On the diversity of land plants[1]

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Abstract: To understand the current patterns of plant diversity, it is necessary to consider the various controlling factors within the broad range of both spatial and temporal scales. We briefly review historical and geographical evidence for the evolutionary context. We concentrate on recent studies investigating the processes that control plant diversity to outline our present knowledge of plant diversity. Most of the research is drawn primarily, though not exclusively, from data collected in wetlands, although there are parallels to terrestrial systems. Future directions for the study and conservation of diversity are recommended.
Keywords: wetland plants, experimentation, evolution, species pool.

Résumé : Pour comprendre le portrait actuel de la diversité chez les plantes, nous passons en revue les différents facteurs pouvant l'expliquer, que ce soit au niveau spatial ou temporel. Nous analysons les facteurs historiques et géographiques ayant influencé la diversité des plantes, le tout dans un contexte évolutif. Nous nous concentrons sur les études récentes traitant des processus qui influencent la diversité des plantes pour mettre en évidence les connaissances actuelles en la matière. La plupart de ces études se rapportent aux milieux humides, mais nous faisons ressortir certaines similarités avec les milieux terrestres. Nous suggérons quelques pistes de recherche sur la diversité végétale, notamment en matière de conservation.
Mots-clés : plantes de milieux humides, expériences, évolution, pool d'espèces.

Introduction

How many kinds of plants are there? And why do some areas have more plants than others? Both Hutchinson (1959) and May (1988) have addressed an analogous question in papers that are now benchmarks in ecology. However, both papers concentrate on patterns of diversity in the animal kingdom. Hutchinson (1959) writes in his essay entitled "Homage to Santa Rosalia" "[W]hy are there so many kinds of plants? As a zoologist I do not want to ask that question directly, I want to stick with animals but also get the answer." May (1988) makes one single statement (without a reference) on plant diversity, in his paper entitled "How many species are there on Earth?", that "The fungal and plant kingdoms represent roughly 22% of species," at which point May moves on to a discussion of animal diversity! Yet, plants constitute roughly one-quarter of a million species (Groombridge, 1992) and 99% of the world's biomass (Whittaker, 1975), while the number of species of fungi has been estimated at 1.65 million (Hawksworth, 1990).

Our goal was to review the factors that allow so many different species of plants to occur and to coexist. This project had two components: (*i*) to determine which environmental factors are correlated with plant diversity, and (*ii*) to determine which methods have provided evidence about the nature of these patterns? In addition, we illustrate many of these patterns using wetland plants. Much of the evidence used in recent work concentrates largely, or even exclusively, on a subset of the terrestrial plants. If nothing else, we hope to expand the data base for exploring questions of plant diversity, but we also intend to ask whether plants of wet habitats have any distinctive patterns that complement results obtained with other floras. Plants of wet habitats can be included as part of the terrestrial flora since they are all secondarily derived from terrestrial species (Sculthorpe, 1967; Hutchinson, 1975; Tomlinson, 1986), and have largely failed to recolonize the oceans (the genus *Zostera* being one of the very few exceptions). We leave the topic of oceanic algae to better qualified authors. The answers to our initial questions, of course, depend on the scale at which one chooses to pose the question. We will begin with the largest scales and then move to the smallest.

The evolutionary context of the problem

At the largest scales of space and time, three events need to be emphasized. First, about 400 million years ago, early land plants evolved, entering new habitat into which adaptive radiation could occur (Benson, 1959; Scagel *et al.*, 1969; Stewart & Rothwell, 1993). *Rhynia* and *Asteroxylon* are two well-known examples. Second, about 200 million year ago, the Gymnosperms solved the problem of reproducing in dry environments; seeds are found independently in a number of different orders including the Gnetales, Ginkgoales, Welwitschiales, Cycadales, and Coniferales, as well as three extinct ones (Pteridospermales [seed ferns], Bennettitales, and Cordaitales). Only the Coniferales is a common component of today's terrestrial communities, having eight families, some 50 genera, and hundreds of species. Gymnosperms range from the largest of all trees, *Sequoiadendron giganteum* of California, to the bizarre *Welwitschia mirabilis*, which consists of only two spreading leaves and a bowl-like stem supporting strobili, and is found in a small area of the southwestern deserts of Africa.

The third event occurred some 130 million years ago in the Cretaceous period, with the appearance of angiosperms. There was rapid radiation by the angiosperms, plants which were capable of producing flowers, protecting the ovules within a bract called the megasporophyll (carpel or pistil), and had double fertilisation. After this point, the total number of species increased dramatically, but the number of plant groups other than angiosperms declined (Figure 1). Angiosperms now dominate all terrestrial plant communities, except for at high latitudes and altitudes, where conifers are still abundant (Archibold, 1995).

One important feature of angiosperms was their ability to shorten the life cycle by reducing the gametophyte stage to little more than a few cells borne on the sporophyte. This drastic reduction in the complexity of the gametophyte allowed for a relatively short generation time, hastening natural selection and evolution (Figure 2). In addition, some angiosperms started using beetles to efficiently carry pollen from one plant to another (Percival, 1965). The gymnosperms, in contrast, remain dependent on wind pollination, and have vast numbers of microstrobili to dispense clouds of pollen into the atmosphere. This pollen is passively spread into any nearby receptive ovules in megastrobili; the use of insect vectors by angiosperms is much more precise. While it is widely understood that insect vectors greatly reduced the amount of pollen produced, a second consequence seems to have been generally overlooked. Clouds of wind-dispersed pollen place a severe restriction on the number of coexisting species (and possibly also on rates of speciation), since neighbours will flood one another with pollen grains. In contrast, flowers allow for a nearly endless diversification of reproductively isolated species, even if they occur within close proximity. Each can remain reproductively isolated

behind barriers erected by flower design and type of insect used for pollination (see Ehrlich & Raven, 1964; Percival, 1965; Futuyama & Slatkin, 1983; Crepet & Friis, 1987 for further discussions on co-evolution). We suggest that this was the key step in both the rapid evolution and persistence of angiosperm diversity. It may be noteworthy that existing stands of conifers still consist of only a few species represented by large numbers of individuals of each kind. In contrast, in the tropics, where one finds a vast array of complex flower types and complex methods of cross pollination, each species may be represented by a few individuals widely separated from one another. This feature of the angiosperms is beautifully expressed in Perry's (1986) book on tropical forest canopies:

Some tropical trees produce massive amounts of flowers in an opulent display of color and aroma that can be seen for miles around. Since individuals of the same species may be separated by hundreds of yards or even miles, it is thought that these flowers act as "billboards" to help pollinators locate familiar sources of pollen and nectar within the confusing array of hundreds of tree species that make up a jungle community (p. 59).

In other words, the evolution of insect pollination allowed for the partitioning of biomass into many more reproductively isolated units, and this simply could not have happened to the same degree in the Gymnosperms, given their reproductive system.

SCALE AND PATTERN

The scales at which we look for pattern can range from the diversity (or to be more precise, the pool) of the global biota to the occupants of a single quadrat of 0.25 m^2 (or even smaller). Similarly, we can ask about diversity patterns present today, or look back in time to diversity patterns in previous geological eras. The scales of ecological inquiry are very broad, and apparent discrepancies in results can often be attributed to different temporal or spatial scales (Delcourt & Delcourt, 1988).

To better understand current plant distributions, we turn to the conditions of the world during and just before the Cretaceous. During the Triassic and Jurassic, Gondwanaland separated from Laurasia as the Tethys sea opened (*ca*. 250 million years BP). Many surviving ancient plants are found today in regions of the world that were derived from Gondwanaland: South America, Africa, Australia, New Zealand, and India (Scagel *et al*., 1965; Archibold, 1995). Some of these families have radiated extensively: the family Proteaceae, for example, has diversified to about 50 genera and 1000 species (Benson, 1959), and the Restionaceae to some 30 genera and 350 species in the southern hemisphere.

A major catastrophic event, probably a meteorite (Alvarez *et al*., 1980), at the Cretaceous-Tertiary boundary also seems to have contributed to the current distribution of vascular plants. Tschudy *et al*. (1984) and Wolfe (1991) show paleobotanical evidence that the vegetation at the end of the Cretaceous was largely destroyed, leading to the abrupt extinction of a number of plant species. Plant refugia must have remained, however, as recolonization did occur. Ferns were the first invaders, followed by angiosperms (Tschudy *et al*., 1984; Wolfe, 1991). Such a disturbance would have provided the opportunity for new biotic radia-
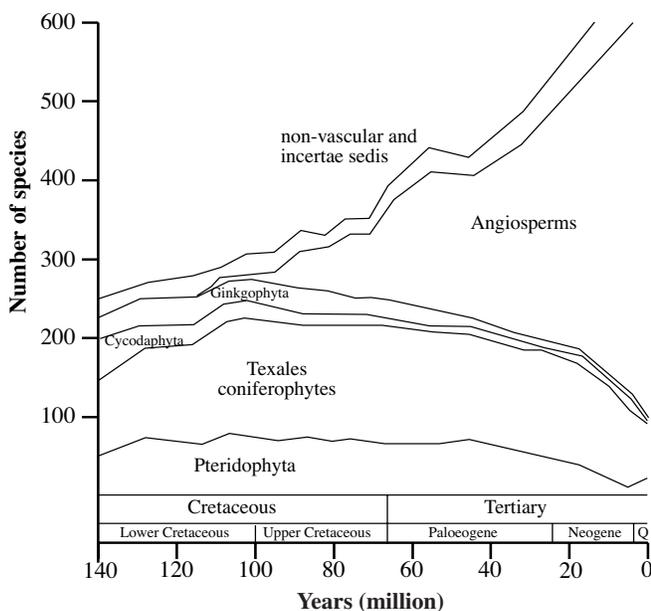

FIGURE 1. Changes in the diversity (at the species level) of suprageneric taxa represented in the Late Mesozoic and Cenozoic. Owing to the sources of data (predominantly from North America, Europe and Asia), these graphs more properly reflect changes in plant diversification for the Northern Hemisphere. Rates of speciation measured in million years (from Niklas *et al*., 1985, with permission).
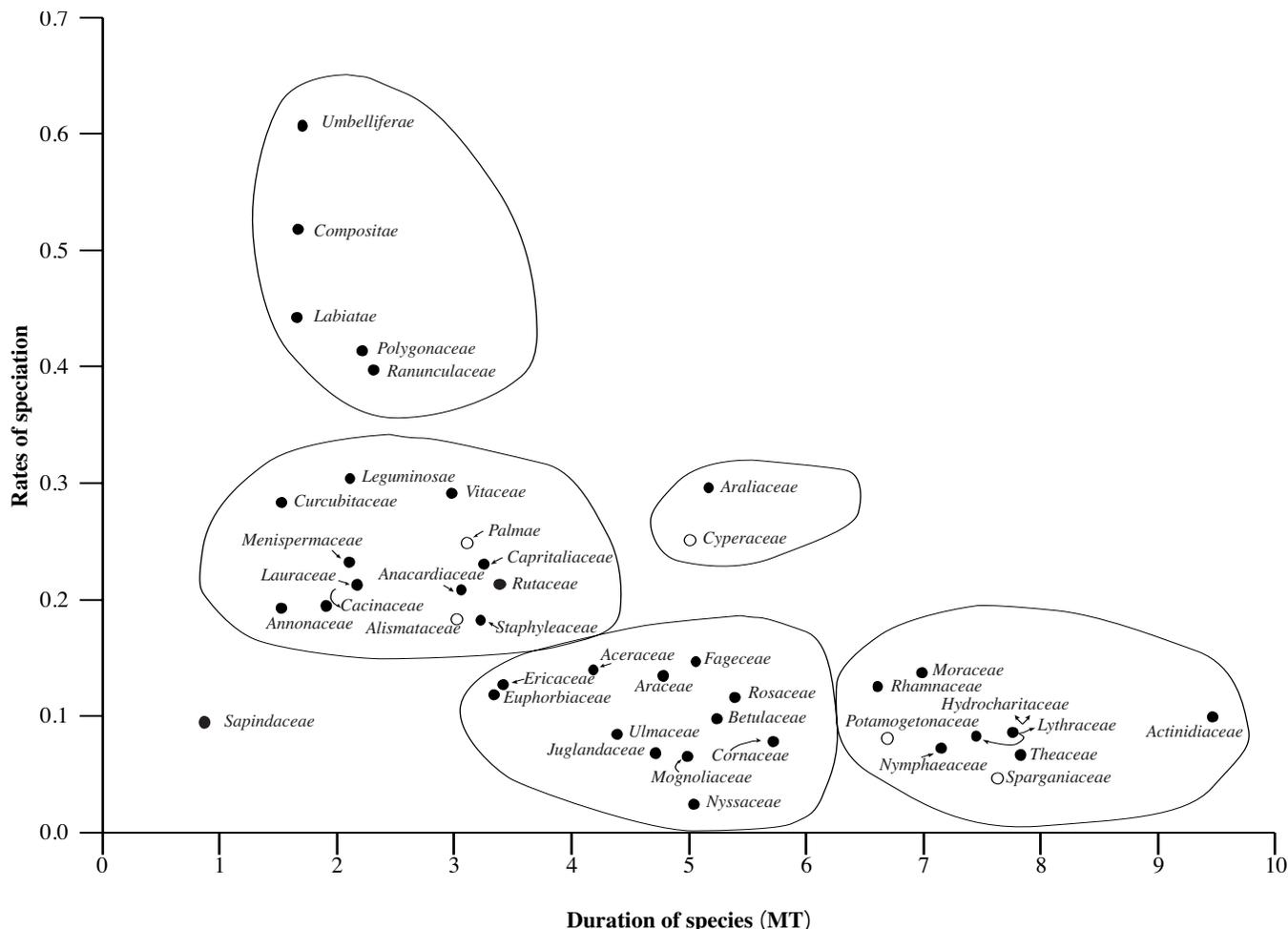
FIGURE 2. Plot of mean species-origination rate *versus* mean species duration for representative families of angiosperms (filled circles - dicotyledonous families; unfilled circles - monocotyledonous families). The solid lines drawn around groups of families are subjective. (From Niklas *et al.*, 1985, with permission).

tions, resulting in a potentially very different plant kingdom. Certainly, Alvarez *et al.* (1980) argues that this critical event allowed mammals to replace dinosaurs.

In conclusion, there are many problems for paleobotanists to solve concerning the origin and diversification of plants, and angiosperms in particular. But based on current understanding, both the present distribution of ancient plant genera (*e.g.*, *Araucaria, Podocarpus*, *Nothofagus*) and the present diversity in other genera (*e.g.*, *Acacia, Eucalyptus, Banksia*) can best be explained by events that happened millions of years before the present.

More recent studies have sought to better quantify these patterns of diversity. Woody plants have been examined on large scales (Currie & Paquin, 1987; Specht & Specht, 1993; Austin, Pausas & Nicholls, 1996), confirming that diversity is strongly correlated with productivity, measured as potential evapotranspiration rate. As a result, Currie & Paquin (1987) and Currie (1991) show that cold climates support few woody species. Energy availability is greatest in tropical regions. The tropics, therefore, may have greater species diversity as a consequence of high energy availability (Wright *et al.,* 1993). Latham & Ricklefs (1993a) tested this proposition and concluded that Currie & Paquin's (1987) North American model failed to predict regional species

richness in other parts of the world. However, Francis & Currie (1998) re-analysed the Latham & Ricklefs (1993a) data, combined it with the Currie & Paquin (1987) data, and found evidence consistent with the richness-energy hypothesis. The main argument Francis & Currie (1998) make is that Latham & Ricklefs' (1993a) data are ambiguous due to strong collinearity between annual evapotranspiration rate and region, making it impossible to distinguish between the effects of these two variables on species richness.

History is probably important as an ultimate cause of species diversity, although testing an hypothesis based on an historical explanation is often difficult (but see Alvarez *et al.*, 1980; Tschudy *et al.*, 1984). One alternative, and historical, hypothesis to the richness-energy hypothesis is provided by Axelrod (1970), who observes that far back in the fossil record tree species were restricted to "equable conditions", by which he apparently means absence of freezing conditions or severe drought. Latham and Ricklefs (1993a, b) postulate that the current distribution of diversity still betrays the Cretaceous origins of this flora in warm regions, and that there has been insufficient time to produce woody forms adapted to colder climes.

It may also be the case that woody forms of plants are simply unable to cope with the cold conditions (freezing

tolerance) at higher latitudes. The tree growth form is just one end of a continuum of size and woodiness in plants. Therefore, when exploring hypotheses about tree species diversity, we are required to consider two different hypotheses: (*i*) that the number of plant species may change, and (*ii*) that the proportion of species with tall woody growth forms may change. The shift away from the tree growth form at high latitudes was documented early this century when Raunkiaer (1908) classified plants into ten life forms, depending on the degree of protection provided to apical meristems. Phanerophytes, *i.e.*, trees and shrubs with buds (meristems) borne above the surface of the ground, were most sensitive to freezing because the buds were not buried in the soil. Raunkiaer collected data from many different climatic types showing that the proportion of tree species always declined in abundance in cold climates (Table I). Nanophanerophytes (shrubs with meristems that could be buried beneath snow) or cryptophytes (with meristems buried in the soil) increased at higher latitudes. The theory of cold adaptation offered by Raunkiaer is a parsimonious explanation for changes in growth form with latitude. Since these sorts of physiological constraints may well have operated millions of years ago, there is little reason to doubt the opinion of Axelrod that trees were always more common in the wet tropics.

Raunkiaer not only described these patterns, but constructed what is probably the first null model in ecology, his "biological normal spectrum". He begins his discussion with the observation that Nanophanerophytes are abundant in the Seychelles.

"But what do these numbers mean? Are we to conclude from the fact that the Nanophanerophytes are the best represented life-form that it is the Nanophanerophytes that are particularly characteristic of the humid and hot tropical regions? By no means! The large number of Nanophanerophytes (sic) might perhaps mean that this life-form is common in the world taken as a whole ... what we lack is a standard, a 'normal spectrum' with which to compare the spectra of the various regions, and by means of which the value of the individual numbers can be determined. It is most reasonable to suppose a normal spectrum of the whole world, that is to say the percentage of each life-form in the flowering plants of the world." (Raunkiaer, 1908; p. 115)

Raunkiaer selected 1000 species at random from the world's flora, paying close attention that no two species were from the same genus, and constructed a life form spectrum which he then used as a reference against which to compare the life form spectra of specific climates (Table I). His data show that in the case of cold, there was a shift in growth

away from Phanerophytes towards Nanophanerophytes and Cryptophytes (Hemicryptophytes, Geophytes, and Helophytes). Further, this shift away from the tree growth form could be measured against departures from what appear to be the first null model in ecology: the biological normal spectrum.

Rosenzweig (1995) departs from an energy-based climate view, suggesting that the increase in the species pool with decreasing latitude is due largely to a concurrent increase in land area (*i.e.*, the species-area relationship; but see Rohde, 1997). Remarkably, Crow (1993) reports that the latitude-richness patterns observed in many groups of organisms (MacArthur, 1972; Pielou, 1979) do not occur in aquatic plants, and if anything the flora is richer in the temperate zone (see also Rejmankova *et al*., 1995). Although knowledge of tropical floras is insufficient, and not all the data are strictly comparable, Crow's compilation suggests that something is fundamentally different about global patterns of richness in wetland plants compared to terrestrial plants.

THE PHYSIOLOGICAL CONSTRAINTS ON DIVERSITY ARE ADDITIVE

We currently lack a general theory of how constraints restrict evolutionary diversification; however, it seems likely that each physiological constraint acts as a barrier (or filter; Keddy, 1992) to a certain subset of the flora. This barrier exists either because of the lack of an evolutionary solution to a particular stress, or more likely because the solution as such a high metabolic cost. A quantitative example is provided by Werf *et al*. (1988), who measured the respiratory costs of ion uptake in a species of sedge, finding that the proportion of ATP demand for ion uptake alone ranged from 10 to 36%! Perhaps consistent with the decline in diversity with latitude is the decline in diversity with salinity (Chapman, 1940; Sculthorpe, 1967; Tomlinson, 1986; Adam, 1990). A set of extreme conditions challenges the tolerance limits of a species by presenting new evolutionary challenges to the physiology of the organism. Even if these challenges are solved, there may well be added metabolic costs. In flooded and saline environments, these added costs would include the need to cope with anaerobic soil environments. This requires either inefficient energy extraction by fermentation instead of respiration, or specialized structures for transporting oxygen to the roots. Salinity further raises the cost of maintaining osmotic balance; there must be mechanisms to exclude the uptake of unnecessary sodium and chloride ions, or else special organs are needed to excrete them. Even herbaceous plants have had difficulty occupying the combination of flooding and salinity. The difficulty woody plants have had meeting this challenge is

TABLE I. Selected life-form spectra from Raunkiaer (1908). S = stem succulents; E = epiphytes; MM = mega- and mesophanerophytes (> 8 m); M = microphanerophytes (2-8 m); N = nanophanerophytes; Ch = chamaephytes; H = hemicryptophytes; G = geophytes; HH = hydrophytes; Th = therophytes

Regional Flora	Approx. latitude	Number of species	S	E	MM	M	N	Ch	H	G	HH	Th
Denmark	55° N	1 084			1	3	3	3	50	11	11	18
St. Thomas and St. Juan	5° N	904	1	2	5	23	30	12	9	3	1	14
Seychelle Islands	5° S	258	1	3	10	23	24	6	12	3	2	16
Aden	12° N	176	1			7	26	27	19	3		17
Clova (Scotland)	57° N	373			2	2	5	9	58	7	5	13
Spitzbergen	78° N	110					1	22	60	13	2	2
Normal spectrum		1 000	2	3	8	18	15	9	26	4	2	13

illustrated by the very low diversity of mangrove swamps, even in tropical regions where nearby freshwater flood-plains have some of the most diverse woody plant floras on Earth (Grubb, 1987; Gentry, 1988). Levitt (1977) and Larcher (1995) review the many physiological stresses that restrict growth of plants. Forested wetlands are potentially subject to a high number of environmental stresses, the most obvious being flooding. Keogh (unpubl. data) found that the greatest tree species richness within forested wet-lands was in tropical freshwater environments (Figure 3). Tree species richness progressively decreased with the addition of major constraints (*e.g.,* cold [tropical to temperate], peat, salinity).

Competition may provide a further limitation. The presence of neighbours raises the metabolic constraints on plants by increasing the cost of acquiring light and nutrients (Keddy, 1989). Hence, the first species to solve an evolutionary problem (such as a mangrove invading flooded saline conditions) receives a great added advantage by being able to occupy a habitat without neighbours. The metabolic benefits to all later species invading this habitat are automatically reduced by the canopy and roots of the first species. The pressures of competition, combined with those of the metabolic costs of adaptation, may well place an upper limit on the diversity of habitats with extreme environments. Of course, a mutualistic association would have the opposite effect (Boucher, 1985; Bertness & Shumway, 1993; Bertness & Callaway, 1994; Bertness & Leonard, 1997), making it difficult to disentangle the various effects of biotic interactions on evolution. However, clearly mutualistic interactions have not produced high-diversity mangrove swamps.
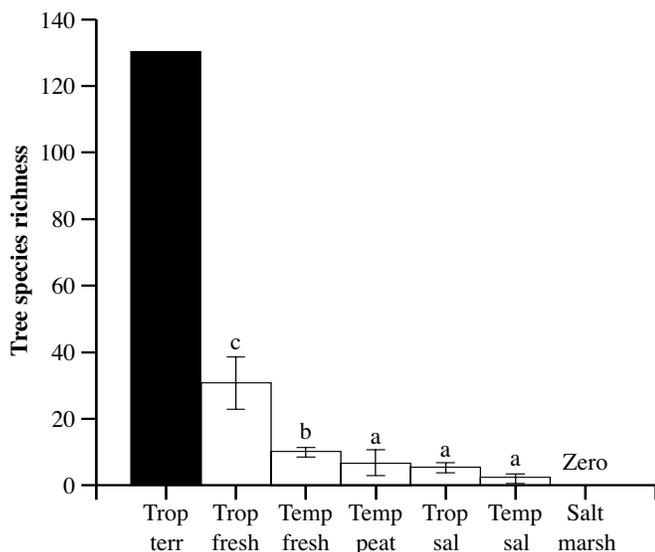

FIGURE 3. Effect of the addition of environmental constraints on tree species richness in forested wetlands. In this figure, Trop = tropical; Terr = terrestrial; Temp = temperate; Fresh = fresh water; Peat = peat lands; Sal = saline. 'Trop Terr' and 'Salt Marsh' are provided as reference points to compare tree species richness in forested wetlands with environments that have few stresses (Trop Terr), and many major stresses (Salt Marsh). Bars not sharing the same letter are significantly different using Tukey's test. Error bars represent 95% confidence limits (Keogh *et al.*, 1999).

TABLE II. Species pools of flora from a range of regions around the world (from Bond, 1997)

Region	Area (10^3 km^2)	Number of species	Species diversity (10^3 km^{-2})
Mediterranean climate regions			
Cape Floristic Region	90	8578	95.3
Cape Peninsula	0.47	2256	13.7
California Floristic Province	324	4452	13.7
SW Australia	320	3600	11.25
Greece	130	6000	30.8
Temperate Regions			
British Isles	308	1443	4.7
Eastern North America	3238	4425	13.7
Europe (Flora Europea)	10 000	10 500	1.05
Tropical Rainforests			
Panama	80	*ca* 8300	103.75
Malaysian Peninsula	130	*ca* 8000	61.5
Ivory Coast	320	*ca* 4700	14.7

Species pool

The word pool describes the complete list of species for a habitat or geographic locale (see Table II for examples of species pools in a variety of regions). Eriksson (1993) has provided a simple model to help explore the relationships between community richness (the number of species in a local community), and the number in the pool. Let the rate of change of the number of species in a particular community, dS/dt, be a function of local colonization and extinction, just as the number of species in the pool, N, is a function of speciation and extinction. The local colonization rate is then proportional to the number of species in the species pool, N, minus the number of species that are already present in the community, S, that is, the number of potential colonizers left in the pool. The local extinction rate, however, is a function of only the number of species already present, assuming the relationship is a first-order (linear) process. If we add in two proportionality constants for the rates of colonization (c) and extinction (e),

$$dS/dt = c(N - S) - eS \qquad [1]$$

and at equilibrium the value of S is

$$S^* = N (c / c + e) \qquad [2]$$

This simple expression yields some predictions. First, if the local extinction rate, e, is very low, then S^* will be close to N; that is, the local community will contain most of the species in the pool. Second, if the rates of colonization and extinction are equal, that is $c = e$, then $S^* = 1/2N$; the local community will have one half of the species in the pool. Third, if extinction rates are much higher than colonization rates, the community will be species-poor, despite the fact that the number of invading species per unit time will be relatively high. Therefore, one simple explanation for communities having many species is the existence of a large species pool, which Eriksson calls the species pool hypothesis. Depending on the values of e and c, however, a variety of other scenarios can be constructed.

In many cases, ecologists do not have data on the entire community, but rather on the number of species in a series of samples from that community, such as the number of species in a quadrat. In the very unlikely case where all of the quadrats are identical in composition, then the species

richness of one quadrat will be the same as the pool. The greater the difference between each pair of quadrats, the greater will be pool size relative to quadrat size. Since species richness (or number of species per quadrat) varies along biomass gradients, perhaps pool size also varies along the same gradient.

Connell & Orians (1964) predict that pool size will be highest in high biomass communities because these have the most energy to allocate among species. Alternatively, pool size may be simply a direct mirror of alpha diversity, and high pool diversity may occur where high alpha diversity also occurs (Preston, 1962a,b; Taylor, Aarsen & Loehle, 1990; Eriksson, 1993). Although this latter hypothesis may seem the most likely, particularly based on what is known about global diversity patterns, it is founded on the assumption that the degree of similarity among quadrats does not differ along local gradients, such as a fertility gradient on a hillside or a disturbance gradient along a lakeshore. Wisheu & Keddy (1996) tabulated data for 640 quadrats from shoreline marshes across eastern North America, plotting both species richness and pool size against biomass (Figure 4). Both reached maxima in similar habitats with approximately 50 g/0.25 m^2. Alpha diversity was a nearly constant percent of pool diversity, irrespective of the biomass of the sites examined.

The ecological processes that cause this pattern in pool size remain unclear. Is the pool pattern (produced by large-scale evolutionary processes and dispersal) causing the well-known 'humped-back' (*sensu* Grime, 1973) model? Or is the alpha diversity pattern (produced by local ecological processes such as stress, disturbance, and competition) causing the pool pattern (Zobel, 1997)? These sorts of basic questions have important consequences for the ways in which we design and manage nature reserve systems.

EXAMPLE: PLANT DIVERSITY IN MEDITERRANEAN CLIMATE REGIONS

Five areas of the world have Mediterranean types of climate with warm dry summers and cool, wet winters. In order of decreasing size, these are the Mediterranean basin, California, south-western Australia (kwongan), central Chile, and the cape of South Africa (fynbos). The species pool for each region has been estimated by Cowling *et al*. (1996a) in Table III, and fynbos ranks as one of the highest. Many of the species are sclerophyllous shrubs that appear superficially similar, but Cowling *et al*. (1996a) attribute the high plant diversity to relatively low growth rates and the reshuffling of competitive hierarchies after fires. There are some distinctive features of the species pools in these areas. The southern hemisphere family Proteaceae is very well-represented in both the fynbos and kwongan. These two areas also appear to have converged in a number of other ways: they share high diversity, a high incidence of species with obligate dependence on fire for reseeding, serotinous seed storage in the canopy, and seed dispersal by ants (myrmecochory; Cowling *et al*., 1994). Other genera have rapidly diversified into this habitat, including *Eucalyptus* (> 300 species), *Acacia* (> 400 species) and *Erica* (> 500 species). Across all five regions there is a clear relationship between species richness and area (Figure 5).

Gradients and gaps

Environmental gradients play an important role in determining diversity. Gradients, such as elevation (Whittaker, 1956; Peet, 1978; Cowling *et al*., 1996b), soil depth (Gagnon & Bouchard, 1981; Belcher, Keddy & Twolan-Strutt, 1995; McDonald, Cowling & Boucher, 1996), or salinity (Grace & Pugesek, 1997), increase the heterogeneity of a site so that more species can coexist. On a small scale, the diversity of particular sites is determined by their position along gradients. Lakeshore vegetation is an ideal habitat for studying gradients because the plants form an obvious zonation where species occupy different positions relative to the water level (Hutchinson, 1975; Keddy, 1983). Keddy (1984) tested whether increased diversity is correlated with increased specialization along gradients, the degree of specialization for each species being measured as the mean depth range occupied. The results, based on 30 transects
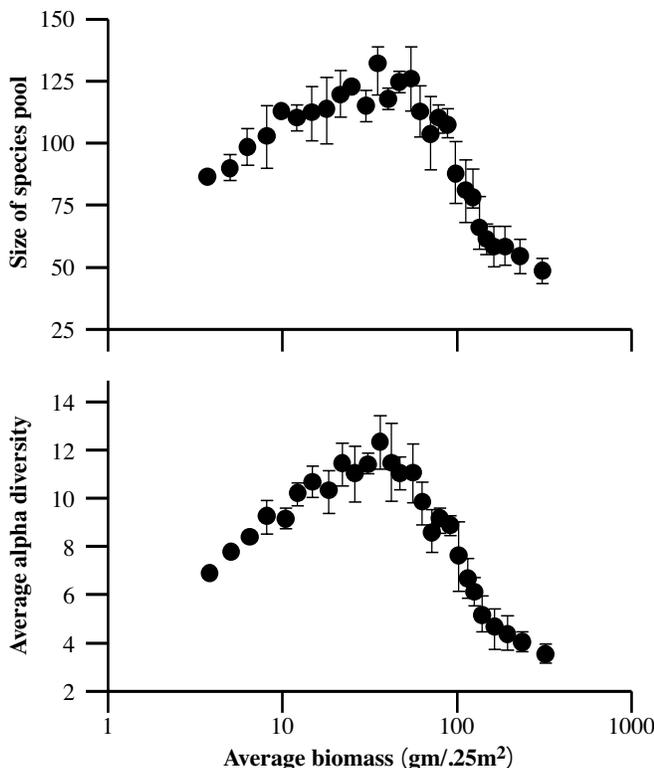

FIGURE 4. The size of species pools (top) and average alpha diversity (bottom) plotted against the average biomass of wetland habitats. Each dot represents mean values calculated from five randomly selected sets of 50 quadrats each, with bars representing 95% C.I.'s of the means. (From Wisheu and Keddy, 1996, with permission).

TABLE III. Plant species diversity of Mediterranean-climate regions (from Cowling *et al*., 1996)

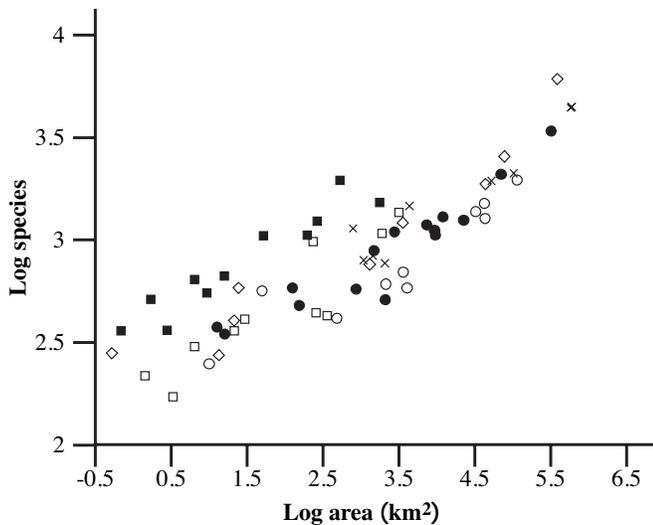| Region	Area (10^6 km^2)	Native flora
California	0.32	4300
Central Chile	0.14	2400
Mediterranean Basin	2.30	25000
Cape (fynbos)	0.09	8550
SW Australia (kwongan)	0.31	8000

FIGURE 5. Species richness in samples of different area from Mediterranean-climate regions. Diamonds, SW Australia; filled squares, Cape (SW); unfilled squares, Cape (SE); crosses, Mediterranean Basin; unfilled circles, Chile; filled circles, California. (From Cowling *et al.*, 1996, with permission).

from 0.5 m above to 0.5 m below the water line, showed no significant correlation between the number of species in a transect and the mean depth range colonized. In other words, tighter packing of species at particular depths does not appear to increase the overall number of species that occur along a gradient. Therefore, specialization along the water-depth gradient does not explain the variation in number of species on a lakeshore.

Increased species diversity is often associated with greater topographical heterogeneity (Whittaker, 1956; Huston, 1994). Coexistence in spatially structured communities may be facilitated by interspecific differences in factors such as dispersal ability between patches, germination microsite preferences, resource requirements, environmental tolerances, and mortality (Skellam, 1951; Horn & MacArthur, 1972; Slatkin, 1974; Grubb, 1977; Tilman, 1982; Keddy, 1984). Such differences are thought to lead to changes in competitive interactions in heterogeneous environments (Chesson & Huntly, 1989). On a large topographic scale, vegetation types are associated with elevation, geology, and moisture combinations (Figure 6), prompting du Rietz (1931) to write:

The more different habitats there are in a country, the greater will be the number of species; the more uniform the habitats, the smaller will be the number of species. A plain has not as great a chance of attaining wealth in species as a mountain country.

Similar processes may occur at the micro-topographic scale and, indeed, facilitation of coexistence in heterogenous environments has been demonstrated in several multi-species communities (Fitter, 1982; Grime *et al.*, 1987; Vivian-Smith, 1997).

Within homogeneous areas, there is evidence that tree species alternate with one another, saplings of one species establishing under the canopy of another (Fox, 1977; Woods & Whittaker, 1981). Further, there is constant dis-

turbance within forests, from the relatively large gaps carved out by severe storms to small ones created by individual trees falling. This creates an array of different gap sizes with different light regimes (Grubb, 1977; Denslow, 1987; Seischab & Orwig, 1991; Dirzo *et al.*, 1992; Denslow & Hartshorn, 1994). Depending on their light requirements, different tree species may come to occupy the clearing (Denslow, Ellison & Sanford, 1998). Thus, even where sites are at first relatively homogeneous, the tree canopy and different gap sizes create a form of biological heterogeneity.

To study the role of gap regeneration in maintaining tree species diversity, Phillips & Shure (1990) surveyed an area of mixed mesophytic forest to determine the relative abundance of tree species. They then cut gaps of four different sizes: 0.016, 0.08, 0.4, and 2.0 ha, and monitored regeneration in these gaps. Two years after cutting there were marked differences. *Liriodendron tulipfera* (a member of the magnolia family) had the highest regeneration in the smallest gaps. *Robinia pseudoacacia* (a member of the pea family) showed a striking preference for the largest clearings. *Quercus robur*, like *Liriodendron*, grew best in the smallest gaps, but unlike *Liriodendron*, it established very poorly in the larger gaps. *Quercus prinus* and *Carya* species showed very low regeneration in the gaps, possibly reflecting a requirement for fire to remove leaf litter. Even in apparently homogenous landscapes, different patch sizes can control the germination and establishment of different species, thereby generating a diversity of adults.

Quadrats

Most descriptive studies have measured diversity at the quadrat scale. There is a long history concerning the use of quadrats (Pound & Clements, 1897). Lloyd, Grime & Rorison (1971) outline the advantages of using small quadrats of fixed dimensions for mechanistic studies of herbaceous plant community structure and diversity:

...Data collected from a quadrat of 1 m^2 ... is sufficient to permit accurate measurement of the relative frequency of individual species, but is not so large that there is serious risk of including different components of the vegetation mosaics... The metre square provides a sampling unit which is relatively insensitive to small-scale variation in species composition and species density arising from the morphology of subsidiary components of the vegetation or from (other) factors (Lloyd, Grime & Rorison, 1971).

One of the most well-documented relationships with diversity to emerge from the use of quadrat data was Grime's model (1973; 1979) of above-ground biomass *versus* species richness. Grime (1973) observed that in British grasslands, habitats with intermediate levels of biomass appeared to have the largest numbers of plant species. He postulated that there is a general unimodal relationship in vegetation between species richness and above-ground biomass. Grime suggested a mechanism: that species richness was low at low biomass because of high levels of stress or disturbance, whereas richness was low at high biomass because of dominance from a few strong competitors. Some studies support the patterns of Grime's model (Al-Mufti *et al.*, 1977; Wheeler & Giller, 1982; Moore & Keddy, 1989;

a)

[Boreal forests]   [Healt bald]

Beach mesic type | Forests sedge type

White oak- Chestnut forest

Grassy Bald

Cave forests

Hemlock forest

Red oak - Chestnut forest

Chestnut oak - Chestnut forest

Table mountain pine heath

Chestnut oak - Chestnut heath

Pitch pine heath

Red oak - Pignut hickory forest

Virginia pine forest

Elevation (ft): 2000, 3000, 4000, 5000, 6000

Caves | Flats | Draws | Sheltered Slopes | Ridges & peaks NE E W S N NW SE SW | Ridges & peaks

Canyons | Ravines

Mesic ·········· Dry

b)

Alpine   40 Krummholz   Alpine

Picea engelmonnii   Abies tasiocorpa forest   Pinus flexilis forest

31   22   13   22

Pinus contorja forest

40   31

Mixed mesic forest

49   Pinus ponderosa pseudotsuga forest   Pinus ponderosa woodland   40

58

Riparian forest

Grossland   Pinus ponderosa, cercocorpus shrubland

Elevation gradient (m): 1700, 1900, 2100, 2300, 2500, 2700, 2900, 3100, 3300, 3500

Right axis: 6 000', 7 000', 8 000', 9 000', 10 000', 11 000'

Ravines | Sheltered slopes | Open slopes NE E SE | Exposed ridges

Wet | Mesic | N | NW | W | SW | S | Xeric

Topographic-moisture gradient

c)

Vegetation types

| Renosterveld
D Undifferentlated cliff communities
⚘ Forest and ticket
▼ Ericaceous fymbos
Ⅴ Upland restiod fymbos
Ⴕ Wet restiod fymbos
▽ Dune asteraceous fymbos
△ Sandplain proteoid fymbos
■ Wet mesotrophic proteoid fymbos
● Mesic mesotrophic proteoid fymbos
□ Wet oligotrophic fymbos
○ Mesic oligotrophic proteoid fymbos

Geology

■ Malmesbury Group (shale)
▫ Cape Granite suite
□ Grastwaler Formation (mudstone, miltstone) } Table mountain group
▦ Peninsule Formation (quartzitic sandstone) }
■ Old dune sands
■ Young dune sands

Table Mountain

A   B
Lion's Head   Kirsten-bosch
Sea Point

Altitude (m): 0, 500, 1000

C   D
Swartkoptirq   Falsa Bay
Atlantic Ocean   Cape of Good Hope Nature Reserve
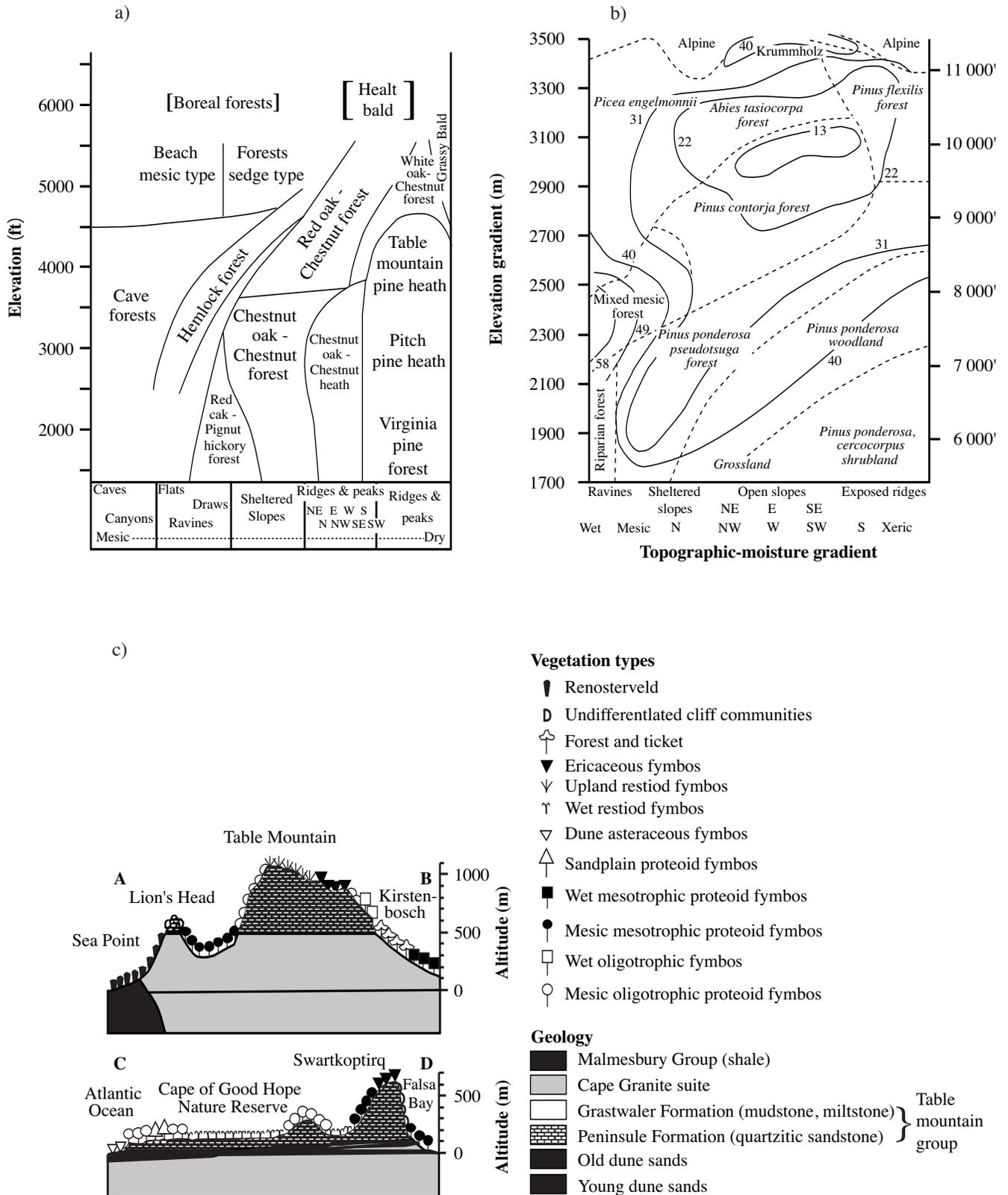
Altitude (m): 0, 500

FIGURE 6. Transects across (a) Great Smokey Mountains, U.S.A. (from Whittaker 1956), (b) Colorado Front Range, U.S.A. (from Peet, 1978), and (c) Cape Peninsula, South Africa (from Cowling *et al.*, 1996b) showing the relationships between vegetation type and geology, altitude and slope/aspect combinations.

Muotka & Viranen, 1995), others do not (Vermeer & Verhoeven, 1987; Gough, Grace & Taylor, 1994). A recent paper even questioned the relevance of this model, suggesting that some results are simply an artifact arising from the use of small samples of constant size (Oksanen, 1997; 1998). Instead, Oksanen proposes the 'no-interaction model' (Oksanen, 1997). Oksanen's no-interaction model predicts that the number of species are related to the number of individuals within a small quadrat. The model is similar to the self-thinning law (Yoda *et al.*, 1967), which states that as the number of individuals decrease, the size of the plants increase. Rapson, Thompson & Hodgson (1997) provide data which challenges the no-interaction model when applied to British herbaceous communities (see also Maranon & Garcia, 1997; and Grime, 1997 for comment).

Data from more than 400 quadrats in eastern North America (Figure 7a) show that maximal richness occurs in wetlands with biomass in the range of 50 g/0.25 m². Furthermore, if rare species alone are considered, the vast majority of nationally rare wetland species occur in very low standing crop habitats (less than 100g/0.25 m², Figure 7b). There is, however, a great deal of variance in species richness at any given biomass in Figure 7a. There are at least three ways to proceed. First, one could try to reduce the scatter around the curve by adding a second predictor variable in addition to biomass. Shipley *et al.* (1991) included the proportion of species that were functional
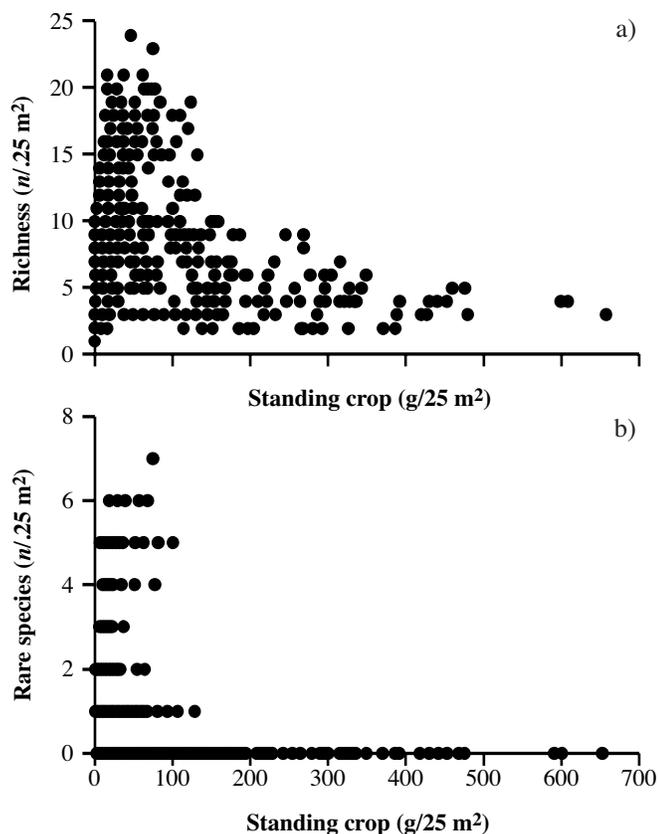
annuals as a surrogate for disturbance. Using both biomass and the proportion of plants that were perennial, it was then possible to predict plant richness with greater success (see also Gough, Grace & Taylor, 1994 and Grace & Pugesek, 1997, for a similar approach).

A second tactic would be to examine the unexplained variation by breaking the data down into smaller units. That is, instead of comparing across many vegetation types, one could look for relationships within selected vegetation types. By applying this approach, Moore & Keddy (1989) did not detect a pattern consistent with Grime's model. Of course, Moore and Keddy (1989) found that each vegetation type generally had a shorter biomass gradient because long biomass gradients were the result of comparing across many vegetation types. Whichever factors and processes produce the peak at intermediate biomass, they apparently arise out of large-scale comparisons across vegetation types.

A third approach reconsiders Grime's original work, noting that he actually referred to potential species diversity. Potential diversity, unlike observed diversity, cannot be measured, so most workers have used curve fitting techniques which assume that all data points have equal weighting. However, if the original wording is taken precisely, Grime proposed that there is an outer envelope or upper limit to species richness, and that this is the form of the relationship he was drawing. For example, Marrs, Grace & Gough (1996) re-analysed Gough, Grace & Taylor's (1994) data set and concluded that even though biomass and species richness were weakly correlated (r^2 of 0.02), there were few plots that had both high biomass and high diversity. Of course, there are few statistical techniques for fitting upper limits (Scharf, Juanes & Sutherland, 1998), but establishing an upper limit changes the question. Instead of trying to account for scatter around the line, as Shipley *et al.* (1991) attempted to do, we are instead asked to explain why many sample units fell below the line.

Experimentation

Experimental manipulation of independent variables, such as nutrients, is regarded by many ecologists as the only way to determine cause and effect relationships. This is certainly true for understanding local patterns of species diversity, but global patterns of diversity are harder to explore with manipulative experiments simply because the scale of manipulation is practically impossible to achieve (but, see Carpenter *et al.*, 1995 for a review of large-scale manipulative experiments). Therefore, most experimentation is conducted at the local, quadrat-scale level. There are two main methods of experimentation: laboratory studies and field studies.

LABORATORY STUDIES

The objective of laboratory (or microcosm) studies are quite different from field studies in that they sacrifice realism for precision (Diamond, 1986). The advantage of microcosms for community-level research is the degree of control over independent variables. The role of microcosms in terrestrial community ecology research has increased dramatically over the last decade (Fraser & Keddy, 1997). A

FIGURE 7. a) Species richness *versus* biomass, and b) number of nationally rare species *versus* biomass in 401 0.25 m² quadrats from wetlands located in Ontario, Québec, and Nova Scotia. (From Moore *et al.*, 1989, with permission).

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number of recent microcosm studies have been published which directly address questions regarding biodiversity (Grime *et al.*, 1987; Naeem *et al.*, 1994; Weiher & Keddy, 1996). Let us consider two examples, one from fields and the other from marshes.

Grime *et al.* (1987) examined the functional significance of mycorrhizal infection, soil structure, and grazing for the floristic diversity of a synthesized calcareous grassland community. They found that mycorrhizae can increase diversity by raising the biomass of the subordinate plant species relative to that of the dominant canopy species. The results suggested that transfer of mineral nutrients and assimilates through mycorrhiza may be one of the factors that reduces intensity of competition and encourages species coexistence on fertile soils. Prior progress in the field has been limited because important factors, such as mycorrhizal infection and soil structure, were not amenable to precise field measurement or manipulation.

Weiher & Keddy (1996) examined the effect of 24 different habitat treatments on species composition of wetlands for a five-year period. They began with a standard pool of 20 species, ranging widely in functional classification type (Boutin & Keddy, 1993). After five years, species richness was strongly affected by fertility level and year for all treatments, but only two of the environmental variables were strongly significant: water depth and fluctuation in water depth, where high water level or fluctuations in water level were associated with lower species richness. The microcosms that were started 28 days after the others had greater richness than did the control treatments. The resulting community assembly was modelled as a series of environmental filters.

FIELD STUDIES

Experimental manipulation of independent variables in the field is more realistic, but burdened with the problem of complexity and how to disentangle the myriad natural factors that influence community pattern. Furthermore, Huston (1997) has shown that there are problems associated with the methodology of some biodiversity experiments, which he has termed 'hidden treatments'. Two of the most common field manipulations are based on the two fundamental forces that structure plant communities: fertility and disturbance (Grime, 1979; Tilman, 1982; 1988). There has also been at least one field experiment that has manipulated species pools (Tilman, Wedin & Knops, 1996), but the methodology was criticized for using a limited selection of plant functional types (Huston, 1997).

The longest-running manipulative experiment is the Park Grass Experiment at Rothamsted, England. Begun in 1856, the treatments involve different fertilizer regimes on hay-meadow grassland. Silvertown (1980) and Wilson *et al.* (1996) show that, over the years, species diversity has progressively declined in the nutrient-enriched treatments (corresponding with an increase in biomass). The pH of the soil was found to be another important factor controlling species richness, where soils with lower pH had lower species richness. Decline in species richness with nutrient enrichment has been found in many other studies (Grime, 1973; 1979; Huston, 1979; Austin & Austin, 1980; Tilman, 1982),

including wetlands (Willis, 1963; Moore *et al.*, 1989; Verhoeven, Koerselman & Meuleman, 1996).

Depending on the shortage of a particular nutrient, the limiting nutrient may differentially affect species composition of a plant community (Verhoeven & Schmitz, 1991; Verhoeven, Koerselman & Meuleman, 1996, Koerselman & Meuleman, 1996). Plant growth in mires and moist grasslands is commonly limited by the availability of nitrogen, phosphorus, or (less frequently) potassium, or a combination of these elements (Verhoeven & Schmitz, 1991; Olff & Pegtel, 1994). Plant species adapted to nitrogen-limited environments are different from those adapted to phosphorus-limited environments. Verhoeven, Koerselman & Meuleman (1996) showed that if the ratio of nitrogen to phosphorus concentration in herbaceous vegetation was 15:1, neither the nitrogen nor the phosphorus was more limiting than the other. However, If N:P was lower than 14:1, plant growth was N-limited in 18 out of 21 cases. Furthermore, if N:P was higher than 16:1, plant growth was P-limited in 14 out of 15 cases. Finally, at ratios between 14:1 and 16:1, either N or P was limiting (Figure 8). Annual summer harvesting and a base-rich water supply have been shown to control for N- or P-limited plant growth. Therefore, a low availability of N and/or P in mires produces species-rich communities (Verhoeven, Koerselman & Meuleman, 1996), and the ratio of N:P generates further diversity along nutrient gradients.

Future Directions

There are both evolutionary and ecological forces that determine plant diversity at the global, regional, and local scale (Delcourt & Delcourt, 1988). Table IV summarizes the causal factors at each scale. Based on our review, we propose seven ways in which we can advance our understanding of plant diversity.
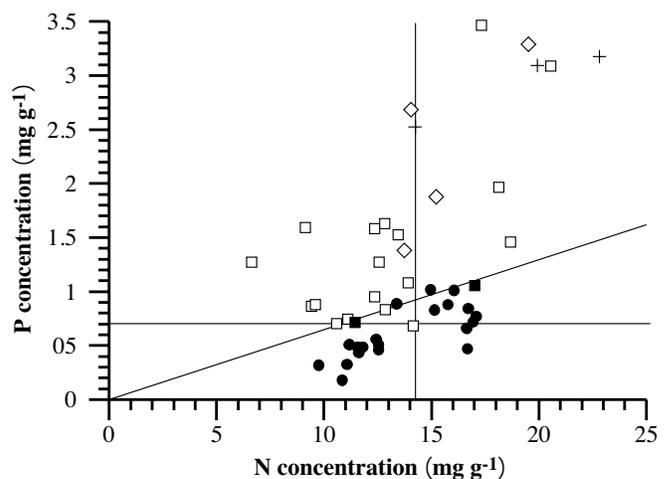

FIGURE 8. Nitrogen (N) and phosphorus (P) concentrations in the herbaceous vegetation in the control treatment of fertilization experiments reported in the literature. The horizontal and vertical lines indicate the 'critical' p and N concentrations, respectively. The line through the origin represents an N:P ratio of 15. Symbols: unfilled square, N-limited; filled square, N- and P- limited; filled circle, P-limited; diamond, N- and K-limited; plus, K-limited. (From Koerselman & Meuleman, 1996, with permission).

Table IV. A summary of the major factors, based on different temporal and spatial scales, hypothesized to control diversity in plant communities

Large temporal and spatial scales global species pool)

(1) The isolation of continents allows increased plant diversity by permitting the evolution of new species and persistence of different floras on different continents.
(2) The angiosperm life cycle allows for greatly increased rates of speciation.
(3) The angiosperm method of pollination allows more species to coexist within a landscape.
(4) Strong constraints (drought, infertility) create opportunities for evolutionary diversification.

Medium temporal and special scales (regional species pool)

(1) Gradients allow for the coexistence of more species within a landscape, and the longer the gradients and more kinds of gradients, the more species can be found.
(2) Within any segment of a gradient, disturbance and gap dynamics allow more species to coexist.
(3) There is little evidence that habitat specialization on narrower sections of gradients allows more species to coexist.
(4) Multiple physiological constraints on plant growth (*e.g.*, salinity and flooding) reduces the species pool for a site.

Small temporal and spatial scales (local species pool)

(1) A few species always dominate a site at the expense of most others.
(2) Increased productivity associated with factors such as higher soil fertility or longer growing season tend to increase the degree of dominance by these few species.
(3) Species density reaches a maximum at intermediate levels of fertility and disturbance.
(4) Patches with extreme infertility or disturbance tend to support distinctive species, thereby increasing the size of the local species pool.

1. Increase the collection of species pool data over a wide range of communities around the world. Descriptive studies are generally no longer conducted because they do not lead to explanations of patterns. However, a global database of species pools would be invaluable for the examination of null models and for generating hypotheses.

2. Compare species richness patterns to environmental variables and develop general models. Prediction is probably the most important function of any science (Peters, 1981; Rigler & Peters, 1995). Although it need not drive all ecological experimentation, the prediction of future states should be the ultimate goal. Quantitative relationships also provide a means of testing for differences in patterns among geographical areas.

3. Determine the major physiological constraints that may limit species richness. We have evidence that temperature, fertility, salinity, and flooding are major constraints on plant growth, and that they may limit speciation. We require more information to determine the quantitative effect of each constraint on species richness as well as the cumulative effect of multiple constraints.

4. For mechanistic explanations of diversity, put more emphasis on small-scale gradients (*e.g.*, altitude, soil depth, and fertility). Small-scale gradients limit the possibility of co-varying factors that inevitably obscure interpretation at a larger scale.

5. Determine scale-dependence of richness-environment relationships. Each quantitative relationship can be expected to have limitations. Explicit constraints (*e.g.*, domain and range) need to be given for each model of diversity.

6. In the paleoecological context, more data on fossil floras and fossil environments are needed. Past events produce future states. Studies of continental drift and catastrophic events provide a means for exploring effects of phenomena that occur at larger time scales than humans can observe. They can also provide a means to test whether present-day patterns (*e.g.*, richness and temperature relationships) apply to floras that are different from those living today.

7. Conservation implications demand continued and expanded attention. Ecological management and conservation is a burgeoning field. There are a number of new journals as well as stated objectives for the maintenance of native biodiversity (Noss & Cooperrider, 1994; Table V). Conserving biodiversity, which is an important conservation goal (World Conservation Monitoring Centre, 1992; Reid *et al*., 1993; Noss, 1995), requires us to think about the full species pool for an area. At the largest scale, our challenge is to maintain the species pool of the entire planet, or at least of a region. Most managers, though, must focus on maintaining or increasing diversity at only one location. Therefore, managers should focus on the factors that affect diversity at the local or regional scale, with special attention to rare and endangered species.

Conclusion

Two very different methods of investigation (descriptive and experimental) can be used to study patterns of diversity in plant communities. This paper began with a discussion of large-scale historical and geographical phenomena and then moved on to smaller-scale examples of descriptive and experimental studies. In spite of the fact that descriptive studies are important, there has been only limited success in predicting species richness from environmental factors. Our inability to predict such simple state variables in plant

Table V. The four fundamental objectives of maintaining the native biodiversity of a region (from Noss & Cooperrider, 1994)

1. Represent, in a system of protected areas, all native ecosystem types and seral stages across their natural range of variation.
2. Maintain viable populations of all native species in natural patterns of abundance and distribution.
3. Maintain ecological and evolutionary processes, such as disturbance regimes, hydrological processes, nutrient cycles, and biotic interactions.
4. Manage landscapes and communities to be responsive to short-term and long-term environmental change and to maintain the evolutionary potential of the biota.

communities points us towards two conclusions. First, we are remarkably ignorant of the factors controlling community properties, and further work will require a careful mixture of description and experimentation. Second, if we cannot yet predict basic ecological properties such as diversity, we need to approach conservation management with caution or we risk making situations worse rather than better. In the short term, we must clearly set the priority of constructing nature reserve systems that efficiently represent the largest possible pool of species, combined with the rarest of species (Scott *et al*., 1987; Pressey *et al*., 1993; Myers, 1988, Noss & Cooperrider, 1994; Cowling *et al.,* 1996). This will buy time while we design management methods to ensure the persistence of biodiversity through time. The common assumption that increasing local diversity must be good (even if it decreases global diversity) is a perfect example of the misapplication of ecological theory in management. Given the rising number of endangered species in the world, a great deal remains to be done.

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