intentionally imprecise) terms local-scale, landscape-scale and macro-scale (see O'Brien et al., 2000). However, the distinction made by Whittaker (1977) between inventory and differentiation diversity is an important and useful one, as is the recognition that each of these concepts can be applied at different scales of analysis.

AREA

As radically different types of data and indices are typically employed in analyses at local, landscape and coarser scales, it is clearly important that those undertaking meta-analyses based on previous studies do indeed compare like with like. For instance, a study of 0.1 ha data from local inventories each sampled intensively on single occasions at a suite of scattered locations, provides data for comparisons of variation in richness across geographical space (Clinebell et al., 1995) but remains a local (alpha) scale study, likely to retain signal from factors that vary measurably on local scales, such as soil nutrient status. This is entirely different from a study based on species range maps that are each based on decades of general floristic inventory from numerous localities, and which are then converted to richness values across a set of grid cells. The latter is far more likely to reveal climatic correlates of richness. This is not to say that meta-analyses must be limited to studies of precisely identical protocols, as this would be unduly restrictive. Whilst studies of radically different grid cell size (orders of magnitude apart) are not strictly comparable, the difference between studies using 10,000 km^2 and 25,000 km^2 is unlikely to be substantial. For instance, an analysis for bats and marsupials, using a nested series of quadrats from 1000 km^2 to 25,000 km^2 suggested that the form of the geographical gradient in richness may be relatively invariant with respect to area within those bounds (Lyons & Willig, 1999), although it is too early to say if this finding can be generalized.

If we start from the premise that in order to examine the relative roles of different environmental variables, area should be held constant in analysis, it follows that at the macro-scale, equal area grid cells should be used. Attempts to fix data based on latitudinal–longitudinal grids by regressing out area (a commonly used fix) involve the danger of obscuring variables that happen to co-vary with the geographical pattern of grid cell size; ideally this should be avoided. Cells that are reduced in their effective area because

they overlap water bodies should also be avoided as they may smuggle in area effects. By analysing the geographical gradients in richness based on these protocols the confounding effect of area on the analysis (see debate in, e.g. Rosenzweig & Sandlin, 1997; Rohde, 1998; review in Brown & Lomolino, 1998) is bypassed, the 'area hypothesis' is rendered essentially redundant (but see Synthesis, below) and the first order climatic pattern emerges (O'Brien, 1993, 1998). For woody plant species richness, it then becomes evident that the macroscale pattern across the globe consists of a mixture of largely latitudinal patterns, largely longitudinal patterns, and in some regions a combination of the two, broadly mimicking the spatial patterns shown by the major biomes. Arguably, we should stop thinking of these geographical richness patterns as 'latitudinal gradients', as (1) they are not universally latitudinal, and (2) it no longer appears unreasonable to label them 'climatic gradients'.

SPECIES RICHNESS THEORIES: FROM MACRO- TO LOCAL SCALES

Historical vs. Dynamic hypotheses of richness

There are numerous theories and hypotheses relating to spatial patterns of richness. A fairly typical short list modified from Fraser & Currie (1996) is provided in Table 3. Area has been dealt with above – it is largely a confounding factor to be controlled in analysis – leaving six other 'general' hypotheses, which we discuss in relation to their scale of applicability. In essence, our case is that at the macro-scale they collapse to dynamic hypotheses (based on climate) and historical contingency, and that as distinct ecological hypotheses the relevance of the other hypotheses (4–7 in Table 3) is largely to local-to-landscape scales of analysis. The use of the phrase 'distinct ecological hypotheses' is stressed, as we are not arguing that these mechanisms and processes have no role in macro-scale patterns, but that in so far as they do, it is a role largely dictated by, and thus not independent of climate.

The distinction between historical and dynamic hypotheses is based on the repeatability or probability of recurrence of a particular state or form. Thus: (1) historical, or time-bound knowledge, refers to the analysis of complex states having very small probabilities of being repeated, i.e. states of low recoverability; whilst, (2) physical, or dynamic, or timeless knowledge, refers to the analysis of states having a high degree of probability of being repeated, such analysis leading to the formulation of laws of general validity (Schumm, 1991).

The search for dynamic hypotheses of species richness can thus be likened to the search for the general laws of ecology (Brown, 1999), from which historical contingency supplies the deviations (see Synthesis section, below). Whereas the 'historical' focus of the entry in Table 3 is at the macro-scale, historical signals may in fact be evident on a range of scales, from continental glaciations to the creation of forest gaps in relation to an ENSO (EL Niño Southern Oscillation) cycle: in this sense 'history' has a bearing on each of the following sections.

Climate and energetics

Dynamic models may take different forms. The equilibrium theory of island biogeography (ETIB) (MacArthur & Wilson, 1967) is one form of dynamic hypothesis. It invokes a general relationship between extinction and immigration (plus speciation), controlled by a few obvious environmental parameters, to regulate patterns in species-area regressions. Although it is not a climatic model, it is based on the premise that the resource base of an island dictates richness in a predictable fashion. An increasingly popular model, which was built upon the ETIB, is Wright's (1983) species-energy hypothesis. Wright took the apparently simple step of replacing 'area' as the independent variable predicting richness with 'available energy', where this refers to the rate at which resources available to the species of interest are produced on the island as a whole. In effect, for plants, he multiplied the annual rate of actual evapotranspiration (AET) averaged over each island (taken from a global map of AET) by the area of the island. The islands in Wright's analysis ranged over two orders of magnitude in both area (1200 km^2 for Jamaica to 770,500 km^2 for Australia) and species number (137 species on Spitzbergen to 12,000 for Australia), and both variables were logged prior to analysis. Despite the usual improvement that this transformation brings, only 70% variance was accounted for in the regression. Wright's paper has nonetheless proven influential, perhaps in part because it coined the 'species-energy' theory or hypothesis, since adopted by others engaged in

General hypothesis	Argument
Area	Richness reflects sampling effects and environmental heterogeneity
Historical factors	Glaciation effects, dispersal, higher speciation rates
Available energy	Partitioning of energy among species limits richness
Environmental stress	Fewer species are physiologically equipped to tolerate harsh environments
Environmental stability	Fewer species are physiologically equipped to tolerate varying environments
Disturbance	Disturbance prevents competitive exclusion
Biological/ecological interactions	Competition and predation affect niche partitioning

Table 3 Commonly cited general hypotheses of diversity. Modified slightly from Fraser & Currie (1996, Table 1)

macro-scale studies of species richness (e.g. Turner *et al.*, 1988; Fraser & Currie, 1996; Lennon *et al.*, 2000) (see below).

The basic idea in the species-energy hypothesis is that the amount of available energy sets limits to the richness of the system (Wright, 1983; Currie, 1991; Table 3). Studies under this rubric have used a variety of measures of energy, including: temperature, AET, primary productivity and potential evapotranspiration (PET), where each of these measures may be annual or seasonal values, and where a variety of alternative formulations of each is available (compare, e.g. Richerson & Lum, 1980; Currie & Paquin, 1987; Turner *et al.*, 1988, 1996; Adams & Woodward, 1989; Currie, 1991; Ricklefs *et al.*, 1999; Lennon *et al.*, 2000). It needs to be understood that these indices of 'energy' differ in kind and may exhibit strongly contrasting patterns at the macroscale (see, e.g. O'Brien, 1993; Hulme *et al.*, 1996). For instance, AET can be crudely characterized as an estimate of the amount of water used to meet the environmental energy demand. It thus estimates water balance and is recognized as a good correlate of plant productivity, i.e. it measures use of energy by plants (thus in turn available to animals) rather than climatic energy *per se*. Temperature is the simplest measure of environmental or climatic energy, and may provide good correlates with, e.g. birds; but may be anticipated to be less powerful in models of the richness of solar ectotherms such as butterflies (Turner *et al.*, 1988, 1996; Lennon *et al.*, 2000). The point here is a simple one – and an ecological truism – that it isn't just a question of the amount of energy, but of its availability to the trophic level or taxonomic group in question that matters. Heat and light are both necessary for photosynthesis. Thus, a good measure of climatic energy regime for plants should incorporate both. In contrast, net primary production (NPP) does not measure the inputs for plants, but is an indicator of the availability of energy (in chemical form) for heterotrophs.

O'Brien (1993, 1998) has developed a theoretical model of plant species richness at the macro-scale that is consistent with the ideas of species-energy theory, but which is more satisfactory and we believe more general than previous formulations (Whittaker & Field, 2000). Her insight is that it is the interaction between water and energy that is foundational to an understanding of spatial variation in photosynthesis, and thus biological activity, and through this activity, spatial patterning in the capacity for plant species richness to be supported. In general, richness should be anticipated to increase as a linear function of rainfall and a parabolic function of energy (heat and light); the latter as photosynthesis is dependent on a narrow range of temperature conditions below which water freezes and above which it vapourizes. The emphasis on considering the water balance as well as the energy regime in modelling vegetation has of course been noted by other authors (e.g. Stephenson, 1990; Currie, 1991; Kleidon & Mooney, 2000). O'Brien's 'water-energy dynamics' theory is more fundamental because it generates clear expectations as to the form of the relationship between climate and richness. In her studies

of southern African woody plants, the most powerful simple model of richness was found to be a two-variable model based on a linear relationship with annual rainfall and a parabolic ($x–x^2$) relationship with minimum monthly PET (Thornthwaite's formula). Subsequent analyses demonstrate that this holds for species, genus and family richness (O'Brien *et al.*, 1998) and that it can be developed into an interim general model capable of reproducing known patterns of richness elsewhere on the planet (i.e. for regions of other climates and biogeographic histories), irrespective of whether they are latitudinal or longitudinal in form (O'Brien, 1998).

A simple 'capacity rule' (*sensu* Brown, 1981) encapsulates these ideas, as follows: whatever the geographical pattern of variation in water-energy dynamics, it will tend to be matched by the geographical pattern of variation in the amount and duration of chemical energy production, in biological dynamics and thus (over geological time) in the capacity for taxonomic richness (O'Brien *et al.*, 1998). Given this rule, climate can be conceptualized as setting the general form of the predictable macro-scale pattern in richness, i.e. the 'climatic potential for richness' (*sensu* O'Brien, 1998). The model is capable of improvement, most simply by the inclusion of a measure of topographic relief (O'Brien *et al.*, 2000, and unpublished), but appears to be capable in its original two-variable form, of capturing the first order macro-scale pattern of variation in woody plant richness globally. It is not to be anticipated, for good ecological reasons, that the spatial patterns in all other taxa will follow this relationship, but it may nonetheless provide a foundation for building a more general understanding of richness variations in other taxa (e.g. for mammals, see Andrews & O'Brien, 2000).

Notwithstanding the substantial body of work on climatic relationships to richness, the debate persists as to the underlying mechanisms (e.g. Loehle, 2000), with several authors pointing to inconsistency of diversity–productivity relationships. In practice, this inconsistency is the result of comparisons being made at vastly different spatial scales (Fig. 1; and see: Weiher, 1999; Gross *et al.*, 2000; Morin, 2000; at the alpha/local scale, see: Oksanen, 1996), and whereas the relationships being revealed by work at the macroscale are generally consistent, at local scales of analysis, climatic controls are less evident as other factors that exhibit greater heterogeneity at these scales kick in with their signal (cf. Purvis & Hector, 2000).

Stress, stability, disturbance

The ideas that fewer species are physiologically equipped to tolerate harsh or varying environments and that disturbance prevents competitive exclusion, are similar in at least one respect: they are founded on the implications of environmental variability for the persistence of species in an area. As Colinvaux (1993) notes, the basic answer as to why 'stressful' habitats such as hot springs, salt flats and mountaintops tend to support few species is that they are rare, scattered and sometimes ephemeral. The problems of species' adaptation to
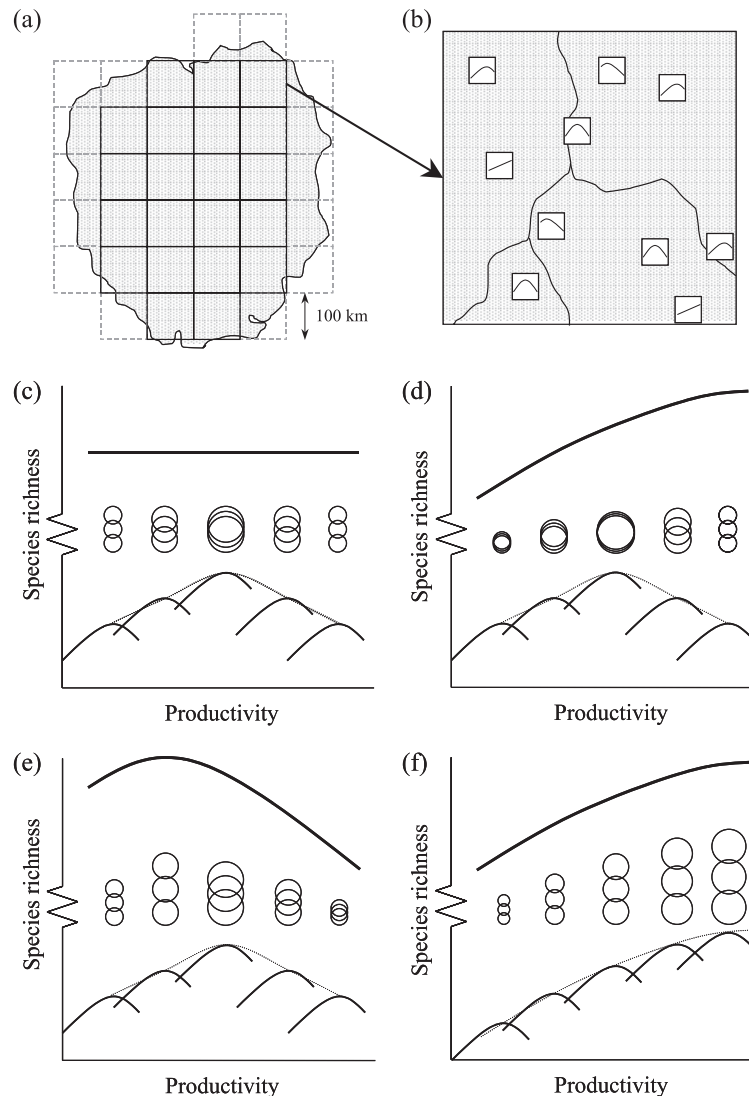
Figure 1 Hypothetical productivity–diversity relationships at different scales of analysis. The figure indicates how different relationships could theoretically be obtained between inventory diversity and productivity at the local and macro-scales, by varying patterns of differentiation diversity (species turnover) across landscapes or regions. (a) depicts a hypothetical land mass, over which has been placed a grid cell system of fixed shape/area cells. Species richness counts are derived based on presence of native species within each cell, discounting cells that contain significant areas of ocean (as, e.g. O'Brien, 1993); (b) depicts a cell from this grid, in which a number of local-scale studies have been conducted, using small (e.g. 1 or 10 m^2) fixed area quadrats. These hypothetical studies vary in their findings (shown as curves within small squares), but in general appear to show a unimodal response of richness to productivity variation. A river system is shown for the purposes of illustration. In (c) to (f), the lower (thinner) curves represent local-scale studies of inventory richness from small (e.g. 1 m^2 or 10 m^2) plots; the upper solid lines represent macro-scale studies of inventory richness that might be derived using the macro-scale (approx. 10,000 km^2) grid cell data and the circles in the middle of each figure indicate varying amounts of differentiation diversity, wherein circle size is scaled roughly to local inventory richness and circle overlap represents the proportion of species in common between local-scale plots. (c) to (f) assume that a unimodal relationship for small plot inventory richness pertains, each solid curve below the break in the y-axis showing the series of data points sampled within a small area: the series of these curves representing a set of comparative small-plot studies from across a large region. (c) to (e) involve identical local scale findings, but varying trends in differentiation diversity, and thus three radically different patterns at the macro-scale. (d) and (f) involve identical macro-scale patterns, underlain by varying patterns from the overall series of small plot studies. In practice, although there have been numerous studies using small plots, we can only infer the macro-scale patterns from existing data. Satellite-derived productivity estimates, combined with macro-scale inventory data, would seem an obvious way of exploring what form these relationships really take. For woody plants, according to O'Brien's (1993, 1998) water-energy dynamics theory, we would expect to find the macro-scale pattern shown in figures (d) and (f) to pertain, with figure (f) the most likely general representation of the four figures given.

such environments, their small size (or, in cases, extreme unproductivity), and the difficult of migrating between such sites provides elaboration of the case. Considering harshness and variability of environments in respect to their nature and causes, most sites that are unfavourable and have a low richness for these reasons are either localized and relate to plate tectonics, e.g. hot springs, mountaintops, serpentinite outcrops, or are regionally distributed as a function of climate, e.g. extreme desert environments. Mangroves may be considered as occupying harsh or stressful environments and as a further illustration of this class of systems. Mangroves are the woody plants that occupy estuaries and intertidal zones throughout the tropics and subtropics. These ecotonal systems between the marine and terrestrial worlds support a relatively low diversity of the dominant higher plants, with thirty to forty species in the most diverse areas and only one or a few in many places (Field *et al.*, 1998). These environments are subject to pronounced environmental fluctuations dictated by tidal conditions, involving extreme edaphic conditions of high and varying salinity. Whilst the pattern of variation in gross richness between the Indo-West Pacific and the Atlantic, Caribbean and Eastern Pacific region appears best explained by historical scenarios associated with the origins of mangrove taxa (Ellison *et al.*, 1999), patterns of richness at the local scale within large land masses or groups of islands do appear to correlate with a variety of measurable environmental variables, often including precipitation in a leading role (Duke *et al.*, 1998; Field *et al.*, 1998). Despite the importance assigned to climatic factors in some studies, the fact remains that mangrove ecosystems are unusual environments, linearly distributed as narrow, discontinuous ribbons around coastal margins. Area-controlled analyses restricted to mangroves are possible only at a local scale of analysis, and they are at best only a small part of the signal (or noise?) within macro-scale, area-controlled analyses of richness.

Considering the role of disturbance, relatively few aspects of environmental variability on the macro-scale would appear to be independent of climatic controls. For instance, the distribution of high-energy storms (hurricanes, cyclones, typhoons), and of large fires are both functions of the general circulation, and of interannual variations in circulation such as ENSO (e.g. Kitzberger *et al.*, 2001). On a longer time-scale of variation, glaciations of temperate latitudes could be considered under this rubric, as large-scale 'disturbances' through which climate-richness relationships may have been modified to varying degrees in different parts of the globe (below). One category that is independent of climate and which can impact powerfully on ecosystem functions is large volcanic eruptions. However, given the ability of plant species to persist as dormant propagules and to bounce back from intensive volcanic activity (e.g. Whittaker *et al.*, 1995, 1999), it is unlikely that volcanic eruption impacts will be detectable in macro-scale plant richness, although they may well be detectable locally (e.g. in species numbers on Krakatau, cf. Whittaker *et al.*, 1997). The impact of disturbance on richness may not be simply negative of course, rather, as suggested in the next model considered, richness may have a parabolic relationship to disturbance.

The Intermediate Disturbance Hypothesis (IDH) (Connell, 1978) is essentially a patch-dynamics or successional model, invoking conditions for maximal diversity whereby repeated local disturbances occur that are frequent enough to prevent competitive exclusion over an entire area, but not so frequent as to eliminate most species. As Wilson (1990, 1994) notes, both actual physical scale and frequency must be commensurate with the physical size and generation times of the organisms concerned for this model to operate. In his assessment of the relevance of the IDH to New Zealand plant communities, Wilson (1990, 1994) argues that the processes involved, such as fires, floods, tectonic processes, landslips, etc., operate at spatial scales too large for there to be mosaics within areas of 10^3 m^2, the upper limit he uses for alpha or within-community diversity, except in the context of forest gaps. He therefore places the IDH as essentially a landscape-scale model. In practice, it is hard to see how the IDH can be tested at the macro-scale, as this requires a simultaneous measurement for each grid cell of all important disturbance phenomena, their area of impact, intensity of impact and frequency, including, e.g. fires, severe storms, landslips, volcanic eruptions, etc., and it is not at all clear how a meaningful quantification can be obtained by this means (see, e.g. Peterson & Parker, 1998). Most grid cells will contain patches that are little disturbed and patches that are very disturbed, hence it seems unlikely that disturbance regime will in fact vary measurably at the macro-scale. Examination of recent papers citing the IDH in the ISI Web of Science data base confirms that evaluations of the IDH tend to be landscape (or local to landscape) in scale and that even at this scale it has mixed success (see, e.g. Bornette & Amoros, 1996; Schwilk *et al.*, 1997; Townsend *et al.*, 1997; Sheil, 1999; Beckage & Stout, 2000). The closest to a test at a regional or geographical scale that we encountered is the study by Hiura (1995), although in fact the data he uses are from small patches of forest and are thus based on local inventories rather than species range data. Similarly, Loehle's (2000) interesting attempt to develop a model accounting for richness variations, which incorporates biological traits in respect of disturbance regime, is essentially operationalized at the landscape scale, requiring climatic inputs to enable regional calibration.

Biological interactions

Although Table 3 identifies commonly cited general hypotheses, there are of course innumerable specific theories and hypotheses of diversity, particularly so at local scales of analysis (e.g. see Silvertown *et al.*, 1999; Hugueny & Cornell, 2000; McCann, 2000; Tilman, 2000). As an illustration of the difference between explanation at the local and geographical scale, Wilson (1990; see 1994) identifies twelve possible mechanisms by which alpha-scale species diversity patterning may be determined, i.e. for how the species of a local community coexist without competitive exclusion occurring. In his meta-analysis, he evaluates each of these mechanisms for data from indigenous vegetation of

New Zealand. He finds some support, with diminishing confidence, for the following mechanisms: (1) gradual climate change (fluctuation), (2) cyclic successional processes, (3) spatial mass effect, (4) niche diversification, and (5) aggregation. He finds little support for, (6) the intermediate(– timescale) disturbance hypothesis at the alpha scale, except for small forest gaps (see above). In addition (7) equal chance, and (8) life-history difference mechanisms may be involved and some conditions necessary for (9) the pest pressure hypothesis do appear to pertain. Three other ideas he dismisses as unimportant or non-existent at this scale are: (10) initial patch composition (11) circular competitive networks and (12) stabilizing coevolution. Simply reporting the various postulates involved in this single meta-analysis would take more space than we wish to devote here. Rather, we have chosen to focus on just one of these mostly biological ideas, the pest-pressure hypothesis (PPH) (Janzen, 1970) for broader evaluation across scales.

The PPH postulates that tree recruitment is depressed near conspecific adults because of host-specific predation or pest/pathogen attack. This suppresses the expression of competitive dominance and ensures that most species are sparsely distributed at a local scale and thus allows more species per unit area in the tropical rain forests, where conditions are ideal for pests and pathogens. This mechanism was proposed as one explanation for the high diversity of tropical moist forests, but at what scale does the PPH operate? One answer is that, if operating at all, it is a process measurable and testable only at the local scale of analysis (as, e.g. Nichols *et al.*, 1999; Barone, 2000). In its original formulation (Janzen, 1970) the PPH fails to identify any particular theoretical relationship to climate, but does refer to 'favourableness' and variability of climate. Thus, whilst the PPH is of broader heuristic value, as a basis for model building at the macro-scale, it is incompletely specified. Only by the accumulation of numerous comparative studies at the local scale in different climatic regimes can the PPH mechanism be evaluated. For it to contribute to an understanding of macroscale or geographical richness patterning it must be shown to operate to a consistently greater degree in tropical than temperate forests.

In fact, evidence for its operation in the lowland tropics is equivocal at best (e.g. compare Givnish, 1999; Nichols *et al.*, 1999; Harms *et al.*, 2000). Some studies find evidence, contra the PPH, of aggregated rather than dispersed populations of tropical moist forest species (e.g. Condit *et al.*, 2000). Few tests appear to have been undertaken in temperate regions, but at least one recent study has suggested that the mechanism of 'pest pressure' operates for a temperate forest species (Packer & Clay, 2000), thus raising further doubts as to whether this mechanism does distinguish clearly between tropical and temperate forests. Setting these doubts aside, if the PPH does indeed operate preferentially in the lowland tropics, the explanation is that conditions for biological activity are very favourable in these regions, enabling more generations of pests per year, and with no cold winter season to limit outbreaks (Janzen, 1970). In short, the argument for the PPH at the macro-scale

is directly based on climatic conditions enabling a longer duration (within the year) and thus greater amount (over a year) of biological activity. It thus constitutes one particular linkage mechanism whereby climatically regulated water-energy dynamics allows a higher capacity for richness in the lowland tropics than in boreal forests.

Parenthetically, one of the commonest questions posed of (or even by!) those promoting explanations of macro-scale patterns based on climatic variables is 'but what is the mechanism?' We envisage that there are in fact numerous linkage mechanisms that have operated over time (and will continue to do so) to contribute to the accumulation of more species per unit area in the tropical forests than at higher latitudes. Another such mechanism is provided by various hypotheses concerning niche differentiation, e.g. in response to light conditions in the understorey (Svenning, 2000). See also, e.g. Givnish (1999) and Tokeshi (1999). In short, our rejoinder to the question is that there isn't one linking mechanism, but a plethora! We have chosen to discuss only one for illustrative purposes, and not because other mechanisms are unimportant. The general case being made here is that biological/ecological mechanisms are either local in scale of application, or if regional in impact, are dependent upon climate for their patternation, and thus constitute secondary or 'linking mechanisms', rather than in their own right constituting first-order independent controls setting the pattern.

EQUILIBRIUM AND NON-EQUILIBRIUM WITHIN DIVERSITY HIERARCHIES

Isolation and impedance

Returning to insights from island biogeography, it is not always the case that empirical studies display a positive species–area relationship, although this is commonly the case. Two different scenarios can be put forward for exceptions to the general pattern, and they are not necessarily mutually exclusive. First, in cases where there is little variation in 'island' areas but significant variation in other factors (e.g. isolation, edaphic factors, climate), the species-area effect may be swamped by these other factors. Secondly, exceptions occur where the response times of the biota are too slow to enable an equilibrium pattern to develop. The first scenario is exemplified by Lomolino & Perault (2001), who find no species-area effect in a data set for forest fragment mammals, which they suggest is because their data set considers only small fragments and thus other factors swamp the area effects. Two studies of insect groups on remote oceanic islands neatly illustrate the second, non-equilibrium response, in having negative relationships between area and richness, but significant positive relationships between island age and species richness (Paulay, 1994; Borges & Brown, 1999). In both cases cited, this relationship has developed through *in situ* evolution of taxa on remote islands. The lengths of time necessary for highly derived taxa to evolve and great radiations to develop are often of the order of hundreds of thousands, or millions of years, even in essentially favourable circumstances (e.g. the Hawaiian or

Galápagos finches, reviewed in Whittaker, 1998). Whilst recognizing the importance of such long-term lag effects, it is noteworthy that micro and macro-fossil data indicate apparently rapid re-adjustment of continental species richness gradients in response to switches between glacial and interglacial climates (e.g. see Silvertown, 1985). Indeed, recent analyses of macro-fossil remains from Northwest Europe (Kullman, 1998) indicate that range adjustments of tree species, which might be anticipated to be amongst the slowest taxa to respond, because of the immobility of adults and other life cycle considerations, were far more rapid than hitherto assumed.

A crucial difference between the island cases and continental data cited in the previous paragraph lies in the ability of species of the plants and animals concerned to move between areas. As noted many times (e.g. Lomolino & Perault, 2001), the impedance of terrestrial landscapes varies hugely and in ways that vary greatly from species to species. It is also to be expected that landscape impedance varies significantly through time, such that for instance, the potential for forest trees to migrate through early postglacial landscapes may be quite different from their ability to migrate through today's landscapes. Isolation in an ocean is also not simply a function of distance (e.g. wind and sea current, and migration routes may be important), but is arguably simpler to assess than terrestrial landscape impedance. The point here is that predictable (climatic) patterns may be anticipated to occur where there is sufficient flow of biota across land-or sea-scapes, and sufficient time for biotic processes (e.g. migration, succession) to run their course, and 'unpredictable' patterns to occur when these conditions do not apply. Both conditions can apply, of course, such that studies may find in favour of different labels – equilibrium or non-equilibrium, climate or history – depending on choice of taxa, and the geography of the study system. Given which, every ecological hypothesis of diversity is born refuted. However, this is not to say that there are not universal laws and principles at work underpinning the predictable patterns in richness. Our ability to model these predictable gradients at the macro-scale (e.g. O'Brien, 1998; Kleidon & Mooney, 2000) provides evidence supporting the existence of such ecological laws. Whereas some authors take evidence of historical legacies in richness (or diversity) variation to refute climatic explanations, we contend that these deviations from predicted pattern are to be expected and, within a general explanation of diversity variations, can be seen to be broadly consistent with a first order climate-based model.

The saturation question
According to Rohde (1992, p. 524) 'the widespread view that diversity is limited by some environmental factor is based on the unsupported belief that all habitats are filled to capacity.' It is probably conceptually simpler to rationalize ideas of equilibrium patches occurring within non-equilibrium regions than the reverse. Yet, we contend (contra Rohde, 1992) that the reverse can occur, i.e. there may be a broadly equilibrial pattern at the macroscale,

within which local areas may be non-equilibrial (see also: Gaston, 2000; Loreau, 2000). By way of exemplification, for woody plants, the macroscale relationship can be envisaged as being set by the water-energy dynamics capacity rule (O'Brien *et al.*, 1998, 2000; O'Brien, 1998). But, this acknowledges that regions exhibit both significantly higher levels and lower levels of richness than predicted by the elegantly simple interim models thus far developed. The notion of non-equilibrium patches occurring within a broadly equilibrial macro-scale pattern can be understood by a consideration of the patchy nature of species ranges and of the differing forms of data considered at local and regional scales. Species range boundaries are more-or-less continuous envelopes containing far more spaces than objects. This is because of (1) the existence of large amounts of suboptimal or unsuitable habitat, (2) the presence of interacting species (competitors, predators, etc.), (3) temporal environmental variability, and (4) impedance of species movements within landscapes, meaning that not all suitable habitats are occupied at any one time (cf. metapopulation models).

There has been increasing debate as to whether local communities are indeed saturated, with much evidence indicating that they often are not (compare: Wilson, 1994; Kellman, 1996; Hugueny & Cornell, 2000; Loreau, 2000). Intriguingly, some recent analyses suggest that conditions of local dynamic equilibria (i.e. involving turnover of species through time, with constant richness) may be more commonly obtained in conditions of minimal effective isolation (impedance to species movement), than in recognizably 'insular' localities (Brown *et al.*, 2001; Ernest & Brown, 2001; Parody *et al.*, 2001). In these circumstances, local population adjustments as a result of fluctuating environmental conditions, allow communities to change in composition but retain a fairly constant number or density of species, as a function of basic energetic controls on ecosystem function. In contrast, real islands may commonly be neither equilibrial nor saturated with species (Heaney, 2000).

Interestingly, as noted above, palaeoecological/palaeobotanical data indicate that tree species range boundaries are capable of far more rapid adjustment than hitherto anticipated, in favourable conditions via jump dispersal at low densities (Kullman, 1998). Thus, species may respond individualistically to changing climatic conditions in adjusting the range boundary envelope, whilst vast amounts of 'holes' remain within the range. This is consistent with the persistence through time of spatial patterns in richness at the macro-scale as a function of basic energetic (climatic) controls.

MACROECOLOGICAL INSIGHTS

'The increase in species richness from the poles toward the equator described by earlier workers is now thought to be closely and mechanistically associated with other relationships, including decreasing size of geographical range (Rapoport's rule), increasing hab-

itat specificity, more even distribution of abundance among species, and contrasting roles of abiotic stresses and biotic interactions in limiting species ranges....' (Brown, 1999, p. 6).

Bigger cakes mean more slices

One of the questions commonly posed in response to diversity theories incorporating a productivity argument is 'why don't a small number of species monopolize the available energy?' (e.g. Rohde, 1992). The coexistence of species with similar habitat niches in areas of high productivity ('capacity' for richness) can be understood, according to Auerbach & Shmida (1987), in terms of variation in other niche components, and in terms of interactions with other trophic levels. The case advanced by Auerbach & Shmida (1987) is that diversity controls are scale-dependent (i.e. as advanced in the present article, that heterogeneity of different causal variables changes with spatial scale of analysis), and that within this framework, it is not necessary to assume equilibrium assemblages, nor to ignore the role of stochastic environmental variation at local scales. Phenological differences between species that result in temporal division of resources, differences in growth form, regeneration niche, responses to disturbance, pollination and dispersal syndromes, etc., are all mechanisms that result in the larger cake being distributed amongst more mouths, rather than the same number of mouths simply meaning more bloated stomachs (see, e.g. Tokeshi, 1999). In theory at least, many species of similar trophic niche (Auerbach & Shmida (1987) term them trophic equivalents), can be seen to be capable of coexisting, when the patchy distribution of resources and temporal environmental variation, are taken into account.

Recent macroecological analyses (studies of the emergent statistical properties of ecological data sets) provide additional important insights. As Brown (1999, p. 4) states 'The promise of macroecology is that it offers evidence that such general ecological laws must exist, and it provides some hints about how they work.' For instance, underpinning the high diversity of tropical forests are optimal or near-optimal conditions for biological activity, yet even in these systems, energetic constraints can be detected via macroecological analyses. This is shown by recent analyses of allometric relationships in dry tropical forests in Costa Rica by Enquist *et al.* (1999). They demonstrate, from a sample of 2283 trees of forty-five species measured 20 years apart, that when variations in wood density are accounted for, the data for tree growth variation with size fit remarkably tightly onto a quarter-power scale relationship. This indicates energy equivalence between species and supports the existence of an evolutionary constraint implying that, in whatever ways species may differ in terms of niche, to coexist they must all be capable of optimizing their growth rates so that their energy budgets balance (Enquist *et al.*, 1999; Whittaker, 1999). Underlying this constraint are physical and biological constraints on the distribution of water and materials in solution (nutrients, energy) through the plants' internal distribution networks (West *et al.*, 1999; Brown & West,

2000). This finding is interesting because it demonstrates that energetics (and water-energy dynamics) are important at all scales, down to the stand, even in benign climates, and notwithstanding that climatic regime varies little on this scale, such that alpha and beta diversity patterns are accountable primarily through other local-scale factors and processes (above).

Trade-offs

Following this line of reasoning, if we are arguing that communities are often unsaturated, and that they are typically variable in space and time, what determines the range boundaries that go to make up the macro-scale gradients in plant richness? Are they 'hard' boundaries, set environmentally, or are they 'soft' boundaries, set by competitive and other biotic interactions? Given the difficulties of demonstrating competitive exclusion on the local scale, it is hard for many ecologists to credit that the boundaries of species ranges might be set competitively, but data do clearly point in this direction (e.g. Stevens & Enquist, 1998). The explanation for contrasting roles of biotic and abiotic factors in setting different range boundaries may lie in trade-off mechanisms that are also consistent with the size-growth scaling relationship reported by Enquist *et al.* (1999).

One such mechanism has been suggested by Loehle (1998). He has examined the northern and southern range limits for twenty-two species of North American trees. Whilst noting the importance of water balance (drought) in range limits, he identifies temperature as the key parameter determining tree distributions. He notes that forest growth models typically assume a unimodal growth response in relation to various measures of energy, i.e. such that growth typically declines to zero at northern and southern range boundaries. However, he observes that in practice, the best growth is often found at the southern end of the range, or even further south when trees are planted as exotics. His explanation for this is based on a trade-off between the costs of cold hardiness and maximum growth rate. No one species can optimize energy use in all climates, the problem at the northern (high latitude) end being to maximize use of the available growing season without being caught out by early or late cold. At the southern (low latitude) end of the range, trees are in essence too conservative, i.e. grow too slowly and/or are active too little of the potential growing season. Southern range limits are thus set not by too much heat, but by competition with superior competitors, i.e. a suite of species with faster growth rates. Competition in this context is diffuse and involves interactions with pests, pathogens, etc. as well as direct competition for, e.g. light and water. Whilst local communities and patches may be variously unsaturated, saturated or even super-saturated, species range boundaries settle down to a pattern of geographical overlap, within which many species are constrained well within their fundamental niche. A further contributory macroecological pattern is that species show high abundances only near the centre of their ranges, and appear to have typically low abundances near their range limits (e.g. Enquist *et al.*, 1995;

Brown *et al.*, 1996). Together, these features of species distributions provide through time for relatively rapid reactions even to significant changes in climate, thus allowing for the persistence through space and time across much of the globe of the climatic pattern of species richness at the macroscale (O'Brien, 1998).

Rapoport's rule and its place in the hierarchy
Rapoport's rule is another latitudinal trend, whereby the mean size of species' geographical ranges decline toward the equator. Stevens (1989), who gave the rule its name, suggested that it might be an explanation for the latitudinal gradients in richness. He argued that accidentals at the range margins persist by the 'rescue effect' and that towards the equator the ratio of rescue effect area to geographical range increases, creating more opportunity for species richness to be inflated. Taylor & Gaines (1999) present mathematical simulation models suggesting that the Rapoport and rescue effects cannot on their own account for the grand cline in richness. They found that only by introducing the effects of competition and certain unrealistic assumptions (e.g. that all points on the earth's surface are filled to saturation), could the Stevens hypothesis explain the gradient. Moreover, as Kerr (1999) points out, first, not all empirical studies support the existence of Rapoport's rule (see also: Gaston & Blackburn, 2000), and secondly, the mechanism put forward to account for it is essentially a climatic argument, concerning the degree of climatic variability. In his analyses of two insect taxa and the class Mammalia, Kerr found that a measurement of ambient climatic energy accounted for most of the observed variance in richness (using variable area quadrats of $2.5° \times 2.5°$ and $2.5° \times 5°$) across North America, with climatic variability providing very poor models. While there may well be links between the species richness gradients and other macroecological phenomena, including Rapoport's rule (Brown, 1999), the latter clearly occupies a less fundamental position in the hierarchy of explanation, than the water-energy dynamics capacity rule. We therefore concur with Brown (1999) when he wrote '…. many of the statistical patterns of body size, abundance, distribution, and diversity or over space and time can be attributed ultimately to the effects of limited energetic and other resources. The macroecological patterns reflect general principles which govern the division of these resources among individuals and species and over space and time….' (Brown, 1999, p. 8).

SYNTHESIS

'Since processes which produce biological diversities operate differently, and at different rates according to the position of biological phenomena along the scales of space, time and change, many theories and paradigms are probably more complementary than conflicting.' (Blondel, 1987).

We argue above for area to be held constant, and for model building to begin with dynamic models of richness. It will be appreciated, however, that it is not quite so easy to dismiss

area and history from consideration, and that in particular geographical circumstances, both may be evident. If the extent of a land mass is limited, e.g. as with an island, or a peninsular, then a large environmental perturbation, such as the climatic changes associated with glacial–interglacial switches, could result in the loss of a portion of the species once found there, as the region fails to provide habitat within their climatic envelope (Brown & Lomolino, 1998). As others have noted, the occurrence of frost (a physical change in the state of water) appears to be one particularly important threshold that large numbers of plant species have failed to cross (Latham & Ricklefs, 1993; Turner *et al.*, 1996) and which could eliminate species from an enclosed (water or mountain-bounded) region during a cold climatic episode. By such means, the species complement of a region of this sort could be significantly reduced for periods longer than the Holocene has yet run (McGlone, 1996).

This particular historical/area effect concerns the continguity of habitats in space and through time, avoiding sampling effects (see also Gaston, 2000). As palaeoclimate scenarios improve and with better understanding of land-sea configurations through the Quaternary, it becomes possible to develop *a priori* hypotheses as to those regions where macro-scale richness (at scales of *c.* 10,000 km^2 or more) should indeed be depressed below the values predicted from area-invariant climate-based models. It is difficult, however, to develop climate-based models capable of identifying such effects on the basis of empirical data from study areas that have been heavily influenced by precisely those climate-chance driven episodes of species removal. It is this problem that seems to lie at the heart of the debate (e.g. Francis & Currie, 1998; Ricklefs *et al.*, 1999) as to whether it is history or climate that provides the first-order model of diversity.

The development of models from areas where Pleistocene glaciations have had less drastic impact, appears to provide a basis to circumvent this problem (O'Brien, 1998). Theory development requires that biogeographical hypotheses, such as alluded to above, are integrated into the general theory of diversity, but we regard them not as the first step in explaining richness variations, but rather as a complement to the climate-based models. The stress in a number of recent articles on a dichotomy between climate and history, which we crudely characterize as pointing, respectively, to the existence of a dynamic pattern based on underlying capacity rules or ecological 'laws' (Brown, 1981, 1999), and to the role of contingencies and events, is hindering progress towards a 'complete' understanding of richness variation and a more complete theory of diversity. Calls for integration have come from both sides of this divide. For instance, the palaeoecologist, McGlone (1996, p. 313) writes 'Ecological and biogeographical processes work continuously through time, and the current situation must reflect past ecologies. These past ecologies are largely under the control of past distributions of energy and moisture, and so in turn are related to current latitudinal energy gradients.' This we concur with. McGlone goes on to state that '…No matter how well large-scale climate-species diversity correlations may predict current species richness, they essentially have no

explanatory power.' It is right to caution that explanatory power is not simply a question of r^2 values, particularly given the troubling question of what autocorrelation may mean for r^2 values derived from contiguous grids (Lennon, 2000). However, explanatory power can be derived from statistical models built upon a clear theoretical case, and especially so when the model developed can be shown to have some predictive power.

Another line of argument focused on an aspect of area, specifically geometric constraints on species ranges, has been advanced by Colwell & Lees (2000). They use null models that generate a so-called 'mid-domain effect', a peak in richness in the middle of a study region or domain. This, they argue to be a logical consequence of placing data sets of species of varying range size (whether empirically or theoretically generated) randomly within a bounded domain. Their models point to the possibility of geographical patterns in richness that happen to be correlated with putative causal variables, being indistinguishable in practice from patterns generated by a model that assumes geometric constraints on the range boundaries of all species, but which contains no other biological or ecological rules. We can gain interesting insights and cautions from such 'experiments', but as ever the case when null models are applied in biogeography (Gotelli, 2001), it is important to look at the assumptions involved in these mid-domain analyses. Two appear particularly important: (1) ranges are treated as continuous between the northern and southern extremes (or other geographical axis), and (2) the analysis is restricted to species bounded by, i.e. endemic to, the region under analysis. The corollary of this is that the null models are inapplicable to studies that do not involve either or both of these restrictions. Examples would be any studies of richness patterns based on all native species (e.g. of birds, or mammals, or woody plants), using grid cell systems wherein the presence of a species in a cell in the data set is based on firm evidence that it actually occurs there (e.g. O'Brien, 1993; Andrews & O'Brien, 2000). In so far as a region abuts another (e.g. North and South America) or has in the past exchanged species, the legacy of shared species would seem to constitute a normal feature of biogeography (Brown & Lomolino, 1998). It therefore seems odd, if the aim of the exercise is to understand controls on geographical variation in richness of a particular life form, to ignore native species that happen to occur outside the target region.

In developing the 'water-energy dynamics' theory, O'Brien (1993, 1998; O'Brien et al., 1998) stresses the necessity of thinking about the diversity problem through space and time simultaneously. According to this line of thinking, the persistence of a planetary-scale climatic gradient through time (albeit subject to modification) has provided the basis for the generation and persistence of macro-scale variations in biological activity, beginning with photosynthesis, and in turn generating the response of spatial variations in richness. This is not to claim that the pattern will have remained static or fixed in amplitude. Were the data available for millions of years back or forward in time, they would doubtless reveal changes in detail of the pattern and in amplitude, but not in

the existence of the grand cline (re: the historical evidence, see: Crane & Lidgard, 1989). Whereas evolutionary rates of gain and/or loss of species may vary across the globe, it is ecological controls (based on energetic constraints) that set the limits, within the constraints of the biotic and abiotic interactions of the time. So, at the macro-scale, there will always be more tree species where optimal energy conditions are combined with abundant moisture, than at the poles.

In this article, we have advocated the development of a hierarchical theory of diversity, favouring a top-down approach to the problem (see also Gaston, 2000). Whilst there is a rich tradition of bottom-up ecology, and it undoubtedly has its part to play in the understanding of diversity (e.g. Tilman, 2000), we are unconvinced that the reductionist approach lends itself to the identification of the general laws and 'rules' that are the mark of a maturing discipline (for more general advocacy of top-down approaches in ecology see: Allen & Starr, 1982; Brown, 1995; Maurer, 1999). We have also argued for the importance of controlling scale explicitly in analysis and evaluation. Our review has focused on species richness (species density) variations, and the idea that different factors exhibit measurable variation – and have explanatory value – at different scales of analysis (cf. Peterson & Parker, 1998). To restate this, no matter how important we know an environmental factor to be to the ecology of a group of organisms, if it happens to exhibit no variation across a series of sites, it is incapable of influencing the pattern of richness therein. In essence, the building blocks of this account of richness variation begin at the macro-scale with plants, energetics and climate (water and energy). The 'capacity rules' for richness at the macro-scale described to date constitute first-order generalizations, from which deviations are climatically 'unpredictable'. Such deviations are, however, to be predicted from a knowledge of other ecological and biogeographical factors. Within these macro-scale patterns we may then refine a nested sequence of landscape to local-scale analyses and theories.

This is, however, but one part of a general theory of diversity. A general theory must accommodate variations in biogeographical distinctiveness (i.e. patterns of endemism) at a variety of taxonomic levels, from orders to subspecies and populations, and how historically, these patterns may have arisen. We contend that these elements of theory must also address the question of scale, in both space and time (Table 2). There is a general tendency, in at least some classes of biogeographical pattern, for there to be positive linkage between space, time and change, i.e. patterns evident over greater distances involve greater changes over long time periods than patterns evident over smaller distances. However, this linkage is imperfect (Blondel, 1987) and becomes more complex the more response variables are given simultaneous consideration. Hence, it must be recognized that a general theory of diversity implies a plurality of purpose, addressing multiple patterns. A general theory of diversity cannot be solely equilibrial, nor non-equilibrial, nor can it be based solely on geometry, nor can it be entirely historical, nor ahistorical, rather it

must incorporate all of these things. Such a body of theory is not resolvable to a simple equation or in verbal form a single sentence (unless horribly lengthy!). Elements of this general theory can, however, be of this form. As Brown (1999) contends, '…One implication of many macroecological patterns, such as the latitudinal gradient of diversity and the inverse relationship between body size and population density, is that limited energetic and material resources powerfully constrain the organization of ecological systems.' These patterns and these constraints, if further supported and developed, provide a basis for the construction of transcalar theories of diversity, encompassing not only the ecological phenomena of richness variation, but also the biogeographical phenomena.

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