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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-

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-

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

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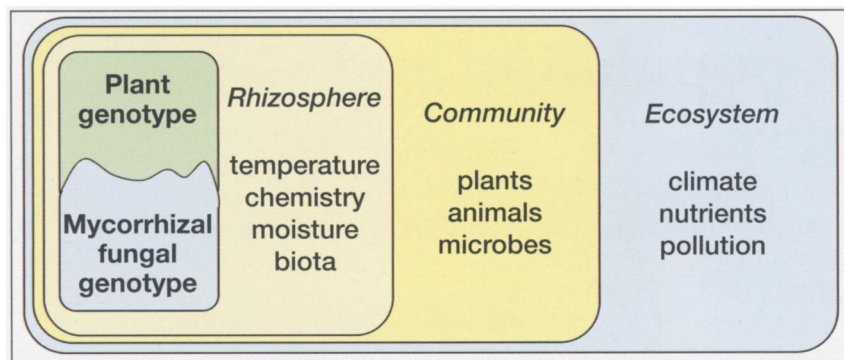


Figure 1. Context dependence almost always affects interactions among species. For example, mycorrhizal associations are a manifestation of the interaction between plant and fungal genotypes and the hierarchy of environmental factors that determine the functioning of mycorrhizas along a continuum from 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

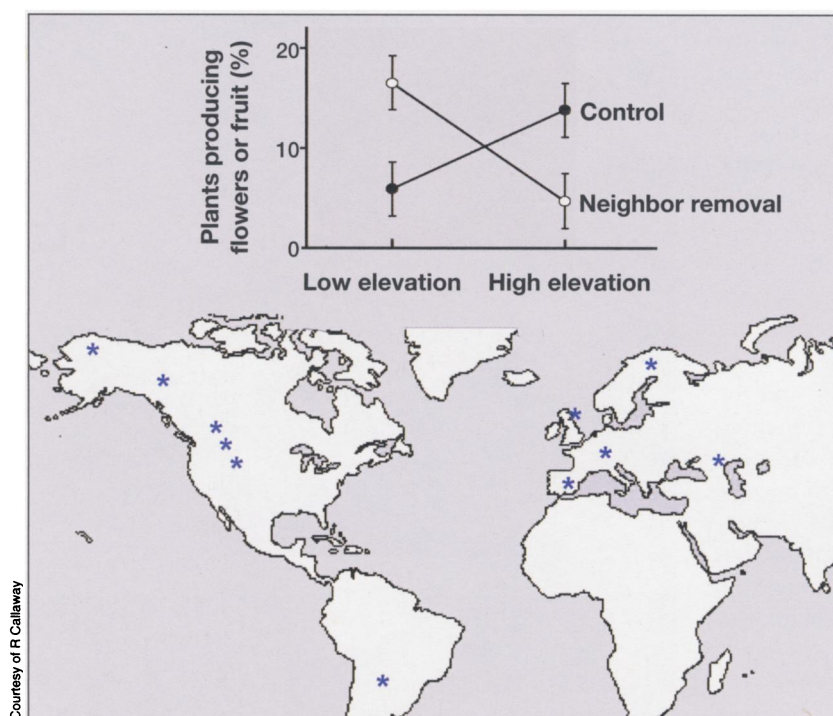


Figure 3. Using environmental gradients to understand variation in the outcomes of interspecific interactions: plant–plant interactions vary predictably along a gradient of environmental harshness. Working in 11 study sites (asterisks), Callaway *et al.* (2002) demonstrated that, at low elevations, competition 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

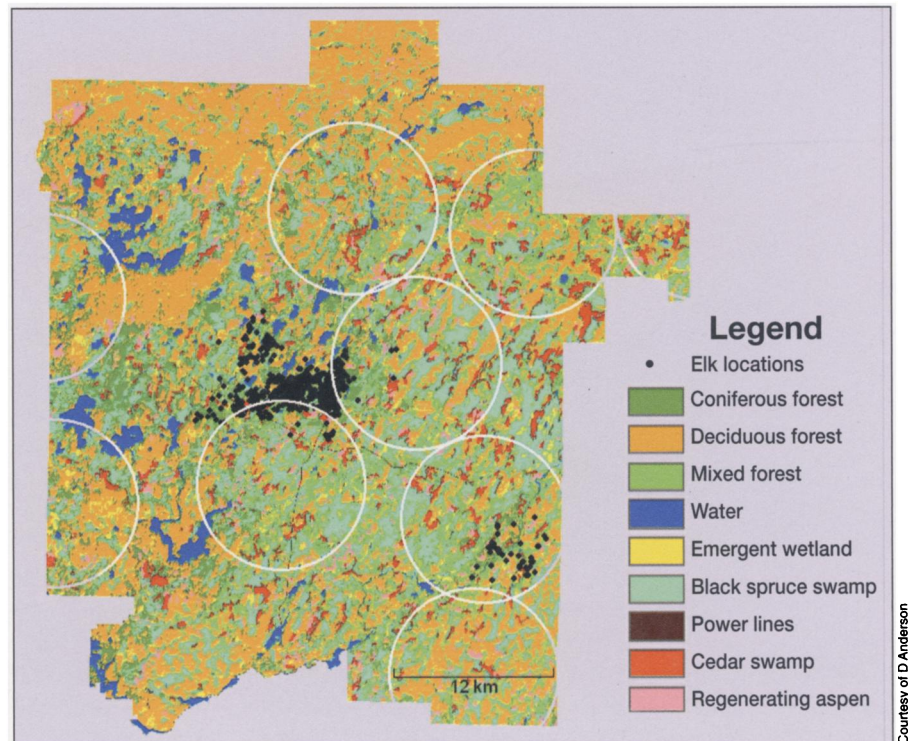


Figure 4. Reciprocal interactions (ie ecological feedbacks) are ubiquitous but rarely studied. For example, a tri-trophic feedback is likely at the landscape scale among habitat selection by wolves and elk and vegetational production. Elk (black dots) selected areas with lower predation risk (by wolves; 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.

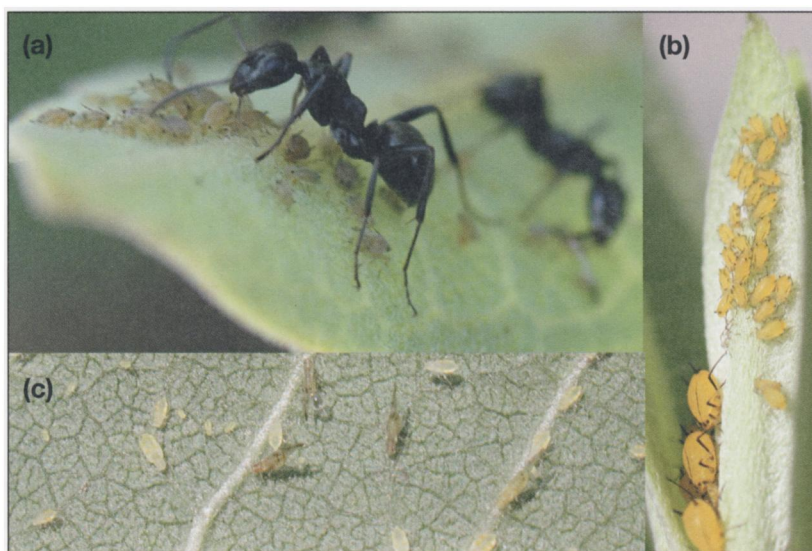


Figure 5. Multiple factors allow for the coexistence of species. For example, three aphid species coexist on the same host plant, *Asclepias syriaca*, (and on the same resource from that plant, phloem sap): (a) *Aphis asclepiadis*, (b) *A. nerii*, and (c) *Myzocallis asclepiadis*. Each species has distinct 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

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

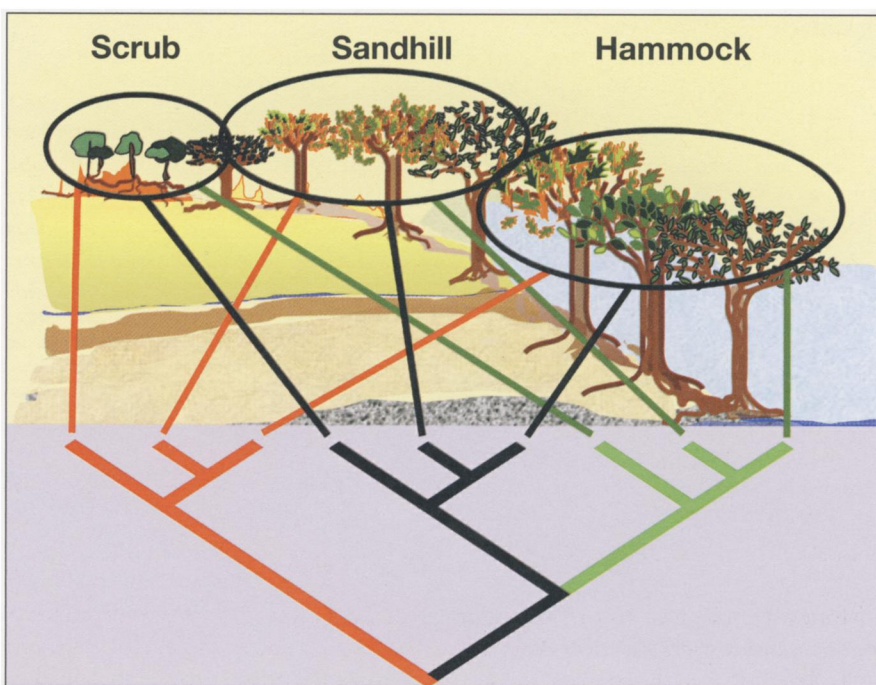


Figure 6. Using knowledge of evolutionary history to understand community assembly. This figure presents a schematic of phylogenetic overdispersion (phenomenon of co-occurring species being less related to each other than expected by chance) in three major oak-dominated communities in Florida (adapted 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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