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Filling key gaps in population and community ecology

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We propose research to fill key gaps in the areas of population and community ecology, based on a National Science Foundation workshop identifying funding priorities for the next 5–10 years. Our vision for the near future of ecology focuses on three core areas: predicting the strength and context-dependence of species interactions across multiple scales; identifying the importance of feedbacks from individual interactions to ecosystem dynamics; and linking pattern with process to understand species coexistence. We outline a combination of theory development and explicit, realistic tests of hypotheses needed to advance population and community ecology.

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Ecology is concerned with understanding the abundance, diversity, and distribution of organisms in nature, the interactions among organisms and between organisms and their environment, and the movement and flux of energy and nutrients in the environment. Along with an understanding of the principles that shape funda-

In a nutshell:

- Ecology will become a more quantitative and predictive discipline if research is focused on how the strength of interactions between species changes with biotic or abiotic context
- Interactions among ecological entities – be they individuals, populations, or ecosystems – are almost always bidirectional, but are rarely studied as such; the explicit examination of feedbacks is critical for understanding ecological dynamics
- Theory on species diversity and species coexistence has outpaced experimentation, so empirical tests that distinguish among competing theories are needed
- The role of historical events in driving ecological patterns and processes is increasingly recognized and must be accounted for in both theory and experimentation

mental parameters, such as the organization of communities and the cycling of resources in ecosystems, the basic knowledge of ecologists should include information from other physical and environmental sciences to address today's most pressing environmental issues. In January 2006, the US National Science Foundation convened a panel to discuss the “frontiers of ecology” (www.nsf.gov/funding/pgm_summ.jsp?pims_id=12823&org=DEB&from=home) and to make recommendations for research priority areas in population and community ecology. This article summarizes the panel's recommendations.

The last such panel was convened in 1999 (Thompson *et al.* 2001), and we therefore report on recent progress and research goals for the next decade. Although we agree with many of the previous recommendations, we have chosen to highlight areas of inquiry still in need of expansion. In particular, our approach was not to redefine the field or identify “hot topics”. Instead, we stepped back to ask: what are the outstanding questions that, if answered, would substantially advance the discipline? Here, we highlight several rapidly developing conceptual areas that have the potential to reshape ecology in the near future. We have not highlighted fields such as microbial ecology or invasion biology, as these areas are already growing fast and are rightfully receiving attention in terms of funding and intensive study. Nor have we based our discussion on under-investigated systems, although we highlight some underutilized systems and approaches, which present great opportunities for understanding ecological pattern and process (WebPanel 1). Instead, we seek to highlight underexploited but potentially fruitful areas of research that, if pursued, would build upon recent conceptual advances in ecology.

At the most general level, we propose that ecologists must understand the implications and limitations of three key assumptions which, by unfortunate necessity, have often provided the implicit framework for previous ecologi-

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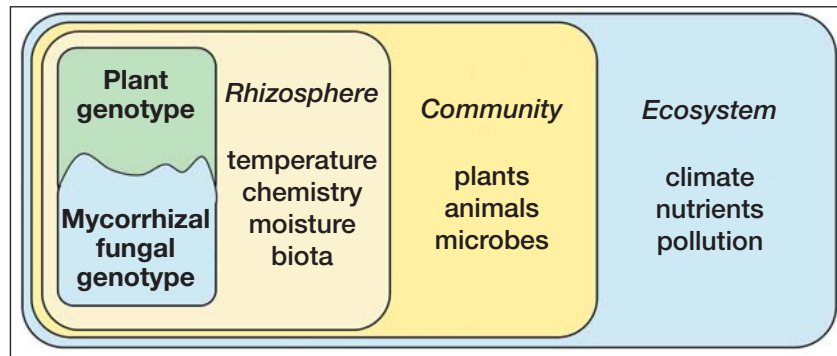


Figure 1. Context dependence almost always affects interactions among species. For example, mycorrhizal associations are a manifestation of the interaction between plant and fungal genotypes and the hierarchy of environmental factors that determine the functioning of mycorrhizas along a continuum from mutualism to parasitism. Adapted from Johnson *et al.* (1997).

cal research: (1) that the effects of multiple factors (eg competition, predation, nutrient availability) are independent of one another and are manifested in a consistent fashion across scales and contexts; (2) that the traits of interacting entities are uniform and unchanging; and (3) that feedbacks inherent to ecological interactions, scaling from individuals to communities, may be ignored without corruption of our understanding of complex interactions. Today, the number of ecologists thinking within this framework is in decline, but we have not yet relaxed these simplifying assumptions and embraced the resulting complexities in our theoretical, conceptual, and empirical models.

Below, we focus on advancing three major themes in population and community ecology: the strength and modification of species interactions across multiple scales, the importance of feedbacks within and across ecological scales, and pattern and process of species coexistence. Like Thompson *et al.* (2001), we value the role of historical and evolutionary perspectives for addressing ecological questions. However, we depart from their recommendations in important ways. Theory development in community ecology has been so rapid in the past decade that empirical data, including tests of theory, are sorely needed. A focus on organismal traits, shaped by environmental variation (plasticity), natural selection, and phylogenetic history, is a timely and key avenue of research. In the area of individual and community feedbacks, we argue that both theoretical and empirical advances are needed, as these processes may generate unanticipated outcomes. Although most of our recommendations for research lie in the realm of fundamental population and community ecology, we also consider important issues relating to emerging aspects of global change (WebPanel 2).

■ Community context and the strength of species interactions

Organisms contend with abiotic stresses, compete for resources, eat each other, and engage in mutually beneficial relationships. Historically, the principal approach in com-

munity ecology has been to evaluate how each process separately influences population dynamics or community structure. This approach has been fruitful: in the past 40 years, ecology has transitioned from the view that competition alone structures communities to a more inclusive and nuanced perspective incorporating predation, mutualism, and parasitism (Wootton 1994; Stachowicz 2001). Moreover, we now recognize the importance of conditional outcomes of interactions (Bronstein 1994), indirect effects (Wootton 1994), trait-mediated interactions (Preisser *et al.* 2005), and intraspecific genetic variation (Agrawal 2003, 2004).

Advances in this area are currently limited by a lack of knowledge on:

- how biotic and abiotic contexts shape the strength of species interactions;
- the degree to which the distribution and abundance of a given species are influenced by interspecific interactions (with the exception of predator–prey interactions);
- how biotic and/or abiotic factors interact and vary in magnitude over time or space; and
- how variation in the abundance of particular species influences variation in the abundance of the species with which they interact.

Modern population and community ecology is poised to move beyond lists of community-structuring factors to a predictive framework for where, when, and how multiple factors may work, both individually and in combination, to structure communities. Substantial progress now comes from asking not only whether particular factors have *detectable* effects on community structure, but also quantifying the magnitude of effects to ascertain their *relative* importance. Furthermore, we now recognize that both the strength and outcome of interactions can change as a function of biotic and abiotic context. For example, many studies have demonstrated a substantial influence of landscape or local conditions on species abundance and the outcomes of species interactions (eg Hebblewhite *et al.* 2005). Mycorrhizal fungi interact mutualistically with their host plants under nutrient- or moisture-poor conditions, but become parasitic in nutrient- and moisture-replete environments (Johnson *et al.* 1997; Figure 1).

Variation in experimental outcomes due to non-additive dynamics of interactors (ie emergent properties) has led to disagreement when investigators working in parallel systems reach different conclusions on the nature of interspecific interactions. Understanding how these different results can be reconciled to elucidate general ecological principles is key. Our view is that understanding context-dependency is critical for such reconciliation. For example,

classic studies in certain intertidal communities showed the primacy of local species interactions in determining community composition and diversity (Connell 1961), but similar studies in different geographic locations failed to yield the same results (Gaines and Roughgarden 1985; Figure 2). Further work showed that regional oceanographic conditions mediated this disparity: in regions where currents limited larval supply, recruitment patterns drove community composition, and species interactions were of lesser importance. In contrast, when oceanographic conditions facilitated the return of larvae to shore, recruitment was high, resources became limiting, and the importance of interspecific interactions increased (Connolly and Roughgarden 1999). We need more work that explicitly examines or manipulates environmental attributes to determine how distinct components of environmental variation contribute to changing interaction strengths across environmental gradients (eg Crain *et al.* 2004). Though not a new agenda, we still have remarkably few studies that compare the relative importance of multiple factors and estimate non-additivity among factors.

Metrics for quantifying interaction strength, or effect size, are leading to important insights into the sources of variation in community structure, although care must be taken in choosing the appropriate metric for a particular effect type (Berlow *et al.* 1999). Effect size metrics have been used to compare and summarize results of multiple studies that each measure the effect of a factor in a different community. This meta-analytic approach has been a great improvement over the “vote counting” approach of past literature reviews and, importantly, has allowed ecologists to correlate among-study variation in effect strength to non-experimental covariates that differ among communities.

While meta-analysis can generate hypotheses about the drivers of variation in the strength and outcome of interactions, multi-factorial studies can experimentally test these dynamics within communities. For instance, several recent studies have compared the individual and combined effects of predation and competition on plant and animal performance (eg Hambäck and Beckerman 2003). A related approach has been to study the influence of a single factor along an environmental gradient (eg plant–plant facilitation along gradients of abiotic stress; Callaway *et al.* 2002; Figure 3). With either approach, calculating effect sizes within multi-factor experiments provides a common currency to compare the strength of effects both within and among experiments (Berlow *et al.* 1999). Moreover, multi-factorial approaches permit rigorous and quantitative comparison of the *relative* effects of several factors in a single ecological context (site, community, environmental conditions). Finally, this approach allows us to determine whether such factors act independently or non-additive dynamics are associated with the combination of factors. Work to date indicates that non-additive effects are probably the norm, not the exception. As a result, accurately characterizing the net strength of biotic and abiotic influences within a community requires understanding not only



Figure 2. Interactions among species in the marine intertidal zone have played an important role in the conceptual development of ecology. This image shows the mid-intertidal zone of Fleming Island in Barkley Sound, British Columbia, Canada. Shown are a number of different color morphs of sea stars (*Pisaster ochraceus*), mussels (*Mytilus californianus*), and two barnacles (*Balanus glandula* on mussels and the larger *Semibalanus cariosus* attached to the rocks).

the individual factors, but also the emergent properties of those factors in combination. Such interactive effects also lead to non-linear dynamics, an area currently undergoing important theoretical development. Yet to date, most experimental manipulations employ only exclusion and control treatments; understanding how multiple non-additive factors structure ecological communities requires quantifying interaction strengths at multiple (ie three or preferably more) species densities concentrated within the natural range of variation (Abrams 2001).

In our view, a necessary step forward is a more explicit consideration of mutualisms, and formal comparisons of the relative importance of mutualism and negative interactions (eg competition, predation, pathogens) in structuring ecological communities. Although mutualisms are receiving increasing attention in ecology, the impacts of such “positive interactions” on community structure and function have not been well integrated with general theory (but see Bruno *et al.* [2003]), and empirical tests and further development of theory are needed.

Although experimental approaches will always be

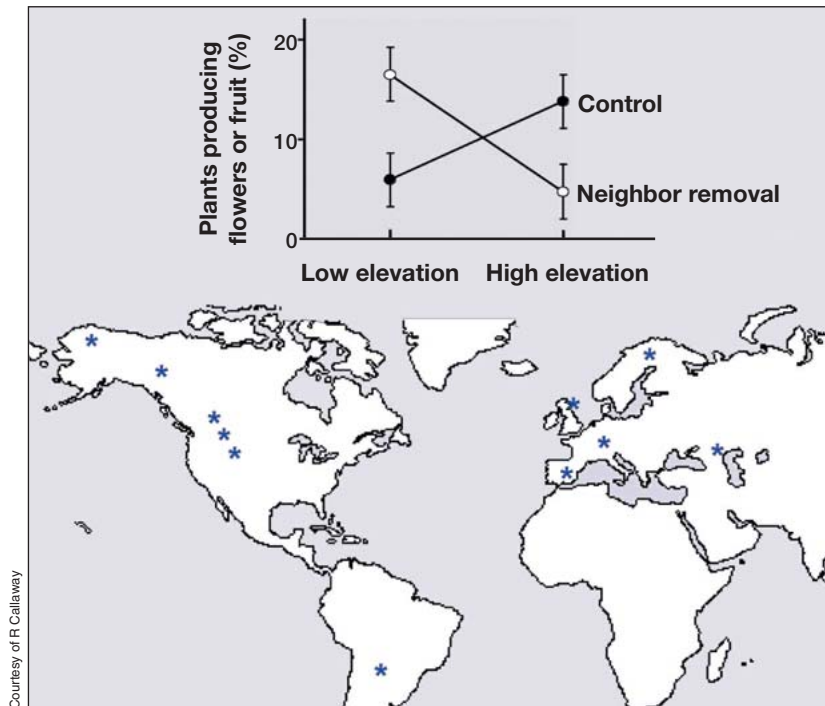


Figure 3. Using environmental gradients to understand variation in the outcomes of interspecific interactions: plant–plant interactions vary predictably along a gradient of environmental harshness. Working in 11 study sites (asterisks), Callaway *et al.* (2002) demonstrated that, at low elevations, competition is the main structuring force in communities of plants (ie removal of plant neighbors caused focal plants to increase flowering or fruiting), while facilitation supplants competition in this role at higher elevations (ie removal of plant neighbors diminished flowering and fruiting in focal plants).

required to demonstrate mechanisms underlying ecological phenomena, observational studies complement and expand on what can reasonably be studied in an experimental context. Techniques such as structural equation modeling (eg path analysis) can generate testable hypotheses about such mechanisms. In addition, where mechanisms are unknown, path analysis can reliably deconstruct net effects into component parts with ascribed magnitudes. For example, path analyses have been used to evaluate the relative importance of seed predators and pollinators on plant fitness and floral characteristics (Cariveau *et al.* 2004). The use of path analysis in combination with experimental manipulations can provide non-intuitive insights into the functional relationships between species interactions, environmental variation, and outcomes.

Finally, a novel, trait-based approach provides a means to mechanistically link the phenotypes of organisms to the outcomes of interactions. Two perspectives are valuable here. First, comparative approaches informed by phylogeny offer a powerful tool for understanding the role of particular traits in ecological interactions (eg Cavender-Bares *et al.* 2004a). Second, many species' traits are phenotypically plastic (ie expression of the trait is dependent on the biotic and abiotic environment; Agrawal 2001). Such plasticity may have strong impacts on community interactions, independent of differences in the density of

organisms. For example, a remarkably large portion (often >50%) of the indirect effects that occur between predators, prey, and plants reflect the effects that predators have on the behavior of prey (eg feeding rates, hiding behavior, emigration) rather than direct reductions in prey density (Preisser *et al.* 2005). Predator-mediated effects on prey behavior are an illustration of a much broader process, in which responses of phenotypic traits to the environment change the context of interactions among species, quantitatively altering population dynamics, interaction strengths, and community outcomes.

In sum, addressing classic questions about the organization of communities and the role of interspecific interactions has the potential to lead researchers to a new level of predictability in ecology. This goal should be achievable through well-designed experiments coupled with observational work in various ecological contexts.

■ Feedbacks across multiple ecological scales

The dynamic nature of most ecological processes means that feedback often occurs between factors that are typically considered independent. Predator–prey population cycles, perhaps the classic example of an ecological feedback, have received considerable theoretical and empirical attention. Likewise, the study of coevolution, the reciprocal evolutionary change that occurs in interacting populations, has addressed feedbacks in an evolutionary framework. In contrast, feedbacks between interacting individuals (in their behavior or phenotypes) and community dynamics have received comparatively little attention.

Advances in this area are currently constrained by a limited understanding of:

- how reciprocal interactions mediated by behavior or phenotypic plasticity shape community and population dynamics, stability, and structure;
- the scale dependence of feedbacks between community interactions and environmental conditions;
- the mechanisms driving the relationship between species diversity within communities and genetic diversity within populations; and
- when it is necessary to consider evolution within communities.

Most organisms exhibit phenotypic plasticity, and it is almost certain that feedbacks of reciprocal, plastic responses are common among interacting species. For example, herbivore damage frequently induces defensive responses in plants, which reduce the performance of sub-

sequent herbivores (Karban and Baldwin 1997). In turn, consumption of plant secondary compounds can induce herbivore detoxification enzymes that increase herbivore performance (Krieger *et al.* 1971). Though typically studied as a one-way interaction, reciprocity may often result in escalating (or at least changing) phenotypes. Similar feedbacks are also likely to occur between positively interacting species, such as ants and aphids, or ants and lycaenid caterpillars, which dynamically adjust their investment in mutualistic interactions (Axen and Pierce 1998; Yao and Akimoto 2002). Phenotypic feedbacks may be (1) a primary determinant of an organism's phenotype in nature; (2) an ecological signature of coevolution; and/or (3) a stabilizing factor that prevents runaway exploitation (Agrawal 2001). A critical question that remains unanswered is: what is the strength and ubiquity of these reciprocal effects? There is currently no theoretical framework addressing how reciprocal interactions that influence phenotypes may affect coevolutionary dynamics or community structure.

Despite their absence from theory, there is growing appreciation for the potential of reciprocal effects to influence important community attributes. Feedbacks between plants and soil microbes have been implicated in maintaining community structure and coexistence of plant species (Klironomos 2002). A key frontier of biodiversity research in community ecology is identifying the feedbacks among the environment, biodiversity, and species interactions. Separate research programs have provided strong support for the unidirectional linkages among these three areas (ie productivity drives species diversity, diversity in turn affects productivity). More generally, we know that the composition of a community can affect characteristics of the environment and that the environment can affect species interactions, but we have a poor understanding of the mechanistic linkage, especially at larger landscape scales (eg Pastor *et al.* 1998; Figure 4). Is one direction of the feedback loop stronger than the other? Are these processes scale-dependent? Are there "equilibrium" states? At what time scales do feedbacks operate? Similarly, the trophic composition of a community can have strong impacts on prey diversity, and prey or resource diversity can, in turn, shape predator impacts. The feedback among diversity, consumer effects, and ecosystem level dynamics remains largely unexplored (Downing and Leibold 2002), but deserves greater attention. We predict that many classically studied, one-way

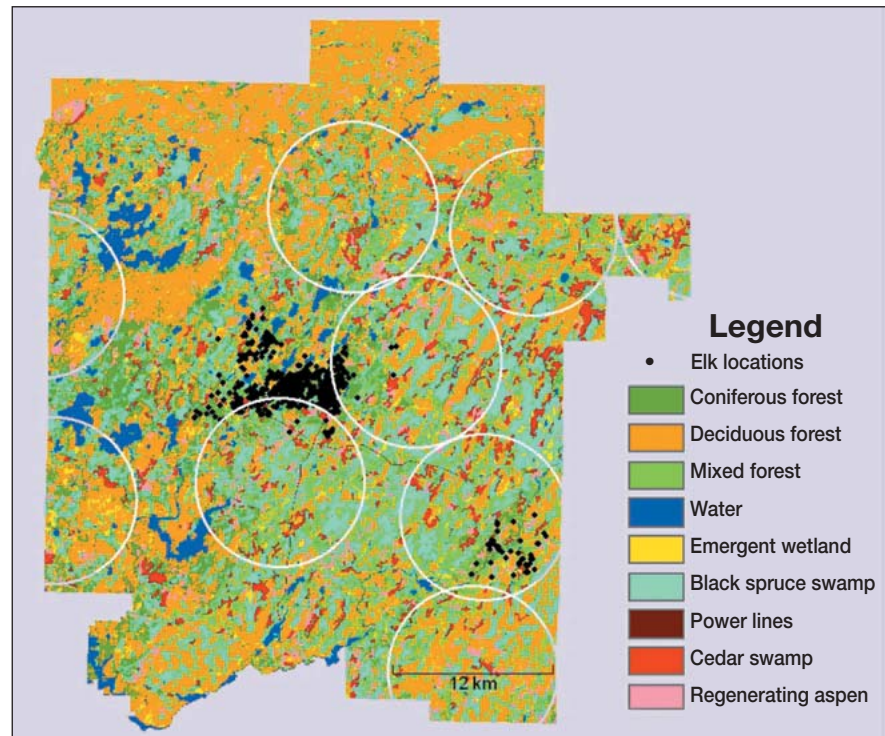


Figure 4. Reciprocal interactions (ie ecological feedbacks) are ubiquitous but rarely studied. For example, a tri-trophic feedback is likely at the landscape scale among habitat selection by wolves and elk and vegetational production. Elk (black dots) selected areas with lower predation risk (by wolves; territories shown by white circles) and more forage in the Great Divide District of Chequamegon National Forest, WI. Thus, habitat selection by elk results in their spatial concentration and may reciprocally shape predator and vegetation dynamics (Anderson *et al.* 2005)

interactions (eg impacts of biodiversity on ecosystem function) will be overshadowed by the reciprocal effects (eg ecosystem properties drive biodiversity), at least at some scales. Theory and experiments are needed to address these questions.

Understanding the feedbacks between community diversity and genetic diversity within species is also a novel area of recent inquiry (Vellend and Geber 2005). Theoretical work predicted that species diversity within communities and genetic diversity within populations would positively covary. Biotically rich communities, for example, may exert conflicting selection on traits of component species and thereby maintain genetic diversity (Strauss and Irwin 2004), and/or promote stabilizing selection. In recent studies manipulating genetic diversity of plant species, but not species diversity, resulting species diversity was highest in study plots with the greatest intraspecific genetic diversity (Booth and Grime 2003). Similarly, genetic diversity speeds the recovery of eelgrass communities after grazing by geese (Hughes and Stachowicz 2004). Genetically diverse plant communities also support greater arthropod biodiversity, and this can reciprocally affect plant fitness (Johnson *et al.* 2006). From these and other studies, it appears that intraspecific variation within a species may play an important role in shaping community structure and diversity.



Figure 5. Multiple factors allow for the coexistence of species. For example, three aphid species coexist on the same host plant, *Asclepias syriaca* (and on the same resource from that plant, phloem sap): (a) *Aphis asclepiadis*, (b) *A. nerii*, and (c) *Myzocallis asclepiadis*. Each species has distinct demographic rates, interactions with other species (only *A. asclepiadis* has a mutualistic relationship with ants), and tendencies to disperse, which may contribute to their ability to coexist.

More generally, models that incorporate the evolution of one or more players in a food web often predict dramatically different outcomes from models that consider only ecological interactions among species with fixed traits (eg Loeuille and Loreau 2005). Feedbacks among species interactions, genetic change, and community structure are an important reality for all communities. These dynamics may occur much more rapidly than previously believed, in part because of non-equilibrium conditions. Although definitive experiments that demonstrate the importance of evolution for population and community structure may be limited to laboratory microcosms (eg Yoshida *et al.* 2003), a combination of field experiments, modeling, and comparative work could provide a strong test of these ideas.

■ Mechanisms of species coexistence

The related challenges of understanding species diversity and coexistence lie at the heart of community ecology. At issue is what determines the number of coexisting species within a community and what, if anything, prevents competitive exclusion and thus allows those species to coexist.

Advances in this area are currently limited by a lack of:

- linkages between theory on how multiple effects generate coexistence and ways in which different mechanisms can be tested empirically;
- empirical data at appropriate spatial and temporal scales to test theoretical predictions of species coexistence;
- phylogenetic data in studies of coexistence; and
- evolutionary approaches to ecological mechanisms of community assembly and maintenance.

Recent and rapid advances in coexistence theory have fundamentally changed the questions that must be addressed in this area. Historically, the question has been phrased in terms of the external factors or niche differences among species that might be large enough to allow coexistence (Figure 5). Recent theoretical findings have

counterintuitively suggested that similar species may coexist more easily than ones with greater niche differences, and that a multitude of external factors are each sufficiently powerful to generate coexistence (Chesson 2000; Hubbell 2001; Chave 2004). One of the most useful distinctions is between processes that promote equality in mean population fitness across species (“equalizing forces”) versus those that lead to positive population growth rates when species are rare (“stabilizing forces”; Chesson 2000; WebPanel 3).

Explicit empirical tests of the predictions and assumptions of competing coexistence theories will be critical in evaluating mechanisms underlying invasion, persistence of rare species, and, generally, the maintenance and determinants of diversity in communities. Three priorities follow closely from the theoretical issues outlined above. First is the design of field studies that can be used to test multiple coexistence mechanisms in the same community and that enable a ranking or quantification of their relative importance. Second is the need for the careful treatment of spatial scale and dispersal dynamics in investigations of the maintenance of coexisting species. Many of the mechanisms thought to be important for the coexistence of species rely on spatial effects, including aggregation due to limited dispersal abilities or habitat heterogeneity (Ives and May 1985; Chesson 2000; Hubbell 2001); designing field studies that can estimate the processes driving these spatial effects presents a major challenge. Third is the need for studies that measure dynamics or even community patterns over the lengthy time scales most relevant to many coexistence theories. For example, paleoecological analysis of small mammal communities in North America demonstrates greater temporal stability of community structure than can be plausibly predicted based on a neutral model of ecological drift (McGill *et al.* 2005). A related issue is reconciling the time scales at which stable coexistence may occur with the time scales of community assembly and disassembly due to climatic and geological change.

Phylogenetic approaches to community ecology show particular promise because they have the potential to integrate the evolutionary history of the regional species pool with local analyses testing for non-random processes of community assembly (Webb *et al.* 2002; Figure 6).

Since Darwin, it has been argued that individuals of closely related species will be phenotypically and ecologically similar and, as a result, will compete more strongly. The co-occurrence of distant relatives may thus provide evidence for the role of competition and/or ecological differentiation in the assembly of communities. Recent studies within relatively narrow clades suggest that co-occurrence of distant species may be prevalent (eg species of oaks; Cavender-Bares *et al.* 2004a,b). In contrast, studies of co-occurrence in more divergent groups find the opposite. For example, a recent study of California grasslands showed that exotic species distantly related to plants in the invaded community were more invasive and ecologically harmful than were exotics more closely related to plants in the invaded community (Strauss *et al.* 2006). At larger phylogenetic scales, related species appear to cluster by habitat, reflecting shared environmental tolerances (Webb *et al.* 2002). Studies are needed across a range of ecological and phylogenetic scales to permit a broad, quantitative synthesis of these contrasting patterns. Additionally, further experimental studies are needed to formally test the prediction that close relatives compete more intensely or share similar susceptibility to pathogens and predators. Experimental community studies using assemblages with more or less closely related species would be valuable to directly test these ideas, although it will be important and challenging to experimentally separate phylogenetic and functional diversity (WebPanel 4).

■ Conclusions

Filling the gaps in knowledge outlined here will require a diversity of approaches. This pursuit includes testing and enhancing the reality of existing theory, developing new theory, and working out new and creative ways to combine experimental work with observational studies or comparative analyses. Where possible, it will require increasingly sophisticated experiments that shed light on the relative importance of multiple and potentially interacting effects. Finally, quantitative experimental designs (in place of traditional qualitative presence/absence studies) may be particularly useful, because this can reveal the influence of natural variation in abundance of particular species. While these conclusions may seem to imply simply that more research is needed, we argue that the time is right not for

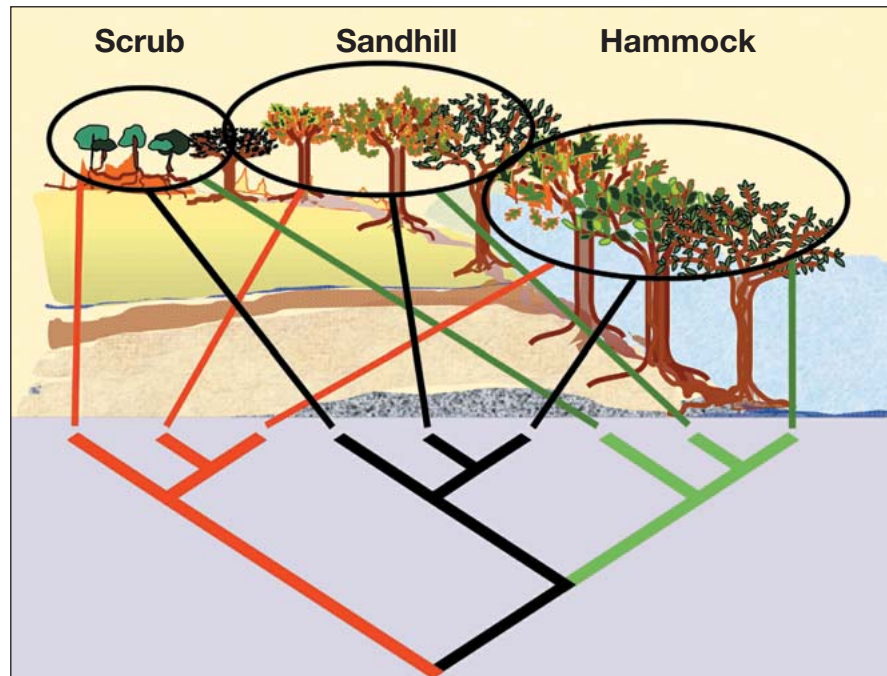


Figure 6. Using knowledge of evolutionary history to understand community assembly. This figure presents a schematic of phylogenetic overdispersion (phenomenon of co-occurring species being less related to each other than expected by chance) in three major oak-dominated communities in Florida (adapted from Cavender-Bares *et al.* 2004 a,b). Oaks within each of the major phylogenetic lineages occur in each community (with respective physiological traits apparently matched to each environment), indicating convergent evolution. The alternative pattern of co-occurring species being closely related (ie phylogenetic clustering) can be generated when the environment filters species based on traits shared among close relatives.

more research across the board, but for a greater integration of disciplines, individual studies, and research directions to produce an emergent field of ecology.

We have highlighted the importance of ecological context and individual phenotypes in shaping the outcome of interactions, and suggest that these factors may lie at the heart of accurately predicting effects on communities. Trait-based approaches that focus on trait variation generated by phenotypic plasticity, genetic variation, and evolutionary divergence among species show particular promise, especially if linked to studies examining their role in propagating indirect effects through communities. Finally, feedbacks, though long-recognized, require greater integration into the mainstream ecology of individual and community interactions.

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WebPanel 1. Understudied systems and underutilized approaches in ecology

The fundamental questions in ecology apply to all populations, communities, and ecosystems. Traditionally, ecologists have focused on systems that are accessible in a variety of ways, and on organisms that are easy to reach, view, and identify. We encourage additional work on the following systems and approaches.

The semi-natural matrix. Ecological studies often investigate pristine systems, but many organisms now persist in the fringes of habitat around highly disturbed areas (Brauer and Geber 2002). Although much work has been conducted in some of these areas (eg eastern North American old-fields, much of Europe) and despite a growing interest in urban ecology, the semi-natural matrix is still mainly unexplored, its ubiquity notwithstanding.

Scavengers and decomposers. These organisms recycle nutrients from all trophic levels, yet we are just beginning to understand their population and community dynamics (Allison 2006).

Pathogens, with a particular focus on viruses, fungi, and nematodes. Although microbial ecology, with a focus on bacteria, is an expanding area in both population and community ecology, less attention has been paid to some of the more cryptic groups, such as viruses, fungi, and nematodes (Arnold *et al.* 2003; Forde *et al.* 2004; Cattadori *et al.* 2005; Ezenwa *et al.* 2006). The roles of these organisms shift easily among pathogen, commensal, and mutualist, providing opportunities to investigate variation and changes in ecological roles and the interplay of evolution with ecology.

Chemical ecology. Although the study of chemical mediation of interactions among species has been one of the core areas of ecology, technological advances and interest in a broader group of taxa, beyond plants and chewing herbivores, opens additional questions. Furthermore, hormonal and biochemical data can be used to gain insight into the interactions of individuals with one another and with their environment. Predictive theory from biochemists has yet to be tested in ecologically realistic settings (Mopper and Agrawal 2004).

Ecological stoichiometry. Understanding the relative chemical needs and composition of species may provide a key link between population/community ecology and ecosystem science. Nutrient ratios and dynamics have moved well beyond measures of carbon, nitrogen, and phosphorus in predicting ecological outcomes. In particular, recent hypotheses about stoichiometric relationships, diet breadth, and trophic structure are important areas of conceptual and empirical development (Elser *et al.* 2000; Fagan *et al.* 2002).

Geographic range limits. The spatial distribution of a species is set by a combination of abiotic and biotic factors that represent adaptive limits. Constraints on range expansion include limited genetic variation, tradeoffs in performance across habitats, and gene flow that swamps local adaptation. Theoretical models to explain the limits of geographic ranges have received inadequate empirical investigation. Given the expected importance of climate change, an understanding of the ecological and evolutionary determinants of species' ranges is a critical issue in landscape ecology and conservation biology.

Merging paleo- and neocological perspectives. Although paleoecological insights into the composition of past (especially plant) communities have contributed to theory in community ecology, a synthesis of paleo- and neocological perspectives is needed to better understand how modern dynamics may be linked to both recent and distant ecological history. For example, such a synthesis may help to explain how neocological dynamics in North America may be shaped by the loss of Holocene megafauna. Does community composition converge or diverge through time? How different are past and present biotic assemblages? More broadly, such space–time linkages could be important for predicting responses to climate change.

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WebPanel 2. Applying ecology to global change frontiers

In an era of unprecedented environmental change, ecologists are seeking to understand the effects of global change on populations, communities, and ecosystems, and to provide the means by which ecological principles can be applied to mitigate the consequences of global change. Below we outline a few of the emerging areas.

Distribution-wide dynamics. A wealth of studies have examined the role of climatic variability and associated changes in population dynamics of species. Nonetheless, projections of the impacts of climate change on species (rather than on individual populations of species) remain rare in the absence of distribution-wide analyses. Our understanding of the effects of climate and landscape, natural enemies, and conspecifics on species' responses to climate change can be improved through analyses that incorporate populations of focal species throughout their distributions, with a particular focus on the edge of species' range. Analysis of population dynamics of species throughout their distributions has the potential to reveal population "hot-" and "cold-spots" in species' responses to climate change (Post 2005).

Extreme events. The frequency of extreme climatic events, including hurricanes, floods, and droughts, is expected to increase as a function of global climate change. The role of such extreme events in population dynamics and community structure, and in disease outbreaks and dynamics, is not well understood. Advances in climate change modeling allow the frequency and location of these events to be predicted more accurately. Extreme events represent substantial ecological perturbations that can result in switches among ecological equilibria, leading to the loss of species, changes in species abundance, and alteration of fundamental biogeochemical processes. More cryptic effects are likely to be important and require attention, such as the potential of extreme events to bring spatially structured populations into synchrony, increasing the likelihood of extinction and outbreaks of pests and epidemics (Cattadori *et al.* 2005). How resilient are communities to extreme events? How quickly do species and communities respond, how long do they take to recover, and what form can recovery take in the context of anthropogenic change (Spiller *et al.* 1998)?

Several approaches are needed to assess the consequences of extreme events: small-scale experiments to identify processes, large-scale experimental manipulations to determine if these processes scale up, and modeling of non-linear processes that identifies thresholds in how systems respond to these events. Some insight into these issues could be obtained by an examination of paleoecological records that reveal the consequences of past large-scale events (Davis and Shaw 2001).

Species deletions. With increasing rates of habitat destruction and modification, changes in global climate, and localized human activity such as illegal poaching, communities throughout the world face accelerating losses of native species. A central challenge is to understand how these species deletions influence the structure and function of the communities and ecosystems in which they are embedded. While our understanding of how reductions in plant diversity influence invasibility and production at small scales is growing (Elton 1958; Loreau *et al.* 2001; Hooper *et al.* 2005), we lack insight into the impact of species loss on diverse ecosystems with complex food webs, where species loss is of greatest concern. Local or global extinctions are usually non-random and, often, large-bodied predators and mutualists are at greatest risk (Peres 2000). In turn, the fate of microbial symbionts is poorly understood, reflecting a dearth of knowledge regarding these and other cryptic organisms. We lack insight into how loss of these potentially influential species may impact the systems from which they are removed. Theory concerning the relationship between diversity and stability is contradictory (McCann 2000) and poorly tested, especially in complex natural systems. Central to understanding the ecological importance of species losses in complex food webs is determining whether functional redundancy buffers systems from the negative impacts of these losses. There is often substantial overlap in the prey, pollen, or seeds utilized within generalist predator, pollinator, or disperser guilds. Can species that are "functionally redundant" compensate for the loss of functionally similar species? Is there always a relationship between diversity and functional redundancy in complex systems?

Emerging diseases. Climate disruption may well have an important influence on the emergence of new diseases for humans and wildlife. As temperatures increase, simple degree-day models predict linear effects on the development time of free-living parasites and vectors; however, some studies indicate that there may be rapid non-linear increases in disease exposure. Climate disruption may also influence minimum and maximum temperatures and cloud formation in some systems, a pattern suspected of having precipitated disease outbreaks that are driving widespread amphibian extinctions in Central America (Pounds *et al.* 2006). In several well-documented cases, geographic ranges of vector organisms are expanding, and changes in climate are allowing diseases to invade areas not previously colonized (eg West Nile virus). The causal relationship of global change to disease emergence requires further study.

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WebPanel 3. Theoretical issues in species coexistence research

In species coexistence theory, some processes are thought to promote equality in mean population fitness across species (“equalizing forces”), while others lead to positive population growth rates when species are rare (“stabilizing forces”; Chesson 2000). Neutral theories of community structure (Caswell 1976; Bell 2000; Hubbell 2001) provide some of the best models for investigating equalizing forces. These explanations of coexistence assume demographic equivalence at the individual level (ie equal probability of mortality and offspring establishment), reducing any deterministic trend toward competitive exclusion, and thus increasing the average time to local extinction. However, non-neutral models of coexistence can also be “equalizing” by generating demographic equivalence when no population is increasing or decreasing (Chave 2004). In this case, demographic equivalence may arise due to specialization for alternative habitats in a heterogeneous landscape, or due to interactions among distinct combinations of physiological traits (Marks and Lechowicz 2006). Thus, the fact that species differ in physiological and functional traits that might promote specialization or differentiation in resource use is not in itself a refutation of the importance of equalizing forces in promoting coexistence. In this vein, we predict that studies that connect functional traits to fitness, and ultimately demography, will be particularly helpful in distinguishing between these two broad models of coexistence.

Stabilizing forces promote coexistence among species by niche differentiation, temporal and spatial storage effects (Warner and Chesson 1985), aggregation effects (Ives and May 1985), enemy escape (Janzen 1970), and density-dependent mechanisms (eg Lotka-Volterra criteria for intra- versus interspecific competitive effects and predator switching behavior that targets common prey). Trade-offs between life-history attributes, such as competitive ability and dispersal, can also promote co-existence. These and many other stochastic and deterministic mechanisms tend to favor uncommon species and hence stabilize community composition by depressing the risks of local or global extinction. Importantly, equalizing and stabilizing forces closely interact. Chesson’s theory, in particular, demonstrates that similar species (in terms of average demographic performance) are able to coexist with only very weak stabilizing forces. Our recent understanding of this interplay emphasizes that surprisingly subtle species differences may be sufficient to maintain diversity.

With many mechanisms capable of maintaining diversity in communities, the most striking aspect of current coexistence theory is its complexity and its disconnectedness from data and from clear criteria for testing alternative mechanisms (Chave 2004). This is intended not as a criticism of the burgeoning theoretical developments, but as a comment on what is needed next. In terms of theory, three priorities are especially evident. First, and most striking, is the need for coexistence models to simultaneously consider temporal and spatial heterogeneity; for example, models of the storage effect, with its emphasis on temporal fluctuations, have not been brought into the parallel framework that considers spatial heterogeneity and aggregation (Ives and May 1985). Recent work by Snyder and Chesson (2004) merges several spatial mechanisms into a single framework and thus sets the stage for a synthetic theory that may allow quantitative comparisons of the importance of spatial and temporal heterogeneity in promoting coexistence. Second, the field of coexistence theory has increasingly moved from consideration of whole communities, including not only a single guild of potential competitors, but also their consumers and mutualists. Earlier, and more testable, whole-community and multi-trophic theories of coexistence (eg Paine 1966) need to be brought back into the fold of ideas considered in coexistence studies. Finally, criteria from theory are needed with which to clearly compare, contrast, and synthesize the results of empirical coexistence studies. Similar patterns of species abundance can arise from very different processes, undermining their use in discriminating among competing theories. Theoretical and empirical examination of coexistence based on increase from very low numbers (ie invasion criteria) may have greater potential to generate direct tests of different coexistence mechanisms than do theories focused on static patterns in abundance (eg Wills et al. 2006). Such theories may also shed light on the role of rare species in community function, an area that has received relatively little attention.

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WebPanel 4. Phylogenetic diversity: from clades to landscapes

The evolutionary relationships among coexisting species are encapsulated in phylogenies. Using modern phylogenetic methods, comparative biology provides a useful toolbox for ecologists, assisting in the diagnosis of conservation priorities, the interpretation of community structure and function, and the measurement of biodiversity at multiple scales. Rapid development of molecular tools, which allow diagnosis of taxonomic units when phenotypic characters are lacking or misleading, coupled with an increased use of phylogenetic tools in evolutionary ecology (Webb et al. 2002), has led to the increased use of phylogenetic diversity measures as a complementary approach to traditional measures of species richness and diversity (Vanewright et al. 1991; Faith 1992). As originally described, phylogenetic diversity represents the sum of pairwise distances between taxa on a phylogenetic tree (Faith 1992). Simply stated, the distance between two taxa (*a* and *b*) is represented by the sum of the lengths of the branches on the path between them, given branch lengths that are proportional to elapsed time since the most recent common ancestor or cumulative evolutionary change.

Phylogenetic diversity (PD) measures offer two advantages over traditional approaches: (1) they take into account the phylogenetic distance among organisms present in a sample, and thus provide an indication of the genetic diversity (or disparity) among taxa; and (2) they do not rely on species definitions (or the designation of other taxonomic units). The utility of PD is illustrated by the example of two communities, each with equal species richness, that differ dramatically in the taxonomic relatedness within each species pool. Ecologists using standard measures of diversity would consider the two communities to be equally diverse, overlooking the contribution of ancient lineages, species-poor clades, or genetic disparity in making one community more diverse than the other. In this way, PD has been used to inform ecologists about the “biodiversity value” of particular geographic regions, as well as focal lineages in the tree of life: bryophytes (Shaw and Cox 2005), bumblebees (Vanewright et al. 1991), crested newts (Faith 1992), carnivores and primates (Sechrest et al. 2002), and fungal symbionts (Arnold et al. in press). In turn, the “species-free” approach of PD enables ecologists to avoid ongoing debates regarding species concepts and the objective reality of species while drawing meaningful conclusions about diversity. Especially in microbial ecology, PD provides an indispensable method for measuring diversity of uncultured microorganisms known only by their genotypes, cultured microbes that lack sufficient phenotypic characters to distinguish species using traditional methods, or assemblages of microbes that have been integrated into phylogenetic trees, but for which species concepts remain arbitrary (Arnold et al. in press).

While phylogenetic diversity measures have provided an important tool in conservation biology and are increasingly used in community and evolutionary ecology (Webb et al. 2002), these measures are imperfect. In particular, ecologists need methods to effectively quantify diversity without relying on potentially faulty inferences due to (1) poorly resolved phylogenies, (2) phylogenies that reflect systematic error due to incongruence between gene trees and the evolutionary history of the organisms that carry those genes, (3) limited taxon sampling, which may lead to inaccurate measures of pairwise distances; and (4) inconsistency in branch lengths among clades, reflecting differential rates of evolution due to intrinsic or ecological factors. Furthermore, phylogenetic placement may not provide the desired framework for reconstructing functional roles; convergent evolution and horizontal gene transfer can obscure the relationship between phylogenetic distance and ecological similarity. Finally, the relationships between models of phenotypic evolution and phylogenetic biology need to be clearly defined (Alexandre 2004). Thus, caution is needed when using PD measures. Novel measures of diversity need to be developed and should be compared to both PD and traditional indices.

Even with these limitations, PD is likely to play an important role at the frontiers of ecology. Understanding the phylogenetic diversity of microbial communities has already brought about a paradigm shift in the study of biodiversity and in our understanding of cryptic ecological processes (Arnold et al. in press). The development of methods associated with PD will build much-needed bridges between ecology, systematics, bioinformatics, and genomics, providing new insights into ecological metagenomes, nonrandom processes of extinction, and the ecological processes associated with diversification. One of many potential roles of PD lies in understanding the causal relationship between biodiversity and ecosystem processes: a transition from species diversity to phylogenetic diversity may inform debates regarding the functional equivalence and “redundancy” of the units of biodiversity.

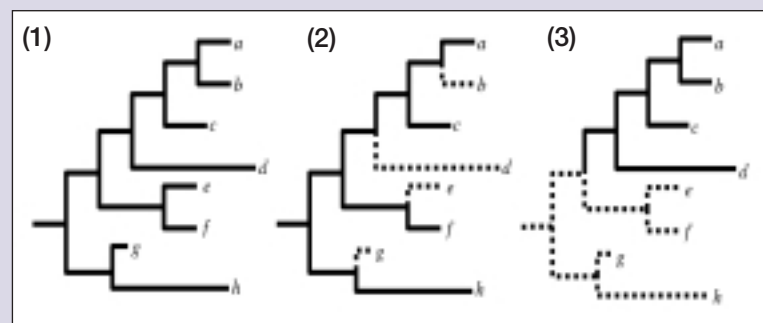


Figure 1. Phylogenetic diversity of communities. (1) Hypothetical phylogenetic tree for organisms *a* through *h*, drawn with representative branch lengths. (2) Hypothetical tree for organisms at site X, with organisms that are present indicated by solid branches, and organisms that are absent indicated by dashed branches. (3) Hypothetical tree for organisms at site Y. Phylogenetic diversity is calculated as the sum of the minimum total length of all phylogenetic branches needed to span a set of taxa on the tree (Faith 1992). In this simple example, although site X and site Y have equal species richness, site X has a markedly greater phylogenetic diversity.

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