

Towards a theoretical basis for ecosystem conservation

IAN DOUGLAS ROZDILSKY,^{1*} JEROME CHAVE,² SIMON ASHER LEVIN¹ AND DAVID TILMAN³

¹*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, United States of America,* ²*Laboratoire d'Ecologie Terrestre, CNRS 5552, 13 avenue Colonel Roche 31029 Toulouse, France* and ³*Department of Ecology, Evolution, and Behavior, University of Minnesota, Minneapolis, MN 55455, United States of America*

Humans have altered the environment so severely that extinction events are now occurring at rates unprecedented in modern history. In order to slow this trend, conservation actions must be taken to protect biodiversity, beyond just saving flagship species. Some governmental and conservation organizations have responded by committing to ecosystem conservation but, as yet, there is no coherent strategy for how this can be carried out. This report introduces many of the theoretical aspects that will need to be considered for the development of a coherent ecosystem conservation policy. The approach includes analyzing a hierarchy of interaction-based local coexistence mechanisms within a regional and historical context. This approach points toward the need for prioritizing sensitive habitats using local interaction models; considering the effects of historical exploitation mechanisms, which are now often missing; and evaluating regional diversity influences further to identify circumstances where system-wide habitat improvements deserve more emphasis.

Key words: coexistence; ecosystem conservation; hierarchy; models.

INTRODUCTION

Humans affect biodiversity on many levels. In California, urban sprawl is now cited as the leading cause of general species imperilment, being responsible for 188 out of the 286 species listed as threatened or endangered (Doyle, Kostyack, McNitt *et al.* 2001). Species-specific examples include the extinction of the California Grizzly, largely by hunters (Storer 1955). Because humans affect ecosystems on many levels, it is necessary for conservation actions to respond on many levels by mitigating the general causes of biodiversity decline (ecosystem conservation) in addition to preserving those species on the brink of extinction (single-species conservation). Ecosystem-based conservation perspectives are gaining increasing international acceptance. For example, ecosystem conservation has been a formal commitment of the US Fish and Wildlife Service since early 1994

(Beattie 1996), and the conservation of ecological integrity was introduced as a prime mandate for the Canadian National Park system in 1988 (Nelson *et al.* 2000). In the marine environment, a recent US National Research Council study recommended ecosystem approaches be used for the management of fisheries (National Research Council 1998). The mandate for ecosystem conservation, however, has not yet been matched by more than vague ideas as to how such a plan can be carried out. In the present study, we outline some of the steps that will be necessary for improving the theoretical basis of ecosystem conservation.

If a theoretical basis for ecosystem conservation is to be useful, it must be closely tied to plausible conservation actions. Conservation initiatives often consist of setting aside regions of land from further development or exploitation of natural resources. Therefore, a primary goal of theoretical models should be to determine how patterns of habitat alteration (often destruction) affect biodiversity. Land use patterns can be modified in a variety of ways to promote ecosystem conservation. In this century, the concept of nature reserves (and national parks) has come to the fore, but many other actions are possible, such as habitat restoration, the creation

*Author to whom correspondence should be addressed. Email: irozdils@princeton.edu

Accepted 29 September 2001.

of wildlife corridors, prevention of sprawl, and general regional improvement of already impacted habitats. Because conservation managers typically operate within very limited budgets, some prioritization of the effectiveness of these actions for various endangered habitats is also needed. Beyond land planning, there are as many additional examples of preventative conservation actions as there are environmental threats. There is inadequate space here for a detailed discussion, but several examples that can play dominant roles deserve a mention. Individual species that may play a key role can be reintroduced, as were wolves to the Greater Yellowstone Ecosystem of the United States. Overexploitation caused by resource extraction, intensive fishing, hunting, and logging operations can be limited. Pollution caused by local and regional sources can be regulated and lessened. Finally, actions that cause large-scale ecosystem disruption, such as dam building, can be prevented or, at least, more carefully evaluated.

The species diversity in a given region is a reflection of a complex collection of influences that span many fields of expertise. There is a huge variety of possible species interactions embedded within a complex environment that has been influenced by historical events. Determining if, where, when, and at what scale theoretical models are appropriate for guiding conservation decisions therefore goes to the essence of the problem at hand. The perspective taken in the present study is to begin by considering the historical context and influence of regional diversity, and then applying local interaction-based models as deemed appropriate.

Perceptions as to the relative influence of historical events and interaction-based mechanisms on local diversity have waxed and waned over the course of the past century (Chesson 2000). Large-scale patterns of diversity are, in great part, a reflection of historical accumulations of species over time (Brown & Lomolino 1998). Biogeographic arguments augmented by historical records of continental movements play a significant role in explanations as to why similar but long-separated environments have substantial differences in aspects of biodiversity. For example, the greater age of Australian desert, as compared to the North American desert, is often cited as a contributing factor to the more massively diverse lizard populations found in Australia (Westoby 1993).

Regional models can be used to explain local diversity in terms of the influence of regional species pools without explicitly considering species interactions. There are now a rich variety of data sets that reveal regional biodiversity trends as a function of latitude, water availability, body size, and many other factors (Rosenzweig 1995). These datasets have spawned several theories of regional diversity. It should be remembered, however, that species do interact and can be driven to extinction if the nature of their interactions changes, regardless of whether their presence is a result of historical events.

Views with respect to the influence of local species interactions on diversity are changing rapidly as a result of increasing attention from the theoretical biology community over the past several decades. The experiments of Gause in the 1930s led to the 'competitive exclusion principle', which states that the number of species coexisting at equilibrium can be no greater than the number of limiting factors (Levin 1970). This foundational theory seemingly contradicts many empirical observations, such as the presence of approximately 320 000 species of terrestrial plants coexisting on, what appears to be, about 30 limiting resources (Tilman 1982; Prance *et al.* 2000). The challenge this contradiction posed prompted much experimental and theoretical research to determine how relaxing the simple assumptions, upon which the competitive exclusion principle is based, makes coexistence possible. Careful experimental observation found that species often partitioned resources in subtle ways (MacArthur 1958), and theoretical studies which relaxed model assumptions related to the effects of space, scale, and non-equilibrium behaviors have uncovered numerous coexistence possibilities (Connell 1978; Levin 1992; Tilman 1994; Chesson 2000; Hubbell 2001). Linking some of the finer points of different possible model assumptions to real systems is often problematic, making empirical verification difficult. In addition, significant unanswered questions remain in relation to food web structures and feedback effects across scales (Chesson 1991; Holt 2001).

Hence, conservation managers are faced with a number of historical/regional arguments and with interaction-based models that are presented in formats that can be difficult for non-specialists to interpret. All of these various explanations come

with limited observational support, address overlapping problems, and can imply very different conservation priorities. There is always likely to be uncertainty as to the relative importance of multiple underlying causes of species diversity but, by narrowing this uncertainty where possible, and more broadly considering the consequences of several competing but plausible theories, a stronger theoretical basis for conservation practices will be gained. In this framework, ecosystem conservation must be looked upon as an active and evolving activity operating under the precautionary principle and must be prepared to change course as more information becomes available.

HISTORICAL INFLUENCES

Historical events that can have strong influences on local diversity include the motions of continental land masses, the formation or elimination of land bridges, and long-term weather patterns (Ricklefs & Schluter 1993; Rosenzweig 1995; Brown & Lomolino 1998). Some continents have long histories of isolation from other large land masses, while others have often been in contact with one another over geologic time (Ernst 1990). In the 19th century, Wallace hypothesized that isolation was partly responsible for the unusual species assemblages present in the Australasian region (mainly Papua New Guinea and Australia), which has long been isolated from Oriental South-East Asia (Borneo, Sumatra, and the Malay Peninsula). Additional diversity anomalies that are thought to be a result of isolation include the general lack of predators on the islands of New Zealand and the lack of large mammals in South America. The formation and disappearance of land bridges also play important roles. The creation of the Bering land bridge during the Pleistocene ice age has affected the diversity of North America significantly by forming a migration route not only for large mammals but for the peopling of the North American continent by Indian tribes. In a similar manner, the emergence of the Isthmus of Panama during the Pliocene epoch allowed for the exchange of North and South American species, and is believed to have caused the extinction of many South American species. A final consideration is the history of long-term climate changes.

Ice ages have triggered the advance of ice sheets, which scoured clean large portions of North America and Europe, but the influence on unglaciated tropical areas is poorly known (Latham & Ricklefs 1993). For example, the relatively low diversity of temperate tree species in Europe and North America's Pacific slope as compared to tropics is thought to be a consequence of the Neogene period of climate cooling and glaciation (Latham & Ricklefs 1993). In parallel, the high species richness of the neotropical world may, in part, be a result of the isolation of rainforest remnants, or refugia, during drier epochs, thus triggering speciation by isolation.

REGIONAL INFLUENCES

Given an historical context, it is possible to consider regional scale influences on diversity. If evidence is present that supports strong regional influences on local diversity, consideration should be given towards shifting conservation priorities toward the maintenance of these regional forces. Evidence for regional influences stem from regional biogeographic data interpreted through models that do not consider explicitly species interactions. As many model systems (both regional and local) produce similar predictions of diversity trends, distinguishing between models that are based on empirical data is often problematic.

The key biogeographic trends have been reviewed many times (Fischer 1960, 1961; Ricklefs 1990; Brown & Lomolino 1998). Greater diversity is often found at tropical latitudes (Latham & Ricklefs 1993), in favorable climates (Richerson & Lum 1980), and in regions where disturbances are of intermediate intensity (Connell 1975). Species–area curves, or measurements of diversity as a function of land area surveyed, have provided added insight. MacArthur and Wilson (1967) found species–area curves of islands to have a linear relationship on a doubly logarithmic plot. They introduced a theoretical model based on a balance between immigration and death rates for an island as a function of its size and isolation to explain empirical trends. A wide variety of studies found similar species–area curves, even when applied to continental study sites. The slope exponent (rate of logarithmic diversity change) was

generally found to be approximately 0.3 for islands and 0.15 for continental locations (Connor & McCoy 2001). At first glance, the species–area relationship provides a simple estimate for how much biodiversity will be lost when a known habitat region is destroyed, but these estimates can be very misleading and should not be used as a basis for conservation actions (Connor & McCoy 1979; Simberloff 1992). Indeed, conservation ecologists too often assume that power-law shaped species–area curves are a realistic canonical model, despite their very poor predictive power in many natural systems (Gleason 1922; Connor & McCoy 1979; Plotkin, Potts, Yu *et al.* 2000). Habitat destruction is typically biased toward diverse regions and will exaggerate species losses (Balmford, Moore, Brooks *et al.* 2001; A. P. Dobson, pers. comm., 2001) and, most importantly, species–area curves are often not suitable for backward interpretation. Finally, there are fundamental differences between comparing connected areas of varying sizes and comparing distinct islands (Chave *et al.* In press; Chave 2001), and the power–law relationship can be especially problematic for the former (Plotkin, Potts, Yu *et al.* 2000).

Beyond species–area curves, there are a variety of additional measures used to address the importance of regional influences. Saturation is a concept used to determine if local species diversity is being limited by local interactions or regional influences, such as the rate of immigration from regional species pools (Loreau 2000; Hubbell 2001). Data showing that local diversity (also called alpha-diversity in this context) is proportional to regional diversity is generally compatible with an unsaturated local community (Ricklefs 1987), but there are several complicating factors (Cornell 1993). There is also the possibility that local populations of a given species act as ‘sinks’ that are unsustainable without ‘sources’ in other locations, the protection of which should be the top priority. More generally, if key species inhabit a variety of environments or move across large spatial scales, regional influences on diversity are likely to be important, thus promoting interhabitat, or beta-diversity (Whittaker 1972). Should evidence point toward strong influences on local diversity from the regional species pool, conservation actions should include a stronger emphasis on protecting these regional forces. If long-distance migrations or pos-

sible source–sink behavior is found, a stronger emphasis should be placed on maintaining the integrity of source locations and migration corridors.

INTERACTION-BASED COEXISTENCE

There are a wide variety of plausible interaction-based coexistence mechanisms, and the applicability of different mechanisms is likely to vary over time and throughout different environments at different scales. For clarity, we introduce more precise definitions of coexistence and scale-related considerations before addressing mechanisms. Other reviews have sought to organize coexistence mechanisms using a variety of other criteria. For example, a review by Levin (1981) considers niche differentiation, temporal partitioning, and various forms of frequency dependence. Tilman and Pacala (1993) focus more on the role of limiting resources within a context of spatial and temporal heterogeneity, and also discuss coexistence based on competition–colonization trade-offs and competitively identical species (see also Hubbell 1995; 1997). Chesson (2000) interprets a wide variety of mechanisms as promoting coexistence by functioning in two major ways: (i) *equalizing* fitness differences; and (ii) *stabilizing*, through increasing the strength of intraspecific versus interspecific interactions. See also Tilman (1982), Schoener (1983), Grace and Tilman (1990), Tilman *et al.* (1994), Crawley (1997), Grover (1997), Tilman *et al.* (1997), Tilman and Kareiva (1997), Tokeshi (1999), Chapin, Zavaleta, Eviner *et al.* (2000), Gaston (2000), McCann (2000), Purvis and Hector (2000), Margales and Pressey (2000), Tilman (2000), and Holt (2001).

Confusion may arise because terms such as coexistence are often used in different ways by different authors. The main uses of coexistence are: (i) the presence of a stable mathematical equilibrium (stability); (ii) the ability of a species when rare to increase in population (permanence); and most broadly (iii) the survival of species over a given time period (persistence). The first definition, stability, is the narrowest and can be difficult to justify from field studies. The second definition, permanence, is now a widely used criterion, and is often stated more precisely as the ability of a species to exhibit a positive long-term growth rate at low densities in the context of the environment

and its competitors. The minor differences between these definitions can be important because species whose populations oscillate (permanent but not stable) can violate the competitive exclusion principle (Koch 1974; Armstrong & McGehee 1980). For a species to have permanence it must be distinguished from other species in ecologically significant ways (Chesson 1991). Species can coexist under the final and broadest definition, persistence, even when they have neither stability nor permanence. Persistence can occur when the rate at which species are going extinct is sufficiently slow in comparison to the time period under consideration. Finally, coexistence is very scale-dependent. From a broad perspective, two species may appear to be intimately mixed, but clustered into patches from which they exclude one another at finer scales of perception (Levin 1974).

Interpretation of interaction-based mechanisms requires carefully linking of the scales over which species interact to the model system used. Landscape scales, which include many ecosystem types such as alpine meadows and lowland swamps, are generally much larger than the scale of typical ecological interactions. However, there are many important exceptions where widely travelling species can have strong influences on distant locations. For example, migrating birds, and a few other species such as salmon, can transfer significant resources between quite distant locations. Scales that approach the size of an individual organism are generally smaller than the range over which species interact. These rough upper and lower boundaries set the spatial scales within which species interactions have their most direct effects. The temporal scale of interest varies with the conservation issue and species of interest. In many cases, a temporal scale that stretches across many generations of the longest-lived organism which interacts strongly with a species of interest is appropriate. Longer temporal scales require the consideration of a variety of complicating details, such as climate change and human influences.

There are several complications that can make the simplistic notions of relevant scale, which were introduced in the previous paragraph, inadequate. Interactions between species can have complex feedbacks across large spatial and temporal scales and within complex and changing food webs. It has long been known that the presence of forests

can influence the local temperature, which can, in turn, influence the growth of trees over long time scales (Larson 1922). Likewise, the anthropogenic release of carbon dioxide into the atmosphere might fertilize forests, and the latter could act as atmospheric carbon sinks (Prentice & Lloyd 1998; but see also Caspersen *et al.* 2000). There is increasing acceptance that most biological systems must be examined as open systems because nutrient flows across habitats can alter biodiversity substantially (Polis & Hurd 1996). The importance of these complications is a subject of many debates, but one conception of how simple models can guide or misguide the development of ecosystem conservation priorities can be gathered by considering trends in modern farm practices.

Modern farming techniques attempt to increase crop yields by using chemicals to control weeds, destroy pests, and increase soil fertility. Fertilizers and pest-destroying toxins are usually introduced to crops with little, if any, consideration for feedbacks over long time periods or for interactions within complex insect/soil-centered food webs. Even this quite naïve approach has vastly increased farm productivity and helped to usher in the 'green revolution' (Barker *et al.* 1995). In fact, this simplistic perspective has been so successful that fertilizers and pest-destroying toxins are often applied, at significant cost, without adequate evidence that they improve productivity. This overconfidence is rather cavalier, and it has been shown that insecticide sprays applied by default to Philippine rice fields simply modify the insect food web to promote alternative insect pests without actually benefiting yields (Schoenly *et al.* 1996). Official government policies are now shifting toward integrated pest management (IPM), such as the Indonesian program (The Indonesian National IPM Program 1991), using approaches that bear similarities to ecosystem conservation mandates. Several long-term feedback mechanisms have also become apparent. Farming methods that degrade topsoil, leading to erosion, have contributed to disastrous feedback mechanisms, such as the famous American dustbowl of the early 1930s (Steinbeck 1940). Programs such as Canada's National Soil and Water Conservation Program (NSWCP) have been developed to integrate knowledge of these long-term feedbacks with modern farming practices. In general, simple models have been very

successful in promoting increases in crop production but, in hindsight, a more precautionary approach should have been taken to avoid negative long-term feedbacks when they became apparent.

MECHANISMS UNDERLYING COEXISTENCE

A wide variety of biological mechanisms undergird coexistence. In this section, we discuss a sampling of the most important.

Multiple limiting resources

Perhaps the simplest mechanism that can promote stable multispecies coexistence is the presence of several limiting resources in an environment. There are a wide variety of possible limiting resources for carnivores and herbivores, including water, light, minerals, and food sources. Extensions of the competitive exclusion principle tells us that in a uniform well-mixed environment where there is an adequate supply of only one limiting resource, the species that can survive on the lowest level of that limiting resource will drive all others to extinction (Tilman 1982). If several limiting resources are present, however, as many species as there are limiting resources can coexist stably without violation of the competitive exclusion principle (and more can exhibit permanence if fluctuations are allowed; Armstrong & McGehee 1980). For example, phosphate and silicate are known to be limiting resources for certain algal species in Lake Michigan, United States. In a series of papers by Tilman (Tilman & Kilham 1976; Tilman 1976; Tilman 1977) the growth rates of two diatom species, *Asterionella formosa* and *Cyclotella meneghiniana*, were measured as functions of phosphate and silicate concentrations. Predictions were then made as to what resource combinations allow for multispecies coexistence, and theoretical predictions agreed with experimental studies. Similar trade-offs in the competition of plants for limiting resources can be found in Chapin (1980), Reader, Wilson, Belcher *et al.* (1994), and Barbour (1987). For multiple species to coexist at a stable equilibrium on multiple limiting resources, each species must consume relatively more of the resource that limits its growth

at equilibrium. Stable coexistence through trade-offs in the utilization of several limiting resources is often displayed graphically in a form similar to Fig. 1. The x and y axes represent two limiting resources (R_1 lines represent zero net growth isoclines for species a, b, and c. Along each zero net growth isocline, the species population is at an equilibrium where the death and growth rates are equal. A detailed analysis reveals that various positions in the x - y plane, which represent different resource concentrations, can support the stable coexistence of zero, one, or two species at a stable equilibrium, but not more than two. For a thorough development, refer to Tilman (1982).

Spatial patterning

Another crucial assumption of the competitive exclusion principle is that the environment is homogenous and species interactions are well-mixed. The spatial patterning of an environment can promote stable coexistence in a variety of ways. The famous study of warblers by MacArthur (1958) is an example of how the behavior of a collection of species can partition resources in space and thus avoid competitive exclusion. If limiting resources vary in space, biodiversity can be greatly enhanced because subregions are present in which different combinations of species can coexist stably. Referring to Fig. 1, if the resource concentrations in a given region vary within circle 1, two species can coexist, and for circle 2, all species can coexist. There are many occasions where spatial variation of limiting resources would be expected. For example, nutrient concentrations in soils that act as limiting resources for plants can have strong spatial variation on the scale of meters (Tilman 1982). Levin (1974, 1976) discusses more thoroughly a variety of ways in which spatial effects can enhance coexistence.

Even in potentially homogenous environments, localized disturbance or stochastic effects, coupled with dispersal limitation can enhance coexistence. Indeed, any mechanisms that limit the ability of species to mix and compete with one another can facilitate coexistence, in homogenous or heterogeneous environments. Most plant species are sessile, as adults and, hence, interactions are strongly influenced by seed dispersal patterns. Strong trade-offs often exist between the ability to colonize new

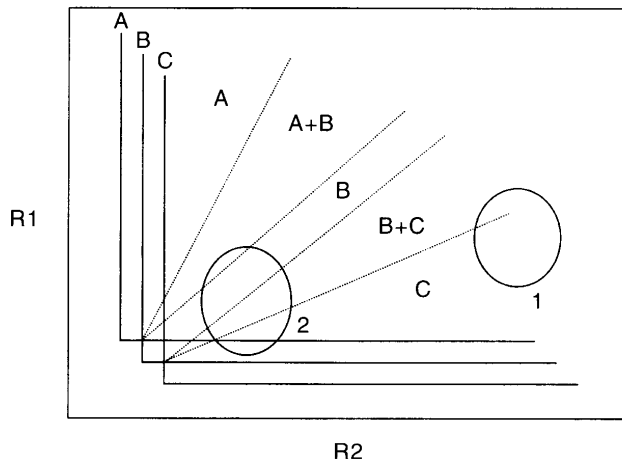


Fig. 1. Competition between three species for two limiting resources. The x and y axes represent two limiting resources R_1 and R_2 , and the solid lines are zero net growth isoclines for species a – c . The dashed lines have divided the resource plane into regions where one or two species can coexist stably. If the environmental variability of limiting resources lies within the circle labeled 1, regions will exist where species c will dominate and where species b and c coexist. Within the circle labeled 2, all three species can coexist stably.

habitats and the capability to compete for space (Levin & Paine 1974; Werner & Platt 1976; Grubb 1986; Gaines & Roughgarden 1985; Harrison *et al.* 1988; Hanski 1990; Sale 1991; Shorrocks 1991; Doherty & Fowler 1994; Tilman 1994). The presence of such trade-offs is intuitive because species that expend large amounts of energy attempting to colonize new territories are likely to fare worse in competition than those that conserve their energy by not attempting to colonize new territories as vigorously. Furthermore, the very traits that may facilitate long distance movements and rapid population growth, such as small size, should often diminish competitive ability. Model-based systems have examined the coexistence of species that have trade-offs between coexistence and competitive ability, with evidence that the poorest colonizers (and, consequently, the best competitors) often go extinct first as habitat is removed (Nee & May 1992; Tilman 1994; Tilman & Kareiva 1997).

Temporal patterning

Anyone familiar with the progressive sequence of spring flowers has an intuitive sense of how tem-

poral patterns can promote the stable coexistence of many species. In most environments, resources are not available uniformly over time. The energy received by plants from the sun varies in strength by day, by season and, in a complex manner, is related to weather systems and cloud cover. Water is another important resource for plants and can vary in complex ways during drought and monsoon cycles. Many adaptations have evolved across the plant community to deal with such feast or famine water conditions (Barbour 1987; Crawley 1997). Some common adaptations include waiting out dry periods in the form of relatively impermeable seeds, and dropping leaves to prevent evaporation during the hottest season. These adaptations, in combination with the temporal patterning of water availability, permit the potential coexistence of many species (Chesson 2000).

Variation of the physical environment

A variation of the physical environment (with regard to factors that are not consumed) can make it possible for many species to coexist stably on a few limiting resources (Hutchinson 1959). The physical environment can vary in a variety of ways, including changes in temperature, pH, and exposure to sunlight and wind. For example, in the Northern Hemisphere, east–west ridges create north-facing slopes where the air and soil temperatures are cooler than south-facing slopes due to the direction of incoming sunlight. The many possibilities for leaf shape and root structure allow plant species to have trade-offs in their abilities to utilize limited water or nutrient resources in different temperature and weather regimens (Barbour 1987; Crawley 1997). In central California, north-facing slopes are often covered by oak woodland while south-facing slopes are covered by chaparral, and variation of the physical environment is a likely cause for the stable coexistence of these two modes of vegetation. As a physical factor varies, there is no limit theoretically to the fine distinctions of competitive ability that can result (as with mechanisms 2, 3, and 5). Figure 2 graphically displays possible resource requirements for four species on the single limiting resource R (possibly nitrogen) with respect to a physical variable V (possibly temperature). The curves drawn for each species (A , B ,

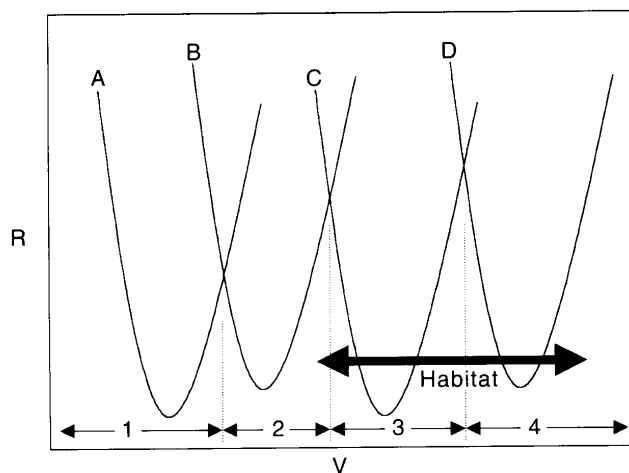


Fig. 2. Competition between four species for one limiting resource with a variation of the physical environment. The vertical axis, R , could be any limiting resource in general, such as nitrogen, and the horizontal axis, V , represents a variation of the physical environment, such as temperature. The U-shaped curves labeled a–d represent the minimum resource requirements for each of the species as a function of the physical variable. In the regions labeled by arrows 1–4, species a–d, respectively, will dominate and exclude others. If the habitat has physical variations in the range shown by the thick arrow, three species (b, c, and d) can coexist stably.

C, and D) represent the minimum resource requirements for each species as a function of temperature and, therefore, the species with the smallest resource requirements for a given V is the superior competitor and will eliminate all other species. If a habitat varies in the range of the large thick arrow, it is possible for species B, C, and D to coexist stably (Tilman 1982; Tilman & Pacala 1993).

Exploitation

Exploitation-like behaviors can by themselves promote the stable coexistence of many species on a small number of limiting resources. For convenience, in the present report, exploitation will be used broadly to refer to a wide variety of top-down mechanisms including predation, herbivory, parasitism, and disease dynamics. Exploitation-type interactions, depending on their characteristics, can either reduce or enhance the species diversity in a given region. Heavy exploitation generally reduces species diversity by raising the resource

threshold required for species persistence, allowing only a few of the original species to coexist stably. In other situations, prey-switching behaviors which concentrate exploitation on the prey species that is most abundant, provide stabilizing forces that promote multispecies coexistence. Janzen (1970) and Connell (1971) have suggested that frequency-dependent seed/seedling predation could be the mechanism responsible for high tree diversity in the tropics, but the full significance of this effect has not yet been resolved (Hammond & Brown 1998; Harms *et al.* 2000). An exploitation mechanism of this form can favor a large diversity of rare species.

DISCUSSION

The diversity within any given ecosystem is the result of a complex hierarchy of local coexistence mechanisms embedded within a historical framework and regional influences that change across scales and with time. The present study proposes that a useful approach is to begin by considering the historical context and influence of regional diversity, and then to apply local interaction-based models as deemed appropriate. This discussion will focus on a few areas in which continued research using such an approach can provide more specific guidance on priorities for habitat conservation/restoration and will suggest alternative ecosystem conservation perspectives. The application of theoretical models to ecosystem conservation should be carried out in a precautionary manner because it will be always difficult to identify with certainty which coexistence mechanisms are operating and the relative influence of regional and local factors. By further narrowing the possible list of diversity mechanisms, and more broadly considering the consequences of several competing but plausible theories, a stronger theoretical basis for conservation practice can be developed. Many theoretical approaches are likely to be compromised by gaps in basic knowledge with regard to the characterization (and even identification) of insect species and soil microfauna and the characterization of food web structure. The following brief list discusses a few more specific areas in which progress can be made along these lines to improve conservation planning.

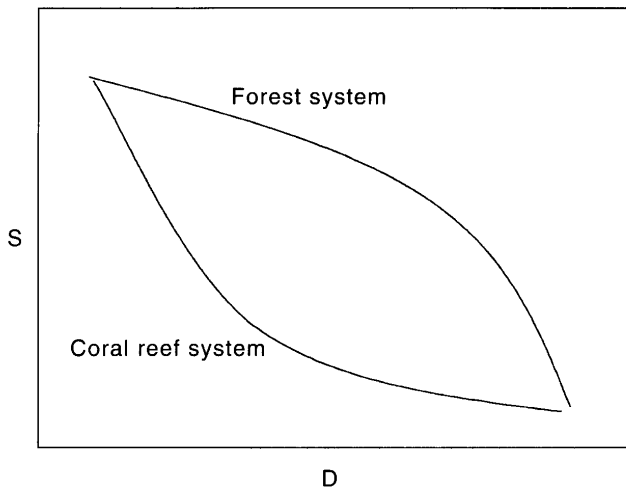


Fig. 3. Effects of habitat destruction on forest and coral ecosystems assuming a coexistence mechanism of spatial patterning based on colonization/competition trade-offs. The vertical axis, S , is the amount of species present and the horizontal axis, D , is the fraction of habitat destruction (inspired by Stone 1995).

1. *Further research regarding local coexistence mechanisms based on spatial patterning can aid the development of priorities for the preservation/restoration of habitats.*

The main tool that conservation managers have for carrying out ecosystem conservation is changing land use patterns, often through the designation of new nature reserves. Questions that need to be addressed for the development of a comprehensive conservation policy include: Which local communities will lose species most rapidly as a consequence of habitat degradation?

There is supporting evidence that spatial patterning as a result of a trade-off in colonization/dispersal and competitive abilities can support rich species diversity (discussed earlier). This suggests that spatial patterning is likely to be a mechanism that contributes to species diversity, especially in regions that have historically developed very diverse species assemblages, in a temporal scale encompassing many generations, and a spatial scale relative to the pattern of species variation. Both forest and coral reef systems can fit these requirements. For forest systems, theoretical models predict that as habitat is destroyed biodiversity declines slowly at first; but for coral reefs, where the majority of species have poor dispersal ability, even modest habitat destruction can cause great biodiversity loss (Fig. 3; Stone 1995). This

result stems from the distribution of colonization and competitive abilities for each system. Coral reefs are more sensitive to disturbance because the majority of species have poor dispersal abilities. These preliminary results indicate that coral reefs could be more sensitive than forest systems to small amounts of habitat destruction and greater vigilance may be warranted from a perspective of ecosystem conservation. Further empirical and theoretical studies detailing the applicability of such models and the relationship between all the factors which affect colonization and competition trade-offs are needed to develop a firm theoretical foundation for identifying those ecosystems that are most sensitive to habitat alteration.

2. *Ecosystem conservation goals must consider historical exploitation mechanisms that often increased system diversity.*

The mechanisms that support local coexistence for a given region can change over time, and awareness that different local coexistence mechanisms may require different conservation priorities can help to avoid ineffective actions. From a historical point of view, one of the most notable changes mankind has imposed on the environment is the extermination of large mammals across most of the terrestrial planet and other selected creatures deemed to be a nuisance. One example of this is the decimation of prairie dog populations across the central United States because they were deemed to be a nuisance by the ranching industry. Prairie dog 'towns' exert strong top-down effects on grassland ecosystems through increasing the local exploitation of grasses, thereby promoting the diversity of flowering plants. This is likely to have subtle but important effects on the grazing patterns of bison, which often prefer the greater density of flowering plants available in prairie dog 'towns'. The presence of prairie dogs also makes it possible for a wide diversity of organisms, such as snakes and raptors, to exploit them in varied ways. Because prairie dog populations exploit those mechanisms that greatly increase diversity, this should make their re-introduction one of the top priorities for ecosystem conservation in medium and short grass prairies of North America.

Efforts to deal with the historical alteration of exploitation mechanisms, which more than likely contributed significantly to ecosystem

functioning, raise several additional controversial issues. If the restoration of these exploitation mechanisms requires the reintroduction of large mammals, which need large regions of land now often compromised by human developments, will society deem this aspect of ecosystem conservation of sufficient importance to alter development patterns? In regions such as the eastern United States, intensive urban and suburban development has prompted great population increases for a few well-adapted species, such as white-tailed deer. Their intensive exploitation of plant communities has complex consequences that will likely lead to decreased community diversity. Should ecosystem priorities include reintroducing predators and restoring large regions of already developed habitat to replace a former balance of exploitation mechanisms that may have promoted greater plant diversity? As this would require a substantial adjustment of current societal values, the limitations placed upon ecosystem conservation without controlling white-tailed deer populations must be considered seriously.

3. *Identification of systems in which diversity is influenced strongly by regional forces may lead toward an increased priority for broader region-wide habitat improvements.*

Deciding whether ecosystem conservation is best served by protecting a collection of small reserves or by slightly improving large regions of already degraded habitat depends on the relationship between regional and local diversity and the level of anthropogenic pressure. Current evidence suggests that the diversity of some organisms, such as herbivorous insects, is not governed by local interaction-based mechanisms but by regional patterns of colonization, speciation, and extinction (Farrell & Mitter 1993). Indications of regional influences include source-pool effects and metapopulation dynamics. Tall grass prairies of the Midwestern United States were almost obliterated completely by modern farming, which is likely to have led to drastic changes in the pollinating insect populations present. Ongoing restoration efforts have achieved much success but cannot yet compete with the diversity of remaining prairie remnants. Further research is needed to determine if insect pollinators could aid in the restoration of prairies with higher diversity. Should research

reveal an important influence by insect pollinators, and should insect population dynamics be under a strong regional influence, an increased priority on restoring many smaller remnants may be appropriate.

ACKNOWLEDGEMENTS

We thank the David and Lucile Packard Foundation, award #8910-48190; and the National Science Foundation, award #INT-9725937, for their support.

REFERENCES

- ARMSTRONG R. A. & MCGEHEE R. (1980) Competitive exclusion. *American Naturalist* 115: 151–170.
- BALMFORD A., MOORE J.L., BROOKS T., BURGESS N., HANSEN L.A., WILLIAMS P. & RAHBEK C. (2001) Conservation conflicts across Africa. *Science* 291: 2616–2619.
- BARBOUR M. G. (1987). *Terrestrial Plant Ecology*. The Benjamin/Cummings Publishing Co., Menlo Park, CA.
- BARKER R., HERDT R.W. & ROSE B. (1985) *The Rice Economy of Asia*. Resources for the Future, Washington, D.C.
- BEATTIE M. (1996) An approach to fish and wildlife conservation. *Ecological Applications* 6: 696–699.
- BROWN J. H. & LOMOLINO M. V. (1998). *Biogeography*, 2nd edn. Sinauer Sunderland, Massachusetts, MA.
- CASPERSEN J., PACALA S. W., JENKINS J. C., HURTT G. C., MOORCROFT P. R. & BIRDSEY R. A. (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science* 290: 1148–1151.
- CHAPIN III F. S. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*. 11: 233–260.
- CHAPIN III F. S., ZAVALA E. S., EVINER V. T., NAYLOR R. L., VITOUSEK P. M., REYNOLDS H. L., HOOPER D. U., LAVOREL S., SALA O. E., HOBBS S. E., MACK M. C. & DIAZ S. (2000) Consequences of changing biodiversity. *Nature* 405: 234–242.
- CHAVE J. (2001) Spatial patterns and persistence of woody plant species in ecological communities. *American Naturalist* 157: 52–65.

- CHAVE J., MULLER-LANDAU H. C. & LEVIN S. (In press) Comparing classical community models: Theoretical consequences for patterns of diversity. *American Naturalist*.
- CHESSON P. (1991) A need for niches? *Trends in Ecology and Evolution* 9: 26–28.
- CHESSON P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- CONNELL J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations*. (eds P. J. den Boer & G. R. Gadwell) pp. 298–313. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- CONNELL J. H. (1975) Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In: *Ecology and Evolution of Communities*. (eds M. L. Cody & J. Diamond) pp. 460–490. Harvard University Press, Cambridge, MA.
- CONNELL J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 661–696.
- CONNOR E. F. & MCCOY E. D. (1979) The statistics and biology of the species–area relationship. *American Naturalist* 113: 791–833.
- CONNOR E. F. & MCCOY E. D. (2001) Species–area relationships. In: *The Encyclopedia of Biodiversity, Vol. 5*. (ed. S. A. Levin) pp. 397–411. Academic Press, New York.
- CORNELL H. V. (1993) Unsaturated patterns in species assemblages: The role of regional processes in setting local species richness. In: *Species Diversity in Ecological Communities*. (eds R. E. Ricklefs & D. Schluter) pp. 243–252. The University of Chicago Press, Chicago.
- CRAWLEY M. J. (1997) *Plant Ecology*, 2nd edn. Blackwell, Oxford.
- DOHERTY P. & FOWLER T. (1994) An empirical test of recruitment limitation in a coral reef fish. *Science* 263: 935–939.
- DOYLE K., KOSTYACK J., MCNITT B., SUGAMELI G., WHITAKER C., WHITCOMB-BLAYLOCK K., BYRD J., STULL G. & CZECH B. (2001) Paving paradise: Sprawl's impact on wildlife and wild places in California. National Wildlife Federation, Washington, DC.
- ERNST W. G. (1990). *The Dynamic Planet*. Columbia University Press, New York.
- FARRELL B. D. & MITTER C. (1993) Phylogenetic determinants of insect/plant community diversity. In: *Species Diversity in Ecological Communities*. (eds R. E. Ricklefs & D. Schluter) pp. 253–266. The University of Chicago Press, Chicago.
- FISCHER A. G. (1960) Latitudinal variation in organic diversity. *Evolution* 14: 64–81.
- FISCHER A. G. (1961) Latitudinal variations in organic diversity. *American Scientist* 49: 50–74.
- GAINES S. & ROUGHGARDEN J. (1985) Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences* 82: 3707–3711.
- GASTON K. J. (2000) Global patterns in biodiversity. *Nature* 405: 220–227.
- GLEASON H. A. (1922) On the relation between species and area. *Ecology* 3: 158–162.
- GRACE J. B. & TILMAN D. (1990) *Perspectives on Plant Competition*. Academic Press, San Diego.
- GROVER J. P. (1997). *Resource Competition*. Chapman & Hall, London.
- GRUBB P. J. (1986) Chapter 12. In: *Community Ecology*. (eds J. Diamond & T. Case) pp. 207–226. Harper & Row, New York.
- HAMMOND D. S. & BROWN V. K. (1998) Disturbance, phenology and life-history characteristics: Factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: *Dynamics of Tropical Communities* (eds D. M. Newbery, H. H. T. Prins & N. D. Brown) pp. 51–78. Blackwell Science, Oxford.
- HANSKI I. (1990) Chapter 8. In: *Living in a Patchy Environment* (eds B. Shorrocks & I. R. Swingland) p. 127–145. Oxford University Press, Oxford.
- HARMS K. E., WRIGHT S. J., CALDERON O., HERNANDEZ A. & HERRE E. A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493–496.
- HARRISON S., MURPHY D. D. & EHRLICH P. R. (1988) Distribution of the Bay Checkerspot Butterfly *Euphydryas-Editha-Bayensis*. *American Naturalist* 132: 360–382.
- HOLT R. D. (2001) Species coexistence. In: *The Encyclopedia of Biodiversity, Vol. 5*. (ed. S. A. Levin) pp. 413–425. Academic Press, New York.
- HUBBELL S. P. (1995) Towards a theory of biodiversity and biogeography on continuous landscapes. In: *Preparing for Global Change: A Midwestern Perspective*. (eds G. Carmichael, G. Folk & J. Schnoon) pp. 171–199. Balogh Scientific Books, Champaign, IL.
- HUBBELL S. P. (1997) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16: S9–S21.

- HUBBELL S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- HUTCHINSON G. E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93: 145–159.
- THE INDONESIAN NATIONAL IPM PROGRAM. (1991) *Farmers As Experts*. Indonesian National IPM Program, Jakarta Pusat, Indonesia.
- JANZEN D. H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501–528.
- KOCH A. L. (1974) Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. *Journal of Theoretical Biology* 44: 387–395.
- LARSON J. A. (1922) Effect of removal of virgin white pine stand upon the physical factors of the site. *Ecology* 3: 302–305.
- LATHAM R. E. & RICKLEFS R. E. (1993) Continental comparisons of temperate-zone tree species diversity. In: *Species Diversity in Ecological Communities*. (eds R. E. Ricklefs & D. Schluter) pp. 294–314. The University of Chicago Press, Chicago.
- LEVIN S. A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* 104: 413–423.
- LEVIN S. A. (1974) Dispersion and population interactions. *American Naturalist* 108: 207–228.
- LEVIN S. A. (1976) Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics* 7: 287–311.
- LEVIN S. A. (1981) Mechanisms for the generation and maintenance of diversity in ecological communities. In: *The Mathematical Theory of the Dynamics of Biological Populations II*. (eds R. W. Hiorns & D. Cooke) pp. 173–194. Academic Press, London.
- LEVIN S. A. (1992) The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.
- LEVIN S. A. & PAINE R. T. (1974) Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the United States of America* 71: 2744–2747.
- LOREAU M. (2000) Are communities saturated? On the relationship between alpha, beta, and gamma diversity. *Ecology Letters* 3: 73–76.
- MACARTHUR R. H. (1958) Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39: 599–619.
- MACARTHUR R. H. & WILSON E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- MARGULES C. R. & PRESSEY R. L. (2000) Systematic conservation planning. *Nature* 405: 243–253.
- MCCANN K. S. (2000) The Diversity Stability Debate. *Nature* 405: 228–233.
- NATIONAL RESEARCH COUNCIL (1998) *Sustaining Marine Fisheries*. National Academy Press, Washington DC, (on-line) <http://books.nap.edu/books/0309055261/html/index.html>
- NEE S. & MAY R. M. (1992) Dynamics of metapopulations: Habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61: 37–40.
- NELSON G., LAWRENCE P. & BLACK H. (2000) Assessing ecosystem conservation plans for Canadian national parks. *Natural Areas Journal* 20: 280–287.
- PLOTKIN J. B., POTTS M. D., YU D. W., BUNYAVEJCHEWIN S., CONDIT R., FOSTER R., HUBBELL S., LAFRANKIE J., MANOKARAN N., SENG L. H., SUKUMAR R., NOWAK M. A. & ASHTON P. S. (2000) Predicting species diversity in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America* 97: 10850–10854.
- POLIS G. A. & HURD S. D. (1996) Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: Examples from the ocean–land interface. In: *Food Webs*. (ed. G. Polis) pp. 275–285.
- PRANCE G. T., BEENTJE H., DRANSFIELD J. & JOHNS R. (2000) The tropical flora remains undercollected. *Annals of the Missouri Botanical Gardens* 87: 67–71.
- PRENTICE I. C. & LLOYD J. (1998) C-quest in the Amazon basin. *Nature* 396: 619–620.
- PURVIS A. & HECTOR A. (2000) Getting the measure of biodiversity. *Nature* 405: 212–219.
- READER R. J., WILSON S. D., BELCHER J. W., WISHEU I., KEDDY P. A., TILMAN D., MORRIS E. C., GRACE J. B., MCGRAW J. B., OLFF H., TURKINGTON R., KLEIN E., LEUNG Y., SHIPLEY B., VANHULST R., JOHANSSON M. E., NILSSON C., GUREVITCH J., GRIGULIS K. & BEISNER B. E. (1994) Plant competition in relation to neighbor biomass: An intercontinental study with *poa pratensis*. *Ecology* 45: 1753–1760.
- RICHERSON P. J. & LUM K.-L. (1980) Patterns of plant species diversity in California: Relation to weather and topography. *American Naturalist* 116: 504–536.
- RICKLEFS R. E. (1987) Community diversity: Relative roles of local and regional processes. *Science* 235: 167–171.

- RICKLEFS R. E. (1990). *Ecology*, 3rd edn. W.H. Freeman, New York.
- RICKLEFS R. E. & SCHLUTER D. (1993). *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago.
- ROSENZWEIG M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- SALE P. F. (1991). *The Ecology of Fishes on Coral Reefs*. Academic Press, New York.
- SCHOENER T. W. (1983) Field experiments of interspecific competition. *American Naturalist* 122: 240–285.
- SCHOENLY J. E., COHEN J. E., HEONG K. L., ARIDA G. S., BARRION A. T. & LITSINGER J. A. (1996) Quantifying the impact of insecticides on food web structure of rice arthropod populations in a Philippine farmer's irrigated field: A case study. In: *Food Webs* (eds G. A. Polis & K. O. Winemiller) pp. 343–351. Chapman & Hall, New York.
- SHORROCKS B. (1991) Competition on a divided and ephemeral resource: A cage experiment. *Biological Journal of the Linnean Society* 43: 211–220.
- SIMBERLOFF D. (1992) Do species-area curves predict extinction in fragmented forests? *Tropical Deforestation and Species Extinction* (eds T. C. Whitmore & J. A. Sayer) pp. 75–89. Chapman & Hall, London.
- STEINBECK J. (1940). *The Grapes of Wrath*. The Viking Press, New York.
- STONE L. (1995) Biodiversity and habitat destruction: A comparative study of model forest and coral-reef ecosystems. *Proceedings of the Royal Society of London B* 261: 381–388.
- STORER T. I. (1955). *California Grizzly*. University of California Press, Berkeley.
- TILMAN D. (1976) Ecological competition between algae: Experimental confirmation of resource-based competition theory. *Science* 192: 463–465.
- TILMAN D. (1977) Resource competition between planktonic algae: An experimental and theoretical approach. *Ecology* 58: 338–348.
- TILMAN D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- TILMAN D. (1994) Competition and diversity in spatially structured habitats. *Ecology* 75: 2–16.
- TILMAN D. (2000) Causes, consequences, and ethics of biodiversity. *Nature* 405: 208–211.
- TILMAN D., MAY R. M., LEHMAN C. L. & NOWAK M.A. (1994) Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- TILMAN D., LEHMAN C. L. & YIN C. J. (1997) Habitat destruction, dispersal, and deterministic extinction in competitive communities. *American Naturalist* 149: 407–435.
- TILMAN D. & KAREIVA P., eds. (1997) *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, NJ.
- TILMAN D. & KILHAM S. (1976) Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semi-continuous culture. *Journal of Phycology* 12: 375–383.
- TILMAN D. & PACALA S. (1993) The maintenance of species richness in ecological communities. In: *Species Diversity in Ecological Communities*. (eds R. E. Ricklefs & D. Schluter) pp. 13–25. University of Chicago Press, Chicago.
- TOKESHI M. (1999) Species coexistence. *Ecological and Evolutionary Perspectives*. Blackwell, Oxford.
- WERNER P. A. & PLATT W. J. (1976) Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *American Naturalist* 110: 959–971.
- WESTOBY M. (1993) Biodiversity in Australia compared with other continents. In: *Species Diversity in Ecological Communities*. (eds R. E. Ricklefs & D. Schluter) pp. 170–177. University of Chicago Press, Chicago.
- WHITTAKER R. H. (1972) Evolution and measurement of species diversity. *Taxon* 21: 213–251.