



12 | ON THE INTEGRATION OF COMMUNITY ECOLOGY AND EVOLUTIONARY BIOLOGY: HISTORICAL PERSPECTIVES AND CURRENT PROSPECTS

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12.1 | INTRODUCTION

In this chapter, I provide a personal reflection on a topic that is both perennial and persistently unresolved—namely, the relationship between ecology and evolution—with a focus on the community level of organization. Ecological communities are surely among the most complex entities tackled by scientists, inasmuch as communities contain many species (e.g., thousands), each with unique attributes and historical origins, interacting in all sorts of idiosyncratic ways. The structure and dynamics of communities are likely to reflect the imprint of historical processes, including evolution. Conversely, the pattern and rate of evolution is likely to be influenced by community processes.

A major intellectual (not to mention educational and sociological) challenge in the early decades of the twenty-first century is to achieve the seamless integration of the disciplines of ecology and evolutionary biology. The companion chapter by Day (Chapter 13) crisply

summarizes the vigorous and continuing development of theoretical evolutionary ecology. As his overview shows, evolutionary ecology has traditionally been concerned with the traits of single species or pairs of interacting species. The interaction between community ecology and evolutionary biology is by comparison still in its infancy, but I suspect that we are poised on a threshold of exciting developments at this interface. Several authors have addressed, from different perspectives, the interplay of community ecology and evolution (e.g., see Eldredge 1995, Brooks & McLennan 1991, Orians 1962, Collins 1986, Silvertown & Antonovics 2001, Price 2003, Webb *et al.* 2002, Levin 1999, and articles in Agrawal 2003), and I will not pretend to give a thorough overview of this giant issue. Instead, I start with some general reflections on the relationship between community ecology and evolution. I then give a quick tour through high points in the history of this relationship, from the early years of the twentieth century to the present, using as a point of departure key documents that defined the discipline of community ecology and emphasizing the evolutionary perspectives taken by the authors. I am not a professional historian but rather have the vantage point of a practitioner, who read and responded to the publications I mention; doubtless I have a distorted and limited view both of the historical facts and of their societal and intellectual drivers. The theme of the interplay of ecology and evolution richly deserves the attention of professional historians of science. In the last part of this chapter, I explain some key questions that seem to me to be particularly ripe for further development at the community ecology–evolution interface. I have chosen not to dwell on explicit, formal mathematical theory but instead to reflect on the conceptual grounding that underlies all such theory.

12.2 | BACKGROUND REFLECTIONS

All biologists know Dobzhansky's famous quip, "Nothing makes sense in biology except in the light of evolution" (Dobzhansky 1973; see Box 12-A). Presumably this includes the core questions of community ecology—such as elucidating the causal underpinnings of patterns of species composition and richness of entire communities. Yet, as Webb and his colleagues (2002) note, the "integration of evolutionary biology and community ecology remains elusive". Hamilton (1995) likewise criticizes the discipline of community ecology for its "relative neglect of . . . the genetical and evolutionary change occurring within species" because "populations and species cannot be treated as entities resembling molecules any more than individuals can." I think it

is accurate to state that many (most?) community ecologists do not directly consider evolution in their work. This is not a damning criticism, far from it. Much valuable work can be carried out in community ecology with little attention paid to evolution. An ecologist colleague of mine once likened his role to that of an analyst of card games: his mission is to interpret what happens when the cards are dealt, not to explain where the cards come from or how they acquired their face values. This is often a reasonable stance. A typical example is a book on marine communities (Berness, Gaines, & Hay 2001) that synthesizes major patterns and processes in marine systems. A few chapters deal with genetics and evolution, but most do not, and they do not really need to do so to provide substantial insights into these systems.

Box 12-A

What about turning Dobzhansky's quip on its head? What would evolution be like without ecology? Would evolution make sense? Do these questions even make sense? I do not know the answer, but it is worth considering this issue briefly. Certainly a great deal of evolutionary biology can be (and is) carried out with scant or no direct reference to ecology. In particular, phylogenetic reconstruction using cladistic methods depends on the assumption of ancestor-descendent relationships and the identification of shared, derived characters using appropriate outgroup comparisons. Phylogenetic techniques do not in any obvious way depend on understanding how organisms interact with the environment or how species interact with one another.

However, I must wonder if the seemingly ecology-free phylogenetic mission simply takes for granted (*viz.* sweeps under the rug) key ecological forces implicitly involved in the origin, maintenance, and diversification of species and ultimately in the generation of phylogenies. For instance, would species even exist in the absence of ecological forces? The cohesive forces that are believed to keep species persistent as evolutionary units (e.g., sexual reproduction, leading to reproductive isolation; gene flow; and stabilizing selection) are hard to understand in the absence of ecology. A prime theory for the evolution of sex is that it reflects the antagonistic evolution of parasites and their hosts providing the right kind of fluctuating selection to favour recombination (Segger & Hamilton 1988). Without these interspecific interactions, sex

summarizes the vigorous and continuing development of theoretical evolutionary ecology. As his overview shows, evolutionary ecology has traditionally been concerned with the traits of single species or pairs of interacting species. The interaction between community ecology and evolutionary biology is by comparison still in its infancy, but I suspect that we are poised on a threshold of exciting developments at this interface. Several authors have addressed, from different perspectives, the interplay of community ecology and evolution (e.g., see Eldredge 1995, Brooks & McLennan 1991, Orians 1962, Collins 1986, Silvertown & Antonovics 2001, Price 2003, Webb *et al.* 2002, Levin 1999, and articles in Agrawal 2003), and I will not pretend to give a thorough overview of this giant issue. Instead, I start with some general reflections on the relationship between community ecology and evolution. I then give a quick tour through high points in the history of this relationship, from the early years of the twentieth century to the present, using as a point of departure key documents that defined the discipline of community ecology and emphasizing the evolutionary perspectives taken by the authors. I am not a professional historian but rather have the vantage point of a practitioner, who read and responded to the publications I mention; doubtless I have a distorted and limited view both of the historical facts and of their societal and intellectual drivers. The theme of the interplay of ecology and evolution richly deserves the attention of professional historians of science. In the last part of this chapter, I explain some key questions that seem to me to be particularly ripe for further development at the community ecology–evolution interface. I have chosen not to dwell on explicit, formal mathematical theory but instead to reflect on the conceptual grounding that underlies all such theory.

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might not exist, in which case species would not be bounded by reproductive isolation. In like manner, the evolution of dispersal (permitting gene flow) often seems to reflect either local competition for scarce resources or spatiotemporal variability in the external environment (see chapters in Clobert *et al.* 2001). Without these ecological drivers, a researcher might see little dispersal. Many forms of stabilizing selection (e.g., on body size) clearly involve interactions between organisms and their environments. Organisms do not inherit just their genes from their ancestors; they also inherit their environments, which can lead to a commonality in the selective regime experienced within a lineage (Holt 1987, Holt & Gaines 1992, Harvey & Pagel 1991, Odling-Smee, Laland, & Feldman 2003). Without cohesive forces based in ecology, it is thus not clear that a researcher would expect to see well-defined lineages—species—at all.

There thus may be a sense in which phylogenies of discrete species only exist (or at least are discernible against the background noise of mutational variation) because of the unfolding of ancestor-descendent relationships in an ecological context providing cohesion to lineages. Moreover, much of the history of life at the grandest scale potentially reflects the imprint of interactions between organisms and a variable physical environment (see Rothschild & Lister 2003 for an excellent overview). Even in a constant environment, biotic interactions within and among species can generate a ceaseless evolutionary dynamic. Without such “Red Queen” forces, abstract theoretical models suggest that evolution long ago would have ground to a halt (Stenseth & Maynard Smith 1984).

A community is a collection of species found in a particular place and time that can potentially interact (Morin 1999). Among the concerns of community ecologists are to understand how interactions among species within a community affect each species' mean abundance and pattern of fluctuations, to gauge how interactions do (or do not) influence which species co-occur in local communities (Tokeshi 1999, Holt 2001), and to ascertain how these local processes combine with forces at larger scales to determine patterns of species richness (Ricklefs & Schlüter 1993, Holt 1993, Rosenzweig 1995). Traditionally, community ecology has been dominated by a concern with local mechanisms (e.g., keystone predation). Important developments in recent years have been a broadening of the spatial and temporal scales of inquiry and a growing

recognition that regional and historical processes may be essential determinants of local community structure (Ricklefs 2004, Webb *et al.* 2002; see also later sections of this chapter). Ricklefs (2004) has argued that this increasing scale requires integrating evolution into community theory, because the timescale of ecological processes such as competitive exclusion becomes comparable to that of macroevolutionary processes (speciation and diversification). Whether evolution should be explicitly considered in an ecological investigation depends on questions of timescale separation.

To address the timescale issue, it is useful to step back from all the details and ask at the most basic level what we do as scientists. I think much of what we do can be boiled down into two questions. First, for a given system, what is an appropriate joint specification of the states of that system, and the forces acting upon it, that describes how it changes with time? Second, how does a scientist combine an understanding of multiple systems (all analyzed in terms of a joint specification of states and forces) to arrive at a more synthetic understanding of them all?

Theoretical community ecology is largely devoted to analyzing systems of coupled differential or difference equations that depict how communities change over time and across space. The *state* in this case is typically a vector of species abundances, defined at a particular spatial scale; the *forces* are the functional forms of the population growth equations, with parameters describing interspecific interactions such as predator functional responses and intrinsic growth rates, that allow a scientist to predict species abundances through time. But if species' properties can change because of evolutionary forces, the parameters and functional forms of the *force* equations can themselves change (see Chapter 13 for examples) and so, in some situations, may be variables over ecological timescales rather than fixed quantities. There are an increasing number of examples of rapid evolution in traits related to interspecific interactions across a range of taxa in both natural (Reznick & Ghalambor 2001) and laboratory (Mueller & Joshi 2000) settings. Most species are very small (e.g., microbes, nematodes, or collembola) and correspondingly have short generation lengths and large population sizes. Evolutionary dynamics (including speciation) of these community members may easily occur at timescales that are small, scaled against the timescale of changes in abundance of the longest-lived community members (e.g., trees or vertebrates). For instance, in studies of plant competition in terrestrial plant communities, the effect of long-lived plant species on one another may be mediated partly by how they influence both the ecological and the evolutionary dynamics of the soil microflora.

Speciation or extinction in effect changes the state vector. A consideration of macroevolutionary dynamics is essential when considering broad comparative or biogeographical questions about species richness or community composition (e.g., what explains the latitudinal diversity gradient?). In comparative studies, if the systems in question have been separated long enough, observed patterns will typically reflect both ecological and evolutionary processes.

The very definition of a *community* brings out an important difference in the frames of reference used in evolution and community ecology, respectively, which one could refer to as *Eulerian* versus *Lagrangian*. In classical fluid mechanics, a Eulerian frame of reference takes as its basic unit a bit of space (e.g., volume) and tracks the fluid fluxes coupling this unit with other such units and the local interactions. By contrast, in a Lagrangian frame of reference, the basic unit is a bit of fluid, which is followed as it moves across space (Symon 1960, p. 313). Neither frame of reference is the "correct" perspective, as both illuminate reality in usefully different ways. A community ecologist focused on dynamics in a particular spatially defined habitat, for instance, the interactions among tit species in Wytham Woods, is a Eulerian. By contrast, an evolutionary biologist concerned with history, say, the phylogenetic relationships of those same tits or the degree to which their life history variables reflect selective pressures, would properly be concerned with a spatiotemporally bounded lineage of past populations of tits in whatever local environment they happened to inhabit; this evolutionary biologist implicitly takes a Lagrangian stance. Elsewhere (Holt & Gaines 1992) I suggested that one way to link these two approaches is to develop a *phylogenetic envelope* for each species. In effect, for the individuals in each population in a local community in a given time step, the scientist identifies in the previous time step the environments (in both real space and abstract environmental space) inhabited by the parents of those individuals. Recursively, going back in time, the scientist can in principle reconstruct the actual environments and spatial locations experienced by the lineages that generated the local community (see Fig. 1 in Holt & Gaines 1992 for a graphical example). If the phylogenetic envelopes of two species overlap only in the current generation, and not before, then it is obvious that coevolution between them is irrelevant to their current interaction. If for a given species in each generation the phylogenetic envelope in prior generations was located elsewhere, the local population may be demographically a *sink* population, which is likely to be maladapted to the local abiotic and biotic environments (Holt & Gaines 1992).

The seminal ecologist C.E. Hutchinson (1965) once wrote an elegant book memorably titled *The Ecological Theatre and the Evolutionary Play*. This title (although not the author) seems to me to miss part of the fundamental dialectic that governs living systems. Namely, the basic evolutionary processes of adaptation and speciation largely (although by no means exclusively) reflect ecological forces, constraints, and opportunities. Conversely, ecological processes are mediated by individuals, species, and interacting suites of species, whose behavioral, morphological, and physiological traits have arisen as products of evolutionary processes; moreover, even abiotic forces can reflect the imprint of evolution. It is as if the props and stage in the "ecological theatre" are themselves constantly being constructed, destroyed, and moved around as the "evolutionary play" unfolds.

It can be difficult to even define the "environment" of an organism independent of the organism itself (Lewontin 1985, Brandon 1990). This is particularly the case when the organism modifies its environment so that it directly affects the selective regime it or its offspring experience (e.g., *ecological engineering* in Jones, Lawton, & Schachak 1994 or *niche construction* in Odling-Smee, Laland, & Feldman 2003). One of the most important conceptual developments in evolutionary theory in the last half-century has been the recognition that although in the short-run the environment selects adaptations, in the long run those adaptations shape and determine the selective environment, particularly when the environment includes species that are themselves evolving (Nowak & Sigmund 2004). Thus, the height of trees reflects as much competition among trees as selective influence of the physical environment on plant form and function (Falster & Westoby 2003). This dialectic between organism and environment makes evolutionary dynamics more like the unfolding of the surprising twists and turns of a game than like climbing the fixed peaks of a rigid adaptive landscape.

This is clear when considering interactions among individuals, within and among species (see Chapter 13). But even the abiotic environment can be strongly influenced by evolution. The recent literature suggests that feedbacks between organisms and ecosystem processes can take surprising and even outrageous forms. For instance, many ecosystems are dominated by fire. Yet, wildfires depend on the availability of highly flammable fuels. At first glance, it is hard to understand why some plant species generate highly flammable dead tissues, which make it more likely a fire will kill the plant that produces such tissues. Schwick and Kerr (2002) demonstrate that if interactions and dispersal are localized, flammability can evolve because parents that burn can leave open areas to

be monopolized by their offspring. As another example, consider the quintessential abiotic factor—the weather. Hamilton and Lenton (1998) provocatively proposed that microbes and small phytoplankton “have evolved to seed cloud formation to create local dispersal vehicles for themselves, winds and clouds” (the mechanism involves the production of dimethylsulphide in localized clones of algae, which can potentially influence both wind and cloud production and thereby facilitate dispersal of algal spores concentrated near the surface of water bodies). This fascinating hypothesis is not yet proven, but it points out that almost any feedback loop, from organismal activity to ecosystem process back to components of organismal fitness, could in principle have substantial evolutionary consequences. (For other examples, see Odling-Smee, Laland, & Feldman 2003.)

These ecosystem effects of evolution surely have many effects at the community level (e.g., flammability can determine the intensity and temporal pattern of fire disturbance regimes, which can influence species richness and composition), but the knock-on effects of evolved ecosystem feedbacks for community dynamics are mostly unexplored (although see, e.g., Loreau 1998 and Mazancourt, Loreau, & Abbadie 1998). Among the many challenges we face as community ecologists, understanding the coevolution of organisms and their environments may be “the most central one in understanding natural communities and ecosystems” (Lewontin, quoted in Levin 1983).

12.3 | A CAPSULE HISTORY OF THE RELATIONSHIP BETWEEN EVOLUTION AND COMMUNITY ECOLOGY

The disciplines of ecology and evolutionary biology have had intertwined histories since their inception (although the relationship has often been a nodding acquaintance rather than an intimate marriage). Charles Darwin was as great an ecologist as he was an evolutionist, and his corpus of work is imbued with a keen awareness of the concrete environmental context of evolutionary processes. The very term *struggle for existence* is an ecological concept, involving the interplay of demography (births and deaths) and constraints on population growth (e.g., resource limitation), arising from interactions among individuals and between individuals and the external environment.

A seminal work in the founding of community ecology was the monograph *Animal Ecology*, written by Charles Elton (1927) when he was only 27 years old (reprinted in 2001 with useful commentaries by the Uni-

versity of Chicago Press). This book introduced many core concepts that even today permeate community ecology, such as food webs, the niche, succession, and the interplay of community and ecosystem dynamics. Elton paid particular attention to population processes such as fluctuations in abundance and dispersal, linking community ecology with population dynamics. This book preceded the modern synthesis in evolutionary biology, yet it is sprinkled with comments about evolution, many prescient of current themes and concerns. A founding father of the discipline, Elton was certainly aware of the interplay of ecology and evolution (for examples, see Box 12-B). The first lines in the book (Preface, p. vii) are “Ecological methods may be employed in many different branches of biology. For instance . . . in the study of evolution and adaptation”. Yet Elton immediately states that “structural and other adaptations [are] . . . the final results of a number of processes in the lives of animals, summed up over thousands or millions of years. . . . [And] although of great intellectual interest and value, a knowledge of these throws curiously little light on the sort of problems which are encountered in field studies of living animals.” This assumption of a rigid decoupling of timescales is still quite common in ecology, as in the anecdote about playing cards noted previously (and indeed is the practice of much theoretical evolutionary ecology even today, as described in Chapter 13).

Box 12-B

Elton's text contains many comments that suggest the germ of potential linkages between evolutionary and ecological processes, linkages that did not emerge until much later in intellectual history. Here I provide a few examples. For instance, in Chapter 4 of *Animal Ecology*, Elton describes the sorting of species in response to limiting factors along environmental gradients. He evokes the importance of adaptation and natural selection when he notes that a scientist can “use the psychological reactions of animals as an indication of their physiological ‘abilities’” and can assume that conditions are unsuitable simply because animals avoid places where they occur, a pattern “presumably brought about by the process of natural selection acting over very long periods, since animals which chose a habitat which turned out to be unsuitable would inevitably die or fail to breed successfully. . . . By making the assumption that animals are fairly well adapted to their surround-

ings we certainly run a risk of making serious mistakes in a few cases, because owing to the lag in the operation of natural selection animals are not by any means always perfectly adapted to their surroundings. But the rule is useful in a general way" (p. 41). This is an interesting passage because it suggests that a scientist should view the habitat distributions of organisms as a reflection of adaptive responses to the environment, including behaviour. Elton's thought here presages the study of habitat selection as a key force by vertebrate community ecologists (e.g. Rosenzweig 1987, Morris 2003). The passage also shows that Elton is not a Panglossian, because he recognizes the potential for imperfect adaptation, particularly in changing environments, presaging current concerns with *ecological traps* and other ecological expressions of maladaptation.

In Chapter 5, Elton introduces the core concepts of a food web and the ecological niche (as the *role* of a species in its community). Evolutionary considerations are rather oblique, but he hints that the linkage pattern of food webs should reflect adaptive behavioural choices by consumers in that there is an "optimum size of food which is the one usually eaten, and the [upper and lower prey size] limits actually possible are not usually realized in practice" (p. 60). Chapters 8 and 9 focus on determinants of population abundance. Much of the description seems implicitly to involve group selection (viz. the notion of an "optimum" density), but there is a clear appreciation of how evolution in species' traits can influence population dynamics, as in the following passage (pp. 114–115): "the habits and other characteristics of the species . . . are continually changing during the course of evolution, and any such change is likely to cause a corresponding alteration in the optimum density of numbers. For instance, if the cats on Tristan da Cunha had possessed poison fangs like a cobra they might have been able to maintain themselves with a small population." ("The cats were introduced to eliminate rats, but the latter fought back and were sufficiently abundant to overwhelm the cats—an instance of what we now call *intraguild predation*; see Holt 1997).

The only chapter in the text squarely concerned with evolution is Chapter 12. Despite the preceding passages, it is clear that Elton felt that ecology existed as a discipline largely apart from evolutionary biology: "It may at first sight seem out of place to devote one chapter [Chapter 12] of a book on ecology to evolution." Although I find the thinking in this chapter rather unclear, it ends with two provocative assertions about the potential importance of

ecology for evolutionary biology: "Ecological studies upon animal numbers from a dynamic standpoint are a necessary basis for evolution theories, and an important result of the periodic fluctuations which occur in the numbers of animals is that the nature and degree of severity of natural selection are periodic and constantly varying." These are important insights that are still being actively developed.

Scientists must be careful not to over-interpret texts from the past, viewed through the lenses of today; nonetheless, in rereading Elton, I am struck with how, despite his initial dismissal of evolution, a conscious concern with using insights from evolution pervades his text (see Box 12-B). He points out the importance of considering traits of organisms as adaptations to their environments and how these adaptations have ecological consequences, ranging from the determination of food web structure, to influencing average abundance, to underpinning patterns of dispersal. His notion of *optimal* population size requires that selection operate on levels of organization greater than that of the individual organism (for recent thoughts along these controversial lines, see, e.g., Wilson 1997). He notes that differences among species perceived by taxonomists may not translate into differences in how those species are regulated in their distribution and abundance, a key assumption of contemporary *neutral* models of community organization (Hubbell 2001, Bell 2001).

A later important textbook by Robert Whittaker (1975) in many ways echoes the evolutionary stance taken 50 years earlier by Elton. The book is sprinkled with interesting thoughts about the adaptive underpinnings of community and ecosystem patterns and about how "diversity begets diversity" over long timescales. Much of Whittaker's thinking strikes me as either explicitly or implicitly *group-selectionist* (e.g., aspects of community organization are viewed as *super-organismal* adaptations), and there is little sense of the potential importance of rapid evolutionary change. Nonetheless, a concern with the evolutionary dimension of ecology is clear.

By contrast to Elton and Whittaker, in perusing the text by Eugene Odum (1971), for many years *the* canonical textbook of ecology, it is striking the degree to which evolution is decoupled from ecology. I suspect that this neglect of evolutionary perspectives arose because Odum and the school of ecosystem ecology he helped found emphasized holistic approaches to ecological systems (e.g., aggregate variables such as energy flows and nutrient stocks). Odum defined ecology as "the

totality or pattern of relations between organisms and their environment" (p. 3) and stated "ecology is concerned largely with system levels beyond that of the organism" (p. 4). Because most adaptations are of organisms struggling with their environments, this holistic stance automatically leads to a diminished concern with evolutionary processes.

It would not be fair to state that Odum's text ignores evolution. Odum writes that "organisms are not just slaves to the physical environment; they adapt themselves and modify the physical environment so as to reduce the limiting effects of temperature [etc.]. Such . . . compensation is particularly effective at the community level . . . but also occurs within the species. Species with wide geographical ranges almost always develop locally adapted populations . . . [with] optima and limits of tolerances adjusted to local conditions" (p. 109). The chapter on the individual level of organization considers evolution, but compared with the authoritative feel of most of the text, the material here is somewhat disjointed and perfunctory (my feeling is that this material was included more out of a sense of obligation to the student to be comprehensive rather than out of a heartfelt belief that these themes were essential to the conceptual foundations of ecology). Overall, I think it is fair to say that the role of evolution in the conceptual framework of ecology provided in Odum's text is rather muted.

The main evolutionary chapter in Odum's text (Chapter 9), titled "Development and Evolution of the Ecosystem", focuses mostly on succession. Odum says "the 'strategy' of succession as a short-term process is basically the same as the 'strategy' of long-term evolutionary development of the biosphere, namely, increased control of, or homeostasis with, the physical environment." He briefly describes how selection pressures shift during succession (from *r*- to *K*-selection). A consideration of evolution comes up explicitly in a treatment of biosphere changes over geological timescales (pp. 270–273), echoing Elton's sense that evolution mainly deals with processes over vast geological epochs. Odum concludes by noting that ecologists are intrigued by the possibility of natural selection at higher levels of organization than those of conventional neo-Darwinism (he mentions coevolution and group selection). The notion that there can be "adaptations" at these higher levels has for some decades been anathema to many biologists (following the critique of Williams 1966). However, the degree to which features of these higher levels of organization can be viewed as adaptive is still a matter of active debate (e.g., see Agrawal 2003; Leigh & Vermeij 2002; Leibold & Norberg, in press; and Leibold, Holt, & Holyoak, in press).

Much of ecosystem and community ecology over the last 50 years developed in Odum's footsteps without explicit linkage to evolutionary

biology. Allen and Hoekstra (1992), for instance, remark that although "ecosystems depend on evolved entities . . . evolution is only tenuously connected to ecosystems." In a 500-plus page monograph reviewing the literature on competition (a central theme in community ecology), Keddy (2000) touches only glancingly on evolutionary themes. A reviewer of a paper of mine (Holt 1994) once argued that knowledge of processes than provided by just knowing the set of species present and their demographic and ecosystem parameters. In his fine community ecology text, Morin (1999) only slightly refers to evolutionary issues. Many otherwise excellent undergraduate textbooks hardly consider evolution (although some do—e.g., those by Ricklefs and by Pianka). In 1987 the British Ecological Society carried out a survey of its members to compile a list of the 50 most important concepts in ecology (Cherrett 1989). Of these 50, 7 have an evolutionary flavour (#9, life history strategies; #12, ecological adaptation; #24, coevolution; #33, *r*- and *K*-selection; #34, plant–animal coevolution; #37, optimal foraging; and #40, ecotype). Yet less than a third of the respondents chose "ecological adaptation" as a key ecological concept. Phylogenetics, speciation, and other concepts related to macroevolution and macroecology are not even mentioned in the list. It would be an interesting exercise to repeat this survey today to see if this lack of connection with evolution is still the norm.

Ricklefs (2004) has provided a crisp overview of the development of community ecology, emphasizing the development of a worldview in which population processes and competitive exclusion in local communities determined patterns of species diversity. A central player in the articulation of this body of ideas was Hutchinson (e.g., see Hutchinson 1959), who formalized ideas about constraints on community membership and niche theory. These ideas stimulated work on topics such as limiting similarity and community assembly in the 1970s and 1980s. The papers collected by Hazen in a volume of readings (Hazen 1970) for students of that era encapsulated the core concerns of community ecology. In many of these papers, a consideration of evolution and genetics is absent. A notable exception is the paper by Harper (1967); although his main focus is on single-species demography, he notes the potential for genetic shifts in competition to facilitate the coexistence of competing species (as suggested by Pimentel *et al.* 1965). Reference to adaptation opponents dealing with trophic level regulation; for instance, Hairston, Smith, & Slobodkin note that the absence of obvious evolved mechanisms for interference competition among many herbivores argues for their

limitation by factors other than food availability (e.g., predation), whereas Ehrlich and Birch (1967) counter that herbivores could be limited by food because many plants are well adapted to escape herbivore effects. (It should be noted that evolutionary ecologists now recognize that there can be a decoupling of the importance of a given environmental force as a limiting factor in population dynamics and as a selective factor in evolutionary dynamics, particularly in trophic interactions; see Abrams 1986 and Holt, Hochberg, & Barfield 1999). The famous "Santa Rosalia" article by Hutchinson (1959) on the regulation of diversity explicitly invokes natural selection leading to divergence as a determinant of species coexistence (p. 146).

Hazen's collection also included several influential papers by a student of Hutchinson, Robert MacArthur, who throughout his career incorporated explicit evolutionary thinking into his ecological theories (see Box 12-C). Elsewhere (Holt 2003) I have outlined how MacArthur's perspectives on the dynamics of species' ranges included important evolutionary issues, such as the evolution of specialization and dispersal, that are still the focus of active research. The famous monograph *The Theory of Island Biogeography* (MacArthur & Wilson 1967) has a chapter devoted to evolutionary changes following colonization, including both microevolutionary shifts in traits and increases in species richness during speciation. However, it is fair to say that MacArthur tended to underemphasize both the role of history in determining present-day patterns in ecology and the potential for rapid evolution occurring at timescales commensurate with ecological dynamics.

Box 12-C

A central figure in the field of community ecology was MacArthur, who in contrast to Odum embedded evolutionary perspectives into his thinking. Even in his 1958 graduate thesis (which appeared in the Hazen (1970) collection), he used an argument based on natural selection on foraging behaviour to discount one possible mode of niche differentiation among closely related species. In his final book-length testament, *Geographical Ecology* (1972), MacArthur proposed that biogeographical patterns (including those in community structure) reflected four essential ingredients: the structure of the environment, the morphology of the species, the economics of species behaviour, and the dynamics of population change. The term *economics* indicates the importance of

natural selection and adaptation. He was writing this book the last years of his life, by which point I had come to know him.

His thinking, as expressed in conversation and class, moved readily between ecological and evolutionary perspectives. I still recall the first essay question given in his biogeography class the fall of my sophomore year (which I took despite being a physics major because I was [and still am] a keen birder, and MacArthur was the closest thing to an ornithologist on the faculty at Princeton University). We were to choose one of the following two thought experiments: what would life be like on the Earth if the day lasted 48 hours, rather than 24? or what would life be like on the Earth if it took 10 times as long to rotate around the sun? (This is from memory, so these numbers may be approximate.) What he expected were essays outlining how biomes would shift, life histories would be altered, and so on, if evolution played out on these "new worlds"; in effect, we were expected to work through the ideas in Chapter 1 of *Geographical Ecology*, "Climates on a Rotating Earth," with these new conditions and think through the biological consequences. For me, as I recall I picked the second one, which was a piece of cake. I was an amateur astronomer, so I knew Kepler's laws, which describe how there is a mathematical relationship between how long it takes a planet to go around the sun and how far the planet is from the sun. A short calculation shows that with the longer year, the earth would be far enough away from the sun that water would doubtless be frozen all year. Voilà, no life. End of essay. A very short essay.

This was not the answer MacArthur was expecting, so he had me stop by his office, where we had the first of several long conversations about ecology, evolution, and science and life in general. He ended up becoming my undergraduate advisor at Princeton in a special programme and invited me to tag along on his last lengthy field trip with other faculty and graduate students (a spring month in the splendid landscapes of southeastern Arizona). This was a wonderful experience. I recall conversations around the campfire, moving seamlessly between ecological questions (e.g., determinants of altitudinal range limits in these desert mountains) and evolutionary questions (e.g., implications of temporal variation in the desert for life history evolution). I had the good fortune of being clueless about how famous he and various of these other faculty (e.g., John Terborgh and Jared Diamond) were, and in any case I had no idea that I would ever be making a living as an ecologist, so I was not abashed about entering into this talk. I will always be

grateful for the kindness and generosity shown to me by Dr. MacArthur and these other ecologists, who perturbed me onto a new career path and led me to appreciate throughout my research and teaching career the desirability of viewing ecological systems through evolutionary lenses.

What has happened in the 30-plus years since MacArthur's death? There have certainly been several attempts made to nurture links between community ecology and evolution. For instance, a volume commemorating MacArthur's brief life brought together the thinking of MacArthur's students and friends (Cody & Diamond 1975). Several contributors dealt with explicitly evolutionary themes. Levins, for example, dealt with the effect of selection on population parameters on the stability and population abundances of interacting species in complex communities, and Rosenzweig developed the implications of viewing species diversity as emerging from the interplay of speciation and extinction rates mediated through the effect of diversity on species' range sizes. A later volume edited by Diamond and Case (1986) provided a survey of community ecology, and again several authors explicitly focused on evolutionary themes. Grant, for instance, dealt with the interplay of selection and competition in fluctuating environments; other authors considered topics such as sexual selection (Colwell), major adaptive syndromes in plant competition (Tilman and Cody), and the adaptive implications of indirect effects in multispecies communities (Wilson). The publication of a text by Roughgarden (1979), considering in detail topics at the interface of evolution and ecology (e.g., character displacement, niche evolution, and density-dependent selection) seemed to beckon the final fusion of ecology and evolution by making the needed formalism accessible to graduate students (Case 2000 updates much of this material). An outside observer might conclude that these books in the Hutchinsonian lineage marked the intellectual fusion of ecology and evolution more broadly throughout the discipline.

12.4 | WHAT DERAILED THE FUSION OF EVOLUTION AND COMMUNITY ECOLOGY?

But as noted in the previously cited quote from Webb *et al.* 2002, this fusion did not happen. In 2000 there was a joint meeting of the British

Ecological Society and the Ecological Society of America. The symposium volume produced from this meeting deals with evolution, but with the exception of brief comments by Richard Lenski (2001), the evolutionary issues considered are almost entirely at the level of individual properties (e.g., life history traits).

It is useful to reflect briefly on why the seeming inevitability of a broader unification of community ecology and evolution may have been derailed by issues both within and outside ecology. On the evolutionary side, I feel that this largely had to do with several broad intellectual and sociological currents.

First, there were numerous attacks on *adaptationism*, stimulated (frittered?) by the emergence of sociobiology in the mid-1970s (the history of critiques of adaptationist thinking is crisply summarized in Rose & Lauder 1996). If evolutionists were squabbling among themselves about whether they could even identify adaptations at the level of individual species without enormous effort (despite stout defences, particularly by behavioural ecologists, such as in Reeve & Sherman 1993 and Mitchell & Valone 1990), outsiders such as community ecologists would likely have been disinclined to view their systems in a way that highlighted the importance of adaptive mechanisms and processes.

Second, there was a reinvigoration of the field of systematics. Part of this involved a vigorous attack on the practice of evolutionary taxonomy, which, roughly speaking, combined historical information about ancestor-descendent relationships with notions about adaptive zones and niches to characterize higher taxa (Wiley 1981). This debate was decisively settled in favour of cladistic approaches, which in practice deliberately and necessarily dealt with organismal characters stripped of their environmental context and adaptive significance. Again, however, this meant that an important group of evolutionary biologists (those focused on reconstructing the history of life) to an ecologist seemed largely focused on characters that did not directly pertain to the *struggle for existence*.

Third, the explosion of molecular genetic techniques and information led to an inexorable pull of young evolutionists towards the use of molecular data and mathematical models for analyses of molecular variation, evolution, and phylogenetic reconstruction, issues on the whole well removed from phenotypic evolution and the broader ecological context of life. In the 1950s and 1960s, the field of ecological genetics focused on conspicuous polymorphisms, which could easily be related to patterns of selection from environmental causes (e.g., see Ford 1975). However, starting with protein electrophoresis in the late 1960s and continuing with the development of deoxyribonucleic acid techniques, a

staggering amount of genetic variation was revealed, so much so that it was difficult to imagine classical balancing selection arising from the environment as the primary cause (Lewontin 1974). The neutral theory of molecular evolution (Kimura 1983) proposed that patterns of genetic variation could be explained by the interplay of mutation, gene flow, and drift, with a minor role for selection. This proposal evoked a great controversy (e.g., see Gillespie 1991) and involved many issues far removed from aspects of the phenotype of interest to ecologists.

On the ecological side, I think several factors influenced the relative neglect of evolutionary perspectives in the last three decades of the twentieth century. The part of community ecology that shades into ecosystem ecology was largely dominated by the nonevolutionary stance represented by Odum's text. Beyond this, many of the associates of MacArthur who championed the evolutionary dimension of ecology also emphasized a single ecological interaction—competition—and more often assumed that the world could be viewed as at or near equilibrium. Part of the internal intellectual dynamic of community ecology in this period was an increasing appreciation of the importance of alternative interactions (e.g., predation and mutualism) and of the crucial importance of disturbance and temporal variability. There was also a sharpened concern with the need for experimental manipulations to test ecological hypotheses concurrent with a general scepticism about inferring process from pattern (Strong *et al.* 1984), leading to an increasing (and at times myopic) focus on examining processes at local scales. I wonder if with the proliferation of local mechanisms being considered, and with the emphasis on experimental tests of theory, there was not an incidental submerging of a nascent evolutionary dimension in community theory essentially because of the sociology of science; those ecologists who tended to be thinking about the evolutionary dimension of their systems (in the Elton-Hutchinson-MacArthur lineage) were being sharply criticized for other reasons (e.g., because they were proponents of competition, equilibrial reasoning, etc.), leading to a kind of submergence of evolutionary themes, which were caught in the cross fire of these academic disputes.

Be that as it may, I find it intriguing that the potential avenues suggested by Lewontin (1974) to explain the *paradox of variation* in population genetics all have strong parallels in the intellectual history of community ecology over the last several decades. He suggested three basic changes needed in evolutionary theory: an explicit focus with the concrete history of populations, a concern with non-equilibrial dynamics, and a focus on linkage and interaction among loci. In like manner, with the growth of phylogenetics, community ecologists have become

much more aware of the importance of explicitly weaving history into the study of community assembly (e.g., see Webb *et al.* 2002); disturbance and non-equilibrial dynamics are now considered the norm, rather than the exception, in natural communities, and the pattern of spatial associations of interacting species, interacting locally but dispersing in *metacommunities*, is widely recognized as an essential driver of community dynamics (Holyoak *et al.*, in press).

It is fascinating that, comparable to the neutral theory of genetic variation, a similar theory has emerged in community ecology, in which patterns of local and regional species diversity are explained in terms of speciation, immigration, and extinction, in the absence of niche differences among species—the *neutral theory* first proposed by Hal Caswell then greatly developed, in particular, by Steve Hubbell (Hubbell 2001; see also Bell 2001). This body of ideas explicitly drew inspiration from the neutral theory of molecular evolution. In a literal interpretation of neutral community theory, neither intraspecific evolution nor macroevolution matter, because all species are assumed to be competitively equivalent, regardless of their specific traits. If the neutral theory of community ecology proves to be even approximately true, this makes it more likely researchers would expect neutral evolution of within-species genetic variation (inasmuch as phenotypic differences among individuals in the same species are usually minor compared with differences among individuals of different species). The general utility of neutral theories in community ecology is a topic of considerable debate (e.g., see Leibold *et al.* 2004 and chapters in Holyoak, Leibold, & Holt, in press).

12.5 | POINTERS TO THE FUTURE

One seemingly dispiriting message that seems to emerge from the vast experimental and observational literature of community ecology is that there are relatively few commonalities among communities, viewed at very local scales. As John Lawton (2000, pp. 56–57) notes, “the local rules of engagement, both the details and many of the key drivers, appear to be different from system to system in virtually every published study in community ecology. . . . we have no means of predicting which processes will be important in which types of system. The Devil is in the contingent detail. Almost every place, time and species assemblage is sufficiently different to make general patterns and rules about local community membership and population abundances impossible to find.”

One interpretation of Lawton's remark is that community ecology has now devolved into a disorganized collection of special cases. My own sense is more optimistic. Instead of general theories (in the sense of familiar laws), we seem to have a trend towards developing structured suites of theories tailored to particular situations. Community ecology is in the position of chemistry in the nineteenth century, seeking a small number of organizing principles that can lead to a kind of "periodic table" of communities. There are several fruitful directions being developed. One promising direction is to draw on fundamental models of how organisms work as metabolic machines, extracting resources from their environments, and then to use metabolic principles to generate scaling relationships (e.g., of life history variables versus body size) (Brown & West, 2000; Allen, Brown, & Gillooly 2002). Understanding the adaptive significance of key organismal metabolic traits (e.g., of resource acquisition, stoichiometry, retention, and allocation strategies), as governed by constraints and played out in phylogenies, provides an obvious bridge between community and ecosystem ecology and evolutionary theory (Loehle & Pechmann 1988, Holt 1994).

In my own work, I have championed the utility of what I call *community modules*, which are small number of species (e.g., 3 to 10 species) linked in a specified structure of interactions (Holt 1997). Familiar modules include unbranched food chains, exploitative competition among consumers sharing a single resource, and keystone predation on competing prey. Sometimes, ecological systems closely resemble a particular module (e.g., agricultural pests with their natural enemies). Species in multispecies communities often interact strongly with just a few other species. The operational hope is that modules provide bite-size conceptual units that permit a researcher to discern key aspects of processes operating in full communities (e.g., indirect interactions or the interplay of top-down and bottom-up forces). These are rather modest goals (relative, say, to predicting diversity as a function of *niche packing* rules). Which module pertains to a particular system depends on many contingent details of that system (Holt & Lawton 1994).

Thus, instead of identifying universal laws (as in physics), maybe we community ecologists will end up with clusters of laws, tailored for particular settings, and a metalew that allows us to know which local laws apply to which situation. Several community ecologists have championed such pluralist approaches to the development of community theory. Schoener in particular, in the Case-Diamond volume noted previously sketched a kind of periodic table of communities and pointed out that MacArthur had also been clearly aware of the likely importance of pluralistic perspectives: "The future principles of the ecology of coexis-

tence will be of the form 'for organisms of type A, in environments of structure B, such and such relations will hold' . . . With different initial conditions, different things will happen . . . Initial conditions and their classification in ecology will prove to have vastly more effect on outcomes than they do in physics." (cited in Schoene 1986, p. 468) A concern with initial conditions entails an interest in history, and so leads naturally to an appreciation of the evolutionary dimension of community ecology.

A powerful set of tools provided by evolutionary biology that can be used to craft the "periodic table" of ecological communities is the explicit use of phylogenies (Webb *et al.* 2002). Phylogenetic reconstruction by its very nature permits a community ecologist in principle to identify key organismal traits shared by many species using their shared evolutionary histories. This can lead to novel insights into community assembly and organization. For instance, Webb (2000) showed that in Bornean rainforest there was a strong phylogenetic signal in the distribution of trees across space, with related species more likely to co-occur in environmental space than to be far apart. This in general accords with the growing theoretical appreciation that for species to coexist in communities, it is not enough that they differ along some niche axis; they also must be equalized in their responses to the environment among other niche axes (Holt 2001, Chesson 2000, Chase & Leibold 2003). If species are roughly equal, then even if competitive exclusion occurs, it may do so very slowly and on a timescale commensurate with within-species evolutionary dynamics and even with speciation (Hubbell 2001). A very active area in community ecology is linking the insights of neutral theory with more classical niche-based approaches (McPeck & Gomulkiewicz, in press). Phylogenetic perspectives are essential to this effort.

In the past 20 years there has been a growing appreciation of the need to understand biodiversity dynamics at large spatial and temporal scales, ranging from metapopulation and metacommunity dynamics at landscape and regional scales to macroevolutionary and palaeobiological timescales (Ricklefs & Schlüter 1993; Ricklefs 2004; Rosenzweig 1995; Brown 1995; Maurer 1999; McKinney & Drake 1998; Polis, Power, & Huxel 2004; Holyoak, Leibold, & Holt, in press). Tokeshi (1999) for instance starts his monograph on species coexistence by emphasizing the evolutionary drivers of species origination and differentiation.

The field of community ecology is in flux. As the spatial and temporal scales considered by community ecologists grow, there are many important arenas in which theoretical and empirical community ecology will be enriched when more explicitly linked to evolutionary analyses and theory. Moreover, many questions in evolutionary biology may only be fully resolved when evolutionary analyses are linked with community

perspectives. Carroll and her colleagues (2004) noted that "one of the great genetic surprises of the molecular era is the formidable collection of genes for which no obvious phenotypes have been identified" and go on to suggest that the phenotypic effects of these genes on fitness may only be revealed in natural conditions in which individuals can interact and experience ecological competition. A full understanding of the factors governing the maintenance and expression of genetic variation may thus require analysis of the community context within which species have evolved.

12.5.1 | Evolution and Ecology at

Commensurate Timescales

The timescales of evolutionary change can often be commensurate with those relevant to population and community dynamics. Ignoring evolution can lead to a serious misunderstanding of the processes governing the community, even at local spatial and temporal scales. A key question is thus: what is the role of ongoing evolutionary dynamics in population and community dynamics over short ecological timescales? Theoretical studies (e.g., Abrams 2000) suggest that permitting short-term parameter evolution (caused by evolution by natural selection) can at times qualitatively alter the nature of population dynamics and constraints on species coexistence. This recent theory formalizes David Pimentel's notion of *genetic feedback* (Pimentel *et al.* 1965, Pimentel 1968) as contributing to population stability in predator-prey systems and coexistence in competing guilds (described later).

The issue of how the maintenance of genetic variation influences stability and persistence of ecological systems is important in both single species and community dynamics. There has been a great deal of interest in how (or if) community diversity influences ecosystem stability (e.g., see Loreau, Naeem, & Inchausti 2002). A parallel question at the level of single-species population dynamics is whether the presence of genetic variation promotes population stability. In community ecology the focus is on whether genetic variation and short-term evolution influence the likelihood of stability, given potentially unstable interspecific interactions.

Similar forces may maintain diversity at different levels of biological organization (Antonovics 1976). At the community-ecosystem interface, among-species variation is maintained by mechanisms known to maintain the diversity of interacting species within communities, such as niche differentiation, food web interactions, disturbance, and spatial dynamics. At the level of individual species and small sets of interacting

species, comparable mechanisms can selectively maintain adaptive genetic variation within species. Diversifying spatial and temporal heterogeneity in selection, with gene flow, provides a potent set of mechanisms for the maintenance of genetic variation, broadly comparable to the forces that maintain diversity in communities (e.g., see Levin & Muller-Landau 2000). Broadly speaking, the stabilizing factors through which biodiversity is believed to stabilize entire ecosystems (e.g., the *insurance hypothesis* and *niche complementarity*; Yachi & Loreau 1999, Loreau 2000) should also pertain to the stabilizing influence of genetic variation on population dynamics.

Species diversity may be particularly important in maintaining ecosystem functioning in changing environments (Norberg *et al.* 2001). Similar processes can operate within species, through shifts in genetic composition, because genetic variation is required for adaptation to facilitate persistence in changed environments (Lande & Shannon 1996).

Microevolutionary processes may play a role in determining some of the most basic processes considered by community ecologists. Realized patterns of community richness reflect controls on both colonization and extinction rates. The process of community assembly involves "testing" local communities with propagules of invading species drawn from a regional species pool; community structure arises from sequences of successful invasions, failures, and extinctions of prior residents. Most ecological theory of assembly dynamics assumes that species' properties remain fixed. In the initial stages of invasion, a species will typically be rare locally and prone to extinction for that reason alone. Yet if genetic variation is present, natural selection can increase the growth rate of the population in the local environment and thus facilitate invasion. Among species with otherwise similar responses to the local environment (e.g., in resource requirements), those with more genetic variation (e.g., because of their mating system) should be more responsive to local selection and thus should be more likely to increase when rare.

The relationship between population size and extinction risk is a core concern of island biogeography (MacArthur & Wilson 1967) and related areas such as metapopulation ecology and conservation biology. What is the relative importance of purely ecological factors versus genetic and evolutionary factors in determining the extinction risks of small populations? There are numerous genetic factors that potentially enhance extinction risks in small populations, including inbreeding depression, accumulation of deleterious mutations, and the loss of adaptive potential. Newman and Pilson (1997) described an experiment with the annual plant *Clarkia pulchella* in which they manipulated the genetic effective

population size but maintained a fixed census population size. They found that lower genetic effective sizes substantially increased extinction risk. If extinction dynamics is an important determinant of community structure, then microevolutionary processes that alter extinction risk could have effects at the community level.

For instance, consider the determinants of species-area relationships. Such relationships are almost universally observed, whether the researcher is considering nested mainland samples or samples drawn from islands differing in size. However, the relationship is usually weaker for the former (e.g., as measured by the slope of a log(species) versus log(area) regression). A general explanation for this is that colonization rates are lower on islands than in similar-sized areas of the mainland (MacArthur & Wilson 1967, Rosenzweig 1995). Another explanation is that local extinction rates are similarly lower for the latter. The greater immigration rate expected within a continuous continental area both enhances recolonization of sites that have experienced extinction and makes extinction less likely in the first place. There are purely ecological reasons that enhanced immigration might reduce extinction risk (as in the *rescue effect* of Brown & Kodric-Brown 1977), but genetic mechanisms may be important as well. Immigrants can reduce the effect of local inbreeding and replenish stocks of genetic variation that can be acted on by natural selection (e.g., to deal with local edaphic conditions or temporal variability; Lande & Shannon 1996, Gomulkiewicz & Holt 1995). With recurrent immigration, evolution can draw on genetic variation available at much larger scales than just the local population, so the phenotypes of local populations can be sculpted to match local environments; this may eventually permit a species to occupy a wider range of habitats than would otherwise be possible. When these evolutionary effects are iterated across many species, researchers might expect a shallower species-area relationship to emerge (because species can be more widespread, having adapted to a wider range of environments). An open question in community ecology is thus determining the potential relative contributions of genetic and evolutionary versus ecological explanations for explaining the shallower species-area relationships observed in continental communities compared with sets of oceanic islands.

Evolution can influence interspecific interactions at short timescales. Thompson (1999), for instance, asserts that "dozens of species interactions are known to have evolved during the past 100 years." He suggests "the stability of communities may rest on the ability of species to make short-term evolutionary changes to each other." The classic example of a rapid evolutionary shift in an interspecific interaction may be the

interaction between the myxoma virus and the introduced rabbit in Australia. The virus initially had a strong effect on rabbit abundance, but because of selection towards both increased resistance in the rabbit and decreased virulence in the virus, the strength of the interaction gradually waned. In agricultural systems, genetically homogeneous monocultures can suffer devastating outbreaks of pests. This suggests that in natural systems, genetic diversity in prey and hosts may be essential in reducing the effect of any given natural enemy and may contribute to community stability.

For each model of a community module that I have described in Holt (1997), researchers can revisit issues such as coexistence, stability, and alternative states and ask how the model predictions would be modified by incorporating ongoing evolution into the model parameters, occurring at roughly the same timescale as ecological dynamics in numbers. Theoretical studies by Levin, Abrams, Hochberg, and others suggest that evolutionary dynamics can either stabilize or destabilize predator-prey or host-parasite dynamics. A microcosm experiment by Hendry and his colleagues (2000) showed that ongoing evolutionary change could contribute to the generation of predator-prey cycles. The interplay of evolutionary and population dynamics is of immense practical importance, for instance, in the control of pest species. Abrams (e.g., see Abrams 2000) in particular has championed how incorporating evolution into dynamic models of predator-prey interactions can have a major effect on the expected behaviour of the system. The specific effects of such coevolution depend on the details of how a focal predator-prey interaction is coupled with the remainder of the food web (see also Levin, Segel, & Adler 1990).

Rapid evolutionary responses within species may at times foster the maintenance of diversity within trophic levels of competing species. This is not a new idea. Pimentel (Pimentel 1968, Pimentel *et al.* 1965) explored the idea that genetic feedbacks could permit species declining because of competition nonetheless to persist in the community. The basic idea is that if a dominant species is pushing a subordinate species towards extinction, selection in the former will be dominated by intraspecific interactions, whereas selection in the latter will be increasingly dominated by the need to cope with interspecific competition as its numbers decline. This asymmetry in the target of selection could potentially permit the maintenance of species in communities. Wardle (2002, p. 205) argues that the ability of soil organisms (e.g., microbes) to adapt rapidly to changing conditions could be an important contributor to observed high levels of diversity in soil communities. It strikes me that

elucidating the influence of ongoing evolution to community stability and the maintenance of diversity is a question worth a great deal more empirical and theoretical scrutiny.

12.5.2 | Final Thoughts on the Interplay of Ecology and Evolution

Even if species' traits are relatively fixed, evolutionary perspectives can help enrich comparisons among communities. This is not a new point and, indeed, is implicit in several of the historical references noted previously. We need a new, tempered, phylogenetically sensible, adaptationist perspective to help organize the numerous contingent facts noted by Lawton (2000). Webb and his colleagues (2002) and Ricketts (2004) point out several important questions that can be addressed using phylogenetic techniques.

Over ecological time-scales, community assembly requires sampling species already present in regional species pools (MacArthur & Wilson 1967, Holt 1993, Rosenzweig 1995). Over evolutionary timescales, community assembly reflects the processes of speciation and adaptive radiation. Gillespie's (2004) study of Hawaiian spider communities reveals that the adaptive radiation of habitat associations is not random, that similar sets of *ecomorphs* arise through both dispersal and evolution, and that species diversity is maximal for communities of intermediate age. She suggests that "the similar patterns of species accumulation through evolutionary and ecological processes suggest universal principles underlie community assembly." Sorting of species along environmental gradients can permit communities to exhibit the properties of 'complex adaptive systems', with adaptive matches between the distributions of phenotypes and local environmental conditions (Leigh & Verweij 2002, Leibold, Holt, & Holyoak, in press).

The last few years have seen a resurgence of interest in the structure and dynamics of food webs (e.g., see Polis, Power, & Huxel 2004), but most of this work has to date not directly dealt with evolutionary questions. As one example of a food web attribute that may require an evolutionary explanation, consider food chain length. Pimm (1982) distinguished four basic hypotheses for why food chain length may be limited: energy flow, size and other design constraints, optimal foraging, and local dynamic constraints. More recently, other authors have proposed that ecosystem size (Post *et al.* 2000) and metacommunity dynamics (Holt 1997) could also constrain food chain length. Of this set of alternative hypotheses, two (body size and optimal foraging) are essen-

tially evolutionary in nature. As another example, consider patterns of connectance. There are purely dynamic forces that can influence connectance in food webs (Pimm 1982), but it must also be true that connectance reflects the evolutionary dynamics of trophic specialization and generalization, and coevolutionary arms races, across various trophic levels. The relative importance of evolutionary dynamics, versus ecological dynamics and constraints such as ecosystem productivity and size in determining food web attributes is an open and important question that needs much more focused work.

Moreover, whether a species' traits are fixed or not is not an absolute but depends on the structure of the environment in which species live and the traits in question. Evolutionary analyses can help sharpen our understanding of when we can reasonably assume that a species' traits are fixed for the purpose of a particular ecological analysis. A second important question is thus: when does the *absence* of evolution reflect ecological constraints?

It is clear that, at times, population dynamics may be decoupled from evolutionary dynamics. Moreover, sometimes the ecological structure of a system can preclude an important role for evolution, even though genetic variation is present. I, with Hochberg (1997), argue that in heterogeneous landscapes, a factor may be strongly limiting (in terms of its effect on distribution and abundance) without it necessarily being a strong selective factor. For instance, consider a predator-prey system with an effective predator that is nonetheless stabilized because a spatial refuge is present. Prey individuals in the refuge can breed without fear of predation and tend to stay there. If they nonetheless generate emigrants who leave the refuge, this "surplus" can stably sustain the predator. Yet because most successful reproduction occurs in the refuge, if this movement rate is low there is an automatic bias in adaptive evolution towards maintaining adaptation to this habitat at the expense of improvement in adaptation outside. Hence, a predator may effectively limit prey abundance and distribution (largely to the refuge) without simultaneously generating strong selection on the prey species to withstand predation when it is exposed outside the refuge. The effect is particularly strong when the predator-prey system is dynamically unstable (Holt, Hochberg, & Barfield 1999).

A striking phenomenon that suggests the existence of constraints on the basic ecological properties of species is *niche conservatism* (Peterson, Soberon, & Sanchez-Cordero 1999; Holt & Gaines 1992). I should note that here I am using the word *niche* in a sense that goes back to Grinnell (via Hutchinson), as a summary of the requirements a species must meet to persist in a given environment (i.e., be able to

increase when rare), rather than in Elton's sense, which has to do with the *role* of species in communities. The niche is an abstract character of a species, in effect a mapping of expected growth rate, when rare, onto an abstract environmental space (with axes of temperature, soil moisture, food levels, etc.). Niche conservatism is to be expected if species experience environmental change sharply enough (in time or across space) such that new environments are associated with high probabilities of extinction (as in the experiments on thermal tolerance in *Escherichia coli* describe by Lenski 2001). I have argued that niche conservatism can be fostered by demographic asymmetries among populations (Holt & Gaines 1992, Holt 1996, Holt & Gomulkiewicz 2004; see also Kawecki 1995, 2004). Broadly speaking, this is because niche evolution is self-referential in a way that most other character evolution is not. Consider the familiar evolutionary catechism: evolution by natural selection occurs if there is (1) variation that is (2) heritable and that (3) leads to different expected fitnesses by individuals bearing different phenotypes. But fitness is always relative to a particular environment, because it is always a joint function of the phenotype and of the environment; if we change the environment, we can often change fitness. For instance, optimal beak size may vary with fluctuations in the food supply (as occurs in Darwin's finches; Grant & Grant 1989). What defines the environment in which a researcher evaluates niche evolution? To a first approximation, it is the niche itself! Environmental states well outside the niche are those in which a species is expected to go rapidly extinct—and there is little scope for evolution in extinct populations.

There are many other issues that could be considered when contemplating the interplay of evolution and ecological interactions. Evolution depends on heritable variation, but the heritable component of genetic variation depends on the environments in which individuals live (Holt 1990, Hoffmann & Merila 1999). Natural selection is not the only force that can potentially influence community dynamics. Evolutionary forces such as mutation, gene flow, and drift can perturb species from adaptive optima or evolutionarily stable states. This may lead to predictable expectations about when to observe species with trait values far from an optimum (e.g., when local density is low, increasing the importance of drift). Gene flow can also at times facilitate adaptive evolution. Rosemary and Peter Grant (1989) have suggested that low levels of hybridization between closely related species can provide significant sources of variation for selection to respond to environmental shifts; species that are competitors over ecological timescales might be mutualists over evolutionary timescales.

A final important consideration is that the effectiveness of selection on a single character can be hampered by genetic correlations with other characters also undergoing selection. Consider a prey species in a complex food web. It may experience selection to avoid predation by a specific predator, but the evolutionary response to such selection will likely reflect the costs of evolved responses, as measured, for instance, in resource uptake rates or exposure to other predators. An important task for future work is to take the web of interactions impinging on a species, affecting its numerical dynamics (e.g., resource limitation, predation, direct interference, and tolerance to disturbance), and then to translate the interaction web into the interlinked suite of selective forces simultaneously acting upon that species. The absence of evolution may reflect the action of a multiplicity of selective forces, tugging in contradictory directions. Ackerly (2003) has suggested that interspecific interactions, in particular multiple interactions arising in a multispecies context, may provide part of the explanation for observed patterns of niche conservatism. Following a change in the environment, species sorting can permit a locally superior species to supplant a resident species much more rapidly than microevolutionary dynamics can occur in the resident. Conversely, if a species can persist across a range of environments with different adaptive optima, given enough time a researcher might expect speciation to be driven by spatial variation in selection (Doebeli & Diekmann 2003, Gavrillets 2003). Thus, the ultimate explanation for a central conundrum in evolutionary biology—the observation of *stasis* in many species over substantial spans of evolutionary history and bursts of adaptive radiation in other species (Eldredge 1989)—may in the end only be resolved by an explicit treatment of the combined effects of interspecific interactions and community assembly and sorting processes, played out across spatially and temporally heterogeneous landscapes.

12.6 | CONCLUSIONS

Thompson and his colleagues (2001) reported the musings of a National Science Foundation “white paper” committee formed to delineate major frontiers in ecology. These scientists concluded that there are four frontiers in understanding the earth's biological diversity. Two of these frontiers are as much frontiers in evolutionary biology as they are in ecology. It was argued that understanding the “dynamics of coalescence in complex communities” was a key desideratum. The term *community*

coalescence denotes the development of complex ecological communities from a regional species pool, which in turn is generated by evolutionary processes creating species and constraining their phenotypes (e.g., because of adaptive trade-offs) so as to comprise functional groups. Another important frontier is to understand "evolutionary and historical determinants of ecological processes." This led to a consideration of six distinct crucial issues that need to be addressed to develop a theory of ecology that takes into account the genetics and evolution of organisms: the phylogenetic structure of ecological processes, rapid evolution and ecological dynamics, coevolution and ecological dynamics, the spatial scales of evolutionary dynamics relative to ecological processes, genetic diversity and ecological dynamics, and the genomics of ecological dynamics.

As I have argued in this chapter, aspects of an evolutionary perspective can be found even from the earliest days of the discipline of ecology. Only recently, however, with the concordant refinement of phylogenetics and molecular technologies, has there been an appreciation of the critical importance of taking an explicit evolutionary stance when considering the core questions of community ecology. There has also been an underappreciation of the potential for rapid evolutionary change, of the need to incorporate organismal-driven change in the environment into descriptions of evolution, and finally, of the potential for ecological forces themselves to determine whether a scientist observes stasis, versus rapid evolution, in species' ecological traits. Our field is ripe for major advances at the ecology-evolution interface, and in my opinion undergraduate and graduate training, and the directives of funding agencies, should be modified to foster the long overdue intellectual coalescence of these two disciplines.

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