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Siepielski, Adam M. and McPeck, Mark A., "On the Evidence for Species Coexistence: A Critique of the Coexistence Program" (2010). *Dartmouth Scholarship*. 768.
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On the evidence for species coexistence: a critique of the coexistence program

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Abstract. A major challenge in ecology is to understand how the millions of species on Earth are organized into biological communities. Mechanisms promoting coexistence are one such class of organizing processes, which allow multiple species to persist in the same trophic level of a given web of species interactions. If some mechanism promotes the coexistence of two or more species, each species must be able to increase when it is rare and the others are at their typical abundances; this invasibility criterion is fundamental evidence for species coexistence regardless of the mechanism. In an attempt to evaluate the level of empirical support for coexistence mechanisms in nature, we surveyed the literature for empirical studies of coexistence at a local scale (i.e., species found living together in one place) to determine whether these studies satisfied the invasibility criterion. In our survey, only seven of 323 studies that drew conclusions about species coexistence evaluated invasibility in some way in either observational or experimental studies. In addition, only three other studies evaluated necessary but not sufficient conditions for invasibility (i.e., negative density dependence and a trade-off in performance that influences population regulation). These results indicate that, while species coexistence is a prevalent assumption for why species are able to live together in one place, critical empirical tests of this fundamental assumption of community structure are rarely performed. These tests are central to developing a more robust understanding of the relative contributions of both deterministic and stochastic processes structuring biological communities.

Key words: *coexistence; density dependence; empirical evidence; invasibility; phenotypic trade-offs; species diversity.*

INTRODUCTION

Gould and Lewontin (1979) in their spandrels of San Marco critique of the “Adaptationist Programme” questioned the assumption that natural selection shaped most every aspect of the phenotype of each organism. Their critique did not question the importance of natural selection as a pervasive force shaping phenotypic evolution. Rather, their critique criticized the nearly unquestioned—and thus untested—assumption that natural selection is the explanation for every nuance of an organism’s phenotype. In essence, they argued that if natural selection has operated to shape some aspect of an organism’s phenotype, then scientists should devise

critical observational studies and experiments to test this hypothesized mechanism and conduct studies to demonstrate its operation in particular cases. Their critique sparked a revolution in the study of natural selection, with techniques to quantify the action of natural selection in the wild (e.g., Lande and Arnold 1983, Arnold and Wade 1984), methods of historical reconstruction to test for the operation of natural selection in a clade’s history (e.g., Felsenstein 1985, McPeck 1995, Martins and Hansen 1996), laboratory and field experiments testing the operation of natural selection (e.g., Reznick and Ghalambor 2005), and a resulting wealth of information on how natural selection operates in nature (e.g., Endler 1986, Kingsolver et al. 2001, Bell 2008, Siepielski et al. 2009). In addition, it forced evolutionary biologists to grapple with other processes that act to shape phenotypic evolution in addition to natural selection (e.g., genetic correlations [Via and Lande 1985, Schluter 1996], developmental constraints

Manuscript received 21 January 2010; revised 17 March 2010; accepted 22 March 2010. Corresponding Editor: J. M. Levine.

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[Maynard Smith et al. 1985], gene flow [King and Lawson 1995], genetic drift [Orr 1998], absence of genetic variance [Blows and Hoffmann 2005], and historical contingency [Losos et al. 1998], among others). In short, their critique forced biologists to critically test how nature actually does work instead of assuming how nature should work.

Here we apply a similar critique to the issue of whether species coexist in nature. Much of community ecology is built on the conceptual foundation of species coexistence (MacArthur 1972, Chesson 2000, Hubbell 2001). In a local community, many species interact with one another either directly (e.g., via interference competition, predation, parasitism, mutualism) or indirectly (e.g., via altering abiotic conditions, resource competition, apparent competition). Considerable theoretical work is directed at investigating what types of species can persist indefinitely with one another and what types of species cannot (i.e., which will be driven locally extinct via competitive exclusion or other processes). Those that are found to be able to persist indefinitely together are deemed to “coexist” (MacArthur 1972, Chesson 2000).

Species coexist if different relative combinations of ecological factors regulate each species' abundance such that each species will tend to increase when rare (MacArthur 1972, Chesson 2000). In fact, theoreticians typically evaluate this “invasibility” criterion for coexistence (e.g., MacArthur 1972, Holt 1977): Can each species increase when it is rare (i.e., when it is an “invader”) and the other species are at their respective typical abundances in its absence (i.e., the “residents”)? Myriad ecological processes can promote or hinder species coexistence, but invasibility is the hallmark of all mechanisms promoting species coexistence (i.e., a species cannot be driven extinct by species interactions if it can increase when it is rare; Chesson 2000, 2008, Adler et al. 2007). Thus, satisfying the invasibility criterion is definitive evidence for the operation of some coexistence mechanism, even if the specific mechanism has not been identified.

Invasibility is conceptually very simple, but may be quite difficult to evaluate in practice. Imagine a community in which three species at the same trophic level (call them A, B, and C) are found together embedded in an interaction web with many other species (e.g., predators, resources, mutualists, diseases), and we want to evaluate whether these three species are all maintained in the community by some coexistence mechanism. First, consider the case in which this system comes to a point equilibrium. To evaluate the invasibility of species A, A would have to be removed from the community; and once the community (including the residents B and C) has arrived at its new equilibrium, A is reintroduced at low abundance (here, A is the invader). If A can consistently increase in population abundance under these conditions, it satisfies the invasibility criterion. These procedures must then be

repeated for species B and C as the invaders. For communities that fluctuate over time (e.g., no point equilibrium but rather communities displaying limit cycles, chaotic or stochastic dynamics), the resident species must be allowed to arrive at their new long-term demographic dynamics before the invader is introduced. If all three species can increase when rare under these conditions, we can conclude that some mechanism is promoting their coexistence (Chesson 2000, 2008, Leibold and McPeck 2006, Adler et al. 2007), but further studies would be needed to identify and characterize the exact mechanism (e.g., Chesson 2000, 2008, Sears and Chesson 2007).

Species are able to coexist because each has demographic advantages when they are rare and disadvantages when they are common in the ecological network (i.e., trade-offs); the demographic advantages allow them to persist, but the demographic disadvantages prevent them from excluding other species from the system. For example, theoretical studies that link species differences directly to demography have shown that competing consumers can coexist if the abundance of each consumer is more limited by a different resource (e.g., Tilman 1982). Likewise, in keystone predation where species simultaneously compete for a shared resource and are fed upon by a shared predator, two species can coexist if one is the better resource competitor and the other is better at avoiding the predator (Levin 1970, Holt et al. 1994, Leibold 1996, McPeck 1996). Even in a temporally varying environment where no point equilibrium is possible, species can coexist if each has higher fitness when rare under different environmental conditions (Chesson and Warner 1981, Warner and Chesson 1985).

This large body of theoretical work has basically validated Hutchinson's (1959) original heuristic conclusion that species must be different in some way to coexist (Chesson 1991). Derived from this, the criterion for coexistence has, however, typically been reduced to the aphorism that “two species must be different to coexist.” Taken to its logical extreme, this aphorism merely requires the identification of any difference among two or more species that are found together, and from this difference some kind of mechanism is inferred to promote their coexistence. However, not all (or even most) species differences will promote coexistence; the criteria that must be satisfied to demonstrate the action of a coexistence mechanism are much more stringent (Chesson 2000, 2008, Leibold and McPeck 2006, Adler et al. 2007). Only species differences that lead to differential success in the various density-dependent processes that regulate their abundances will promote coexistence, and thus foster the invasibility of each species.

Despite its perceived importance and seemingly widespread acceptance, the issue of species coexistence has recently been brought into sharp relief with the rising prominence of “neutral” community dynamics

(Hubbell and Foster 1986, Bell 2001, Hubbell 2001). Neutral models explore community dynamics when species are ecologically equivalent to one another. Ecologically equivalent species cannot coexist (Chesson and Huntly 1997), and species should randomly go extinct as their relative abundances vary stochastically until only one species remains (Hubbell 2001). Neutral dynamics cannot act to maintain species in a system, but rather only slow the loss of species from local communities (Chesson and Huntly 1997, Bell 2001, Hubbell 2001, McPeck and Gomulkiewicz 2005). Many ecologists are now engaged in debates about the relative importance of these two viewpoints (niche vs. neutral dynamics; Gewin 2006). However, in following and engaging in this debate (e.g., McPeck and Gomulkiewicz 2005, Leibold and McPeck 2006, Siepielski et al. 2010), we began to question the degree to which the coexistence of species was a settled proposition. Namely, how many studies have actually thoroughly tested whether species found together in the field are coexisting? Silvertown (2004) recently reviewed the literature for the importance of niches for plant species coexistence, but unlike our analysis, did not focus explicitly on examining the key demographic criterion for coexistence (i.e., invasibility). Our sense was that coexistence was much like adaptation in the late 1970s; most assumed that species found together are coexisting because “they differ in such-and-such a way” (i.e., a “just so” story of coexistence), but definitive observational or experimental evidence existed for very few systems. However, no a priori reason can be justified to assume that each and every species found together in a local community need be coexisting. We use the term “co-occurring” for two or more species that are found together, but are not coexisting (Leibold and McPeck 2006). The implication of this distinction is that some subset of the co-occurring species are either slowly being driven extinct by others in the assemblage (McPeck 2007, 2008), stochastically walking to extinction via neutral dynamics (Hubbell 2001), or maintained in a local area by dispersal from other areas (i.e., sink populations; Schmidha and Ellner 1984, Pulliam 1988).

Like the operation of natural selection, we have no doubt that many species are coexisting with one another. However, any local assemblage is probably some mixture of co-occurring and coexisting species. Simply assuming that all species are coexisting is as scientifically dangerous as assuming that any feature of an individual’s phenotype is the product of adaptive evolution (Gould and Lewontin 1979). Predictions and inferences that are based on this assumption are only as good as the evidence supporting this assumption. Thus, we set out to systematically survey the literature for evidence that species are indeed coexisting in local assemblages in the field. In so doing, we wanted to determine the degree to which species coexistence was being evaluated by critical empirical tests.

SEARCHING THE LITERATURE FOR EVIDENCE OF LOCAL SPECIES COEXISTENCE

Although many coexistence mechanisms have been proposed that operate on some form of spatial segregation (e.g., Chesson 2000, Amarasekare et al. 2004, Holyoak et al. 2005), we limited our inquiry to species within the same trophic level living together sympatrically. Obviously, this statement has a very high degree of scale dependence. By “living together sympatrically” we mean that individuals of the species in question can reasonably be expected to interact with one another in an ecological web (e.g., compete for the same molecules of nitrogen in the soil, feed on individuals of the same resource species, be fed upon by the same predator individuals, be pollinated by the same pollinator individuals, be infected by the same virus particles). Differential responses of plant species to spatial heterogeneity within one field (or plot within that field) would be a spatial mechanism that promotes coexistence of species found together sympatrically (i.e., locally [e.g., Chesson 2008]), and so studies of these types of communities were included in our database (to the best of our ability to identify them). Hundreds of species within many taxa can be found living in sympatry in small areas, and so the much more salient question is how are all of these species found in one place, rather than why do species segregate in space. Thus, we limited our analysis here to what we perceived as studies of local (as we define it here) coexistence based on the descriptions in the paper, but acknowledge that mechanisms of regional coexistence are important (e.g., Chesson 2000, Amarasekare et al. 2004, Holyoak et al. 2005; see *Discussion*).

We reviewed the primary literature (28 journals; Appendix) by searching the ISI Web of Knowledge database (version 4.2, Thompson Corporation) using a key word search for the following terms: coexistence, local coexistence, and species coexistence. We performed our literature review in May 2009, and the resulting database included studies published up to this point (1972–2009), in addition to a few more recent studies that came to our attention.

For each study, we determined whether authors were considering species assemblages at a local scale (as we defined it previously), and whether they made statements about whether the species in question were or were not coexisting. We then evaluated what evidence was presented to support the claims about coexistence. This evidence could either be presented in the paper, or as a reference to a previous study. For the latter, we then evaluated if the referenced paper presented such evidence.

Obviously, evidence evaluating the invasibility criterion for every species in question is needed to support a claim that species are or are not coexisting. Because we found so few studies that evaluated invasibility, we also recorded whether the studies presented other evidence that would be necessary for coexistence but not

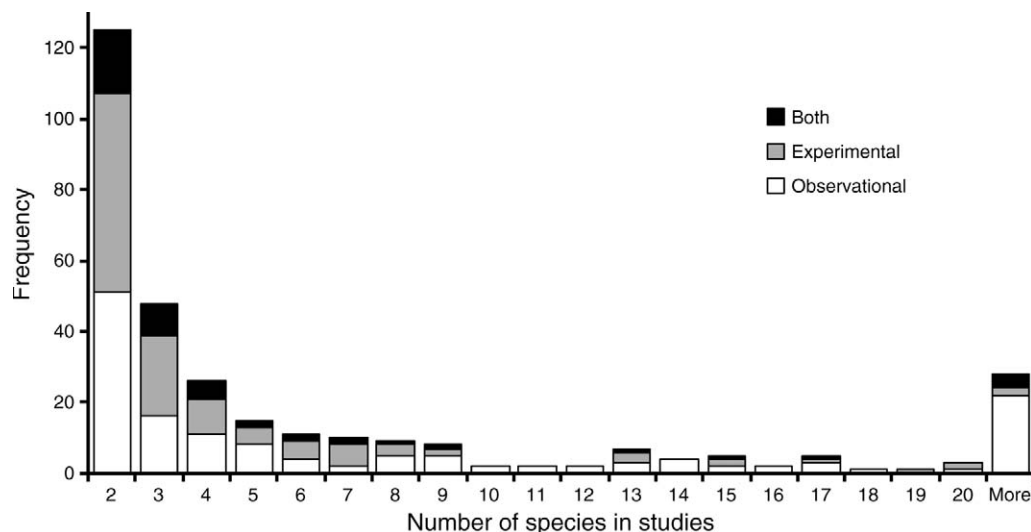


FIG. 1. Frequency histogram of the number of species included in different types of studies. These types were observational (open component of bar), experimental (gray component of bar), or those that included both observational and experimental components (black component of bar) to the analysis. The maximum for observational studies was ~ 4500 species; for experimental studies, 50 species; and for studies including both observational and experimental data, 35 species.

sufficient to make such a definitive conclusion: namely, some form of negative density dependence or frequency dependence in population regulation and some trade-off in ecological performance that would influence population regulation. Negative density or frequency dependence ensures that each species' abundance is regulated; if a species' abundance is not regulated, no demographic force can perpetuate its long-term persistence in a community (Chesson and Huntly 1997). All coexistence mechanisms also imply the operation of some performance trade-off among species (Chesson 2000), and so demonstrating such trade-offs would suggest the possibility of coexistence (e.g., Silvertown 2004). However, coexistence requires a particular balance between the density-dependent fitness advantages that allow the species to persist and disadvantages that prevent the species from driving others from the system. Merely demonstrating the existence of a performance trade-off among species does not prove that this balance is met. We also recorded the proposed mechanism or explanation of species coexistence. Finally, we recorded the number of species evaluated in the community and at what taxonomic level (e.g., species within genera, species in different genera, species in different families, and other taxonomic levels) mechanisms of coexistence were being invoked. The data set is presented in the Supplement.

While we tried to be as objective as possible, this exercise proved to us that determining if a particular paper is evaluating whether some number of species are coexisting can be rather subjective. We sincerely apologize to the original authors for any apparent misrepresentations of their work. We also apologize to any authors whose relevant papers may not have been captured by our search methods. In addition, we suspect

that many researchers may have simply used some form of the word coexist interchangeably with co-occur. We also tried to limit inclusion in the database to those studies that seemed to focus on species coexistence, but acknowledge that our quantitative estimates are probably inaccurate. Nevertheless, our goal here is not to quantify exactly how many species are and are not coexisting, but rather to evaluate the degree to which data are being collected to critically test for the operation of coexistence mechanisms.

Our literature search identified 1589 papers. Of these, 323 were empirical studies of multiple species living in one general location in the field (our criterion for "field" was that the species included in the study are reported by the authors to be found together in nature, but the actual data in the study could have come from laboratory studies [e.g., laboratory studies of phytoplankton or protists that are found together in the field]). We base our analyses on these papers (Supplement). Many papers found in this literature review were not included because they were theoretical papers, were focused on broader regional coexistence, or did not make a clear statement about local species coexistence. Indeed, many studies indicated that the various mechanisms examined could contribute to local coexistence but did not indicate that species were or were not coexisting.

Studies spanned broad taxonomic groups, but plants and insects were particularly well represented (Supplement). Most studies only examined possible coexistence among a few species, with three being the median number of species considered in all studies (Fig. 1). Studies that analyzed only observational data included a median of four species, but the maximum number of species included in an observational study was ~ 4500

TABLE 1. Studies demonstrating key criteria necessary to invoke local coexistence in the maintenance of species diversity.

Taxa	Invasibility	Density- or frequency-dependent population regulation	Phenotypic trade-offs	Reference
Prairie grass species	long-term data showing recovery from low density	negative density dependence because of competitive interactions	species-specific responses to annual variation in climate	Adler et al. (2006)
Desert annual plants	long-term data showing recovery from low density	estimates of r increases at low density	relative growth rate vs. water use efficiency	Angert et al. (2009)
Grasshoppers	not quantified	competitive isocline experiments	implied trade-off in ability to use different resources	Chase (1996)
Freshwater diatoms	long-term experiments showing recovery from low density	population growth rate to equilibrium	trade-offs in growth rates across variation in temperature	Descamps-Julien and Gonzalez (2005)
Prairie plants	not quantified	isocline experiments of R^*	trade-offs in biomass production along soil nitrogen gradient	Dybzinski and Tilman (2007)
<i>Daphnia</i>	long-term data showing recovery from low density	population growth rate to equilibrium	mediated through body size	Gliwicz and Wrzosek (2008)
Protists	experimental data showing recovery from low density	population growth rate to equilibrium	growth rates in different temperatures	Jiang and Morin (2007)
Damselflies	not quantified	experimental data showing decreased density-dependent individual growth and increased density-dependent mortality at high density	growth vs. mortality trade-off shaped by behavior and physiology	McPeck (1998)
Picocyanobacteria	experimental data showing the ability to increase when rare in the presence of a competitor	population growth rate to equilibrium	ability to use different parts of the light spectrum	Stomp et al. (2004)
<i>Tegula</i> snails	estimated model invasibility criteria by substituting empirically estimated parameters into model	experimental data showing negative density-dependent individual growth rates and positive population growth rates with the competitor at equilibrium	behaviorally mediated trade-off between ability to maximally extract food in a patch and maximize the area grazed per unit time	Wilson et al. (1999)

(Fig. 1). Experimental studies or studies that analyzed both experimental and observational data included a median of three species, but the maximum in any particular study was much smaller in these (50 species for experimental studies, and 35 species for studies including both experimental and observational data; Fig. 1).

The taxonomic level of comparisons within communities varied considerably across studies. Comparisons among species in the same genus (108 studies) made up about a third of the comparisons, whereas comparisons among species in different genera (102 studies), species within and between genera (32 studies), species in different families (12 studies), and species of various taxonomic relationships (a cornucopia of taxonomic levels; 69 studies) constituted the bulk of comparisons.

In addition, a small number (13 studies) lumped multiple species together into single taxa.

The majority of studies (78%) made statements about species coexistence but did not present any of the supporting evidence discussed previously to justify these statements (e.g., data testing for invasibility, negative density or frequency dependence, or trade-offs). Most telling, only seven studies evaluated the invasibility of species in some way (Table 1). Evidence for invasibility came from both analyses of long-term data sets of abundances, and from experimental manipulations. We will return to these studies in more detail.

Fifty-one studies (16%) evaluated density or frequency dependence. A variety of approaches were used to assess density or frequency dependence, but typically involved quantifying some demographic parameter (e.g., per capita mortality rate, individual growth [e.g., mass

gain or development] rate) in relation to experimentally manipulated densities, or by showing that the rate of population increase from low density slows over time, which implies density dependence.

Sixty-eight studies (21%) identified phenotypes shaping proposed trade-offs. Evidence of phenotypic trade-offs most often came from showing that some measure of performance in a particular environmental setting for one trait negatively covaried with performance in another environmental setting among species. These included a variety of morphological, physiological, and behavioral differences among species. Although these are all the kinds of trade-offs that could be critical in promoting coexistence, by themselves they do not show that these phenotypic differences translate into demographic outcomes that will allow multiple species to persist.

Three studies tested for density-dependent population regulation and the basis of trade-offs among taxa, but not the invasibility of species (Chase 1996, McPeck 1998, and Dybzinski and Tilman 2007 in Table 1). These three studies were short-term (i.e., lasting less than the generation times of the organisms involved) experimental field investigations. Each demonstrated in different ways that species abundances were regulated by density-dependent interactions, and that species differed in their abilities to engage in these density-dependent interactions in ways that were consistent with the hypothesized mechanism of coexistence. Chase (1996) performed field experiments of competition among three grasshopper species, and showed the degree of diet segregation and differences in competitive ability for overlapping resources could account for their coexistence. McPeck (1998) demonstrated that predation and competition for resources imposed density-dependent mortality and growth on two genera of damselflies, with species in one genus being better at avoiding predators and the other being better at converting resources into their own biomass. Finally, Dybzinski and Tilman (2007) evaluated whether trade-offs in prairie plants for nitrate and light could predict which species could persist in plots along gradients of these two resources. While demonstrating density dependence and the existence of trade-offs are consistent with the operation of some coexistence mechanism, even if met, the species in question may still not be coexisting if the fitness differences among species are sufficiently large. However, if these features were not present in a system, coexistence is impossible. Thus, the results for these studies are suggestive but not definitive.

Seven studies in our survey presented evidence for invasibility (Table 1). We highlight these studies to more concretely illustrate the types of empirical evidence that can be marshaled to test invasibility. Adler et al. (2007) and Chesson (2008) also present a series of experimental designs for evaluating invasibility, and we refer the reader to those papers. Two of these studies used long-term survey data of plant assemblages combined with

statistical modeling approaches to test for higher population growth rates when species are at low abundance (Adler et al. 2006, Angert et al. 2009). Angert et al. (2009) showed in a desert winter annual plant community a trade-off between relative growth rate and water use efficiency that explained long-term population dynamics consistent with recovery from low density. Similarly, Adler et al. (2006) used long-term observational data in a grassland community to show interannual variation in plant performance in relation to varying climatic variables, which increased low-density population growth rates. Both of these studies presented evidence consistent with coexistence via the storage effect (Chesson and Warner 1981). Obviously, evaluations of invasibility in such observational studies as these are only as good as the statistical models used to estimate the demographic responses of species.

Four of the remaining studies were largely laboratory investigations of short-lived organisms (phytoplankton, protozoans, zooplankton) that are found together in the field. For example, in freshwater diatoms, Descamps-Julien and Gonzalez (2005) showed a trade-off between growth rates across a temperature gradient and long-term population growth rates. Similarly, Stomp et al. (2004) showed that a trade-off in the ability to use different parts of the light spectrum by picocyanobacteria contributed to the ability to increase from low population density in the presence of a competitor. Jiang and Morin (2007) showed that certain patterns of temperature fluctuations can permit protozoan species to coexist. Gliwicz and Wrzosek (2008) demonstrated that the trade-off between fish predation and resource competitive ability permit two *Daphnia* species of different body sizes to coexist. All of these tested for invasibility by experimentally starting each species at low abundances and following population dynamics over time.

The final study in our list tested the invasibility criterion using a parameterized modeling approach. Wilson et al. (1999) demonstrated that two species of marine snails exhibited negative density-dependent growth rates and the species differ in foraging modes and resource structure that could promote their coexistence. They also tested for invasibility by substituting empirically estimated parameters into a model of the species interactions. Their parameter estimates fell just outside the parameter space for satisfying the invasibility criterion.

DISCUSSION

Explaining patterns of local species diversity within biological communities has challenged ecologists and evolutionary biologists for decades. More than 50 years have transpired since Hutchinson (1959) eloquently posed this dilemma to ecologists. Considerable effort has since been put forth to describe the theoretical conditions necessary to show local coexistence of species within biological communities (reviewed in Tilman and

Pacala 1993, Chesson and Huntly 1997, Chesson 2000, 2008, Chase and Leibold 2003, Adler et al. 2007). Concomitantly, empiricists have undertaken hundreds of observational and experimental studies to try and understand how multiple species can be found in local areas (e.g., Supplement). Despite these efforts, our review of the literature shows a considerable disconnect between theory and empirical tests (see also Silvertown 2004). We found that surprisingly little empirical evidence has been gathered to test the fundamental criteria needed to show that species locally coexist under any mechanism. Similarly, Silvertown's (2004) review of the importance of niches for plant coexistence failed to find many studies evaluating key trade-offs for niche-based coexistence. Just like Gould and Lewontin's (1979) critique of adaptation, we emphasize that these findings do not refute the importance of local species coexistence in explaining the maintenance of species diversity. Rather, our survey strongly suggests that few critical tests of coexistence are being performed; in other words, we lack the critical empirical evidence to say one way or another whether species coexistence is a pervasive reason why species are found living together.

Obviously, amassing data to test for the operations of mechanisms of coexistence is extremely difficult for many systems (Adler et al. 2007). We note that six of the seven studies testing invasibility were either based on long-term data sets of plants, or laboratory experiments on organisms with generation times of hours to days. For most systems, invasibility may be difficult if not impossible to test directly. First, replicate communities must be established and allowed to come to their long-term demographic dynamics with one species (i.e., the species to be the invader) excluded from each (i.e., an experimental design in which replicate communities with each species deleted as a treatment). Then the invader species is introduced and its population dynamics followed for some number of generations to see if it increases from rarity. Strictly speaking, this straightforward experimental design may only be possible in the laboratory because of constraints of size (e.g., having enough space to establish replicate communities of adequate size) and time (e.g., the experiment must be run long enough for the system to come to its long-term demographic dynamics plus time to evaluate whether the invader is increasing following invasion).

In systems where this is not possible, researchers will have to be more creative. The best course of action is probably to follow the lead of Wilson et al. (1999), by testing for density dependence and trade-offs empirically, and using parameter estimates derived from these experiments in models to test whether features of the system are consistent with each species being able to invade when rare. Chesson (2008) has also recently proposed a combined experimental and modeling approach for assessing coexistence.

Alternatively, when long-term data sets are available on the population dynamics of many species from one

area, invasibility may potentially be assessed through statistical modeling of population demography (e.g., as in Adler et al. 2006, Angert et al. 2009). Here again, time to amass such data may be a limiting factor, given that the data will have to span multiple generations of each species. Moreover, this approach will only be possible in systems that show large fluctuations in abundance over few generations, and so may only be able to detect coexistence mechanisms that have temporal variability as a signature feature (i.e., the storage effect; Chesson and Warner 1981).

Clearly, because of differences in spatial scale and generation time, no single approach to testing for the operation of coexistence mechanisms is the right one for every system. Instead, we advocate that a plurality of observational and experimental approaches be taken that generate multiple reinforcing types of data to assess coexistence. (1) Do observational data on species abundances at different locations along ecological gradients change in predictable ways, suggesting that those ecological factors play a role in the coexistence mechanism? (2) What ecological agents impose negative density or frequency dependence on the species in question; do species differ in the strengths of the density or frequency dependence imposed by these ecological agents; and are trade-offs apparent in their abilities to engage in interactions with these ecological agents? (3) Do manipulations of these important ecological agents cause shifts in the relative abundances of the species or differential alterations of their demographic rates? (4) Can each species increase in abundance when experimentally reduced to low abundance, or alternatively, do the demographic rates of each species become more favorable (i.e., higher survival, growth, and fecundity) when perturbed to low abundance? (5) Do species increase from periods of rarity in long-term observational studies, or is the potential for invasibility supported from statistical models of community dynamics that are parameterized from longitudinal population dynamics data? (6) What phenotypic differences among the species can account for any apparent trade-offs? (7) Do manipulations of the morphological, physiological, or behavioral traits that appear to foster these trade-offs alter demographic performance of species in these ecological interactions? We believe that this full set of questions should guide any robust examination of coexistence. Merely addressing invasibility in one place at one time does not evaluate the generality of the result or identify the mechanism that may be operating. Addressing this full set of questions will.

Our own work on the coexistence of species in two genera of damselflies in freshwater lakes also illustrates the pitfalls of assuming coexistence among every species in the system, even when the operation of coexistence mechanisms is strongly suggested. *Enallagma* and *Ischnura* damselflies seem to coexist because predation imposes density-dependent mortality on them, and their

growth rates in response to limiting resources are density dependent, with the two genera exhibiting phenotypic trade-offs shaping these vital rates: *Ischnura* are better than *Enallagma* at converting food resources into their own biomass, but *Enallagma* are better than *Ischnura* at avoiding their shared predators (fish or dragonflies depending on lake type) (McPeck 1998). Thus, these taxa differ in ways that are completely consistent with the classic mechanism of keystone predation (Levin 1970, Holt et al. 1994, Leibold 1996, McPeck 1996) at the level of the two genera. However, these comparisons are at the generic level. The problem is that in lakes across eastern North America, two to four *Ischnura* species and five to 12 *Enallagma* species can be found sympatrically in most lakes (Johnson and Crowley 1980, McPeck 1990, 1998). We recently conducted an experiment aimed at evaluating whether individual species of *Enallagma* coexist (Siepielski et al. 2010). Results from this experiment showed that species gained no demographic advantage (i.e., higher growth rates or lower mortality rates) at low relative abundance when other species are at high relative abundance, despite the fact that mortality and growth rates of species are strongly density dependent. These studies together therefore suggest that a coexistence mechanism potentially operates to allow the coexistence of the two genera, but no local coexistence mechanism apparently operates within at least the genus *Enallagma*. These results highlight the danger of assuming that because genera coexist, species within genera must also coexist. Further, this study reinforces the importance of studying coexistence of individual species and not simply taxonomically pooled groups of species (as some studies did).

Like the damselfly system, most communities are probably composed of some combination of coexisting and co-occurring species (Hubbell 2001, McPeck 2008). There is simply no a priori reason to believe that all species present in a system are coexisting. Yet, our conceptual basis for theories and empirical explorations of mechanisms maintaining species diversity rests firmly on the assumption of the indefinite persistence of species in niche-based communities, despite the fact that species are transient and ultimately go extinct, and that the loss of species from local communities is not uncommon (Raup 1991, Hubbell 2001). Although examples of species' being driven extinct (particularly on the kind of intergenerational time scale relevant to population demography) from local communities owing to processes like competitive exclusion or especially drift are few (Hubbell 2005), evidence from diverse fields (e.g., laboratory studies of competitive exclusion [Gause 1934], field-based studies of the causes of spatial segregation patterns [Connell 1961, Brooks and Dodson 1965, Paine 1969, Hairston 1980], paleontological studies of the fossil record [Raup 1991, Lawton and May 1995], and paleoecological studies of communities [Overpeck et al. 1992]) all highlight the often transient nature of most species presences in space and time.

Indeed, these examples highlight that at some level our understanding of community structure seems to come mostly from empirical studies demonstrating why species cannot indefinitely persist together (e.g., such classic studies of competitive exclusion as Connell [1961], Hairston [1980]), rather than demonstrating the operation of mechanisms that promote coexistence. A failure to appreciate these very real dynamics of ecological systems has led to what Hubbell (2001:11) has called a "myopic preoccupation with coexistence." Whether myopic or not, our preoccupation with a singular explanation does preclude our ability to comprehensively understand the set of processes shaping patterns of species diversity.

Not only is it that species presences are transient on some spatial and temporal scale, but the notion and hence the perceived importance of species interactions in local communities themselves has been questioned. Pointing to a diverse array of evidence, grounded mainly on the observed tendency for local species richness to increase as a constant proportion of regional species richness (e.g., Ricklefs 1987, 2000, Caley and Schluter 1997), Ricklefs (2008) has argued that studies of local coexistence cannot be used to explain the maintenance of species diversity at either local or regional scales. Instead, local species diversity can only be understood in terms of processes like lineage diversification and adaptation operating over regional scales, along with interactions among species occurring over entire regions, not local communities (Ricklefs 2007).

While we agree with Ricklefs' general thesis, we do not agree that local interactions are irrelevant to understanding patterns of species diversity. However, if local coexistence of species is to be invoked as an explanation for maintaining species diversity, critical empirical tests (observational and experimental; e.g., Table 1) must be performed to distinguish coexistence from co-occurrence in explaining local species diversity. The need for such tests arises because any particular species may be present in a local area for many reasons. Obviously, one is that its demographic rates promote its persistence in this area (i.e., it can increase when rare); in other words, it coexists with the other species present at this location. A second is that the species is slowly being driven extinct locally by the abiotic conditions and interactions with other species. Extinction is a dynamical process, and may take a substantial amount of time to complete, and so the fact that a species will eventually go extinct does not mean it may not be present for a considerable amount of time (McPeck 2007, 2008). Moreover, such a species may persist indefinitely at this location if migration from other areas where it thrives (i.e., "source" populations [Pulliam 1988]) maintain it locally as a sink population (i.e., mass effects of Shmida and Ellner 1984). A third is that the species may be ecologically identical to other species at this location, and so its relative abundance simply drifts randomly (Hubbell and Foster 1986, Bell 2001, Hubbell 2001).

Such a species may also randomly walk to extinction locally, but if local population sizes of equivalent species are large and dispersal occurs among a number of local patches, the time to extinction for this species may be effectively infinite (McPeck and Gomulkiewicz 2005). These simple considerations immediately emphasize the importance of a regional perspective on understanding biological diversity (Ricklefs 2008). However, those regional patterns are complex functions of the local interactions in which each species is engaged. Given that so many kinds of processes can allow multiple species to be present in an area, it should be obvious that evaluating coexistence is, therefore, not merely an exercise in testing what theoreticians think is necessary (see also Miller et al. 2005 for a similar discourse on resource-ratio theory). Critical tests of these criteria are direct tests of the relative importance of various local (e.g., coexistence, drift) and regional (e.g., dispersal, mass effects, source–sink structure) processes to explain patterns of species richness and diversity.

Results from our review of the literature reveal that the “just so story” of coexistence is one where ecologists identify phenotypic differences among locally sympatric species and propose some mechanism for why they are coexisting. Instead of exploring phenotypic trade-offs, many studies simply showed that species differed in ecologically relevant ways. However, just showing that species differ phenotypically or ecologically is insufficient to assign those differences to the kind of trade-off necessary to promote coexistence (e.g., Chesson 2000, Leibold and McPeck 2006). Surely species differ in myriad ways, but what matters for species coexistence is that these phenotypic differences cause trade-offs in the abilities of organisms to engage in the various density-dependent interactions they face.

Moreover, the plethora of cryptic species complexes being uncovered by molecular studies create further problems for explaining why so many ecologically similar species are found together (Bickford et al. 2006). Examples abound of species once thought to be a single lineage harboring many distinct (genetically) species. Genetic analyses of the amphipod *Hyaella azteca*, once thought to be a single species, have revealed it to consist of at least seven different species, with two or more species co-occurring in most lakes (Witt and Hebert 2000). Such examples are not the purview of obscure taxa. For example, cryptic species diversity has been found in such common, ecologically and economically important taxa as bumble bees (Murray et al. 2008) and earthworms (King et al. 2008), which occur sympatrically. One has to wonder what our perspective on diversity maintenance would have been had molecular systematics come first, and ecologists were forced to grapple with high levels of sympatric diversity for species with little or no observable phenotypic differentiation. Presumably, just so stories of coexistence would have been more difficult to construct.

Finally, we wish to discuss the nature of coexistence from a taxonomic perspective. Most studies of “species coexistence” in our analysis were actually at levels above the species level (e.g., comparisons of species in different genera or families), as only about a third of studies were between species within genera. To be sure, the problem of coexistence is the same whether we are asking if two species within the same genus coexist, or if two species in two entirely different families coexist. But what do we make of communities “organized” at high taxonomic ranks (e.g., like families or classes), with such long and varied evolutionary histories? In many systems, the bulk of diversity lies at the level of species within genera. This observation led to studies focused on species:genus ratios (Simberloff 1970), with the idea that more genera relative to species would reflect the occurrence of competitive exclusion, because species within genera were often predicted to be more similar ecologically to each other than between genera. Recently, such inquiries have led to the emerging community phylogenetics framework, which tries to understand whether phylogeny can be a predictor of patterns of species co-occurrence (Webb et al. 2002, Cavender-Bares et al. 2009). Results here are varied, with evidence of both phylogenetic overdispersion (i.e., less phylogenetically distantly related taxa tend to co-occur more often than by chance), and phylogenetic clustering (i.e., more phylogenetically distantly related taxa tend to co-occur more often than by chance) being common. Such variation in community phylogenetic structure itself often varies with spatial and phylogenetic scale (Cavender-Bares et al. 2009). While this approach provides an exciting link between macroevolutionary history and community structure, such analyses cannot test if species coexist. However, some studies do provide a glimpse. Cahill et al. (2008) showed that within some plant groups, competition was more intense among closer relatives, whereas in other groups greater relatedness led to weaker competition. In a second suggestive example, Maherali and Klironomos (2007) manipulated phylogenetic distance in competition experiments of mycorrhizal communities, making comparisons across families and species within families. While this example did not show evidence for coexistence, it did show that realized community richness (i.e., richness after one year of competitive interactions) was often higher when starting species were more distantly related to each other, suggesting a “phylogenetic signal” in the possible outcome of competitive interactions. If patterns of species diversity are a consequence of correlations between ecological interactions and phylogeny, by studying interactions across very distantly related taxa (e.g., between genera or families) we have stacked the odds in favor of finding the widespread operation of coexistence, but our knowledge of species level coexistence remains obscured. Thus, we need studies focused on trying to understand the degree to which many closely related taxa (i.e., species within genera) coexist.

CONCLUSIONS

Assuming the existence of an underlying process by focusing on its perceived outcome and not by performing critical observational and experimental tests is not a new problem to community ecology (e.g., see the collected papers in volume 122, issue 5, of the *American Naturalist*). Many processes can allow multiple species to persist, but not necessarily coexist, together. This exercise revealed that the nature of inquiry into the species coexistence problem is typically to assume that species are coexisting and then test derivative hypotheses based on the operation of the assumed coexistence mechanism. We are uncertain why direct tests of coexistence have been side-stepped. We hope that this critique of the “coexistence program” will motivate a healthy debate about the correct ways to test (particularly experimentally) various coexistence mechanisms and quantify the relative contributions of coexistence and other mechanisms to explaining why various species are found together in a local area. We also hope it serves as a call to action to perform these critical tests in real communities. Great advances can be made in our understanding of how species are organized into biological communities by not simply assuming the operation of mechanisms but rather by performing critical tests of these mechanisms, just as testing for the operation of natural selection has become a necessary component of evidence in studies of microevolution since the publication of Gould and Lewontin’s (1979) critique.

ACKNOWLEDGMENTS

We thank P. Adler, A. Angert, P. L. Chesson, and an anonymous reviewer for thoughtful comments on an earlier version of this manuscript. This work was supported by National Science Foundation grant DEB-0714782 to M. A. McPeck.

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APPENDIX

Journals searched during the literature review (*Ecological Archives* E091-221-A1).

SUPPLEMENT

Tab-delimited text file of studies included in the literature review (*Ecological Archives* E091-221-S1).