Agrawal – Supplementary information

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 mutalist, 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 neoecological perspectives. Although paleoecological insights into the composition of past (especially plant) communities have contributed to theory in community ecology, a synthesis of paleo- and neoecological 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 neoecological 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.

Stablizing 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 Synder 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 phylogenic 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.
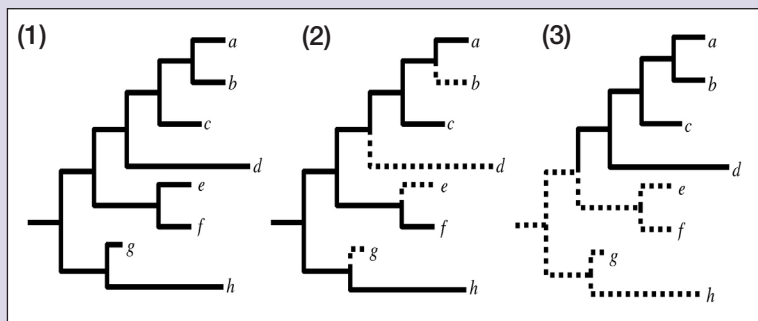
Figure 1. Phylogenetic diversity of communities. (1) Hypothetical phylogenetic tree for organisms a through h, drawn with representative branch lengths. (2) Hypothetical tree for organisms at site X, with organisms that are present indicated by solid branches, and organisms that are absent indicated 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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