

CHAPTER 18: ASSEMBLING AND DEPLETING SPECIES RICHNESS IN METACOMMUNITIES:
INSIGHTS FROM ECOLOGY, POPULATION GENETICS AND MACROEVOLUTION

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Running Headline: Interplay of Ecological Drift and Coexistence

The ecological mechanisms that influence levels of species richness remain elusive, particularly in high diversity systems. Ecosystems often harbor many congeneric and ecologically similar species within local areas, and local richness can be spectacular. Hundreds of beetle species (e.g., Didham et al. 1998; Harris and Burns 2000) and hundreds of butterfly species (e.g., DeVries and Walla 2001) can be found in small areas of tropical forests. The African rift lakes each contain hundreds of endemic cichlid species (reviewed in Kornfield and Smith 2000; Turner et al. 2001). Such impressive levels of biodiversity are not restricted to the tropics or to unique “hotspots”. At least 78 species in 49 genera of chironomid midges inhabit the gravel bottom of one 100 m stretch of stream in southern England, including eight *Orthocladius* and eight *Cricotopus* species (Ruse 1995). Five to twelve *Enallagma* damselfly species co-occur in lakes with fish across eastern North America (Johnson and Crowley 1980; McPeck 1989, 1990, 1998; Shiffer and White 1995; McPeck and Brown 2000). Such examples are easily gleaned from the literature for almost any ecosystem where careful sampling and taxonomic identifications have been done.

In addition to this apparent species richness, molecular phylogenetic studies have identified substantial levels of cryptic local species richness. Several cryptic species of *Chrysoperla* lacewings are often found on the same branch of a bush (Henry et al. 1999). Until very recently, the amphipod *Hyallela azteca* was considered a single species. Recent molecular studies have, however, shown that *H. azteca* is in fact a collection of at least seven species, most of which are morphologically and ecologically indistinguishable and which co-occur in lakes across North America (Witt and Hebert 2000; Witt et al. 2003; G. A. Wellborn, unpublished data). Likewise, nine morphologically indistinguishable rotifer species that were formerly considered *Brachionus plicatilis* co-occur in the lakes of the Iberian Peninsula (Gomez et al. 2002). In both *Hyallela* and *Brachionus*, many of the cryptic species are millions of years old. The literature suggests that such cryptic species richness can be found across the eukaryotes and in almost all ecosystems.

Understanding the mechanisms that promote such high local levels of biodiversity is at the

heart of community ecology, because through sheer numbers these are the mechanisms that maintain the bulk of biodiversity on the planet. However, much of the theoretical edifice of community ecology (e.g., Gause's competitive exclusion principle, niche theory) reinforces the belief that such high local diversity of such closely related and ecologically similar species should not be possible. And yet there it is!

How can so many closely related species all co-occur in local communities? Recent reviews have organized the myriad mechanisms that influence species diversity across the landscape into those that promote the indefinite coexistence of species and those that only reduce the rate of species loss (Tilman and Pacala 1993; Chesson and Huntley 1997; Chesson 2000a). In this paper, we restrict our use of the word "coexistence" to situations where persistence is indefinite for multiple species, and we use "co-occurrence" to imply a less restrictive definition in which species are found together regardless of whether persistence is permanent. Chesson (2000a) outlines an extremely useful framework for considering these mechanisms. In this framework, invasibility – a species' population growth rate when at low density and other species are at their normal abundances – is the criterion for assessing coexistence (see also MacArthur 1972; Holt 1977). Mechanisms of species interactions influence the invasibility of species via their "stabilizing" and "equalizing" effects. Stabilizing effects, often resulting from trade-offs, cause species to be limited by different density-dependent factors (e.g., resources, predators, diseases) such that they depress their own population growth rates more than they depress other species' growth rates; these are the fundamental features of mechanisms that promote the coexistence of species. In contrast, equalizing effects are the consequences of species having similar fitnesses to one another. Equalizing effects are capable of prolonging persistence, but not fostering permanent coexistence.

Mechanisms with stabilizing effects can operate on various spatial and temporal scales (Tilman and Pacala 1993; Chesson 2000a). Typically, we first think of coexistence mechanisms as those that regulate a single, local community to a point equilibrium (e.g., Lotka-Volterra models: see Case 2000). However, temporal heterogeneity can also promote coexistence in a

single local community through some forms of non-linear density dependence (e.g., Armstrong and McGehee 1980; Chesson 1994), through endogenously generated cycles (Abrams et al. 2003), or through species differences that lead to the storage effect (Chesson and Warner 1981; Chesson 1994). Within a metacommunity context, spatial mechanisms operating among a number of local communities can also promote coexistence, with or without temporal heterogeneity, to generate regional species coexistence. In the absence of temporal fluctuations, spatial heterogeneity among patches in a metacommunity can often generate non-linearities or spatial storage effects giving coexistence (Bolker and Pacala 1999; Chesson 2000b; Moko and Iwasa 2000, Amarasekare 2003). Temporal variability (e.g., disturbance or localized individual mortality) and recolonization of sites can promote coexistence among competing species if a trade-off between local competitive ability and dispersal exists (e.g., Hastings 1980; Caswell and Cohen 1991; Tilman 1994; Pacala and Tilman 1994; Hurtt and Pacala 1995; Kinzig et al. 1999; reviewed in Mouquet et al. Chapter 4). Predation can have similar effects on prey diversity (Hastings 1977; Caswell 1978).

Multiple species may also inhabit the same metacommunity simply if different species are better adapted to the ecological conditions found in different patches (Shmida and Ellner 1984). Local conditions may allow one species to dominate all others at any particular site, but different species may be favored at different sites (e.g., Pacala and Tilman 1994, the “species sorting paradigm, discussed in Holyoak et al., Chapter 1). Dispersal among sites could maintain species in patches where they do not dominate, creating a multispecies source-sink system in which each species has a unique but limited number of source patches and each maintains sink populations in the other patches via dispersal. This is termed the “mass effect” perspective in Holyoak et al., Chapter 1.

Equalizing effects alone can only retard the rate of species loss, not give long term coexistence, but they do influence the magnitude of stabilizing effects needed for coexistence (Chesson 2000a). Hubbell (2001) has elaborated a neutral model including only equalizing effects (Hubbell and Foster 1986) at a metacommunity scale. If the fitnesses of all species are

nearly identical, ecological factors will regulate the summed total abundance of all species and not the abundance of each species individually (i.e., a “zero-sum” interaction). As a result, species’ relative abundances on local and regional scales are not affected by local environmental conditions and will undergo a random walk (Hubbell 2001). The ultimate outcome of this “ecological drift” is the extinction of all species save one without the continual input of new species via either speciation in member taxa or immigration from outside the system (Hubbell 2001).

Considerations of stabilizing versus equalizing effects of species interactions focus attention on different aspects of the dynamics of species interactions. When we focus on coexistence via the operation of stabilizing effects, we necessarily focus on the ultimate outcome of species interactions – which species can persist indefinitely with one another – and largely ignore how the system approaches that outcome. Also, because of the mathematical tractability of invasibility criteria for predicting which species will be present at the long term equilibrium, coexistence considerations focus on the dynamics of species when they are rare and increasing in abundance. In contrast, the consequences on equalizing effects of species interactions will only be important to the transient dynamics of an assemblage on the way to its ultimate configuration of coexisting species; thus, this perspective will focus on species as they become rare. If the equalizing effects of species interactions are important to the dynamics of an assemblage, some of the species (i.e., the transient, co-occurring species) are present because the rate at which they are being driven extinct is slow enough to permit them to persist for substantial periods of time in the system before they realize their ultimate fate, and not because local or regional processes foster their indefinite persistence.

Stabilizing effects clearly promote the coexistence of many species in any given local or regional assemblage, but probably not all species in any given assemblage. The stabilizing effects of these mechanisms involving spatial and temporal heterogeneity can allow many more species to coexist in metacommunities than if only local niche partitioning mechanisms dominate (Tilman and Pacala 1993; Chesson 2000a, Abrams et al. 2003; see also reviews in Holt and

Hoopes, Chapter 3, and Mouquet et al., Chapter 4. Moreover, the operation of these mechanisms may involve subtle differences among species that will be hard to document empirically.

However, given the numbers of closely related and phenotypically similar species that co-occur, it is untenable to dismiss the possibility that the equalizing effects of their phenotypic similarities plays a substantial role in their persistence in ecosystems. Simply assuming that stabilizing effects must be operating to maintain all species in a system is as scientifically dangerous as assuming that any feature of an organism is the product of adaptation (Gould and Lewontin 1979). In addition, given that the ultimate fate of all species is extinction (Raup 1991), the indefinite coexistence of species would seem to be a peculiar theoretical yardstick by which various mechanisms are deemed worthy of consideration. Because of these two empirical facts, we have begun to explore the theoretical interplay between stabilizing mechanisms and ecological drift in a metacommunity context. In this paper, we want to highlight some of the basic theoretical and empirical properties of metacommunities that make ecological drift a potentially forceful mechanism influencing patterns of species co-occurrence in ecosystems.

<A>Ecological drift in metacommunities

The processes that shape species richness patterns are highly analogous to the forces of microevolution that shape allelic diversity (see also Amarasekare 2000). The input of new species to a system via speciation or system-level immigration (e.g., species invasions) is analogous to mutation (e.g., Williams 1992). Dispersal of species among patches is analogous to gene flow. Equalizing and stabilizing effects influencing species' coexistence correspond to fitness differences among alleles that generate natural selection. Finally, the dynamics of genetic drift are analogous to those of ecological drift (Hubbell 2001). Clearly, these are merely analogies because evolutionary mechanisms can differ greatly from the ecological analogs. For example the particulars of natural selection among diploids and of species interactions are very different, although they may be quite similar with asexual genetics (e.g., Gerrish and Lenski 1998). In any case, the analogy establishes what we think is a useful mindset for understanding

species coexistence in a dynamically rich setting. Evolutionary theory is typically constructed as a balance of evolutionary forces: allelic diversity within and among populations depends on a balance between mutation and drift (Kimura 1983), or between mutation, selection, and drift (e.g., Bürger 2000), or among selection, drift and gene flow (e.g., Wright 1932). In like manner, we imagine species diversity across the landscape to be governed by a balance of demographic and macroevolutionary forces that shape the distributions and abundances of species on local and regional scales; these forces consist of speciation and system immigration, dispersal, and the stabilizing (coexistence) and equalizing (ecological drift) effects of demography and ecological interactions.

The dynamics of ecological drift are particularly amenable to this analogy, because both the stochastic nature of sampling alleles to pass on to the next generation and the demographic stochasticity that underlies ecological drift are exactly analogous. Hubbell (2001; Hubbell and Foster 1986) uses a birth and death model that closely resembles the Moran (1958) model of genetic drift to model the dynamics of forest trees, illustrating the intimate relationships between this framework and various empirical metrics of species diversity patterns. Here we explore how features of a metacommunity can greatly slow the rate of ecological drift and thus the loss of species from an ecosystem.

Local community drift

Rather than use Hubbell's birth and death model (Hubbell 2001), we will introduce an alternative formulation of ecological drift analogous to the haploid version of the workhorse model for genetic drift: the Wright-Fisher model (e.g., Ewens 1979). We do so because the Wright-Fisher model is the more conventional formulation used to explore genetic drift and thus a greater range of previous analyses are available to draw from and motivate our work. Moreover, the Wright-Fisher and Moran models have largely the same stochastic properties in the limit of large population size (Kingman 1982). To begin with, imagine a closed community that contains J individuals drawn from S different species. Every season these individuals die off

after producing large numbers of offspring, of which J survive to adulthood to form the new community. Let $N_i(t)$ be the number of individuals of species i present and let $F_i(t)$ be the per capita fecundity for that species in year t . To impose Hubbell's zero-sum assumption (Hubbell 2001), we assume $\sum_{i=1}^S N_i(t) = J$ in all years, however ecological drift will occur even if the total community size fluctuates but stays bounded.

If we assume that all offspring compete equally for the J available spaces, then the probability that k members of species i present in year $t+1$, given the sizes and fecundities of all species in year t , is the binomial probability

$$\Pr[N_i(t+1) = k \mid N_1(t) \dots N_s(t), F_1(t) \dots F_s(t)] = \frac{J!}{k!(J-k)!} [p_i(t)]^k [1-p_i(t)]^{J-k}, \quad (18.1)$$

where $p_i(t) = N_i(t)F_i(t) / \sum_{j=1}^S N_j(t)F_j(t)$ is the fraction of newborns produced by species i .

Ecologists will recognize this as a version of Chesson and Warner's (1981) lottery model with non-overlapping generations. In the absence of speciation or immigration to the system, species i will ultimately either become extinct or monodominant. The community as a whole will lose all of its original diversity, becoming dominated by one of the original S species.

A "fully neutral" model akin to Hubbell's assumes that all species are equally fecund, i.e., $F_1(t) = F_2(t) = \dots = F_s(t)$. Then $p_i(t) = N_i(t)/J$, the local relative abundance of species i . Given the zero-sum assumption, the stochastic dynamics of this community are exactly the same as a neutral Wright-Fisher model with haploid genetics and constant population size J . (Geneticists tend to focus on the dynamics of relative abundance, but this is not required; it is easy enough to convert between absolute and relative sizes.) The stochastic properties of the neutral model are well characterized (e.g., Ewens 1979; Kimura 1983). We highlight just two results here: First, the probability of monodominance for species i is equal to its relative abundance. Second, the mean number of seasons to extinction of a species with relative abundance p is $-2Jp \ln p / (1-p)$, conditional on its extinction (Kimura and Ohta 1969). This "exit time" is on the order of J seasons for any moderately abundant species, i.e., any species with relative abundance above about one percent. The mean conditional extinction time for rare

species is much faster, on the order of $\log J$ seasons.

Metacommunity drift

The Wright-Fisher model of local dynamics extends easily to geographically structured communities. Consider a metacommunity containing C local communities such that the i th local community contains $J_i(t)$ individuals belonging to a subset of our S species. The density of species j in community i is $N_{ij}(t)$ at time t , with $\sum_{j=1}^S N_{ij}(t) = J_i(t)$. Assume the zero sum condition applies to the metacommunity as a whole. That is, the total metacommunity size, J_M , is constant: $J_M = \sum_{i=1}^C J_i(t) = \sum_{i=1}^C \sum_{j=1}^S N_{ij}(t)$.

How does geographic structuring affect properties of ecological drift? Some properties are not affected at all, provided no local community is completely isolated from the rest. For example, in the absence of speciation and immigration of new species from outside the system, the metacommunity will eventually lose all diversity and become globally dominated by a single species. Moreover, under the fully neutral model the probability that species i becomes monodominant is equal to its relative abundance across the entire metacommunity. These conclusions follow even when local communities change in size and when dispersal rearranges local species diversities (Maruyama 1970a).

Other aspects of ecological drift can, however, be strongly affected by geographic structuring. Consider the expected time until a species with relative abundance p_M is lost from the entire metacommunity under the neutral model: $-2J_{ME}p_M \ln p_M / (1 - p_M)$ (Kimura and Ohta 1969), where J_{ME} is the “effective size” of the metacommunity (see below). This implies that the expected time for a moderately abundant species to exit the metacommunity is on the order of J_{ME} seasons. Like “effective population size”, which is central to describing random genetic drift in population genetics, we define J_{ME} to be the size of an isolated, unstructured community with the same stochastic features as the metapopulation; the effective metacommunity size.

If dispersal among local communities does not change local community sizes, then the

effective size of a subdivided metacommunity can be related to its census size by

$$J_{ME} = J_M / (1 - F_{ST}) \quad (18.2)$$

(Whitlock and Barton 1997). The parameter F_{ST} accounts for structural aspects of the metacommunity that are critical to ecological drift. It is defined as $F_{ST} = \text{var}(p) / [\bar{p}(1 - \bar{p})]$, where \bar{p} is the mean relative abundance of a particular species, and $\text{var}(p)$ is the variance in relative abundances of the same species across local communities in the metacommunity. F_{ST} lies between zero and one. If the metacommunity is unstructured (i.e., the relative abundances of all species are the same in every local community), $F_{ST} = 0$ and $J_{ME} = J_M$, the metacommunity census size. F_{ST} increases as the relative abundances of species increasingly differ among local communities. The effective size of a structured metacommunity is thus expected never to be less than the total number of individuals that comprise it. Therefore, in the neutral model, the exit of a moderately abundant species is expected to take longer in a structured metacommunity than an undivided one of the same total census size. Moreover, this result emphasizes that the rate of ecological drift is determined by the size of the entire metacommunity: that is, the combined effects of both the number of local communities and the number of individuals in each rather than by just the sizes of the local communities that comprise it.

How does the degree of subdivision affect the rate of extinction? This question can be addressed analytically for certain types of metacommunities, such as island models (Wright 1943; Slatkin 1993), in which all local communities exchange migrants, and stepping-stone models (Maruyama 1970b), in which dispersal is restricted to adjacent communities. For example, the approximation for the island model is $J_{ME} = J_M (1 + (C-1)^2 / (2JmC^2))$ where m is the migration rate, C is the number of local communities, and J is the local community size (Wright 1943; Slatkin 1993). A shared feature is that F_{ST} increases with decreasing migration. Thus the rate at which a species goes extinct in a metacommunity is a declining function of the extent to which the parts of a metacommunity are isolated from one another.

Stabilizing mechanisms

As explained above, coexistence mechanisms are defined to operate when a new species can invade when rare. With drift, however, the invasion of even highly superior rare species cannot be guaranteed since the probability of immediate extinction may be substantial. One must tease out the coexistence mechanisms by minimizing the effects of drift. This is done by assuming that the local community size is very large so that even a relatively rare species is numerically abundant. In later publications, we will consider the joint effects of ecological drift and stabilizing mechanisms. Here we highlight a few of the applicable insights that have been developed in population genetics and molecular evolution.

The fully neutral model has all equalizing and no stabilizing effects. What spatio-temporal patterns of environmental variation and migration will lead to equalization, stabilization, or destabilization? An analogous framework for analyzing these types of questions has been developed for molecular evolution by Gillespie (1991). We will use this framework to understand how environmental variability might maintain community diversity.

Consider the Wright-Fisher model of a closed local community containing S species with different fertilities, $F_i(t)$. (This is expressly *not* a neutral model.) To eliminate drift, imagine that the community size J is extremely large. It is useful to describe the community in terms of relative abundances, which effectively can take on any value between zero and unity. If $p_i(t)$ is the relative abundance of species i then the change in its relative abundance is equal to its theoretical expectation:

$$\Delta p_i(t) = p_i(t+1) - p_i(t) = p_i(t) \frac{[F_i(t) - \bar{F}(t)]}{\bar{F}(t)}, \quad (18.3)$$

where $\bar{F}(t) = \sum_{i=1}^S p_i(t) F_i(t)$ is the mean fertility across the metacommunity in season t .

If the fertilities fluctuate from one season to the next, the species with highest geometric mean fertility will become monodominant (Gillespie 1973). If all S species have the same geometric mean fertility, will diversity be maintained in an infinitely-sized community? The answer, it turns out, is not really (Gillespie 1991; Chesson and Huntly 1997). In the long run, the

community will always be nearly monodominant, with the remaining species hanging on at extremely low relative abundances, except for occasional rapid switches in the identity of the monodominant species. The period between these switches lengthens without bound over time. This suggests that, in a finite community, the rare species will become increasingly vulnerable to extinction by demographic stochasticity. Apparently, temporal variability alone cannot maintain community diversity (Chesson and Huntly 1997).

Can geographical subdivision and spatio-temporal variability maintain community diversity? One way to approach this question is to generalize an ecologically simple model that was originally introduced by Levene (1953) to study analogous questions in population genetics. Imagine a metacommunity with C large local communities. The relative size of the i^{th} community is s_i such that $\sum_{i=1}^C s_i = 1$. At the end of season, the local communities produce a large number of propagules in accordance with local fertilities. These propagules are then freely distributed across the metacommunity landscape.

The dynamics of metacommunity relative abundance for the i th species are described by (suppressing the time variable t)

$$\Delta p_i = \sum_{j=1}^C \frac{s_j \bar{F}_j^\alpha}{\sum_{k=1}^C s_k \bar{F}_k^\alpha} \cdot \frac{p_i [F_{ij} - \bar{F}_j]}{\bar{F}_j}, \quad (18.4)$$

where F_{ij} is the fertility of species i in community j , $\bar{F}_j = \sum_{i=1}^C p_i F_{ij}$ is the mean fertility in community j , and α is a parameter that can range from zero to one (Gillespie 1991). The second factor in the summand is the expected change in relative abundance of species i in community j (cf. Equation 18.3). The first factor describes the fractional contribution of propagules provided by community j to the metacommunity. At one extreme, $\alpha = 0$, in which case the contribution of community j is proportional to its relative size, s_j . At the other extreme, $\alpha = 1$; the relative contribution by a community is proportional to both its relative size and average productivity, as measured by \bar{F}_j . In the population genetics literature, these two extremes are known as soft and hard selection, respectively (Christiansen 1975; Wallace 1970).

It turns out that the extent to which propagule contributions reflect local average productivities is decisive as to whether diversity can be maintained in the metacommunity. Adapting the diffusion methods of Gillespie (1991), it can be shown that when $\alpha < 1/2$, all S species can be maintained under an increasing set of conditions as the degrees of geographic subdivision and heterogeneity increase. This suggests that spatio-temporal variation can serve as a stabilizing mechanism that maintains community diversity. However, when $\alpha > 1/2$, spatial subdivision and variability have just the opposite effect: as they increase, the conditions under which all S species can be maintained become increasingly narrow. We are thus left with the equivocal conclusion that a specific pattern of variability in fitness can be stabilizing or destabilizing, depending on how the metacommunity is structured.

What do these results mean for ecological drift in the face of environmental heterogeneity? Applying Gillespie's results (Gillespie 1991), conditions that support community diversity in the absence of ecological drift (i.e., only stabilizing mechanisms) also slow the rate at which diversity is lost in finite communities compared with a fully neutral model. This means that of the scenarios described above, only spatio-temporal variability with $\alpha < 1/2$ (including the ecological equivalent of soft selection) is consistent with a slower loss of diversity than in a neutral community. By comparison, both temporal and certain kinds of spatio-temporal variability ($\alpha > 1/2$) lead to a more rapid loss of diversity than one would expect under a neutral model.

<A>How have real metacommunities been assembled?

The importance of ecological drift and other consequences of demographic stochasticity discussed above in a metacommunity context will depend in large measure on how close real ecological systems lie to their asymptotic deterministic outcomes (i.e., the long term outcomes of species interactions) and the effective metacommunity sizes (J_{ME}) of assemblages. If the metacommunities we study in nature are already at or near their deterministic equilibria, the dynamics of stochastic species losses will be irrelevant and coexistence mechanisms should

dominate the dynamics and community structures we see. If, however, real systems are not near their long term, deterministic outcomes, the dynamics of approach to those outcomes will be the critical features we see in any particular system and not where it will ultimately arrive (see also Hoopes et al., Chapter 2 for alternative reasons for the importance of transient dynamics). There is also a much larger philosophical point underlying this choice of how we view systems. The theoretical vantage from which we choose to look will define (a) what features of the system we choose to consider, (b) what dynamics we will a priori define as relevant to addressing our larger goals, and (c) how we will interpret features that may have multiple possible explanations (some explanations we will consider and some we will ignore as irrelevant).

The theoretical utility of invasibility criteria to predict which species will coexist in the long term (Holt 1977; Chesson 2000a) naturally draws our attention to what will happen when a new and rare species invades a system that is currently at its long term deterministic equilibrium. “Can a new species increase when it is rare and the others are at their equilibrium abundances?”, is the natural question to ask about the accumulation of species in a system in this theoretical framework. Because the likelihood of long-term persistence of a new, rare species that is nearly ecologically identical to an existing species in the system is exceedingly small, only those species that will deterministically increase when rare (i.e., ones that can coexist with the species already present in the system) would seem to be able to enter the system. Thus from this viewpoint, if only species that can ultimately coexist deterministically have any chance of entering the system, the presence of species that will drift to extinction or those that will ultimately be driven extinct by coexistence mechanisms should be irrelevant to explanations of species diversity and other major features of a multispecies system (e.g., patterns of relative abundance, dominance-diversity relationships, degree of community saturation).

However, this theoretical scenario may not be relevant to many features of real metacommunities if they are not near their long term deterministic equilibria. Growing evidence from many lines of inquiry suggest that today’s ecosystems over large areas of the globe were assembled only recently (on a geological time scale), and that local assemblage membership is

quite fluid. This assembly process was shaped by the movements of animals and plants in response to Pleistocene climatic cycles (e.g., see reviews in Davis 1986: Delcourt and Delcourt 1991: Hewitt 1999). Paleobotanical studies have documented rapid changes in local assemblages of trees and range movements of tree species over large areas of most continents (e.g., Delcourt and Delcourt 1991). Unpredictable range movements and local assemblage changes have been shown in insects (Coope 1979, 1995: Jost-Stauffer et al. 2001) and rodents (Graham 1986: Graham et al. 1996). In fact, modern North American rodent assemblages “have emerged only in the last few thousand years, and many late Pleistocene communities do not have modern analogs” (Graham et al. 1996). Phylogeographic studies of taxa moving out of refugia to colonize deglaciated continental areas provide a similar picture of faunal upheaval and only recent local and regional assembly (reviewed in Bernatchez and Wilson 1998: Hewitt 1999: Avise 2000).

In addition to these changing assemblage compositions across the landscape, many new species came into being during this same period because these same biogeographic processes also promote speciation (e.g., Vrba 1985, 1995). In fact, phylogenetic studies show that many different taxonomic groups radiated during the Pleistocene (e.g., insects, Henry et al. 1999: McPeck and Brown 2000: Knowles 2000, 2001: Barraclough and Vogler 2002; birds, Arnaiz-Villena et al. 1999: Lovette and Bermingham 1999: Price et al. 2000; see review by Hewitt 1996). Not only were local assemblages being destroyed and reassembled into different configurations, but also many new species were being introduced at the same time. Thus, the metacommunities we study today may be only a few thousand to tens of thousand of years old, with many new species having been introduced to the mix over that same time scale.

On top of all this, we must also consider the degree of ecological differentiation of these new species from their progenitors. Speciation can be accomplished by myriad mechanisms (Dobzhansky 1937: Mayr 1942: Otte and Endler 1989: Howard and Berlocher 1998). Many speciation events are accomplished by processes in which lineage diversification accompanies ecological diversification (e.g., Rosenzweig 1978, 1995: Pimm 1979: Schluter 1993, 1996:

McPeck 1996). In these “ecological” speciation mechanisms (Schluter 1996), speciation is simply a by-product of adaptive ecological differentiation. However, many other mechanisms can generate reproductive isolation with no necessary ecological differentiation. Hybridization clearly plays an important role in plant speciation (Stebbins 1950; Barrett 1989; Rieseberg 1997). Chromosomal rearrangements are a primary reproductive isolating mechanism in many animal taxa (reviewed by King 1993). Also, changes in mate recognition systems and sexual selection are also powerful modes of speciation in many animal taxa (Paterson 1978, 1993; Kaneshiro 1983, 1988, 1989; Kaneshiro and Boake 1987; McKaye 1991; Seehausen et al. 1997; Henry et al. 1999; Boake 2002). From these mechanisms species with varying degrees of ecological differentiation may be produced (Carson 1985): some may produce species that are ecologically nearly identical to one another (e.g., insects changing mating songs [Henry et al. 1999] or genital morphology [Eberhard 1988]), whereas others may produce new species that are ecologically quite different from their progenitors (e.g., hybridization [Rieseberg 1997], ecological speciation [Schluter 1993, 1996; Losos et al. 1998; McPeck 1995, 1999, 2000]), and all shades in between.

Given these recent biogeographic and macroevolutionary dynamics, the commonness of closely related and ecologically similar species that co-occur is not at all surprising within a theoretical framework that acknowledges that systems may not be near their long term, deterministic outcomes. For example, consider the recent history of the *Enallagma* damselflies in North America (McPeck and Brown 2000). Permanent ponds and lakes across North America are today inhabited by *Enallagma* species that are derived from the independent radiation of two progenitors that produced 17 species within the last 250,000 years (Brown et al. 2000; McPeck and Brown 2000; Turgeon and McPeck 2002; and in preparation). These radiations appear to have occurred both while various lineages were isolated in glacial refuge areas and as lineages recolonized the deglaciated regions of North America (Turgeon and McPeck 2002; and in preparation). Four of the speciation events were driven by ecological differentiation of lineages associated with habitat shifts back and forth between ponds and lakes that have fish as top predators versus large dragonflies as top predators (McPeck 1995, 1999, 2000; McPeck and

Brown 2000: Turgeon and McPeck, in preparation). However, most of the speciation events appear to have occurred by differentiation of the mate recognition system to generate new species primarily in the fish-lake habitat with little or no apparent ecological differentiation (McPeck and Brown 2000). As a result, 5-12 ecologically very similar *Enallagma* species can today be found co-occurring at most ponds and lakes with fish across much of North America; the members of the local assemblages differ across the continent, but the general pattern of high species richness does not (Johnson and Crowley 1980: McPeck 1989, 1990, 1998: Shiffer and White 1995: McPeck and Brown 2000). In addition, the current ranges for many of these species would have been completely under ice 15,000 years ago, and so much of the metacommunity these species occupy was only recently assembled.

The metacommunities in which *Enallagma* species are embedded are also huge, and differences in relative abundances among lakes should inflate the effective metacommunity sizes even further. Given that population densities of larvae in lakes range between 200-700 larvae/m² in littoral areas (McPeck 1990, 1998), the total abundance of all *Enallagma* species at any given pond or lake containing fish will typically range from 10⁴-10⁶ individuals, depending on the extent of the littoral zone and the overall size of the lake. In addition, many of these species have ranges that encompass literally tens to hundreds of thousands of lakes from the Atlantic coast to the Rocky Mountains. Dispersal among ponds and lakes within a region (e.g., on the scale of 10³ km²; McPeck 1989) or across the entire ranges of species (e.g., on the scale of 10⁶ km²) will link these local systems into a metacommunity with an enormous census metacommunity size (J_M). Also, we can derive an admittedly crude estimate of F_{ST} from the relative abundance data presented in McPeck (1990) among three fish lakes in southwestern Michigan using methods for haploid genetic data (Weir 1996). This estimate of F_{ST} is 0.26 (estimated for $\hat{\theta}$ on page 174 of Weir [1996]), which suggests that the effective metacommunity size (J_{ME}) will be about $1/(1-F_{ST}) = 1.35$ times larger than its census value. The enormity of J_M and J_{ME} for these species will make the loss of these ecologically similar species by ecological drift across the landscape exceedingly slow – on the order of perhaps $J_{ME} \approx$ tens to hundreds of

millions of years for most species to be ultimately lost from the system and thus one species to become monodominant, given that *Enallagma* species have one generation per year. Moreover, as illustrated by Gillespie's (1991) results, stabilizing mechanisms could speed or slow these expected exit times, depending on the exact form of fitness variation among ponds and lakes. But in any case, the fact that so many ecologically similar, and recently derived species, such as the *Enallagma* in fish lakes, co-occur is not surprising when viewed from this theoretical perspective. Similarly, the persistence of cryptic species diversity in such groups as the *Hyallolella* amphipods or *Brachionus* rotifers for ten million years or more may result from similar metacommunity features: local *Hyallolella* abundances are typically an order of magnitude higher than those of *Enallagma* in North American ponds and lakes (McPeck, personal observations).

<A>Conclusions

Rather than considering the structure of natural metacommunities from the perspective of a rare invader into an established system, these data and what we know about the recent upheavals due to climate that occurred across much of the globe strongly argue that we need to alter our theoretical focus for many systems and taxa away from invasibility to consider how natural metacommunities, which have only recently been assembled, are sorting themselves out on regional and maybe even continental scales. In other words, we need a focus that does not abandon the concepts of coexistence, but that does recognize the potential importance of stochasticity and particularly ecological drift at various scales. When considered from this perspective, the ubiquity of ecologically similar and co-occurring species is not surprising. In many taxa, new species have been introduced recently by mechanisms that do not generate much ecological differentiation among species, and these species are now embedded in huge metacommunities, which will make the loss of the ecologically poorer species from the landscape exceedingly slow.

Thus, the correct theoretical perspective for understanding many natural metacommunities may be one that explores how the interaction of various stabilizing and equalizing effects of

species interactions influence the transient dynamics of an assemblage on the way to its ultimate configuration of coexisting species, and one that focuses on species as they become rare. Some, indeed possibly many, species may be present because the rate at which they are being driven extinct is slow enough to permit them to persist for substantial periods of time in the system before they realize their ultimate fates, and not because local or regional processes foster their indefinite persistence. Moreover, it is the very fact that local communities are linked by dispersal into metacommunities that makes ecological drift a potentially important influence on the dynamics of real systems (Hubbell 2001, and results above). Mechanisms with both stabilizing and equalizing effects (Chesson 2000a) influence the dynamics of real metacommunities, and we cannot simply assume that mechanisms promoting coexistence dominate to maintain high biodiversity; many macroevolutionary, historical and ecological features of high diversity systems argue that it is simply not so. Moreover, the interplay of stabilizing and equalizing effects of species interactions may not be straightforward, as Gillespie's (1991) results illustrate. As population genetics and molecular evolution have done (e.g., Ohta 2002), we need to begin to construct a substantial theoretical edifice that can be applied to real metacommunities to explore the dynamical consequences of the stabilizing and equalizing effects of species interactions.

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