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Regulation of diversity: maintenance of species richness in changing environments

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Abstract In order to assess how diversity changes over time at sites undergoing environmental change, we examined three data sets on long-term trends in taxonomic richness and composition: (1) 22 years of rodent censuses from a site in the Chihuahuan Desert of Arizona; (2) 50 years of bird surveys from a three-county region of northern Michigan; and (3) approximately 10,000 years of pollen records from two sites in Europe. In all three cases, richness has remained remarkably constant despite large changes in composition. The results suggest that while species composition may be highly variable and change substantially in response to environmental change, species diversity is an emergent property of ecosystems that is often maintained within narrow limits. Such regulation of diversity requires maintenance of relatively constant levels of productivity and resource availability and an open system with opportunity for compensatory colonizations and extinctions. In addition to studying the effects of diversity on biogeochemical processes, it will often be useful to think of species richness as an emergent consequence of ecosystem processes.

Keywords Birds · Ecosystem processes · Plants · Mammals · Regulation

Introduction

Efforts to use the correlates, causes, and consequences of biodiversity to link population, community and ecosystem ecology have included two primary approaches. One approach considers species diversity as an independent variable and studies its influence on ecosystem processes such as primary productivity, nutrient cycling, and disturbance (e.g. McNaughton 1977; Vitousek 1990; Jones et al. 1994; Naeem et al. 1994, 1996; Tilman 1996; Hooper and Vitousek 1997; McGrady-Steed et al. 1997; Symstad et al. 1998; van der Heijden et al. 1998). The other approach treats species diversity as a dependent variable and studies how it is affected by ecosystem characteristics such as vegetation, soil, climate, and disturbance regime (e.g., MacArthur and MacArthur 1961; Connell and Orias 1964; Pianka 1967, 1986; Cody 1968, 1974; Rosenzweig and Winakur 1969; Brown 1971a, 1981, 1988a; MacArthur 1972; Terborgh 1973; Wright 1983; Currie 1991; Rosenzweig 1992, 1995; Wright et al. 1993; Brown and Lomolino 1998; Kerr and Currie 1999). This second approach implicitly considers species diversity to be an emergent consequence of ecological processes.

To clarify patterns and elucidate mechanisms, both approaches could benefit from long-term studies of particular ecosystems that document changes in species diversity and species composition. In this paper we present data from three case studies of community dynamics of different taxa at varying spatial and temporal scales: (1) a 22-year study of a rodent community from the Chihuahuan Desert in Arizona (Brown 1998; Ernest and Brown, in press); (2) a 50-year record of birds surveyed in northern Michigan (Parody et al. 2000); (3) an approximately 10,000-year record of plant family diversity as documented by fossil pollen data at two sites (Haskell, in press). In all three cases, richness has remained remarkably constant despite large changes in species composition due to local colonization and extinction events. A sampling of the literature reveals that such apparent "regulation" of species diversity within narrow limits by compensatory colonizations and extinctions may be a widespread phenomenon.

A brief review of patterns and mechanisms

Many studies of species diversity have focused on large-scale biogeographic and long-term historical patterns and processes. They have been concerned with the nature

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and causes of such phenomena as species-area relationships, latitudinal and elevational gradients, and mass extinctions (for reviews, see Brown 1988a; Currie 1991; Ricklefs and Schluter 1992; Rohde 1992; Rosenzweig 1992, 1995; Brown and Lomolino 1998; Ricklefs et al. 1999). While the causes of some of these patterns are still debated, the mechanistic hypotheses can generally be divided into two categories, historical and ecological. Historical hypotheses would attribute the patterns to past events of earth history, such as asteroid impacts, tectonic processes, glaciation, and climatic changes, and perhaps to the phylogenetic histories of groups that were influenced by these events (e.g., Latham and Ricklefs 1993; Ricklefs et al. 1999). Ecological hypotheses would attribute the patterns to variation in environmental factors such as productivity, seasonality, abiotic stress, and biotic interactions (e.g., Francis and Currie 1998; Kerr and Currie 1999).

In general, however, these large-scale studies do not focus on how ecological relationships regulate diversity by restricting membership in ecological communities to some subset of the species in a larger regional or geographic species pool. Island biogeography theory suggests that diversity is regulated at some equilibrial level by two opposing processes: colonization from an extrinsic pool and extinction from within the community (MacArthur and Wilson 1963, 1967). The theory predicts that species richness will be maintained within narrow limits despite turnover in composition. Observations that diversity on some islands has changed substantially over time have caused some investigators to question the assumptions of equilibrium and the generality of island biogeography theory (Brown and Lomolino 1998; Whittaker 1999; Lomolino 2000; Brown and Lomolino 2000, and references therein). Some ecologists have applied island biogeography concepts to non-isolated habitats, mainly in comparative studies of species richness across sites that vary in area, disturbance regime, landscape pattern, and geographic and regional species pools (e.g., Rosenzweig 1975, 1992, 1995; Brown and Gibson 1983; Brown 1988b; Ricklefs and Schluter 1993; Schmiegelow et al. 1997; Brown and Lomolino 1998, and references therein). Somewhat related to island biogeography theory are studies that explicitly compare local and regional diversity (e.g., Cox and Ricklefs 1977; Cornell 1985, 1993). Often their aim is to distinguish whether communities are: (1) “saturated” with species, which is inferred when local diversity reaches some maximum value that is independent of the number of species in the pool; or (2) “unsaturated,” which is inferred when local diversity is positively correlated with the number of species in the pool.

Case studies

In this paper we focus on temporal variation in diversity within a site rather than spatial variation among multiple sites. We present three case studies in which local or regional species richness has remained relatively constant over a long time series despite large changes in species composition. We infer that small-scale ecological processes have restricted community membership to a subset of species in the pool so as to maintain an equilibrial or steady-state level of diversity. We present evidence that environmental changes have caused turnover in species composition, but we see no need to invoke legacies of unique historical events to account for the observed regulation of diversity.

Desert rodents at Portal, Arizona

Since 1977, J. H. Brown and associates have studied rodent populations at a study site 6.5 km east and 2 km north of Portal, Cochise County, Arizona (for details about the site, census methods, and changes in climate, vegetation, and rodents see Brown 1998). The study has documented a substantial increase in winter precipitation during the last two decades compared to the century-long average, a concomitant increase in C_3 woody vegetation, and large changes in species composition of the rodent community (Brown et al. 1997). Despite multiple extinctions and colonizations, Ernest and Brown (in press) found that rodent species richness and also total abundance, biomass, and energy use of all rodents exhibited very little variability around the 22-year average.

Birds in Michigan

Parody et al. (2000) analyzed a 50-year time series of avian presence-absence data to determine how community composition responded to changes in habitat. The study area, the northern tip of Michigan’s Lower Peninsula, experienced substantial anthropogenic change during the last century: it shifted from a largely unpopulated, post-logging shrubland to a moderately populated, closed-canopy deciduous forest. Avian community composition varied dramatically over five decades, apparently largely in response to changes in habitat. Nevertheless, overall species richness stayed remarkably constant, and in most years, the number of species present was close or equal to the long-term mean.

Plant families in Europe

Haskell (in press) used fossil pollen data from the European Pollen Database (EPD) (http://www.ngdc.noaa.gov) to examine the impacts of Pleistocene glaciation on the current latitudinal gradient of plant family diversity. For the current study, two sites representing extremes of latitude were selected from the 24 sites used in the original analysis: Lake Xinias, Greece and Akuvaara, Finland. Taxa recorded at these sites were tallied as families to standardize the taxonomic level of pollen identification. For purposes of this paper, we assume that changes in familial richness are correlated with, and provide a conservative estimate of changes in species richness. This was confirmed by analysis of the data at different taxonomic levels (family, genus, or species); using the finest level of taxonomic resolution reported by the original authors gave qualitatively identical results [see Kaufman 1995 and Haskell (in press) for a more complete discussion]. Taxonomic richness at each site remained nearly constant throughout the Holocene, despite substantial changes in the families that were present.

Characterization of species richness

Insofar as possible, we used the same methods to analyze each data set, and thereby to facilitate comparisons among them. However, each study necessarily compiled richness data across time periods of different length and resolution: (1) for the rodents at Portal, monthly trapping data were summed into two 6-month periods for each year; (2) for the Michigan birds, multiple surveys over a breeding season were summed to give one value for each year; and (3) for the European plants, different numbers of sample strata were combined to give one value for each 1,000-year interval for each site.

To claim, as we do, that species richness remains relatively constant, it is necessary to have some standard to measure constancy. One way is to plot colonization and extinction to show whether and on what time scale the two processes are opposing and compensatory. We measured colonization by counting the number of taxa present in one time step that were not present in the previous time step. We determined extinction by counting the number of taxa that were present in one time step that were absent in the subsequent time step. Another way to assess the constancy of diversity is to quantify the changes in diversity that would have been observed if only extinction or colonization were occurring. Therefore, we plotted the actual time series of taxonomic richness as well as the cumulative colonizations (the number of species that would have accumulated if no extinctions had offset the observed colonizations), and the cumulative extinctions (the number of species that would have remained if no colonizations had offset the observed extinctions). In calculating the cumulative colonization and extinction curves, only a single event of colonization or extinction, respectively, was permitted for each species. It frequently happened in the real data sets that a taxon went extinct and subsequently recolonized or vice versa, but in these analyses we counted only the first colonization or the first extinction event for each taxon.

Analyzing the data in this fashion revealed differences between the rodent, bird, and plant systems in the dynamics of diversity (Figs. 1, 2, 3, 4). Such differences are hardly surprising, considering the differences in the kinds of organisms, their environments, time scale of the data, and methods of collecting and analyzing data. These unique features are discussed in the separate papers describing the dynamics of each system (Ernest and Brown, in press, Parody et al. 2000, Haskell, in press). Here we will focus on the similarities in the overall patterns of diversity over time.

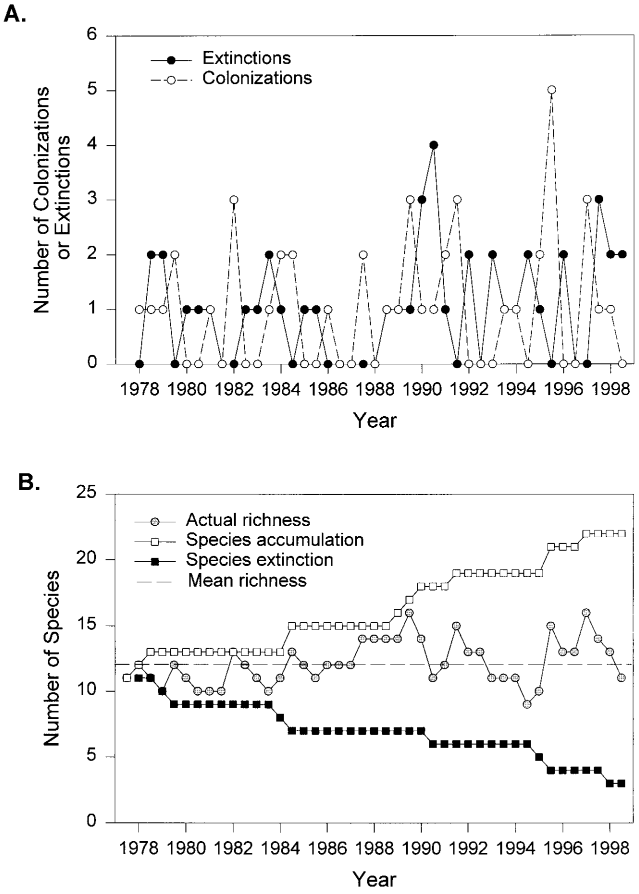

Fig. 1A, B Dynamics of rodent species richness at Portal, Arizona from 1977 to 1998. **A**The number of colonizations and extinctions that occurred between time steps. **B** Temporal variation in species richness (*gray circles*) in comparison to the long-term mean species richness (*dashed line*). Also shown are the cumulative initial colonizations by new species (*white squares*) and cumulative initial extinctions of species that were originally present (*black squares*). In compiling these cumulative curves, only the first colonization or extinction event for each species was used, even though some species colonized and went extinct multiple times

In all three systems, richness remained relatively constant over the duration of the study despite substantial changes in species composition. This apparent regulation of richness occurred because colonization and extinction events, while frequent, were approximately offsetting (Figs. 1, 2, 3, 4).

The effects of these compensatory events are perhaps best seen in the lower panel of each figure, where we have plotted the actual time series of richness, and compared it to the cumulative colonization and extinction curves. In each of these graphs, all three curves start at the same point, the number of species present in the first sample. The divergent final points of the three curves each denote a number of some interest. The end point for the richness curve represents the observed number of species in the last sample. Differences between initial

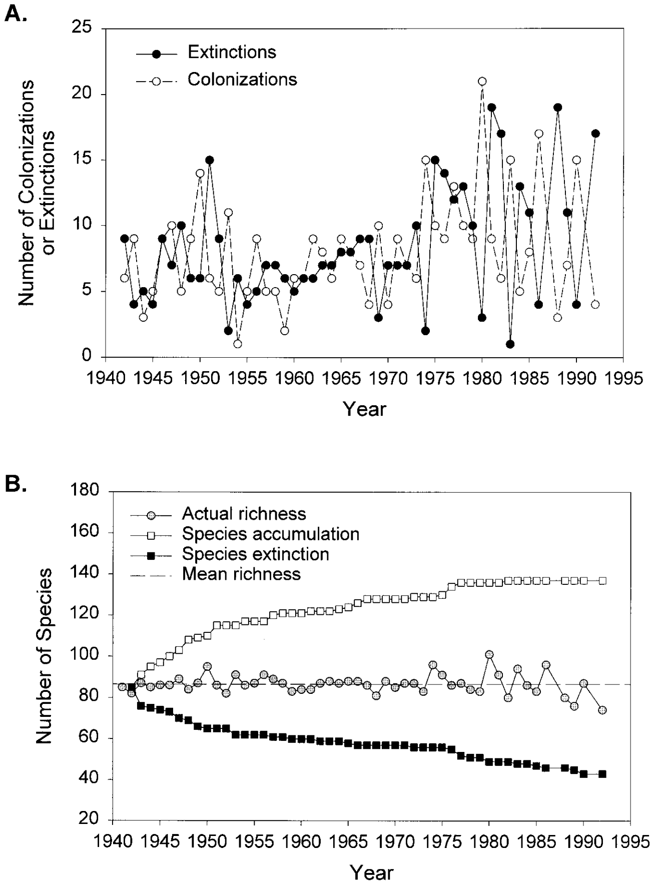

Fig. 2A, B Dynamics of bird species richness in Michigan from 1942 to 1992. **A** The number of colonizations and extinctions that occurred between time steps. **B** Temporal variation in species richness (*gray circles*) in comparison to the long-term mean species richness (*dashed line*). Also shown are the cumulative initial colonizations by new species (*white squares*) and cumulative initial extinctions of species that were originally present (*black squares*)

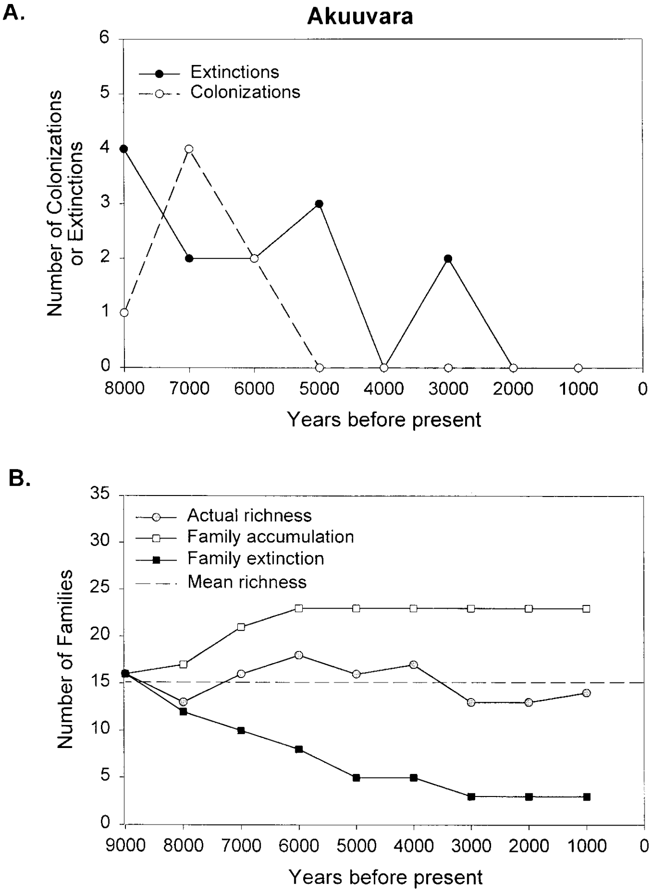

Fig. 3A, B Dynamics of plant family richness at Akuvaara, Finland for 1,000-year intervals from 9,000 to 1,000 years before present. **A** The number of colonizations and extinctions that occurred between time steps. **B** Temporal variation in number of families (*gray circles*) in comparison to the long-term mean familial richness (*dashed line*). Also shown are the cumulative initial colonizations by new families (*white squares*) and cumulative initial extinctions of families that were originally present (*black squares*)

and final values of richness provide one measure of the extent to which some relatively constant diversity was maintained. Deviations between initial and final values range from 0% to 18%, for desert rodents and plant families in Xinias, respectively.

The cumulative extinction curve ends at the number of taxa that were present in every sample throughout the time series. This extinction curve can be treated as a thought experiment, showing the loss of species that might have been expected in a closed or isolated system, where colonization from some regional species pool – including recolonization of species after local extinction – was not possible. The losses of taxa that would have occurred in such hypothetical closed systems are impressive: ranging from 81% (3 of an original 16 families) for plants in Akuvaara to 51% (43 of 85 species) for Michigan birds. While these losses should be interpreted with some caution, they do provide some estimate of the extinctions, and resulting decreased richness, that might have occurred if the study sites were isolated conservation reserves or oceanic islands rather than arbitrarily defined study areas surrounded by a matrix of diverse habitats that supported a regional pool of species.

The cumulative colonization curve ends at the total number of species recorded at the site. This represents a conservative estimate of the time-averaged richness of the regional species pool. By time-averaged we mean the minimum number of species in the pool assuming that the composition of the pool itself did not change due to large-scale colonization or extinction events. For the rodent and bird data sets we know that the pool did not change, because all of the species that colonized the study sites occurred in the surrounding region throughout the time series. This may not be true for the plants, however, because some taxa may have recolonized the regions surrounding the sample sites (especially those at high latitudes) in response to environmental changes related to retreat of glaciers or shifts in climate. Nevertheless, for all three data sets, we believe that the maximum species richness indicated by the end of the cumulative

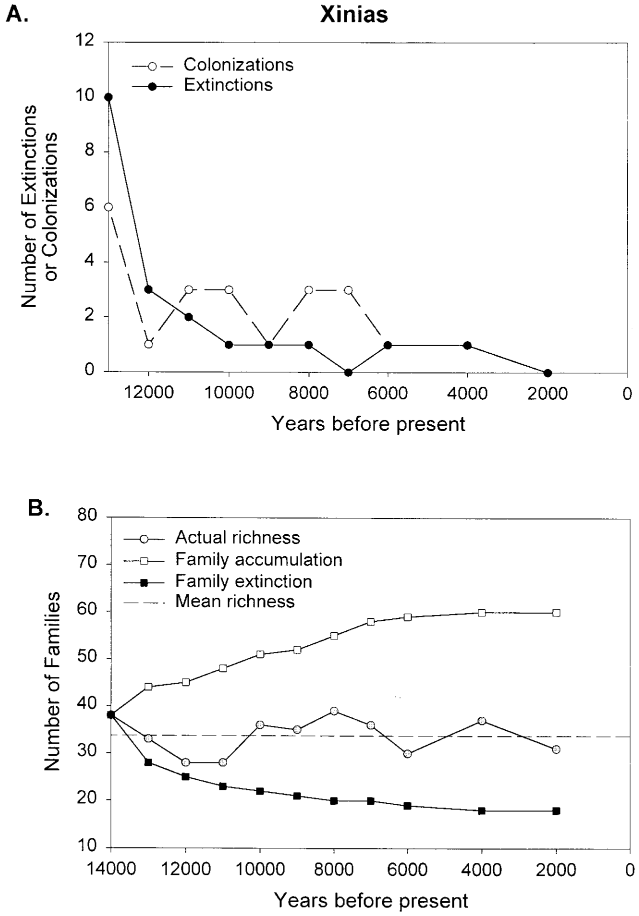

Fig. 4A, B Dynamics of plant family richness at Lake Xinias, Greece for 1000-year intervals from 14,000 to 2,000 years before present. **A**The number of colonizations and extinctions that occurred between time steps. **B**Temporal variation in number of families (*gray circles*) in comparison to the long-term mean familial richness (*dashed line*). Also shown are the cumulative initial colonizations by new families (*white squares*) and cumulative initial extinctions of families that were originally present (*black squares*)

colonization curve is a conservative estimate of the total regional pool. The pool almost certainly contained more than this number, because the cumulative colonization curve did not record all of the species whose geographic ranges overlapped the sample sites during the period of the time series. Again, we know from other records that this was true for the rodent and bird data sets, but we cannot be so certain for the plant system.

The three case studies that have been considered in detail demonstrate remarkable constancy of richness over time. This constancy has been maintained despite environmental changes that caused substantial variation in species composition due to colonization and extinction of species. This phenomenon appears to be very general. Relatively precise regulation of diversity has been observed in diverse taxa, in different ecosystems, on different continents, and over time scales ranging from a few decades to millions of years. A survey of the literature (Table 1) reveals many examples.

Mechanisms regulating species richness

We suggest that regulation of species richness over time within relatively narrow bounds despite substantial turnover in species composition is a frequent but not universal phenomenon. We conjecture that five conditions are both necessary and sufficient for it to occur:

1. Productivity, or more specifically, the availability of energy or other limiting resources, remains relatively constant. This sets a relatively constant “carrying capacity” for the system as a whole. It would be reflected in relatively constant biomass, cover (in plants), total abundance, and other measures of resource supply if these were available.
2. Other abiotic or biotic environmental variables change. The environmental changes favor some species, allowing them to increase in number or to colonize, and disfavor others, causing them to decrease and sometimes to go extinct. Environmental changes cause turnover in species composition.
3. A regional species pool provides a supply of potential colonists. Compared with a local site or habitat, the pool contains substantially more species with a wider range of environmental requirements and tolerances. The existence of the pool implies that local ecosystems are open with respect to migration, so that when conditions change, and some species go extinct, other species can immigrate. This condition holds for many local ecosystems that are embedded within landscapes containing generally similar habitats, such as our local sample sites embedded within continental ecosystems. This condition does not hold for highly isolated systems, such as some oceanic islands and perhaps some reserves surrounded by very different habitats (e.g., patches of prairie or forest completely surrounded by agricultural fields).
4. The species pool must contain a subset of species capable of utilizing all of the available limiting resources and tolerating the altered environmental conditions. This recognizes that the constant whole-system “carrying capacity” referred to above is, in part, a consequence of the resource requirements and environmental tolerances of the species in the pool. Then compensatory shifts in the abundances of species, including colonists, can cause all resources to be used.
5. There is a universal division rule that determines how resources are apportioned among species in a local ecosystem. This division rule is related to the deterministic processes that govern the distribution of relative abundance and other currencies reflecting resource use (cover, biomass, etc.) within a community (MacArthur 1957; Preston 1962; Williams 1964; May 1975, 1986). The division of resources reflects differences in requirements and tolerances among the species, not only within the local ecosystem, but also within the pool. While there is not yet consensus among ecologists about how resources are allocated among species, ranked species-abundance distribu-

Table 1 A sampling of published studies which have reported that species composition changes but taxonomic richness remains constant

Observational data

Taxa	Location	Duration	Citation
Plants	North America	~200 million years	Wing and DiMichele (1995)
Ostracodes	North Atlantic	~130 million years	Benson (1976)
Mammals	North America	50 million years	VanValkenburgh and Janis (1993)
Brachiopods	Oceans	40 million years	Watkins and Boucot (1978) (as described in Rosenzweig 1995)
Ants	West Indies	20 million years	Wilson (1985)
Mammals	North America	12 million years	Webb (1969)
Mollusks	Atlantic Ocean	~7 million years	Allmon et al. (1993)
Benthic Invertebrates	Quebec, Canada	5 million years	Rosenzweig and Taylor (1980)
Plants	Finland	62 years	Virola et al. (1999)
Birds	Channel Islands, California, USA	61 years	Diamond (1969)
Birds	New York, USA	20 years	Lanyon (1981)
Fish	Oklahoma, USA	20 years	Pyron et al. (1998)
Trees	Costa Rica	8–20 years	Kappelle et al. (1996)
Marine Benthic Communities	Atlantic Ocean	2 years	Grassle and Maciolek (1992)
Birds	British Columbia, Canada	2 years	Schmiegelow et al. (1997)

Experimental data

Taxa	Location	Manipulation	Citation
Zooplankton	Wisconsin, USA	Acidification	Brezonik et al. (1993), Frost (1998)
Infaunal community	Ross-shire, Scotland	Removal of pit-digging crab	Hall et al. (1993)
Plants	Tanzania	Nutrient perturbation	McNaughton (1977)
Plants	Rocky Mountains, USA	Grazing	Stohlgren et al. (1999)

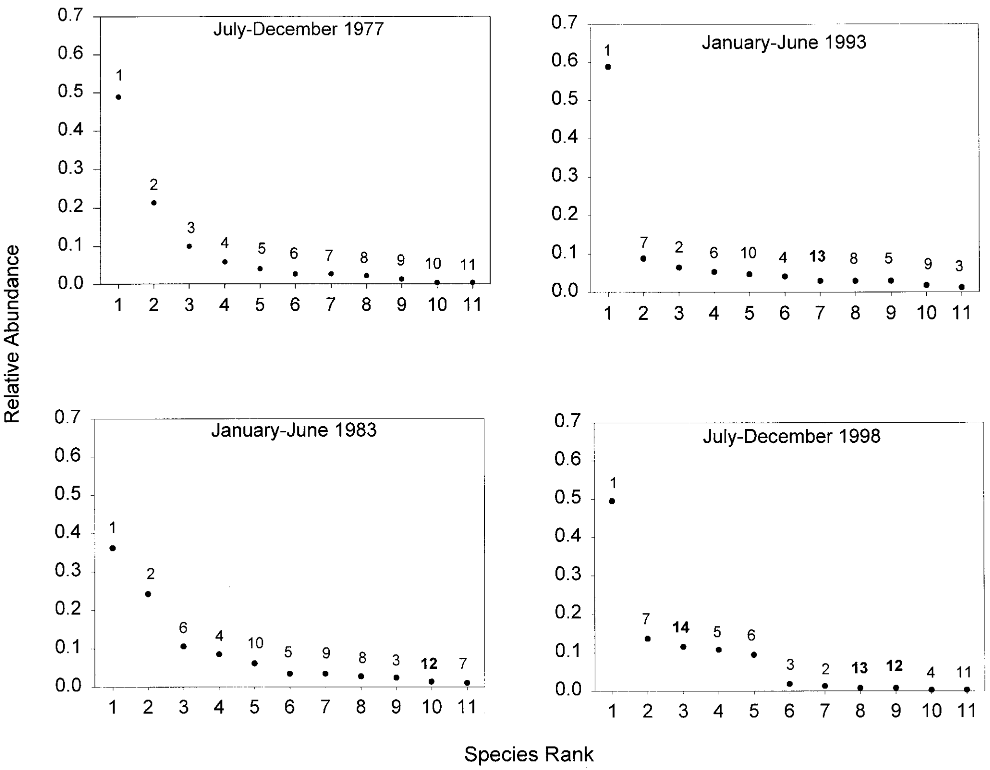

Fig. 5 Ranked species abundance distributions for rodents at Portal for four 6-month periods. Species are numbered from the most to least abundant in the first sample and then in their order of appearance (colonization). Note that there were major changes in the rankings due to shifts in abundance as well as colonization and extinction events

tions have a distinctive form that suggests a universal process (e.g., Fig. 5; Hubbell 2001).

If these conditions hold, it is possible to make some predictions that can be evaluated empirically. We do this for the three case studies.

1. If resource availability does not change, currencies that measure total resource use by the community should also remain constant. Depending on the group of organisms studied, examples of such currencies may include total cover (or leaf-area index), biomass, and energy use by all species combined. For rodents

at Portal we have independent measurements of these currencies. Total abundance, biomass, and energy use of all species did indeed remain relatively constant. While there was some short-term fluctuation, there was no consistent long-term trend, and the magnitude of variation (measured in standard deviation units) was comparable to the modest variation in species richness (Ernest and Brown, in press; see also Boyer 1987, as referred to in Brown 1994).

2. If the turnover of species is caused by environmental changes, these changes should be more predictable or deterministic than expected on the basis of chance alone. Two observations are relevant here. First, if the changes in species composition were just stochastic, colonizations and extinctions should be confined primarily to rare species. Ranked abundance distributions for the rodents at Portal show that this is not the case (Fig. 5). Dominant species have gone extinct, and colonizing species have become dominant. While our data for birds and plants do not allow such precise quantification, it is apparent they showed similar changes in dominance. Second, all three data sets suggest that changes in species composition were due, at least in part, to large, directional environmental changes that have occurred in these ecosystems. At Portal, significant increases in winter precipitation and in the densities of woody shrubs occurred during the 22-year period (Brown et al. 1997). Associated with these changes have been decreases and extinctions of rodents and other animals characteristic of grassland habitats and increases and colonizations of species characteristic of shrubland habitats (Valone and Brown 1996; Brown 1998). For the birds in Michigan, there is a 50-year record of drastic habitat change. In the early 1900s, the study area was heavily logged and burned. By the end of the study period, the vegetation had succeeded to deciduous forest with interspersed human settlements (McCann 1991). These habitat changes were reflected in changes in avian species composition, from predominantly grassland forms early in the study to predominantly forest species in recent years (Parody et al. 2000). The 10,000-year pollen record for high latitudes in Europe documents a transition from herbaceous and shrubby species characteristic of early succession to assemblages dominated by trees and other forest plants.
3. If local ecosystems are open with respect to exchange of species with a regional species pool, this implies that changes in species composition can include colonization and extinction events as well as shifts in abundance of existing species. As indicated above, the minimum size of the pool can be defined operationally by the cumulative number of colonizations. This is conservative, because larger pools would have been obtained by counting all species whose geographic ranges included the study site. Despite this conservative estimate, the species pools were considerably larger than the mean richness observed at any point in time (Figs. 1, 2, 3, 4). Furthermore, many colonization and extinction events were observed in all three ecosystems.
4. If all available resources are used, we should observe compensatory shifts in abundance. Only the rodents at Portal provide data to address this prediction directly. When kangaroo rats were experimentally removed, small granivorous rodents increased several fold in abundance (Brown 1998). Much of the compensation was due to colonization of new species, not just to shifts in abundances of existing species (Valone and Brown 1996; Ernest and Brown, in press).
5. If taxonomic richness is maintained within such narrow bounds as observed in all three studies, there must be some common rule by which resources are allocated among species. Regardless of the exact mechanism and mathematical form of this division rule, there is independent, albeit somewhat indirect, evidence for its existence. The data from the rodents at Portal and European plants included relative abundances (in the latter case, this assumes that abundance of pollen in some way indexes the abundance of plants). Both showed typical species-abundance distributions, characterized by a few common taxa and many rare ones. A plot of the rodent data (Fig. 5) shows that the overall distribution of abundances remained similar over the time series even though the ranks of individual species shifted markedly.

Theory

A major body of ecological theory that addresses the regulation of species richness is the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) and subsequent elaborations and modifications thereof (e.g. Brown 1971b; Gilpin and Diamond 1976; Brown and Kodric-Brown 1977). This theory explicitly predicts that relatively constant species richness is maintained over time within an island or habitat patch. It also predicts that there is turnover in species composition, due to colonization and extinction of species. Our explanation for regulation of species diversity is different from the theory of island biogeography.

The differences can be illustrated by recasting the theory of island biogeography in an alternative graphical form (Fig. 6). In this reformulation, the rate of change in richness (ΔS) is plotted as a function of richness (S). The relationship for each island is depicted (for simplicity) as a straight line with a negative slope, giving an equilibrial number of species (S_K) when ΔS is equal to zero (x-intercept). The maximum rate of colonization occurs when S equals zero (y-intercept); it is predicted to be higher for near or less isolated islands than for far or more isolated ones. The maximum rate of extinction occurs when S equals S_P (where S_P is the total number of species in some regional pool that are potentially available to colonize); it is predicted to be higher for small than for large islands. The rate of change in ΔS is predicted to be more negative for small islands than for large ones. The slope and intercept of the line for a particular island in Fig. 6 reflects the joint influences of colonization and extinction. This reformulation emphasizes that while each indi-

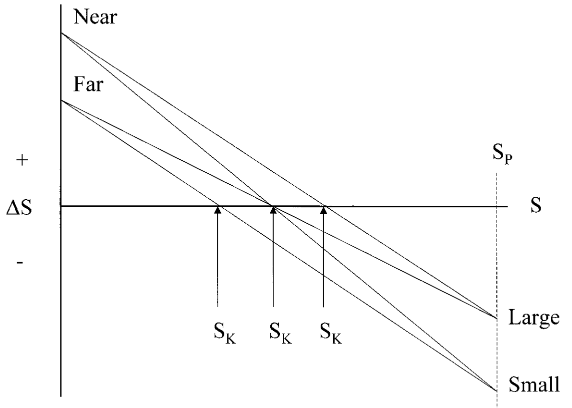

Fig. 6 An alternative graphical model of the MacArthur and Wilson (1967) theory of island biogeography. The rate of change in species richness (ΔS) is plotted as a function of number of species on the island (S). The *vertical lines with arrows* denote the equilibrial species richness (S_K for different combinations of island area (*large and small*) and distance from the mainland (*near and far*). The pool of species (S_P) available for colonization is assumed to be the same for all islands. For simplicity, we depicted ΔS as a function of S using straight lines, but these would be curvilinear if they had the familiar shape shown in MacArthur and Wilson (1967) and Mac Arthur (1972)

vidual island has a particular equilibrial number of species, there is much variation in S_K among different islands due to their physical geographic features: different combinations of area and isolation.

This kind of graphical representation can be generalized to depict the regulation of diversity at a single non-isolated site over time as observed in our data sets (Fig. 7a). Since the site is open to colonization from immediately surrounding habitats and is of arbitrary size, the maintenance of a steady-state richness must be explained in terms of processes other than isolation-mediated colonization and area-mediated extinction. In our depiction the equilibrial diversity, S_K, can be thought of as a “carrying capacity for species” (Brown 1988a): a steady-state level of richness specific to a particular site or local ecosystem, that is set by resource availability and other local conditions and is maintained despite changes in species composition. The precision of regulation will depend on the slope of the line in the vicinity of S_K. While a spectrum of possibilities can be imagined, the empirical results suggest a steep slope with correspondingly small variation around S_K (Fig. 7b).

So, we have depicted a graphical model of richness-dependent regulation of species diversity, analogous to standard models of density-dependent regulation of population size. Just as the number of individuals in a population is regulated by density-dependent births and deaths, the number of species in a local community is regulated by richness-dependent colonizations and extinctions. These colonization and extinction events cause turnover in composition of species, just as births and deaths cause turnover in the identities of individuals.

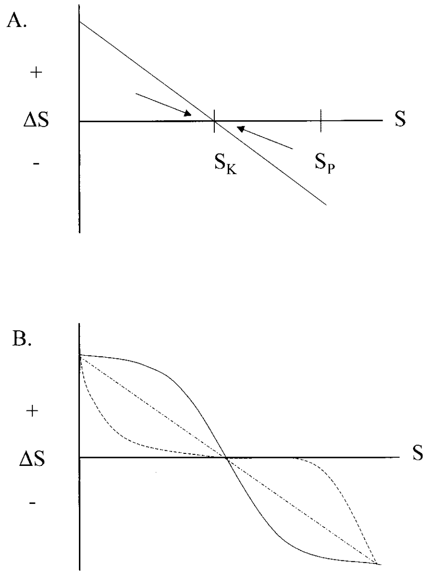

Fig. 7A, B The regulation of diversity at any site open to colonization from a regional species pool can be depicted graphically in a manner similar to the one used earlier (Fig. 6) for the theory of island biogeography. **A** Local ecological conditions rather than isolation and area of the patch are assumed to determine the equilibrial species richness (S_K). **B** How precisely species richness is regulated will depend upon the slope of the line (depicting ΔS as a function of S) in the vicinity of S_K. Our results suggest that often diversity is strongly regulated, implying a steep slope around S_K (*the unbroken line*)

This framework differs from the theory of island biogeography in several important respects. The only similarity is that both theories posit that opposing colonization and extinction events maintain a steady-state value of species richness. There are several important differences. First, our theory attributes the equilibrial value of diversity, S_K, to a carrying capacity for species that is set largely by local ecological conditions, such as productivity, resource availability, and abiotic stress. In contrast, the theory of island biogeography attributes S_K primarily to geographic setting: to island size and isolation. Second, our theory invokes a direct feedback between species richness and colonization and extinction events that is mediated by resources. When $S < S_K$ there is opportunity for species to colonize from the pool, whereas when $S > S_K$ there is a pressure that results in local extinction. Opportunity for colonization and pressure for extinction are determined by the availability of resources and the capacity of the local species to use those resources. In contrast, in island biogeography theory opportunity for colonization is determined not by local conditions but by the geographic isolation of the island, and pressure for extinction comes from the influence of island area on population size, and hence only indirectly from availability of resources. Finally and most importantly, our theory implies that the opposing forces of colonization and extinction should operate most strongly to regulate diversity in non-isolated ecosystems that are open to relatively unrestricted immigration from a rich regional species pool in surrounding habitats. This is in contrast to island biogeography theory, which predicts that the opposing forces of colonization and extinction are sufficiently strong to maintain steady-state levels of diversity in oceanic islands and other highly isolated ecosystems.

Implications

We recognize that species richness, like population size, does not always remain constant. We expect that richness will be regulated within relatively narrow limits, only so long as productivity of the local site remains relatively unchanged and the environmental conditions remain within the tolerances of a sufficient number of species in the regional pool. While some changes in species composition may occur by chance, most will occur due to deterministic interactions of species with the abiotic environment and other organisms. We do not expect that richness will remain constant if the conditions enumerated above are not met, and most importantly if productivity changes substantially, if there are very large changes in the abiotic or biotic environment, or if there are substantial changes in the diversity and composition of the species pool due to a major historical perturbation. We illustrate some possibilities in Fig. 8. For example, we expect S_K to vary with changes in productivity, abiotic conditions, the disturbance regime, or certain biotic interactions (Fig. 8a). We also expect S_K to vary with the size of the species pool (Fig. 8b). Note that, unlike island biogeography theory, it is not necessary to postulate differences in the maximal rates of colonization or extinction (i.e., values of ΔS when $S = 0$ and $S = S_P$, respectively). The implication is that local diversity is primarily influenced by local site-specific ecological characteristics.

Islands and other isolated habitats contrast with the open, unbounded systems that we have studied and modeled here. By open and unbounded we simply mean that local sites are patches that have: (1) arbitrary, investigator-defined boundaries that do not represent major ecological discontinuities; and (2) free interchange of species with the regional pool so that diversity is not colonization-limited. There is a spectrum of openness that extends from such patches to isolated oceanic islands, which for most terrestrial organisms are discrete, naturally bounded ecosystems isolated in an inhospitable matrix that severely limits dispersal.

This leads to the paradoxical conclusion that islands, for which equilibrium theory was devised, should have weak diversity-regulating forces and hence consequently should often be far from equilibrium. Insular ecosystems should show large, long-lasting perturbations in diversity either when environmental changes cause the extinction of native species or when changes in barriers to dispersal result in new waves of colonization. The effects of human-caused perturbations on islands and other isolated ecosystems support these predictions. Thus, for example, when aboriginal humans settled oceanic islands they often exterminated many terrestrial vertebrates and substantially reduced species diversity (Olson and James 1982a, b, 1984; Olson 1989; Steadman 1993, 1995). On Hawaii, human-caused extinctions reduced the number of the native bird species by about 50%. On the other hand, modern humans have greatly increased diversity of some taxa on islands by facilitating invasion of exotic species. Due to human-caused immigration and habitat alteration, the number of plant species on several isolated oceanic islands has increased by more than 40% in the last few centuries (Lonsdale 1999).

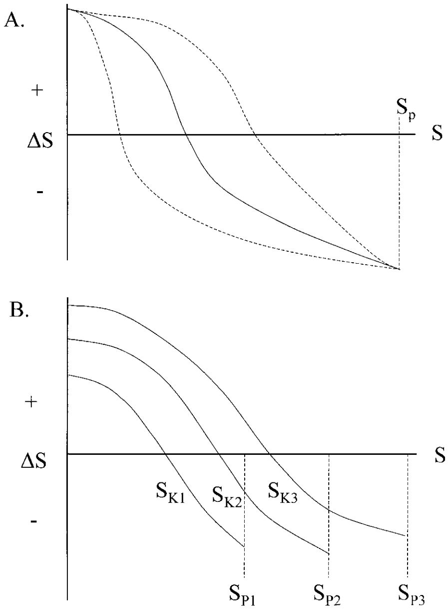

Fig. 8A, B Elaboration of the model for the regulation of diversity (Figs. 6, 7) to illustrate how characteristics of a site can affect the regulation of species richness (*S*). **A** Changes in local ecological conditions, such as productivity, abiotic stress, or intensity of biotic interactions, can change ΔS as a function of *S*, resulting in increases or decreases in the equilibrial number of species (S_K) from the original relationship (*bold line*). **B** Changes in the size of the species pool (S_P) can also change ΔS as a function of *S*, resulting in different numbers of species at equilibrium (S_K)

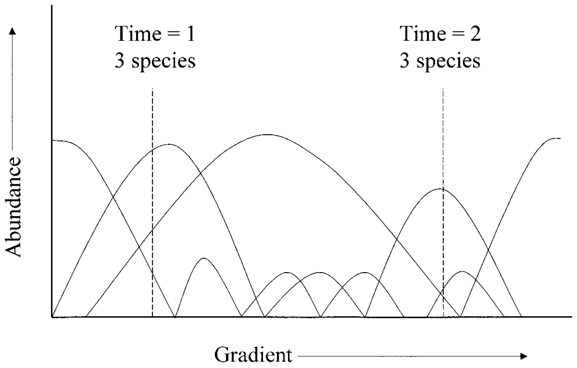

Fig. 9 Whittaker's graphical depiction of species distributions along a gradient can be modified slightly to illustrate how species composition at a single site can change in response to changing environmental conditions, but without changing species richness. In this example, as environmental conditions change from Time=1 to Time=2, there is a change in species composition as two species go extinct and two others colonize, but total diversity remains unchanged at three species

Further insight into how open systems maintain relatively constant species richness can be visualized by adapting Whittaker's (1975) classic graphical depictions of species distributions along environmental gradients (Fig. 9). Implicit in the notion of gradients, is continuous variation and hence autocorrelation in environmental conditions. Temporal changes in the environment can be analogized to the spatial displacement depicted by Whittaker. In fact, we expect a relationship between patterns of environmental variation in space and time. Because of spatial and temporal autocorrelation in abiotic and biotic variables, when environmental changes occur, new conditions at a given site are likely to fall within the range of pre-existing conditions at nearby sites. These adjacent sites with somewhat different environments maintain additional species in the pool and serve as a source of colonists. Like Whittaker, we do not imply that communities are integrated entities of fixed composition that "migrate" across the landscape in response to environmental change. In fact, the fossil record suggests that this rarely occurs; instead species respond "individualistically" (e.g., Cole 1982; Davis 1986; Graham 1986; Jackson and Whitehead 1991; Graham et al. 1996). We do imply, however, that when environmental changes occur, there will often be species within the regional pool that will be favored and able to colonize.

One implication of the observed regulation of diversity is that species are complementary but not redundant. Species must be sufficiently similar in resource utilization and requirements for other environmental conditions so that the changes in abundance and presence/absence are compensatory. Species must be sufficiently different in resource utilization and other niche variables to be favored or disfavored when environmental conditions change. Differences among species are also crucial for the maintenance of a diverse regional species pool. Regional diversity is largely due to spatial variation in the environment and the differential responses of species with varying requirements. Some have argued that many species are "redundant", because manipulation of species composition often results in little change ecosystem processes (Walker 1992; Naeem et al. 1994; Naeem and Li 1997; Tilman et al. 1997; Wardle et al. 1998). Our results imply that the differences among species, even the subtle ones, influence the response of ecosystems to environmental changes. When such changes occur, the extent to which the pool contains species with complementary requirements determines whether or not ecosystem processes will be preserved.

Another implication of our results is that species diversity can be viewed as an emergent property of ecosystems. This provides an alternative perspective to the majority of recent studies on the correlates and consequences of species diversity (e.g. Tilman and Downing 1994; Naeem et al. 1994, 1996; Tilman 1996; Tilman et al. 1996, 1997; McGrady-Steed et al. 1997; Wardle et al. 1998; Symstad et al. 1998; van der Heijden et al. 1998). These studies have considered the effect of species richness on ecosystem properties and processes. Number of species is taken as the independent variable and is manipulated experimentally, and then various ecosystem-level dependent or response variables are measured: e.g. productivity, biomass, nutrient flux, and various measures of stability. This approach is typically motivated by the concern that human-caused environmental changes may cause substantially reduced local and regional diversity. We emphasize the merits of an alternative perspective that takes features of the ecosystem such as isolation, abiotic stress, or productivity as independent variables and measures species richness as the dependent or response variable. This alternative approach is particularly relevant for investigating whether or not human-caused environmental changes lead to changes in species diversity.

Our results imply that while species diversity is influenced by historical events and geographic phenomena, it is also an emergent consequence of local ecosystem-level processes. Despite fluctuations in the environment, so long as the changes are not too severe, species richness is often regulated within narrow bounds by the interaction of local and larger-scale processes. The number of species remains relatively constant because ecosystems respond to environmental change through shifts in species composition: not only compensatory shifts in abundance, but also colonization and extinction events. The implication of this perspective is that when species richness does increase or decrease substantially, including changes in diversity caused by human activities, this reflects the substantial reorganization of ecosystem structure and dynamics. Changes in diversity reflect changes in ecosystem processes, such as productivity, pathways of energy and material flow, disturbance regime, abiotic stress, and biological interactions.

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