MacArthur and Wilson's Radical Theory

This is a book about a new general theory of biodiversity in a geographical context. I define *biodiversity* to be synonymous with species richness and relative species abundance in space and time. *Species richness* is simply the total number of species in a defined space at a given time, and *relative species abundance* refers to their commonness or rarity. This is a less inclusive definition of biodiversity than is commonly used in policy circles, but more in keeping with the classical discipline of ecology as the scientific study of the distribution and abundance of species and their causes. Fragments of a general theory of biodiversity abound in ecological theories of island biogeography, metapopulations, and relative species abundance; but in my opinion, there have not yet been any really successful syntheses.

Among the kinds of diversity patterns I seek to explain with this new theory are those illustrated in figure 1.1. This graph shows patterns of relative species abundance in a diverse array of ecological communities, ranging from an open-ocean planktonic copepod community, to a tropical bat community, to a community of rainforest trees, to the relative abundances of British breeding birds. Each line is a plot of the logarithm of the percentage relative abundance of species on the *y*-axis against the rank in abundance of the species on the *x*-axis, from commonest at the left (low ranks) to rarest on the right (high ranks). The curves differ in many ways, including species richness, the degree of
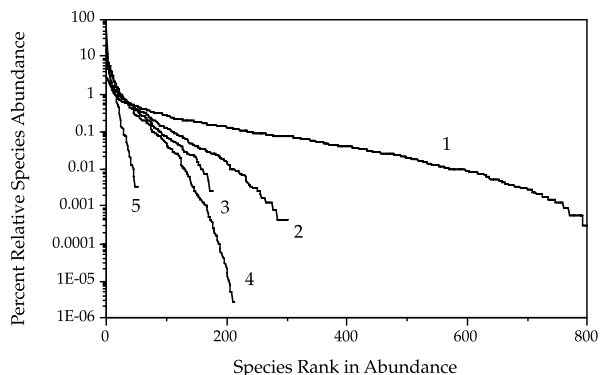
FIG. 1.1. Patterns of relative species abundance in a diverse array of ecological communities. Species in each community are ranked in percentage relative abundance from commonest (*left*) to rarest (*right*). The percentage relative abundance is log transformed on the *y*-axis. 1: Tropical wet forest in Amazonia. 2: Tropical dry decidu-ous forest in Costa Rica. 3: Marine planktonic copepod community from the North Pacific gyre. 4: Terrestrical breeding birds of Britian. 5: Tropical bat community from Panama.

dominance of the community by common species, and the number of rare species each community contains. Neverthe-less, the relative abundance distributions of this heteroge-neous collection of communities all have a curiously similar shape. Some are steeper, and some are shallower, but all of the distributions basically exhibit an S-shaped form, bend-ing up at the left end and down at the right end. Is there a general theoretical explanation for all of these curves? Can we hope even to find a quantitative theory that accurately predicts the relative abundances of the individual species in each of these distributions? I believe so, and I also believe a general theory exists for much more. The development of such a theory is the central theme of this book.

Before proceeding, it is important to issue some caveats and define some terms. Although this purports to be a general theory of biodiversity, in fact it is a theory of

within-trophic-level diversity. There are many aspects of community organization that currently lie beyond the theory's scope, such as the trophic organization of communities (e.g., Hairston et al. 1960, Oksanen 1988), or what controls the number of trophic levels (e.g., Cohen 1978, Pimm 1982, 1991), or how biodiversity at one trophic level affects diversity on other trophic levels (e.g., Paine 1966, Janzen 1970, Connell 1971, Pimm 1991, Holt 1977, Strong et al. 1984).

For present purposes, I define an *ecological community* as a group of trophically similar, sympatric species that actually or potentially compete in a local area for the same or similar resources. Examples might be tree species in a forest, or zooplankton grazing on phytoplankton in a lake. This definition might appear to be closer to what ecologists commonly refer to as an *ecological guild*. However, as I explain in chapter 10, I believe that the theory will often apply more generally to species that are in a particular trophic level but would otherwise be classified in different ecological guilds. While not complete, a theory of biodiversity within trophic levels would nevertheless be a major advance because most biodiversity resides within rather than between trophic levels (i.e., there are many more species than trophic levels). Also, grouping species into trophically similar classes is perhaps the most logical, natural, and tractable way to address questions of species diversity. Not surprisingly, this is the domain for most of the theory about niche partitioning in community assembly (Tokeshi 1993, 1997, 1999). I will also use the term *metacommunity* when applying the theory to biodiversity questions on large, biogeographic spatial scales and on evolutionary timescales. The *metacommunity* consists of all trophically similar individuals and species in a regional collection of local communities. However, unlike species in the local community, metacommunity species may not actually compete because of separation in space or time.

The theory presented here is constructed on the foundation of the equilibrium theory of island biogeography and

owes a great debt to the original insights of MacArthur and Wilson (1963, 1967). It is also an unabashedly neutral theory. I examine the theoretical consequences of assuming that ecological communities are structured entirely by ecological drift, random migration, and random speciation. By *neutral* I mean that the theory treats organisms in the community as essentially identical in their per capita probabilities of giving birth, dying, migrating, and speciating. This neutrality is defined at the *individual* level, not the species level, a distinction whose importance will be explained shortly. The term *ecological drift* is not currently in widespread usage, but it is essentially identical to a concept already familiar to most ecologists as *demographic stochasticity*. While the assumption of complete neutrality is patently false, few ecologists would deny that real populations and communities are subject not only to physical factors and biotic interactions, but also to demographic stochasticity. To study ecological drift theoretically, it is easier to make the assumption of per capita ecological equivalence—at least to begin with. In the plant literature, the notion of ecological equivalence is by no means a new idea (e.g., Hubbell 1979, Goldberg and Werner 1983, Shmida and Ellner 1984).

Before proceeding, I need to be more precise about the meaning of *neutrality* as used in this book. Despite its moniker, the concept of neutrality actually has many meanings in the literature. To most people, the word *neutral* congers up the qualitative notion of "nothing going on." But exactly what people mean by this phrase often turns out to differ from one person to the next. I use *neutral* to describe the assumption of per capita ecological equivalence of all individuals of all species in a trophically defined community. This is a very unrestrictive and permissive definition of *neutrality* because it does not preclude interesting biology from happening or complex ecological interactions from taking place among individuals. All that is required is that all individuals of every species obey exactly the same rules

of ecological engagement. So, for example, if all individuals and species enjoy a frequency-dependent advantage in per capita birth rate when rare, and if this per capita advantage is exactly the same for each and every individual of a species of equivalent abundance (e.g., Chesson and Warner 1981), then such a theory would qualify as a *bona fide* neutral theory by the present definition. The theory of island biogeography is a neutral theory, but it nonetheless has "ecological rules" that govern the rates of immigration and extinction of assumed identical species to and from islands. Thus, *the essential defining characteristic of a neutral theory in ecology is not the simplicity of its ecological interaction rules, but rather the complete identity of the ecological interaction rules affecting all organisms on a per capita basis.* In the present book, I will consider only one class of all possible neutral theories. I examine the consequences of assuming that population and community change arises only through ecological drift, stochastic but limited dispersal, and random speciation. Furthermore, I will consider only one possible mechanism of ecological drift, namely one that I have named zero-sum ecological drift, which I will define and discuss in chapter 3.

Theory aside, it may be hard for many ecologists to accept that ecological drift might actually be important in natural populations and communities. The physicist Heinz Pagels (1982) once observed that there seem to be two kinds of people in the world. There are those who seek and find deterministic order and meaning, if not purpose, in every event. And then there are those who believe events to be influenced, if not dominated, by intrinsically inscrutable, and meaningless, random chance. One of the intellectual triumphs of twentieth-century physics was to prove that both views of physical nature are simultaneously true and correct, but on very different spatial and temporal scales. This dualism remains difficult for many people to accept, however. Even Albert Einstein, whose own work overthrew classical Newtonian determinism, never fully accepted

quantum mechanics and Heisenberg's uncertainty principle (Kevles 1971). Physicists have had to be content with the order discovered in the laws of quantum probability, not in the indeterminism of the quantum events themselves. Ironically, the discovery of deterministic chaos in natural systems has undermined even the once rock-solid faith that determinism ensures predictability (Gleick 1987).

Somewhat analogous philosophical dualisms also run through population genetics and ecology. In population genetics, a long-standing debate has persisted over whether most change in gene frequencies results from random, neutral evolution or from natural selection (Crow and Kimura 1970, Lewontin 1974). In ecology, there are two conflicting world views on the nature of ecological communities which were brought into stark relief by MacArthur and Wilson's theory, although perhaps only in hindsight. The mainstream perspective is what I will call, at the risk of caricature, the *niche-assembly perspective*. This view holds that communities are groups of interacting species whose presence or absence and even their relative abundance can be deduced from "assembly rules" that are based on the ecological niches or functional roles of each species (e.g., MacArthur 1970, Levin 1970, Diamond 1975, Weiher and Keddy 1999). According to this view, species coexist in interactive equilibrium with the other species in the community. The stability of the community and its resistance to perturbation derive from the adaptive equilibrium of member species, each of which has evolved to be the best competitor in its own ecological niche (Pontin 1982). Niche-assembled communities are limited-membership assemblages in which interspecific competition for limited resources and other biotic interactions determine which species are present or absent from the community.

The other world view might be dubbed the *dispersal-assembly perspective*. It asserts that communities are open, nonequilibrium assemblages of species largely thrown

together by chance, history, and random dispersal. Species come and go, their presence or absence is dictated by random dispersal and stochastic local extinction. The theory of island biogeography is an example of such a theory. It asserts that the species in island communities are put there solely by dispersal, i.e., island communities are dispersal assembled, not niche assembled (Hubbell 1997). Although dispersal-assembly theories do not have to be neutral, most are, including MacArthur and Wilson's theory. It is neutral because their famous graphical model assumes that all species are equal in their probabilities of immigrating onto the island, or of going extinct once there. The neutrality of the theory of island biogeography is not always appreciated, however, because MacArthur and Wilson were themselves not completely explicit on this point—about which I will have more to say in a moment.

Neutral theories have had a checkered history in community ecology of creating more heat than light (Strong et al. 1984). Many of the early attempts at constructing neutral models were direct outgrowths of the theory of island biogeography, and some had statistical and other problems that tended to bring misdirected discredit down on the theory of island biogeography itself. The absence of a good neutral theory in community ecology is due in part to the fact that what little neutral theory exists has not been very convincing (Caswell 1976, but see Gotelli and Graves 1996). However, the lack of neutral theory in ecology is also due in no small measure to widespread and, in my opinion, counterproductive resistance to such theories among ecologists.

A recent example of resistance to neutral ideas can be found in an otherwise excellent review by Chesson and Huntly (1997), who argue against the importance of ecological drift (although they did not call it by that name) in structuring ecological communities. The nub of their argument is captured in the following quote: "The unfortunate failure to emphasize that, at some spatial or temporal scale, niche

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differences are essential to species coexistence has allowed logical inconsistencies in the ideas . . . to remain unnoticed" (p. 520). As I will repeatedly demonstrate in this book, however, niche differences are not essential to coexistence, if by "coexistence" we mean the persistence in sympatry of species for geologically significant lengths of time. There is no logical inconsistency in the argument presented here. I prove in chapter 5 that a biodiversity equilibrium will arise between speciation and extinction that results in a long-term, steady-state distribution of relative species abundance. While it is true that all these species are transient, transit times to extinction will be measured in millions to tens of millions of years for most species that achieve even a modest level of total global abundance (chapter 8). Although there is undeniable evidence for niche differentiation among real species in many trophic guilds, this differentiation is not at all essential for coexistence on the timescales usually discussed by ecologists. As I will show, distinguishing the predictions of ecological drift from those made by niche-based theories that predict indefinite species coexistence will often be empirically difficult.

So I believe that we should seriously question *why* our theories in ecology always start with the presumption of the indefinite coexistence of species. All the evidence of which I am aware supports entirely the opposite conclusion—namely, that all species are transient and ultimately go extinct. It seems to me to be a big problem to erect the mathematical expectation of indefinite species coexistence as a sine qua non criterion for whether an ecological theory is acceptable or not. In this entire discussion we seem to have lost sight of the fact that ecology lacks a good *operational* definition of coexistence. The axiomatic premise of coexistence is the real reason why there is virtually no connection between theoretical and empirical discussions of the coexistence question. The loss of a species from a local community is a relatively commonplace observation. However, the

number of cases in which local extinction can be definitively attributed to competitive exclusion is vanishingly small. We no longer need better theories of species coexistence; we need better theories for species presence-absence, relative abundance and persistence times in communities that can be confronted with real data. In short, it is long past time for us to get over our myopic preoccupation with coexistence.

My goals in this book are threefold: first, to develop a formal theory for ecological drift to see "how far we can get with it"; second, to recognize in ecology—as population genetics did quite some time ago—that ecological drift as well as biotic interactions (read genetic drift and selection for population genetics) are *both* potentially important to the assembly and dynamics of ecological communities; and third, to attempt to dispel the pervasive resistance of ecologists to neutral theory by demonstrating its considerable predictive power. Indeed, an intriguing feature of this theory is how surprisingly well it works and how unexpectedly rich it is in nonobvious testable predictions. I will endeavor to show that a neutral theory is not only possible for the origin and maintenance of biodiversity, but also that it generates a quantitative theory for relative species abundance, species-area relationships, and the landscape-level distribution of biodiversity. It also makes testable predictions about modes of speciation and patterns of phylogeny and phylogeography. The theory predicts that different modes of speciation will leave different biodiversity and biogeographic signatures in the distribution of metacommunity relative species abundance (chapter 8).

Neutral theories exist for many ecological patterns and processes at various spatio-temporal scales (Gotelli and Graves 1996). However, the neutral theory presented here is unique to my knowledge in unifying many of them into a single theory. It is the incorporation of speciation into the theory of island biogeography that enables the unified theory to predict relative species abundance from local to

global biogeographic scales. This unified theory also generates a dimensionless biodiversity number, θ, which appears to be fundamental in the sense that it crops up everywhere in the theory at all spatio-temporal scales (chapters 5, 6, 8). Quite remarkably, at least for now, the unified neutral theory does a better job of explaining patterns of biodiversity, relative species abundance, species-area relationships, and phylogeny than current niche-assembly theory does. This state of affairs is likely to change as more synthetic theories develop that include ecological drift as well as niche differences among species. However, regardless of the form that future ecological theories ultimately take, it will no longer be acceptable for these theories to ignore ecological drift.

I begin with a brief review and critique of the original theory of island biogeography, which is the intellectual cornerstone of the unified neutral theory. MacArthur and Wilson erected their theory in part to explain the puzzling observation that islands nearly always have fewer species than do sample areas on continents of the same size. Why is this so? They reasoned that perhaps extinction rates on islands would be higher because of smaller average population sizes (small populations are more extinction prone). Then, once island populations went extinct, it would take the same species longer to recolonize the island than it would take them to disperse among adjacent areas on the mainland. Thus, other things being equal, species would spend a smaller fraction of total time resident on a given island than in the same-sized area of the mainland. Given these assumptions, i.e., a higher island extinction rate and a lower reimmigration rate, one then predicts a lower steady-state number of species on islands than in same-sized areas on the mainland. MacArthur and Wilson captured this simple equilibrium idea in a now famous graph familiar to nearly every high school biology student (fig. 1.2).

By most yardsticks, MacArthur and Wilson's (1963, 1967) simple and intuitive theory of island biogeography has been
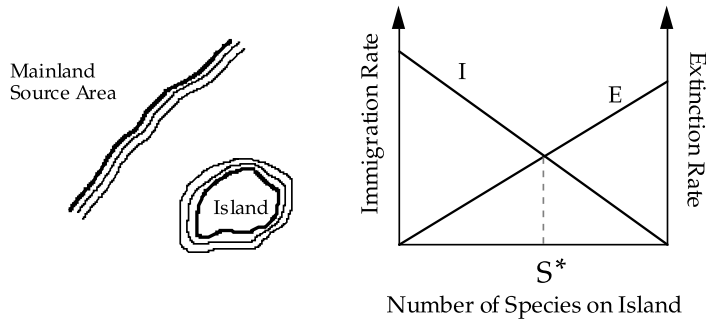
FIG. 1.2.   MacArthur and Wilson's familiar equilibrium hypothesis for explaining the number of species on islands as a dynamic equilibrium (S^*) between the rate of immigration of new species onto the island and the rate of extinction of species already resident on the island. I = immigration rate; E = extinction rate.

a phenomenal and resounding success. The theory revived and sustained a broad interest in questions of biodiversity and biogeography (MacArthur 1972). It spawned a major growth industry in conservation biology by its application to issues such as reserve design (Diamond and May 1975) and the estimation of extinction rates (e.g., Levins 1978, Diamond 1972, 1984, Terborgh 1974, Terborgh and Winter 1980, May and Lawton 1995). It also inspired the fundamental paradigm for the emerging discipline of metapopulation biology (Levins 1969). The literature on island biogeography and allied subjects fills the ecological journals, and in my estimation now numbers in the neighborhood of a thousand papers.

By other measures, however, the theory has been a disappointment, not so much through any fault of its own, as some have charged (e.g., Slobodkin 1996, Hanski and Simberloff 1997), but largely because subsequent development of the theory has languished. Close to four decades have elapsed since MacArthur and Wilson (1963) published their seminal paper in *Evolution*, yet there have been only

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sporadic theoretical advances on the community-level questions that were addressed by the original theory and that have built directly on the foundation of the original insight (e.g., May 1975, Brown and Kodric-Brown 1977). Even more time has passed since the first, independent discovery of the theory by a Cornell graduate student named Monroe, who was studying butterfly biogeography in the Antilles (Monroe 1948, 1953, Brown and Lomolino 1989). In recent years there has been an explosion of empirical and theoretical research on metapopulation biology (Hanski and Gilpin 1997), but this opus consists almost entirely of work on the population dynamics of single species over a set of discrete habitat patches, not on the spatio-temporal dynamics of whole ecological communities.

There is no mystery why so little theoretical development of the equilibrium theory of island biogeography has occurred. MacArthur and Wilson's theory was—and, to a large extent, remains—a radical departure from mainstream thinking in contemporary community ecology. In its fundamental assumptions it is a neutral theory that asserts that island communities are dispersal assembled, not niche assembled. It is something of a misnomer to describe island biogeography as an equilibrium theory: it can only be narrowly construed as such. In this narrow sense, it predicts a steady-state number of species on islands under a persistent rain of immigrant species from mainland source areas (fig. 1.2). However, in contrast to niche-assembly community theory, it does not predict a stable assemblage of particular taxa. It predicts only a diversity equilibrium, not a taxonomic equilibrium.

The theory of island biogeography was radical because it broke away from the conventional neo-Darwinian view of ecological communities as coadapted assemblages of niche-differentiated species residing at or near adaptive and demographic equilibrium. In its place it erected a brave new world view in which ecological communities are seen as

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in turmoil, in perpetual taxonomic nonequilibrium, under-going continual endogenous change and species turnover through repeated immigrations and local extinctions. These turnovers need not be especially rapid, however, and species can coexist for long periods in slowly drifting mixtures and in shifting relative abundances. The theory was all the more remarkable because it was elaborated by MacArthur himself, the leading ecological theorist of his day and champion of the dominant, niche-based equilibrium view.

If communities are largely accidental collections of species whose biogeographic ranges happen to overlap for histori-cal and individualistic reasons, then it follows that species in communities are not highly coadapted or codependent. Setting aside obligate mutualisms and host-parasite relation-ships, which are almost nonexistent between species within the same trophic level (the domain of the present the-ory), then species are rarely so dependent on one another that they cannot persist in the community without particu-lar other species. This view does not deny the obvious exis-tence of niche differentiation. However, it ascribes much less importance to niche in regulating the relative abun-dance and diversity of species in the community. Niche dif-ferentiation, according to this view, is seldom the result of pairwise competition from species sharing similar resource requirements—which helps to explain the apparent rarity of character displacement in nature (Brown and Wilson 1956, Grant 1972, 1975, 1986). Rather, niche differentiation reflects the time-averaged history of the ever-changing biotic and abiotic selective environments to which the species ancestral lineages were exposed during their long, individu-alistic geographic wanderings, the ghost of competition past (Connell 1980).

MacArthur and Wilson's theory raised the possibility that history and chance alone could play an equal if not larger role in structuring ecological communities than do niche-based assembly rules. The idea that random dispersal

and ecological drift could be important in structuring communities was by no means new. Dispersal-assembly theories date back at least to the seminal book, *Age and Area, A Study of Geographic Distribution and Origin in Species,* by a Cambridge University professor J. C. Willis (1922). Similar ideas were independently developed by Gleason (1922, 1926, 1939). However, the success of MacArthur and Wilson's theory brought these old ideas renewed credibility and attention.

According to island biogeography theory, it does not matter which species contribute to balancing immigration and extinction rates on any given island. The only state variable in the model is the number of species on the island. All species in the original theory are treated as identical. Without this assumption, the model's reduction of island community dynamics to counting species does not logically work. Various embellishments on the basic theory do not change this fact. For example, downwardly concave immigration and extinction curves were added to create a more "interactive" version of the theory (Simberloff 1969; fig. 1.3). This makes late-arriving species experience lower successful immigration rates and higher extinction rates. However, this modification does not alter the basic fact that any species arriving late, regardless of whether it is a good colonizer or competitor, will exhibit the same rate changes. Likewise, all species respond in an identical manner to varying the size of the island and its distance from the mainland source area. Other modifications include the "rescue effect" proposed by Brown and Kodric-Brown (1977), who noted that immigration will often interact with and reduce local extinction rates, particularly in local communities in continuous habitats; but again this addition does not alter the fundamental assumptions of the theory.

MacArthur and Wilson's dispersal-assembly hypothesis, when stripped to its bare essentials of total neutrality and species substitutability, will undoubtedly seem extreme to most people. Indeed, it is not clear whether MacArthur
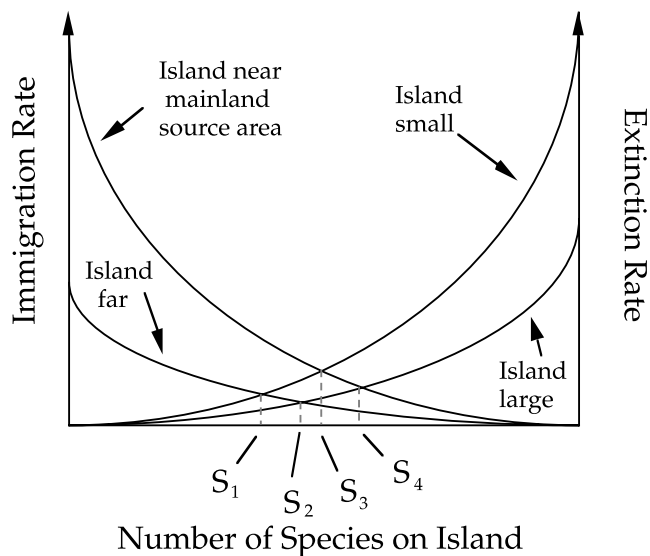
FIG. 1.3. Various enhancements to the basic equilibrium hypothesis of MacArthur and Wilson do not change the dispersal assembly assumption underlying the model. Downwardly bowing immigration and extincton curves were added to characterize the effects of competition on these rates, but all species, whether early or late colonizers, good or bad competitors, experience the same changes in rates. Similarly, the effects of island distance from the mainland and island size on immigration and extinction rates, respectively, operate equally on all species.

and Wilson fully appreciated the implications of this radical assumption. A majority of their 1967 monograph was devoted to discussing such topics as species differences in colonization strategies, causes of species differences in extinction rates, temporal patterning in the order in which species would successfully establish, and so on—all differences *forbidden* by their model! Although MacArthur and Wilson (1967) wrote about traditional ecological processes such as competition, the actual parameters of their model were immigration and extinction rates, distance from

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mainland source areas and island size. These parameters are absent, or virtually so, from most niche-assembly ecological theories.

The assumption of ecologically equivalent species in the theory of island biogeography is simultaneously its strength and its greatest weakness as a neutral theory. The present neutral theory owes its existence in large measure to making a fundamental change in this assumption. In the theory of island biogeography, neutrality is defined at the *species* level. However, in the present theory, neutrality is defined at the *individual* level. This distinction might seem to be subtle and unimportant, but in fact it is key to successfully developing a neutral theory of relative species abundance. Making this change eliminates one of the major objections to the original theory. One of the important ways that species are *not* identical is in their relative species abundances. Relative species abundances, for example, strongly affect the average time it takes a species to go extinct through ecological drift. With this change, there is no longer any need to specify the extinction rate as a parameter—as was necessary in the theory of island biogeography—because the extinction rate can now be predicted by the theory as a function of population size. The ramifications of differences in relative species abundance are the focus of many of the theoretical explorations in this book.

A separate issue from the neutrality assumption is the fact that the theory of island biogeography is conceptually incomplete in a number of important regards. From a biogeographer's perspective, it is incomplete because it embodies no mechanism of speciation. Although species can appear and disappear from islands or habitats in the theory, this is a migration- and local extinction-driven phenomenon. No new species are allowed to originate on islands or in the source area. From a community ecologist's perspective, the theory is incomplete in large part because, as mentioned, it does not predict the relative abundance of

species, only species richness. Relative abundance theory is briefly touched upon in MacArthur and Wilson's (1967) monograph with respect to the species-area relationship. However, the expected equilibrium distribution of relative species abundance on islands was not derived from the first principles of the theory.

The unified neutral theory of biodiversity and biogeography is a conceptual advance over either the theories of island biogeography or relative species abundance taken separately. In current theories of relative species abundance, the number of species in the community is a free parameter that cannot be derived from first principles (Motomura 1932, MacArthur 1957, 1960, Fisher et al. 1943, Preston 1948, 1962, Cohen 1978, Sugihara 1980) (chapter 2). In the unified theory, the equilibrium number of species is a prediction—as in the theory of island biogeography—but so is relative species abundance.

MacArthur and Wilson devoted a large portion of their 1967 monograph to discussing the relationship between island population size and risk of extinction. Without a theory of speciation and relative species abundance, however, they were unable to make headway on many other issues of central importance to community ecology and conservation biology, including expected abundances of species on islands and in the metacommunity and their variances, species incidence functions and times to extinction and recolonization, patterns of island and metacommunity dominance and diversity, species-individual and species-area relationships, and the spatial covariance of populations and of community composition. Much progress has been made on theory for some of these problems individually (e.g., May 1975, Caswell 1976, Coleman 1981, Quinn and Hastings 1987, Caswell and Cohen 1991, Hanski and Gilpin 1997, Durrett and Levin 1996). In the unified theory, many of these problems are now analytically tractable.

Before developing the unified neutral theory, it is useful to give a very brief intellectual history of the niche-assembly and dispersal-assembly perspectives. It is no accident that the perspective to which a person adheres can largely be predicted by the scale on which the person works. Most proponents of niche assembly come out of a strong neo-Darwinian tradition, which focuses on the lives of interacting individuals and their fitness consequences. The concept of niche follows naturally and logically as the population-level summation of the individual adaptations of organisms to their biotic and abiotic environments. Indeed, most ecologists after Grinnell (1917) explicitly grounded niche formalism in the language of fitness and intrinsic rates of increase (Whittaker and Levin 1975).

One consequence of a focus on adaptation and niche assembly has been a tendency to accept an equilibrium and a relatively static view of niches and ecological communities (see critiques by Weins 1984, Pimm 1991). Equilibrium thinking has been aided and abetted by mathematical ecology, which seeks to predict the ecological balance among niche-differentiated competing species, predators and their prey, and so on (Pontin 1982, Weiher and Keddy 1999). For reasons of tractability and hoped-for generality, most theory in population and community ecology focuses on equilibrium analyses and small perturbations around equilibria (Levins 1968, 1975, MacArthur 1972, May 1973, 1981, Maynard Smith 1968, 1974, Pielou 1977, Tilman 1982, Rose 1987). Similarly, theory in evolutionary ecology has elaborated extensively on the idea of the evolutionarily stable strategy (ESS), a concept that assumes the existence of non-invasible adaptive equilibria (Maynard Smith 1968, 1974, Krebs and Davies 1978, Charnov 1982).

This focus on individual variation in fitness, adaptation and niche has led naturally to small-scale, short-term experimental studies of processes of competition, selection and adaptation. Tilman (1989), for example, reviewed several

hundred studies of plant competition and found that nearly half of all studies were on a spatial scale of a square meter or less, and three quarters were done in plots of less than 10×10 m. Only 15% of the studies lasted longer than 3 years, much less outlasted the research career of the original investigator.

Proponents of dispersal assembly, on the other hand, typically work on much larger spatial and temporal scales, using biogeographic or paleoecological frames of reference. Their approach is less experimental and more analytical of large-scale statistical patterns than the niche-based approach, but it is no less scientifically valid (Brown 1995). MacArthur once compared biogeography to astronomy, and quipped that no one has ever faulted astronomy for not being experimental (Rosenzweig 1995). A consequence of working at large spatial and temporal scales is a tendency to be impressed by how spatially variable and ephemeral ecological communities are. For example, the composition and species mixtures of plant communities change greatly from small scales (Whittaker 1956, 1967) to large scales (Gleason 1926, 1939), with few if any sharp community boundaries. On the basis of these patterns, Gleason promulgated his "individualistic" concept of plant distribution, arguing against the extreme niche-assembly view of his contemporary, Frederick Clements (1916). Clements believed that the community was literally a "superorganism," that species were its organs and succession its ontogeny. He argued that each species had an essential role to play in preparing the way for the next seral stage in the succession toward the equilibrium or "climax" plant community. Clements's superorganism theory was discredited by Tansley (1935) on the grounds that it was inconsistent with natural selection at the individual level, and by Gleason (1926) and later by Whittaker (1951, 1956, 1965) as inconsistent with the empirical data on natural plant communities. Improved data on the distribution of organisms has demonstrated that virtually all species, plants

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and animals, are highly clumped and patchily distributed within their overall geographic range (reviewed by Lawton et al. 1994, Brown 1995). This finding has been the empirical inspiration for the new discipline of metapopulation biology (Hanski and Gilpin 1997), which explicitly recognizes the patchy nature of most species distributions.

The best evidence of the ephemeral nature of communities comes from paleoecology. For example, the fossil pollen record from eastern North America and Europe reveals that many pre-Holocene, full glacial, and previous interglacial plant communities are very different from modern communities (Davis 1976, 1986, 1991, Overpeck et al. 1992). Overpeck et al. analyzed 11,700 fossil pollen samples and 1744 modern samples to reconstruct changes in North American vegetation over the last 18,000 years. They document a record of continuously changing plant communities with time. Before the Holocene, vegetation biomes without modern analog were widespread in response to climates and patterns of climate change that no longer exist. The spatial extent of vegetation biomes with no modern analog increases monotonically with greater time depth into the past (fig. 1.4). The data on the geographical history of the paleomigrations of individual species also support Gleason's individualistic hypothesis (Webb 1988, Huntley and Webb 1989, Davis 1991). However, there are other paleoecological studies that reveal cases of long-term community persistence in which a particular suite of species dominates, punctuated by abrupt changes from one apparently stable state to another (Jackson et al. 1996, Brett and Baird 1995). Whether climatic forcing or endogenous processes in the community cause these abrupt changes is generally not known. Whatever the cause, the evidence is strong that communities undergo profound compositional changes, sometimes gradual, sometimes episodic, on timescales of centuries to millennia and longer (e.g., Jackson et al. 1996).
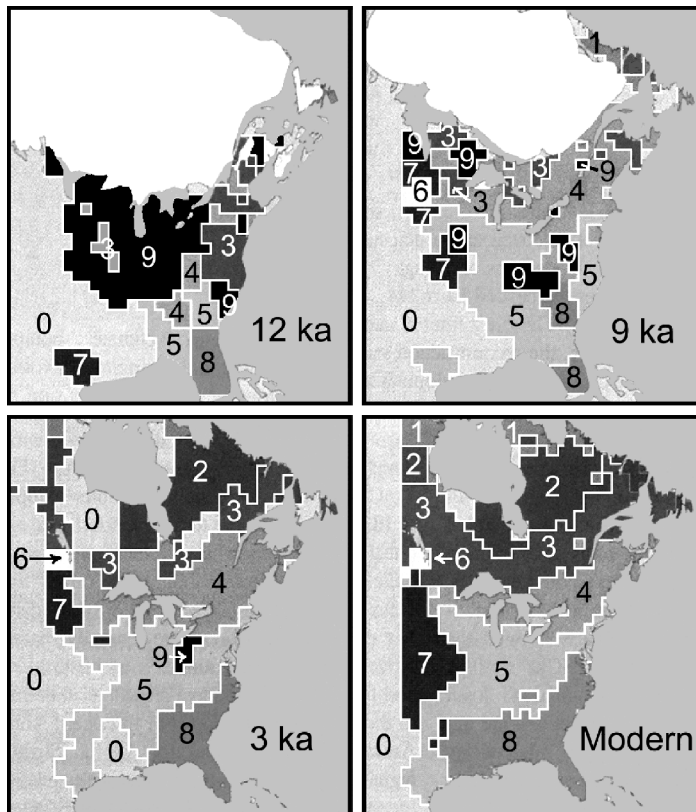
FIG. 1.4. Maps of the paleo-vegetation of eastern North America reconstructed from fossil pollen data, shown at intervals back 12,000 years bp. Mapped vegetation was averaged on a grid cell size of 200 km. The maps indicate continuous change in the distribution of vegetation biomes. Vegetation biomes having no modern analog (in black) become more widespread geographically the farther back in time one goes. Numbers indicate the following areas: 0: No data. 1: Tundra. 2: Forest tundra. 3: Boreal forest. 4: Northern mixed forest. 5: Deciduous forest. 6: Aspen parkland. 7: Prairie/grassland. 8: Southeastern forest. 9. No modern analog. After Overpeck et al. (1992).

Improved data from much deeper in the fossil record are becoming available to test ideas about the stability of fossil assemblages. It is now possible to analyze community changes over mere thousands to hundreds of thousands of years because of much more fine-scale sampling of the spatial and temporal extent of fossil assemblages. Based on detailed studies of Silurian and Devonian faunas, Brett and Baird (1995) proposed the "coordinated stasis" hypothesis (a niche-assembly hypothesis). They reported faunal compositional data on at least fourteen sequential time blocks, each lasting several million years. During these times, faunal composition and relative species abundances were relatively stable, with little species turnover due to extinction, speciation, or migration. These intervals were separated by bursts of rapid change in composition lasting less than 10% of the periods of stasis. However, Patzkowsksy and Holland (1997) have more recently challenged the generality of coordinated stasis based on more detailed temporal and spatial data for Middle Ordovician articulate brachiopod communities. Patzkowsky and Holland report high rates of taxonomic turnover (speciation and extinction rates), even during time blocks exhibiting near constancy in total faunal diversity. These high rates of origination and extinction are not consistent with the coordinated stasis hypothesis by the same statistical criteria that Brett and Baird used to test for coordinated stasis. Their data are more consistent with the view that communities undergo continuous change, comparable to the history of postglacial vegetation change in eastern North America, but on longer timescales.

Actual ecological communities are undoubtedly governed by both niche-assembly and dispersal-assembly rules, along with ecological drift, but the important question is: What is their relative quantitative importance? Falsifying the neutral, dispersal-assembly hypothesis is nontrivial. Observations of

apparent long-term community persistence and resilience in the face of perturbation do not, in themselves, disprove dispersal assembly. For example, community constancy can be mistaken for stability. Constancy in local community species composition will be observed particularly among regionally abundant species. Constancy will be observed even under continual immigration and extinction if the source metacommunity is large, thereby having slow dynamics relative to the local community, due to the law of large numbers (see chapters 5 and 10). For the same reason, drifting species assemblages can also appear to be highly resilient to perturbation. Neutral communities will return to their predisturbance species composition if the disturbance is local and if migration dynamically couples the local community to the size-stabilized metacommunity having slower dynamics.

Falsifying the niche-assembly hypothesis is likewise nontrivial. It cannot be brought down solely on the basis of spatial and temporal change in ecological communities. Proponents of niche assembly have a facile reply to the paleoecologists and biogeographers. To explain most variability in natural communities and still adhere to the niche-assembly hypothesis, one need only posit the existence of sufficient environmental heterogeneity in limiting resources on the appropriate spatial and temporal scale (e.g., Tilman 1982, 1987). On the other hand, while it is not difficult to demonstrate the existence of environmental heterogeneity (Kolasa and Pickett 1991), it is considerably harder to prove that this heterogeneity is actually causing observed patchy species distributions and spatial variability among communities (Naeem and Colwell 1991). Also, by using small-scale heterogeneity as a universal explanation, proponents of niche assembly undermine their case for communities as persistent and predictable assemblages of coevolved niche specialists.

The argument between the niche-assembly and dispersal-assembly perspectives is long-standing. It has persisted so

long precisely because each perspective has strong elements of truth and because reconciling them is nontrivial. This is one of the most fundamental unsolved problems in ecology today. I am convinced that a truly synthetic theory for ecology must ultimately reconcile these divergent perspectives. Applied ecology and conservation biology and policy critically depend on which perspective is closer to the truth, a fact that is not as widely appreciated as it should be. A major motivation for writing this book has been the search for the grail of reconciliation. Reconciling these perspectives is the underlying, if often unstated, theme running through this book. I believe I have made some significant theoretical progress on this question, and in chapter 10 I discuss more fully my ideas for the essential ingredients of such a reconciliation.

The organization of the book is as follows. The intellectual roots of the unified neutral theory are traced in two introductory chapters (chapters 2 and 3). The unified theory follows and is presented in two parts, divided by spatio-temporal scale. The first part considers the relatively fast dynamics of local communities or islands (chapter 4). The second part addresses the much slower dynamics of metacommunities on macroscopic spatial and temporal scales (chapter 5). These two scales are then unified into a single theory of the evolution and equilibrium maintenance of species richness and relative species abundance on continuous landscapes, which forms the basis for a dynamical theory of species-area relationships (chapter 6). Chapter 7 examines the theory in relation to metapopulations and the spatial distribution of biodiversity on the metacommunity landscape. I then explore the theory in relation to phylogeny and the implications of two modes of speciation for the evolution of metacommunity diversity (chapter 8). Chapter 9 focuses on the generality of the theory, and on sampling, parameter estimation, and testing hypotheses under the theory. In the concluding chapter (chapter 10), I revisit the

themes of chapter 1 and speculate about how dispersal-assembly theory might be reconciled with niche-assembly theory and thereby lead to a truly comprehensive theory of biodiversity and biogeography in the future.

This book is by no means the first exercise of these or similar questions (e.g., Brown and Gibson 1983, Pimm 1991, Ricklefs and Schluter 1993, Huston 1994, Brown 1995, Rosenzweig 1995, Hanski and Gilpin 1997), nor will it be the last. However, the present work is unique, to my knowledge, in being the only explicit effort to construct a more general theory of biodiversity and biogeography on the original theory of island biogeography. The premise of this generalized theory is that MacArthur and Wilson were onto something important—namely, that dispersal assembly, ecological drift, and random speciation are reasonable approximations to the large-scale behavior of biodiversity in a biogeographic context. In essence, they took a statistical-mechanical approach to understanding macroecological patterns of biodiversity. I believe that this approach will prove more successful in the long run than attempts to scale up from the reductionistic approach that has preoccupied community ecology for so much of the twentieth century.

My premise in writing this book is that a good neutral theory would be enormously beneficial to the intellectual growth and maturation of ecology. In defense of the unified theory developed here, this is no mere verbal argument. The majority of results must be accorded the status of mathematical theorems because they are proofs that follow inevitably from the assumptions. Therefore, if the theory is "wrong," it will not be because the mathematics is incorrect, but because one or another crucial assumption of the theory has been violated by nature. One of the hallmarks of good theory is to fail in interesting and informative ways. Despite its simplicity, the unified theory generates a host of intriguing, nonobvious, often remarkably accurate, and, above all,

testable predictions about the origin, maintenance, and loss of biodiversity in a biogeographic context.

SUMMARY

1. Ecology currently lacks a good formal neutral theory. This book attempts to develop such a theory on the premise that it would greatly benefit the intellectual growth and maturation of ecology.
2. *Neutrality* in this book is defined as per capita ecological equivalence among all individuals of every species in a given trophically defined community. This definition is not the same as "nothing going on" because it permits complex ecological interactions among individuals so long as all individuals obey the same interaction rules.
3. A new neutral theory of biodiversity in a biogeographic context has been constructed on MacArthur and Wilson's now classical equilibrium theory of island biogeography. The original theory has been modified by including a process of speciation, and by changing the neutrality assumption from the species level to the individual level.
4. Including speciation and changing the neutrality assumption enables the new theory to predict not only species richness on islands and on the mainland, but also the relative abundance of species, species-area relationships, and phylogeny under ecological drift, random dispersal, and random speciation.
5. The theory predicts the existence of a fundamental biodiversity number, θ, that appears throughout the theory at all spatial and temporal scales.
6. The new theory renews the old challenge to reconcile two long-standing divergent perspectives on the nature of ecological communities: the niche-assembly perspective, and the dispersal-assembly perspective.

7. The niche-assembly perspective asserts that ecological communities are limited membership assemblages of species that coexist at equilibrium under strict niche partitioning of limiting resources.

8. The dispersal-assembly perspective asserts that ecological communities are open, continuously changing, nonequilibrium assemblages of species whose presence, absence, and relative abundance are governed by random speciation and dispersal, ecological drift, and extinction.

9. The argument is long-standing because both perspectives have strong elements of truth. Taking the first steps to reconcile these divergent views of ecological nature is the underlying theme of this book.