THE ROYAL SOCIETY

A taxonomic wish-list for community ecology

Nicholas J. Gotelli

Department of Biology, University of Vermont, Burlington, VT 05405, USA (*ngotelli@zoo.uvm.edu*)

Community ecology seeks to explain the number and relative abundance of coexisting species. Four research frontiers in community ecology are closely tied to research in systematics and taxonomy: the statistics of species richness estimators, global patterns of biodiversity, the influence of global climate change on community structure, and phylogenetic influences on community structure. The most pressing needs for taxonomic information in community ecology research are usable taxonomic keys, current nomenclature, species occurrence records and resolved phylogenies. These products can best be obtained from Internet-based phylogenetic and taxonomic resources, but the lack of trained professional systematists and taxonomists threatens this effort. Community ecologists will benefit most directly from research in systematics and taxonomy by making better use of resources in museums and herbaria, and by actively seeking training, information and collaborations with taxonomic specialists.

Keywords: phylogenetics; systematics; community ecology; Internet, taxonomy; biodiversity

1. OVERVIEW

In this essay, I offer my perspective as an ecologist on the interaction between taxonomic specialists (systematists and taxonomists) and community ecologists. I first identify four facets of the current research programme in community ecology to which taxonomy and systematics are particularly relevant. Next, I explain four kinds of information that community ecologists need from taxonomic specialists. My own 'case history' of interactions with taxonomic specialists is described, and I offer some specific advice for both ecologists and taxonomic specialists that will help them work together. I conclude with a plea for more collaborative studies, which is perhaps the most important message of this essay.

2. RESEARCH FRONTIERS IN COMMUNITY ECOLOGY

Much research in community ecology relies on an accurate enumeration of coexisting species and their relative abundances (Morin 1999). Any study in community ecology requires, ideally, that the individuals in a sample be properly counted and identified to species. Therefore, all of community ecology depends very much on current species nomenclature and taxonomic tools for identification. Four areas of current research in community ecology are especially closely linked to work in taxonomy and species identification and are detailed as follows.

(a) *The statistics of species richness estimators*

Community ecologists need the products of taxonomy to properly identify the different species present in an assemblage. Once the identifications are complete, the next step is often a comparison of species richness among different samples. The mantra of biometry is that standardized sampling must be used so that data from different regions or different times can be compared statistically (Sokal & Rohlf 1995). However, the estimation of a species number introduces some subtle problems into efforts to standardize data (Gotelli & Colwell 2001). Species richness in standardized samples (such as pitfall traps, quadrats and transects) rises rapidly at first because most of the common species are captured early in the sampling. As more samples or individuals are added to the collection, species richness continues to rise, but at a much slower rate (Bunge & Fitzpatrick 1993).

In theory, an asymptote will eventually be reached for a local assemblage, at which point additional collecting will yield no new species. (On a wider geographical scale, species–area curves have no asymptote, even in principle; see Williamson *et al.* (2001).) For most assemblages, we do not know what that asymptote is or how much sampling would be needed to reach it. Even worse, different samples often contain very different abundances (Denslow 1995). As a consequence 'standardized samples' may not be comparable on the basis of the number of individuals collected. Ecologists have not always distinguished properly between species density (number of species per sampling unit) and species richness (number of species per number of individuals; James & Wamer (1982)).

There are two general strategies for coping with sampling curves: interpolation and extrapolation. Interpolation methods involve statistical models or computer simulations of random subsets of individuals or samples from the entire collection (Heck *et al.* 1975). A rarefaction curve (Sanders 1968) is a graph of species richness versus abundance that is created by interpolating (or rarefying) the original data to smaller abundance levels (Tipper 1979). The rarefaction curve reveals the number of species that would have been expected in a smaller random subsample of some particular number of individuals (or

---

One contribution of 19 to a Theme Issue 'Taxonomy for the twenty-first century'.

DOI 10.1098/rstb.2003.1443

samples) from the original data. In this way, datasets that may have differed in the number of individuals sampled can be standardized for comparison of species richness.

The extrapolation strategy estimates the asymptote that would be reached if enough individuals were sampled. Extrapolations can be made by fitting nonlinear functions to the sampling curve and extending them outward (Palmer 1990), or by modelling the shape of the relative abundance curve (Longino *et al.* 2002). However, the most promising approaches are non-parametric estimators that are derived from mark and recapture models (Colwell & Coddington 1994; Chao 2004). These estimators use the number of rare species in the assemblage to predict the number of missing species in the assemblage (Shen *et al.* 2003).

Of course, asymptotic estimators are not needed if the sampling curve has already levelled off, but in hyperdiverse communities such as tropical arthropods this seems never to happen. Long-term studies such as the Arthropods of La Selva (see http://viceroy.eeb.uconn.edu/ALAS/ALAS.html) continue to accumulate new rare species as more and more individuals are collected (Longino & Colwell 1997). Both extrapolation and interpolation are computer-intensive methods, and specialized software now exists for these analyses (Colwell 2000; Gotelli & Entsminger 2003). Because taxonomic estimators depend on correct recognition and counts of rare species, they may be especially sensitive to the presence of cryptic species in a dataset, and could change substantially in the face of taxonomic revisions. Unfortunately, it is inevitable that rare species tend to be the last ones discovered and described.

(b) *Quantifying global patterns of biodiversity*

Whereas community ecologists study mechanistic processes operating at small spatial scales (Paine 1994), biogeographers study patterns of species diversity at broad geographical scales (Brown & Lomolino 1998). These different scales typically dictate different taxonomic needs: community ecologists need taxonomic tools to identify their samples, whereas biogeographers need georeferenced museum and herbarium records to delineate geographical ranges and regional occurrence patterns (see Soberón & Peterson 2004).

Recently, these research agendas have begun to coalesce, as both groups of researchers seek to understand the interaction between local processes and regional patterns of diversity (Ricklefs & Schluter 1993). Active research fronts (reviewed by Gaston 2000) include geographical gradients in species richness with latitude (Rohde 1992), depth (Pineda & Caswell 1998) and elevation (Rahbek 1995; Grytnes & Vetaas 2002; Grytnes 2003), the relationship between species number and area (Rosenzweig 1995), productivity (Waide *et al.* 1999) or available energy (Currie 1991), and the assembly of local species assemblages from regional source pools (Cornell 1999).

Many of these topics represent classic questions in community ecology and biogeography. However, recent studies have emphasized scale dependence in patterns and processes (Lyons & Willig 1999; Rahbek & Graves 2000; Crawley & Harral 2001), explicit hypothesis tests through more focused empirical analyses (Roy *et al.* 1998; Chown & Gaston 1999; Ricklefs *et al.* 1999) and comparisons of data with null models (Gotelli 2001) and neutral models (Hubbell 2001), which can generate surprisingly realistic diversity patterns through simple stochastic processes (Colwell & Lees 2000; Jetz & Rahbek 2001). Because these studies all require the analysis of species occurrences at scales larger than a local community, georeferenced museum and herbarium records may be critical for quantifying regional occurrence.

(c) *The influence of global climate change on community structure*

The interest in generating regional species lists goes beyond basic research into the maintenance of community structure. The current 'biodiversity crisis' (http://www.biodiv.org) has generated new demands for easily accessible taxonomic information (Blackmore 2002). Studies of the physiological responses of organisms to global climate change also require current phylogenetic information, because a major research question has been whether related species will react in similar ways to altered climates (Farnsworth & Bazzaz 1995; Hughes *et al.* 1996).

Some of the best evidence for global climate change has come from biogeographers and community ecologists who have documented shifts in species composition and species geographical ranges through time (Walther *et al.* 2002; Root *et al.* 2003). For example, Sagarin *et al.* (1999) recensused intertidal transects on the California coast 60 years after an initial survey by ecologists in the 1930s. Most southern species (10 out of 11) increased in abundance, whereas most northern species (five out of seven) decreased in abundance. These changes were accompanied by an average increase in local seawater temperatures of 0.79 °C. Even stronger evidence for climate change comes from long-term continuous monitoring of a local assemblage. In the highland forests of Monteverde, Costa Rica, local extinctions and population dynamics of birds, reptiles and amphibians were associated with changes in local weather and patterns of dry-season mist frequency, which have all been tracked since the mid-1970s (Pounds *et al.* 1999).

However, once a study moves beyond the scale of a local community, the data cannot be collected entirely by a single ecologist or research team. Some of the most compelling analyses have been for butterflies and birds, two groups for which there is popular interest, a large international base of collectors and hobbyists, and good long-term collection and museum records. In a study of 35 species of non-migratory European butterflies, northern range shifts were documented in 22 species, and southern range shifts in only two species. Most of these changes were documented over the past 20–40 years, although for a few species, good collection records went back as far as 1900 (Parmesan *et al.* 1999). Similarly, range boundaries collated from breeding bird atlases of Britain (Sharrock 1976; Gibbons *et al.* 1993) reflect the expansion of southern species and the retraction of northern species during the 1970s and 1980s (Thomas & Lennon 1999).

At the largest spatial scales, only museum and herbarium records will probably be comprehensive enough to document changes in geographical ranges. For example, Peterson *et al.* (2002*a*) compiled 112 456 occurrence records for all species of birds (1179), mammals (416) and

Papilionid and Pierid butterflies (175) in Mexico. The data were obtained from natural history museums around the world, as part of an ongoing effort to assemble comprehensive distributional data on Mexico's flora and fauna by the Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (http://www.conabio.gob.mx/). Peterson *et al.* (2002*a*) analysed these data with outputs from general circulation models of climate to predict shifts in community structure in the face of global climate change. In general, the larger the spatial scale and temporal scale of the analysis, the more community ecologists will need to rely on museum and herbarium resources to establish accurate species lists and historical occurrence records.

(d) *Phylogenetic influences on community structure*

In addition to species identifications and georeferenced museum and herbarium records, community ecologists increasingly require phylogenetic information from taxonomic studies. The use of biodiversity indices implies that all species in an assemblage are equally different from one another (Peet 1974; Magurran 2003), and analyses that use species as 'replicates' assume that species are statistically independent of one another. However, owing to their shared phylogenetic history, species may not be independent of one another; we expect closely related species to be more similar in all of their ecological attributes than distantly related species. The problem has been recognized for some time, but was popularized by the publication of the important book of Harvey & Pagel (1991) on the comparative method. Since then, there has been widespread interest in community and biogeographic studies that incorporate phylogenetic information (Losos 1996; McPeek & Miller 1996; Webb *et al.* 2002).

In community ecology, two lines of research have used phylogenetic information to varying degrees. The simplest and oldest line of research uses taxonomic ranks, based on the hierarchical classification of species into genera, families and higher taxonomic units to reveal patterns of community structure. For example, there is a long tradition in community ecology of constructing taxonomic ratios, such as the species : genus ratio as indicators of community structure (Järvinen 1982). Elton (1946) and others thought that such ratios reflected competitive interactions, but they failed to take into account the subtle statistical behaviour of such indices in small samples (Williams 1964; Simberloff 1970). More recently, 'taxonomic scaling relationships' of terrestrial plants have been explored with double-log plots of genus and family number versus species number (Enquist *et al.* 2002). For ground-foraging ants, Kaspari (2001) explored how taxonomic level contributed to patterns of local abundance. Although it is still not widely recognized, the statistical problems that arise in the analysis of taxonomic ratios are identical to those that arise in estimating species richness, which is in reality a 'ratio' of species number to abundance (Gotelli & Colwell 2001).

More recently, a second class of community analyses makes use of explicit phylogenies as a type of null hypothesis for community patterns. For example, Webb (2000) refined the analysis of taxonomic ratios by incorporating the degree of relatedness of species in a community. For plots of tropical rainforest he measured the average pairwise phylogenetic distance of coexisting species and compared that with the average in randomly assembled communities. Coexisting species were more closely related than expected, which is consistent with earlier findings of elevated species : genus ratios (more co-occurring species in each genus) compared with appropriate null models (Simberloff 1970). A similar result holds for the phylogenetic similarity of grassland plant communities (Tofts & Silvertown 2000). Other studies have used phylogenies as a basis for the study of taxon cycles (Liebherr & Hajek 1990; Ricklefs & Bermingham 2002), character displacement (Losos *et al.* 1998), adaptive radiation (Schluter 2000) and coevolution (Janz *et al.* 1998). Phylogenies allow for an assessment of the contribution of evolutionary history to patterns in contemporary communities (Cavender-Bares & Wilczek 2003). Not all ecologists are convinced of the primacy of phylogenetic effects (Brown 1995; Westoby *et al.* 1995; Bjorklund 1997), and the measured effects of phylogeny in early studies were not always strong (Ricklefs & Starck 1996). However, this is an empirical issue that is still being resolved (Freckleton *et al.* 2003), and comparative methods no longer imply a simplistic partitioning of variation into phylogenetic and ecological components (Ackerly & Donoghue 1995; Harvey *et al.* 1995). To test historical and evolutionary hypotheses, community ecologists ideally need fully resolved phylogenies, preferably with estimates of branch lengths (Harvey *et al.* 1996).

3. WHAT COMMUNITY ECOLOGISTS NEED FROM SYSTEMATICS AND TAXONOMY

In this section there is a wish-list of phylogenetic and taxonomic needs for community ecology. It might be better to call this a 'dream list' because, for most taxa, these products are unlikely to be generated in the near future. Nevertheless, in order of desirability, community ecologists need the following.

(a) *Taxonomic keys*

We need well-written taxonomic keys based on morphological characters (when possible) for species-level identifications. Special emphasis should be given to keys for arthropods, plants, protists and microbes. These taxa are the most diverse, the least studied, but also the most likely to be used in experimental community ecology. Ideally, a key should be available in print and Internet form for each major biogeographic province on the globe. Although identification of microbes and protists may need to be identified largely by DNA, keys for other taxa should be based on morphological characters. Blaxter (2004) makes a persuasive case for a DNA-based taxonomy, but for now, that seems a remote possibility from my perspective as a community ecologist. Morphological keys should be copiously illustrated (either line drawings or photographs) with diagnostic characters, and the illustrations should be physically adjacent to the text descriptions. Some computer programs (e.g. DELTA) will even generate an interactive key using synapomorphies from a phylogenetic character matrix so they might be easier to generate for groups that are the focus of recent cladistic studies.

The keys should give good details on known geographical ranges, habitat associations, and also contain information on distinguishing easily confused species. Although my preference is for dichotomous keys, they may not be necessary or desirable for some species groups. Existing keys and field guides for birds should be used as the 'gold standard' for what is possible in a well-written and useful key.

(b) *Species names and taxonomic history*

We need a current and comprehensive nomenclature, and a historical record of previously used nomenclature, so that present species lists can be easily compared with those generated in the past.

(c) *Species records*

We need access to museum and herbarium records to be able to compile species occurrence records with spatial and temporal data that are physically associated with the specimen or collection.

(d) *Phylogenetic relationships*

We need to know the current classification of our species and to have a resolved phylogeny (with confidence measures) that illustrates sister taxa and the phylogenetic status of species and entire communities. Ideally, such resolved phylogenies would be based on morphological and molecular datasets and also contain measures of branch length. However, even cladograms that contain only node structure can still be used effectively in some phylogenetic analyses.

The first two needs (§ 3a and § 3b) are most pressing for typical small-scale studies in community ecology. The latter two needs (§ 3c and § 3d) will be valuable for large-scale efforts and conservation studies.

4. TAXONOMY AND THE INTERNET

Godfray (2002) sketches an exciting vision of the future in which all of these products are available free of charge from Internet Web sites, which are continuously updated and overseen by a central committee for a particular taxon that approves a single current Web version of the taxonomy. The Web taxonomy would be periodically updated and archived as new information becomes available. Species might eventually be provided with a DNA-based taxonomic barcode (Blaxter 2003; Hebert *et al.* 2003), and open access to character and distributional data could result in the taxonomic equivalent of GenBank (Agosti & Johnson 2002). The Internet-based taxonomy envisioned by Godfray (2002) and others (Bisby *et al.* 2002) would be a tremendous asset for research in community ecology, and might even result in new research directions for the study of species groups that are notoriously difficult to identify.

Some of this work has already been attempted. For example, the All Species Foundation (see www.all-species.org) proposed to name and describe all living species (somewhere between 4 and 100 million) within a single human generation. Such an effort would require, at minimum, a quadrupling of the rate at which species are currently described (*ca.* 15 000 yr^{-1}) and a doubling of the number of parataxonomists working in developing countries (Gewin 2002). Perhaps more realistic is the Species 2000/ITIS Catalogue of Life, which seeks, more modestly, to create a set of linked databases that together will list all of the species currently known to science. The 2003 Catalogue of Life (www.sp2000.org) already lists 304 710 species (and more than 860 000 associated names and common names) on CD-ROM and the Web (Froese *et al.* 2003).

Species 2000/ITIS Catalogue of Life and the Global Biodiversity Information Facility (http://www.gbif.org/) are working to coordinate international Web-based efforts. Their goal is to make a range of databases on biodiversity available to researchers and policymakers. Numerous other smaller-scale projects demonstrate the utility of Web-based taxonomic tools (Hagerdorn & Rambold 2000; Kendall *et al.* 2000; Kang *et al.* 2002; Struder-Kypke & Montagnes 2002). The Tree of Life (http://www.gbif.org/), Treebase (http://www.treebase.org/treebase/) and Palmkey (http://www.phylodiversity.net/palmkey/) are three excellent examples of the power of Internet-based taxonomy and systematics.

However, there are at least four major obstacles to the development of a comprehensive Web-based taxonomy and phylogeny. The least serious is the technological challenge of linking diverse data sources. The Internet is particularly well suited to this task, and continued advances in hardware and software will allow for maximum flexibility in cataloguing and linking diverse datasets. The second challenge to a Web-based taxonomy is that it will require centralization (or more likely, federation) and consensus. Without a single 'official' Web-based taxonomy for a particular taxon, unauthorized nomenclature and taxonomies will quickly appear in electronic versions, which is already starting to happen (Lee 2000). It is unclear whether existing taxonomic protocols can operate with enough speed and flexibility to be adapted to a Web-based format (Knapp *et al.* 2002) or whether an entirely new protocol is needed (Erwin & Johnson 2000). Consensus will be necessary for such a large coordinated effort (Mallet & Willmott 2003), but there will always remain an inherent tension: species names represent pieces of fixed biological information to community ecologists, conservation biologists and other 'users' of taxonomy (Knapp 2000), but they represent provisional hypotheses to taxonomists and systematists (Thiele & Yeates 2002).

The third challenge is cost. An Internet-based taxonomy would go hand in hand with computer cataloguing of existing museum and herbarium collections, and the projected costs for even this activity are on the order of US$1–10 per specimen (Smith *et al.* 2003). Assuming a global biota of 10 million species, Wilson (2000) estimates the cost of the All Species Project to be US$5 billion, roughly comparable to the Human Genome Project. Given the economic constraints on all scientific research, it may not be possible to secure funds for a large coordinated effort to create a comprehensive Internet-based taxonomy.

But the most serious challenge is neither cost, consensus, nor informatics technology. It is expertise. There are no more than 10 000 professional taxonomists worldwide (Gewin 2002), which is probably at least one order of magnitude too small for the task of cataloguing the world's biota. There have been long-term declines in the numbers of both professional taxonomists (Mallet & Willmott

2003) and amateur collectors (Hopkins & Freckleton 2002), and the US currently spends only US$150 million–200 million each year on systematics research (Wilson 2000). It is the lack of investment in taxonomic training that constitutes the biggest threat to both conservation research and the future of a comprehensive Internet-based taxonomy.

5. A CASE HISTORY

My own interactions with taxonomic specialists have taught me the value of collaborations and the importance of accurate species identification in community ecology. However, these benefits may not be obvious to other ecologists, some of whom publish extensively on community ecology and biodiversity but do not interact with taxonomic specialists. To offer a concrete example, I describe here my own 'case history' of interactions with taxonomic specialists and the benefits that have accrued to my research programme in community ecology.

(a) *Avian biogeography*

As a young graduate student at Florida State University in the early 1980s, I was fortunate enough to share an office with Gary Graves, now an ornithologist at the Smithsonian Institution. Gary and I also shared a common interest in biogeography, but had non-overlapping expertise in null models and statistics, and avian taxonomy and natural history. These different perspectives initially sparked argument and discussion, but soon developed into a long-term collaboration that continues to this day (Graves & Gotelli 1983, 1993; Gotelli & Graves 1990, 1996). These interactions (and time spent at the Smithsonian) gave me an appreciation for the wealth of information available from museum and herbarium collections and the benefits to community ecologists that can come from working with a taxonomic specialist.

For example, Gary was intensely critical of my early work on the biogeography of Caribbean birds, in which I created island source pools by compiling island archipelago lists (Gotelli & Abele 1982). Gary complained that such analyses did not take into account habitat affinities and proximity to mainland source pools. I countered that it was all well and good to criticize, but that the kind of data he envisioned did not exist in the published literature. If he could generate a more biologically realistic source pool list for each island in an archipelago, then we could consider some new kinds of analyses.

To my surprise, Gary took up the challenge, and left for a month-long trip to the American Museum of Natural History. He returned with a remarkable dataset during an era before computerized spreadsheets facilitated the collection and manipulation of large datasets. For seven Neotropical islands (five oceanic and two land bridge), he had created a comprehensive list of all species that occurred within a 300 km radius circle centred on each island. For each species, he determined habitat affinities and categorized geographical range sizes. Null model analyses of these data revealed that most avian families were represented on islands in the same proportion as on the mainland (after accounting for habitat). However, species with small geographical ranges (less than 100 1° × 1° latitude–longitude blocks) were consistently under-represented on islands (Graves & Gotelli 1983).

A taxonomic specialist can categorize species and provide insight into the results of statistical analyses. For example, in a study of species coexistence of the Australian avifauna (Gotelli *et al.* 1997), the ecologist John Wiens provided *a priori* designations of ecological guilds of closely related species, based on the species lists in Blakers *et al.* (1984). The systematist Leslie Christidis (Museum of Victoria) modified our guild lists to reflect recent changes in systematics and taxonomic status of the Australian avifauna. Christidis also pointed out to us that several cases of apparent ecological segregation more probably reflected parapatric and allopatric divergence of sister taxa (Gotelli *et al.* 1997).

Finally, a taxonomic specialist appreciates the limitations of museum and herbarium collections, and can steer you away from projects for which data cannot be reliably obtained. For example, the ant specialist Stefan Cover (Museum of Comparative Zoology, Harvard University) convinced me that, even with extensive museum collections, it would be impossible to reliably reconstruct the ant faunas of the southeastern USA before the invasion of the fire ant (*Solenopsis invicta*) in the 1930s. Therefore, I had to rely on current comparisons of intact versus invaded ant communities to infer the ecological effects of red fire ant invasion (Gotelli & Arnett 2000). All of these studies were tremendously enhanced by interaction and correspondence with taxonomists at museums. The information they provided could not have been extracted from the scientific literature.

(b) *Ant community ecology*

My own struggles with species identification did not begin until 1997. For several years, I had studied the population and community ecology of larval ant lions in western Oklahoma (Gotelli 1993, 1996, 1997). Lionel Stange (Florida Department of Agriculture & Consumer Services) kindly identified my early samples of larvae, and his published key (Lucas & Stange 1981) allowed me to distinguish ant lion species in their larval stages and study competitive interactions (Gotelli 1996). The famous myrmecologist Jeannette Wheeler kindly confirmed the species identification of many ants from Oklahoma for me and my PhD student Marc Albrecht (Albrecht 1995; Albrecht & Gotelli 2001).

With my PhD student Amy Arnett, we expanded the spatial scale of the ant lion research to study the evolution of life-history traits across the geographical range of *Myrmeleon immaculatus* (Arnett & Gotelli 1999, 2000, 2001). Our results pointed to the importance of larval food supply, which we wanted to quantify on a latitudinal transect. In the summer of 1997, we surveyed ground-foraging ants (the principal prey of ant lions) on a 2000 km transect from the Florida panhandle to upstate New York. Although the study was intended as a survey of ant lion food availability (Arnett & Gotelli 2003), it proved even more valuable as a study of the biogeographic effects of the red invasive fire ant *S. invicta*, which was present in the southern portion of our transect (Gotelli & Arnett 2000).

Travelling north from the Florida panhandle, we sampled sites every 50–60 km. At each site, we established two 5 m × 5 m grids of pitfall traps, one in deciduous forest and one in open habitat. Each pitfall trap consisted of a 50 ml plastic centrifuge tube partly filled with soapy water.

Traps were left open for 48 h, then recovered from the field and the contents fixed in ethanol. In retrospect, our field design was far from ideal for censusing ant communities, and would not have been used by a taxonomist or ant collector. Pitfall traps do not sample arboreal or leaf-litter ants very well, and the small size of our traps (27 mm diameter) meant that large-bodied ant species were surely undersampled. The small spatial coverage of our grids meant that populations of many resident species were probably missed, and the single 48 h trapping interval meant that trap yields would be very sensitive to local weather conditions (a few of the grids had to be discarded and resampled owing to thunderstorms). Nevertheless, the large spatial scale of the transect and the use of standardized sampling methods generated a surprisingly strong biogeographic signal, in spite of considerable statistical noise from the limited sampling effort at each site.

Before we could analyse these interesting biogeographical data, however, all of this material had to be sorted and identified. The collection consisted of 1650 pitfall trap yields, with a total of 14 347 individual ants. I sorted and picked the material, and used the recently published keys by Hölldobler & Wilson (1990) and Bolton (1994) to identify samples to the genus level. The new terminology and morphology were difficult for me at first, and my progress was slow. I knew it would be impossible to do a credible job without some expert help.

I initiated correspondence with Stefan Cover, ant specialist at Harvard's Museum of Comparative Zoology. In a letter to Stefan, I described the sampling design of the study, and explained that I wanted to learn how to properly identify ants of eastern North America to the species level. His initial response was not encouraging: 'I cannot advise you to continue this project', he wrote, 'the identifications are not going to be very easy, and you have an awful lot of material to work through'. I politely persisted, explaining that I was not asking him to identify all of this material for me, but to teach me how to do it myself. Stefan replied that the only way for me to learn ant identification skills was to come visit him at the MCZ for a few days and to bring along lots of my material. At the MCZ, Stefan first handed me a stack of taxonomic keys and reprints for xeroxing, and I was able to purchase from him one of the few remaining copies of the out-of-print monograph of Creighton (1950), the last comprehensive treatment of the ants of North America.

Stefan proved to be a natural teacher, and I spent a productive 2 days taking notes and making sketches, sorting my material, and comparing my specimens with the museum collections. Stefan also quickly provided me with labelled identifications for a subset of my material, creating a small reference collection for me. When I returned to Vermont, I began tackling my collection in earnest. I was on sabbatical leave in the fall semester of 1998, and spent 6–8 hours a day at the dissecting scope working through this material. The xeroxed taxonomic keys that Stefan sent me home with were somewhat useful, but I mostly relied on my handwritten notes of Stefan's descriptions of species and diagnostic characters.

Nevertheless, there were still a considerable number of specimens that did not fit with my reference collection, and I continued to make notes on specimens or characters that puzzled me. I made two more visits to the MCZ, bringing with me the troublesome specimens. I also had Stefan spot check some of my previous identifications. I had to make several passes through my collection, and in a few cases (e.g. the genera *Pheidole* and *Myrmica*), had to redo most of my identifications. Nevertheless, my confidence in my identifications increased, and I began to quickly recognize and identify species, and to use some of the published keys without too much effort. In the end, the collection yielded 82 species, including an undescribed and previously undiscovered species of *Tapinoma*, which I was pleased to have recognized as 'suspicious'.

The time spent on ant species identification has had big payoffs and profoundly influenced my research in community ecology. In 1996, I began collaborative work with Aaron Ellison on the carnivorous pitcher plant (*Sarracenia purpurea*) in ombrotrophic bogs of New England (Ellison & Gotelli 2002; Gotelli & Ellison 2002*a*). We quickly discovered that ants are the most important prey of *Sarracenia*, and have since begun studies of the biogeography and community structure of ants in northern bogs and forests (Gotelli & Ellison 2002*b*,*c*; Ellison *et al.* 2002).

Like birds, ants are ideal taxa for the study of community structure. Ants dominate the biomass of most terrestrial animal communities, and are critical plant pollinators and seed dispersers. There are striking biogeographic gradients in ant species richness (Cushman *et al.* 1993), and there are even about the same number of ant species as bird species in the continental USA (roughly 600 described ant species and 700 bird species). Nevertheless, until very recently (Kaspari *et al.* 2000), there have been relatively few studies of ant community structure at a biogeographic scale. I agree with Bolton (1994), who suggests that the paucity of ant community studies reflects the difficulties of species identification. By contrast, there are a wealth of keys, guidebooks, software and Internet resources available for the identification of birds. It is probably no coincidence that studies of avian assemblages have a profound influence in community ecology (Wiens 1989), even though birds are poor subjects for experimental studies of community structure.

6. COMMON GROUND FOR TAXONOMIC SPECIALISTS AND COMMUNITY ECOLOGISTS

Taxonomic specialists and community ecologists sometimes share the common goal of assembling an accurate species list for a given region. However, their approaches and assumptions are quite different from one another. Taxonomic specialists work to accumulate a comprehensive list of species from a region, with a properly mounted specimen as a physical record of each species. Such a collection is critical for comprehensive, revisionary systematics and the construction of stable, well-resolved phylogenies.

Although habitat records for species are an important piece of information that is keyed to each specimen, habitat designations are fairly coarse, and the delineation of habitat affinities is not a primary goal. Relatively little emphasis is placed on collecting effort, and (most) specimens of species already well represented in the museum or herbarium will not be collected or retained. The museum or herbarium collection is thus a composite of samples taken at different times and with different collecting methods and efforts. The goal is to build up a comprehensive collection for a region, with a representative series of specimens for each species. There is naturally an emphasis on rare or undescribed taxa, so that rare species are probably disproportionately more common in museum and herbarium collections than they are in nature.

By contrast, the ecologist wants a standardized sample of species from an area. The data have to be collected in such a way that the sample can be validly compared statistically with samples collected in the same way at other places or times. Although the ecologist would like to have a comprehensive list of species from a site, this is rarely possible. Ecologists have to be satisfied with a representative standardized sample of the diversity in a site or region. An ecological 'collection' will be dominated by common species, and there will inevitably be rare species missing from the collection. However, the relative abundance curve for a properly sampled community should approximate that found in nature. The failure to capture all of the rare species does not just represent a statistical constraint on sampling. Some rare species are transients that may not be maintaining self-sustaining populations in the sampling area, and will emerge only in collections that are made over large spans of time.

Ecologists and taxonomic specialists also differ in the units that they use to quantify biodiversity. For the taxonomic specialist, the individual specimen is the unit of interest, and the associated biogeographic, habitat and sampling information. For the ecologist, it is usually the sample that is of interest. Once the sample has been properly sorted to species, there is little interest in distinguishing the individuals that have already been counted. As a consequence, ecologists and taxonomic specialists often organize their data in quite different ways, which can make collaborative studies a challenge. Some software tailored for museum and herbarium specimens (Colwell 2004) allows for easy conversion between ecological and taxonomic data formats.

7. ADVICE FOR ECOLOGISTS

(a) *Learn to curate material*

Find out how to properly prepare, mount and label your specimens. Although you will probably have too much material to curate your entire collection, you should prepare representative specimens and begin to assemble your own 'in-house' collection. This is an invaluable resource for your future research and teaching.

(b) *Sort and clean samples*

Taxonomists should not have to pick through debris-filled containers. Although all of your material may not be properly mounted or curated, it should at least be cleaned, sorted and labelled before you ask someone else to examine it.

(c) *Learn the terminology*

To key out specimens and work with the taxonomic literature, you need to master the specialized vocabulary and terminology associated with your taxon. Learn to speak this 'language' so that you can communicate accurately and read the taxonomic literature.

(d) *Do your homework*

Before contacting a taxonomist, do as much work as you can on your own with existing keys and guides. Sort your specimens to morphospecies and key them down as far as you can.

(e) *Get into the details*

Correct identification of specimens to the genus and species level requires focus on subtle morphological differences between specimens. When working with a taxonomic key, the statistical perspective of 'approximate' results is not good enough. Remember that in taxonomy, there is only one 'right' answer, and that is what you want to arrive at: the correct identification of your specimen. Careful attention paid to minute details will ultimately yield correct identifications.

(f) *Invest time in studying specimens*

Knowing the diagnostic characters and using the keys is not enough. You also need a handle on variation in the characters within a species across its geographical range, among habitats and among different ages or life-history stages. The only way to get a feeling for this variation is to examine as many specimens as possible of each species. It will be slow going at first, and you may find yourself spending the better part of the afternoon working on a single specimen. You will pick up speed as you gain experience and knowledge, but there is still no substitute for many hours spent studying your material.

(g) *Visit taxonomists and museums and herbaria*

Keys are important and necessary, but they are no substitute for working with an expert and gaining access to an extensive museum or herbarium collection. Make contact with a taxonomic specialist, do your homework ahead of time, and prepare to spend 2–3 days on a museum or herbarium visit. Taxonomic specialists are not 'mail-order ID sources'. You should never send material to a taxonomic specialist for identification without first making contact and obtaining permission. Taxonomic specialists should not be asked to identify large amounts of material, unless you are paying them or they are collaborating with you on a manuscript (see § 7h). If you have a lot of material from an ecological study that you need to have identified, it is your responsibility to learn how to do it yourself.

(h) *Offer collaborative authorship*

Taxonomic specialists are among the most overworked, underpaid and under-appreciated scientists in biology. Everyone wants something from them, such as computerized data, taxonomic keys, identification services, specimen loans, destructive sampling for DNA analysis, museum displays and information for reporters and the public. Why should a taxonomic specialist bother to take the time to teach you (an ecologist) how to use keys and identify material? You should offer collaborative authorship up front, before asking for time and expertise from a taxonomic specialist, and before getting too deeply into your community ecology research. Collaboration that offers the prospect of joint publication makes the project suddenly more attractive to taxonomic specialists than all of the other competing demands on their time, and this strategy recognizes the crucial contribution by the taxonomic specialist. From your perspective, it ensures a stamp of 'quality control' on your data and species identifications. A taxonomic collaborator also ensures that you do not unnecessarily contribute to the confusion over species identifications by publishing papers larded with synonyms or unidentified 'Sp. 1, Sp. 2, Sp. 3, …'.

(i) *Deposit vouchers*

Ideally, voucher material from your ecological study should be deposited in a museum or herbarium. In this way, your work can be built upon in future studies. As the human population continues to increase and anthropogenic influences intensify, voucher material will become especially important for confirming the expansion and contraction of species geographical ranges, verifying population and species extinctions, and tracking phenotypic and genetic changes. However, many museums and herbaria will no longer accept ecological vouchers, or if they do, they require an endowment for the costs of space and maintenance. And no museum or herbarium wants to acquire unlabelled specimens that are not properly prepared and mounted.

(j) *Take notes*

A good taxonomic specialist can tell you things about species identification, range distributions, phylogeny, morphology, ecology, evolution and natural history that you will not find in any publication. Do not let this material slip away. Take copious notes when you visit.

(k) *Test yourself*

During your museum or herbarium visit, pull out both clear-cut and ambiguous specimens from your own samples and attempt to identify them. Ask your taxonomic specialist colleague to check your work and provide feedback on the difficult cases and on your mistakes.

(l) *Ask questions*

Do not just passively absorb material and information from a taxonomic specialist. Repeat it back in your own words, and ask for confirmation on morphological structures and diagnostic characters.

(m) *Offer specimens and material*

You should offer taxonomic specialists any material from your samples to add to their museum or herbarium collection. As always, make sure this material is properly mounted, prepared and labelled.

(n) *Write taxonomic specialists into your grant proposals*

Correct species identification is essential for a successful study in community ecology, and it requires time and expertise. Incorporate expenses for taxonomic help into all of your grant proposals, and consult with taxonomic specialists as you prepare your proposal. Surprisingly, I have not been successful at persuading taxonomic specialists to allow me to write them into my grant proposals. I suspect it is because they do not want to make a firm commitment to make my work a priority ahead of all the other non-paying requests they receive. Also, some taxonomic specialists may be government or state employees, and their contracts may limit their participation in grant-funded activities. In any case, you should always offer to incorporate expenses in your grant for species identification.

(o) *Take a course*

Training courses devoted to species identification are becoming increasingly popular. For example, The Bee Course (http://research.amnh.org/invertzoo/beecourse/), The Ant Course (http://www.calacademy.org/research/entomology/ant_course/) and The Taxonomy & Biology of Parasitic Hymenoptera (http://www.nhm.ac.uk/entomology/hymcours/) are sponsored, respectively, by The American Museum of Natural History and the California Academy of Sciences, and the Natural History Museum in London. These courses bring together expert taxonomists, systematists and collectors to train groups of students in intensive field courses. Such courses will enhance your identification skills, teach you how to properly prepare and curate your material, introduce you to new field-collection techniques and give you a better appreciation for natural history. Perhaps most important, they will help you to establish a network of taxonomists, systematists, ecologists and collectors who work on your organism. This network of scientists is likely to be very different from your working group of ecological colleagues, and may help you to establish new scientific collaborations.

(p) *Teach someone else*

The crisis in taxonomy exists in part because there are too few taxonomists relative to the number of species that need to be described and classified, and the number of specimens that need to be identified. Teaching students elements of species identification will help to prime the pump for the next generation of taxonomists. Among today's undergraduates, there is intense interest in biodiversity and environmental science, and laboratory exercises that incorporate species identification are consistently popular. These kinds of laboratories are also excellent recruiting tools for identifying students with a passion and talent for species identification and classification.

8. ADVICE FOR TAXONOMIC SPECIALISTS

(a) *Be patient*

Although ecologists may be knowledgeable about the natural history of an organism, its population dynamics, and species interactions, they are likely to have little or no training in systematics, taxonomy and species identification. They will usually be ignorant of the procedures and rules for naming and recognizing new species.

(b) *Articulate the details*

When working with an ecologist, you have to be a good teacher as well as a good taxonomist. It is not enough to rely on 'gestalt' impressions and statements such as 'This specimen just looks like species X'. You will have to carefully articulate all of the details and diagnostic characters that you use to recognize different taxa. You will also need to explain to your ecologist colleague not only why the specimen should be recognized as species X, but why it should not be keyed out to species Y. Ecologists need to be taught not only how to use diagnostic keys, but also how to compare their specimens with museum material and with the formal species diagnosis and original description of the species.

(c) *Write a key*

The number of taxonomic experts is alarmingly small, and the problem is getting worse as fewer new taxonomists are trained. Take the time to write a clear easy-to-use taxonomic key for a particular group that you are familiar with. Include drawings or photographs of diagnostic characters for each couplet, and consider posting the key to a permanent Internet Web site. Do not wait until you (or someone else) has completed the definitive taxonomic revision of the group. Instead, create the best possible key for the group in its current taxonomic state. Revisions can always be incorporated later. For now, you may be literally the only person who can who can create a working key, imperfect as it is. From the perspective of community ecology, the need for usable taxonomic keys is much more pressing than the need for comprehensive taxonomic revisions. The editorial boards of journals need to encourage the publication of such keys, even if they do not include taxonomic revisions or new species descriptions.

(d) *Accept rare specimens*

Many taxonomists collect extensive series of individuals from a population, and many times such series are necessary for species determinations (e.g. some ants cannot be keyed to species without males). However, ecological collections will not include such material, and will often consist of rare species that are represented by only one or two individuals in a collection. These 'singletons' and 'doubletons' are quite important for species richness estimation (Colwell & Coddington 1994), and this limited material will have to be identified as well as possible.

(e) *Be willing to examine some unmounted material*

The large size of ecological collections means that specimens will not be properly mounted or pinned, although they should at least contain valid labels. Ecologists who are trying to identify and process a large collection from an ecological survey or experiment will not be able to properly curate and mount every specimen they have.

(f) *Write ecologists into your grant proposals*

For all of the reasons listed here, taxonomic specialists should also initiate collaborations with community ecologists who are working on their taxon. As the funding arena becomes more competitive, single-investigator 'experts' will find it increasingly difficult to get their grants funded. Synthetic multi-investigator proposals are usually more competitive and becoming more and more common. For your next grant proposal, seek out a good ecologist who can provide expertise on quantitative sampling and data analysis.

(g) *Re-emphasize alpha taxonomy*

Delineating and naming species based on reliable morphological characters is a lot less prestigious (and perhaps less publishable) than radical revisionary systematics, but basic alpha taxonomy and stable species names are among the most pressing needs for community ecologists. Although the 'top-down' approach might be resented by some, the suggestion of Godfray (2002) for a single 'official' Internet taxonomy for any particular group would provide welcome relief. Community ecologists are more concerned about having a stable set of usable names than having the most 'current' taxonomy. Radical proposals to dump Linnean taxonomy in favour of cladistic phylogenies based entirely on DNA analyses leave me cold. These technologies are currently not feasible for the kind of species identification I need, and I doubt they will be at any time in the near future.

(h) *Consolidate nomenclature*

Even if species and genus names remain stable, higher-level nomenclature can still result in headaches and confusion. For plants, the Deep Green phylogeny project (http://ucjeps.berkeley.edu/bryolab/GPphylo/) and other phylogenetic analyses have resulted in wholesale revisions and changes at the family level. For example, the plant family 'Scrophulariaceae' was revised out of existence in a recent paper (Olmstead *et al.* 2001). Has the disappearance of the family—and the re-allocation of its species—been adopted by the major species checklist organizations, such as the Species 2000/ITIS Catalogue of Life, the IOPI Global Plant checklist or the Scrophulariaceae database at the NHM, London? Is it formally accepted by the International Code of Botanical Nomenclature (Botanical Code)? How do I know or find out? Again, a single 'official' Internet-based nomenclature is a key solution, but what should I do in the meantime? Taxonomic specialists can help educate ecologists about accepted sources for taxonomic nomenclature.

9. ADVICE FOR TAXONOMIC SPECIALISTS AND COMMUNITY ECOLOGISTS

(a) *Collaborate*

Collaborations between taxonomists and community ecologists will strengthen both research programmes. From the taxonomist's perspective, working with a community ecologist will allow you to participate fully in ecologically structured biogeographic analyses and studies of regional diversity. Ecology has become increasingly mathematical and statistical, and in the past 10 years, there has been a sharp increase in the number of new analytical tools, simulation software, statistical methods and mathematical models for biogeographic and ecological analysis. Even relatively established ideas, such as the measurement of species richness (Gotelli & Colwell 2001) and the existence of the latitudinal gradient in species richness (Colwell & Lees 2000; Colwell *et al.* 2004) are being examined in fresh ways. Collaboration with a community ecologist is the simplest and most reliable entry to these new methods of analysis.

From the community ecologist's perspective, collaboration with a taxonomist does much more than just ensure that species identifications are correct, even though that is the crucial first step for a meaningful community study. A good taxonomist can construct *a priori* source pools, regional species lists and estimates of biogeographic range boundaries. These parameters are vital for the analysis of many ecological models, particularly null models in which community structure is compared with patterns that would be expected in a community organized by stochastic colonization (Gotelli & Graves 1996). In the absence of valid source pool estimates, ecologists are often forced to make unrealistic assumptions. For example, most null model analyses that are based on species presence–absence matrices implicitly assume that all of the sites in the analysis share the same source pool, and that all of the species can potentially colonize all of the sites. A taxonomic specialist will probably be able to improve considerably on such simplifications. Such collaborations make full use of museum and herbarium resources and taxonomic expertise, which is especially important in this era of diminished funding for museums and herbaria.

Paradoxically, it might seem that the success of taxonomists in publishing usable taxonomic keys and guides would render collaboration unnecessary. However, this will never be the case for species identifications. Consider how much trouble bird watchers still have with species identifications, in spite of the wealth of published material (including Internet resources) available. The problem is going to be even more formidable for almost all other groups of organisms for which diagnostic characters are not so discernible (e.g. grasses, ants, fungi). The Internet is a great resource, but it is no substitute for working with experts who have devoted their entire professional careers to species identification and taxonomy. The 'apprenticeship' model of learning how to correctly identify species may be unique in the sciences and needs to be preserved and encouraged.

Nevertheless, much ecological research that uses the products of museums and herbaria does not seem very dependent on living taxonomists. After all, for some taxa such as birds and mammals, there are already numerous field guides, check lists, range maps and species lists that are actively consumed in so-called 'macroecological' analyses. Indeed, a major cottage industry has developed around the analysis of datasets that were neither collected nor verified by the authors. Many of these studies, particularly 'meta-analyses' of previously published results, have allowed useful generalizations to emerge from disparate datasets. Nevertheless, many of the analyses are based on second-hand and even third-hand data sources that were often collected for very different purposes. Ecologists do not always seem cognizant of the potential errors and biases that exist in such data sources (Peterson *et al.* 2002*b*). The same datasets are often recycled in clusters of very similar papers, and the marginal returns on such studies are slim (Gotelli & Graves 1996). Collaboration with a taxonomic specialist is the best antidote to these problems. The best research comes from collaborations between taxonomic specialists and community ecologists who can bring both fresh ideas and fresh analyses to the table, and take advantage of the wealth of information that resides in museum and herbarium collections. The division of labour and mutual dependence (and respect) of a taxonomic specialist and a community ecologist usually results in superior research and better prospects for grant funding.

I thank F. Bisby, R. Colwell, A. Ellison, E. Farnsworth, C. Godfray, G. Graves, J. Longino, P. O'Grady and an anonymous reviewer for comments that improved this manuscript. Supported by NSF awards DEB 0107403 and DEB 0234710.

REFERENCES

Ackerly, D. D. & Donoghue, M. J. 1995 Phylogeny and ecology reconsidered. *J. Ecol.* **83**, 730–733.

Agosti, D. & Johnson, N. E. 2002 Taxonomists need better access to published data. *Nature* **417**, 222.

Albrecht, M. & Gotelli, N. J. 2001 Spatial and temporal partitioning in grassland ants. *Oecologia* **126**, 134–141.

Albrecht, M. C. 1995 New species distributions of ants in Oklahoma, including a South American invader. *Proc. Oklahoma Acad. Sci.* **75**, 21–24.

Arnett, A. E. & Gotelli, N. J. 1999 Bergmann's Rule in the ant lion *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae): geographic variation in body size and heterozygosity. *J. Biogeogr.* **26**, 275–284.

Arnett, A. E. & Gotelli, N. J. 2000 Geographic variation in body size of the ant lion *Myrmeleon immaculatus*: evolutionary implications of Bergmann's Rule. *Evolution* **53**, 1180–1188.

Arnett, A. M. & Gotelli, N. J. 2001 Pit-building decisions of larval ant lions: effects of laval age, temperature, food and population source. *J. Insect Behav.* **14**, 89–97.

Arnett, A. E. & Gotelli, N. J. 2003 Bergmann's Rule in larval ant lions: testing the starvation resistance hypothesis. *Ecol. Entomol.* **28**, 645–650.

Bisby, F. A., Shimura, J., Ruggiero, M., Edwards, J. & Hauser, C. 2002 Taxonomy at the click of a mouse. *Nature* **418**, 367.

Bjorklund, M. 1997 Are 'comparative methods' always necessary? *Oikos* **80**, 607–612.

Blackmore, S. 2002 Biodiversity update—progress in taxonomy. *Science* **298**, 365.

Blakers, M., Davies, S. & Reilly, P. 1984 *The atlas of Australian birds*. Melbourne: Royal Australasian Ornithologists' Union.

Blaxter, M. 2003 Counting angels with DNA. *Nature* **421**, 122–124.

Blaxter, M. L. 2004 The promise of a DNA taxonomy. *Phil. Trans. R. Soc. Lond.* B **359**, 669–679. (DOI 10.1098/rstb.2003.1443.)

Bolton, B. 1994 *Identification guide to the ant genera of the world*. Cambridge: Harvard University Press.

Brown, J. H. 1995 *Macroecology*. University of Chicago Press.

Brown, J. H. & Lomolino, M. V. 1998 *Biogeography*, 2nd edn. Sunderland, MA: Sinauer.

Bunge, J. & Fitzpatrick, M. 1993 Estimating the number of species; a review. *J. Am. Statist. Assoc.* **88**, 364–373.

Cavender-Bares, J. & Wilczek, A. 2003 Integrating micro- and macroevolutionary processes in community ecology. *Ecology* **84**, 592–597.

Chao, A. 2004 Species richness estimation. In *Encyclopedia of statistical sciences* (ed. N. Balakrishnan, C. B. Read & B. Vidakovic). New York: Wiley. (In the press.)

Chown, S. L. & Gaston, K. J. 1999 Patterns in procellariiform diversity as a test of species-energy theory in marine systems. *Evol. Ecol. Res.* **1**, 365–373.

Colwell, R. K. 2000 *EstimateS: statistical estimation of species richness and shared species from samples* (software and user's guide), v. 6. See http://viceroy.eeb.uconn.edu/estimates.

Colwell, R. K. 2004 *Biota2: the biodiversity database manager*. Sunderland, MA: Sinauer Associates, Inc.

Colwell, R. K. & Coddington, J. A. 1994 Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond.* B **345**, 101–118.

Colwell, R. K. & Lees, D. L. 2000 The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* **15**, 70–76.

Colwell, R. K., Rahbek, C., & Gotelli, N. J. 2004 The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.* (In the press.)

Cornell, H. V. 1999 Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience* **6**, 303–315.

Crawley, M. J. & Harral, J. E. 2001 Scale dependence in plant biodiversity. *Science* **291**, 864–868.

Creighton, W. S. 1950 The ants of North America. *Bull. Mus. Comp. Zool.* **104**, 1–585.

Currie, D. J. 1991 Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* **137**, 27–49.

Cushman, J. H., Lawton, J. H. & Manly, B. F. J. 1993 Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* **95**, 30–37.

Denslow, J. 1995 Disturbance and diversity in tropical rain forests: the density effect. *Ecol. Applic.* **5**, 962–968.

Ellison, A. M. & Gotelli, N. J. 2002 Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*. *Proc. Natl Acad. Sci. USA* **99**, 4409–4412.

Ellison, A. M., Farnsworth, E. J. & Gotelli, N. J. 2002 Ant diversity in pitcher-plant bogs of Massachusetts. *Northeastern Nat.* **9**, 267–284.

Elton, C. 1946 Competition and the structure of ecological communities. *J. Anim. Ecol.* **15**, 54–68.

Enquist, B. J., Haskell, J. P. & Tiffney, B. H. 2002 General patterns of taxonomic and biomass partitioning in extant and fossil plant communities. *Nature* **419**, 610–613.

Erwin, T. L. & Johnson, P. J. 2000 Naming species, a new paradigm for crisis management in taxonomy: rapid validation of scientific names enhanced with more complete descriptions on the Internet. *Coleopterist's Bull.* **54**, 269–278.

Farnsworth, E. J. & Bazzaz, F. A. 1995 Inter- and intra-generic differneces in growth, reproduction, and fitness of nine herbaceous annual speices grown in elevated CO_2 environments. *Oecologia* **104**, 454–466.

Freckleton, R. P., Harvey, P. H. & Pagel, M. 2003 Phylogenetic analysis and comparative data: a test and review of the evidence. *Am. Nat.* **160**, 712–726.

Froese, R., Bisby, F. A. & Wilson, K. L. (eds) 2003 *Species 2000 & IT IS catalogue of life 2003: indexing the world's known species*. Los Baños, Philippines: Species 2000.

Gaston, K. J. 2000 Global patterns in biodiversity. *Nature* **405**, 220–227.

Gewin, V. 2002 All living things, online. *Nature* **418**, 361–362.

Gibbons, D. W., Reid, J. B. & Chapman, R. A. 1993 *The new atlas of breeding birds in Britain and Ireland: 1988–1991*. London: Poyser.

Godfray, H. C. J. 2002 Challenges for taxonomy. *Nature* **417**, 16–19.

Gotelli, N. J. 1993 Antlion zones: causes of high-density predator aggregations. *Ecology* **74**, 226–237.

Gotelli, N. J. 1996 Ant community structure: effects of predatory ant lions. *Ecology* **77**, 630–638.

Gotelli, N. J. 1997 Competition and coexistence of larval ant lions. *Ecology* **78**, 1761–1773.

Gotelli, N. J. 2001 Research frontiers in null model analysis. *Global Ecol. Biogeogr.* **10**, 337–343.

Gotelli, N. J. & Abele, L. G. 1982 Statistical distributions of West Indian land bird families. *J. Biogeogr.* **9**, 421–435.

Gotelli, N. J. & Arnett, A. E. 2000 Biogeographic effects of red fire ant invasion. *Ecol. Lett.* **3**, 257–261.

Gotelli, N. J. & Colwell, R. K. 2001 Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391.

Gotelli, N. J. & Ellison, A. M. 2002*a* Nitrogen deposition and extinction risk in the northern pitcher plant, *Sarracenia purpurea*. *Ecology* **83**, 2758–2765.

Gotelli, N. J. & Ellison, A. M. 2002*b* Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. *Ecology* **83**, 1604–1609.

Gotelli, N. J. & Ellison, A. M. 2002*c* Assembly rules for New England ant assemblages. *Oikos* **99**, 591–599.

Gotelli, N. J. & Entsminger, G. L. 2003 *Ecosim: null models software for ecology*, v. 8.0. Jericho, VT: Acquired Intelligence Inc, & Kesey-Bear. See http://homepages.together.net/gentsmin/ecosim.htm.

Gotelli, N. J. & Graves, G. R. 1990 Body size and the occurrence of avian species on land-bridge islands. *J. Biogeogr.* **17**, 315–325.

Gotelli, N. J. & Graves, G. R. 1996 *Null models in ecology*. Washington, DC: Smithsonian Institution Press.

Gotelli, N. J., Buckley, N. J. & Wiens, J. A. 1997 Co-occurrence of Australian land birds: Diamond's assembly rules revisited. *Oikos* **80**, 311–324.

Graves, G. R. & Gotelli, N. J. 1983 Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. *Oikos* **41**, 322–333.

Graves, G. R. & Gotelli, N. J. 1993 Assembly of avian mixed species flocks in Amazonia. *Proc. Natl Acad. Sci. USA* **90**, 1388–1391.

Grytnes, J. A. 2003 Species-richness patterns of vascular plants along several altitudinal transects in Norway. *Ecography* **26**, 291–300.

Grytnes, J. A. & Vetaas, O. R. 2002 Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am. Nat.* **159**, 294–304.

Hagerdorn, G. & Rambold, G. 2000 A method to establish and revise descriptive data sets over the Internet. *Taxon* **49**, 517–528.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford series in ecology and evolution (ed. R. M. May & P. H. Harvey). Oxford University Press.

Harvey, P. H., Reed, A. F. & Nee, S. 1995 Why ecologists need to be phylogenetically challenged. *J. Ecol.* **83**, 535–536.

Harvey, P. H., Leigh Brown, A. J., Maynard Smith, J. & Nee, S. (eds) 1996 *New uses for new phylogenies*. Oxford University Press.

Hebert, P. D. N., Cywinska, A., Ball, S. L. & DeWaard, J. R. 2003 Biological identifications through DNA barcodes. *Proc. R. Soc. Lond.* B **270**, 313–321. (DOI 10.1098/rspb.2002.2218.)

Heck Jr, K. L., Van Belle, G. & Simberloff, D. 1975 Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* **56**, 1459–1461.

Hölldobler, B. & Wilson, E. O. 1990 *The ants*. Cambridge: Belknap.

Hopkins, G. W. & Freckleton, R. P. 2002 Declines in the numbers of amateur and professional taxonomists: implications for conservation. *Anim. Conserv.* **5**, 245–249.

Hubbell, S. P. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Hughes, L., Cawsey, E. M. & Westoby, M. 1996 Climatic range sizes of *Eucalyptus* species in relation to future climate change. *Global Ecol. Biogeogr. Lett.* **5**, 23–29.

James, F. C. & Wamer, N. O. 1982 Relationships between temperate forest bird communities and vegetation structure. *Ecology* **63**, 159–171.

Janz, N., Nyblom, K. & Nylin, S. 1998 Butterflies and plants: a phylogenetic study. *Evolution* **52**, 486–502.

Järvinen, O. 1982 Species-to-genus ratios in biogeography: a historical note. *J. Biogeogr.* **9**, 363–370.

Jetz, W. & Rahbek, C. 2001 Geometric constraints explain much of the species richness pattern in African birds. *Proc. Natl Acad. Sci. USA* **98**, 5661–5666.

Kang, S. C. (and 13 others) 2002 The Internet-based fungal pathogen database: a proposed model. *Phytopathology* **92**, 232–236.

Kaspari, M. 2001 Taxonomic level, trophic biology and the regulation of local abundance. *Global Ecol. Biogeogr.* **10**, 229–244.

Kaspari, M., O'Donnell, S. & Kercher, J. R. 2000 Energy, density, and constraints to species richness: studies of ant assemblages along a productivity gradient. *Am. Nat.* **155**, 280–293.

Kendall, M. A., Paterson, G. L. J. & Aryuthaka, C. 2000 Online exchange of polychaete taxonomic information. *Bull. Mar. Sci.* **67**, 411–420.

Knapp, S. 2000 What's in a name? *Nature* **408**, 33.

Knapp, S., Bateman, R. M., Chalmers, N. R., Humphries, C. J., Rainbow, P. S., Smith, A. B., Taylor, P. D., Vane-Wright, R. I. & Wilkinson, M. 2002 Taxonomy needs evolution, not revolution. *Nature* **419**, 559.

Lee, M. S. Y. 2000 Online database could end taxonomic anarchy. *Nature* **417**, 787–788.

Liebherr, J. K. & Hajek, A. E. 1990 A cladistic test of the taxon cycle and taxon pulse hypotheses. *Cladistics* **6**, 39–59.

Longino, J. T. & Colwell, R. K. 1997 Biodiversity assessment using structured inventory: capturing the ant fauna of a lowland tropical rainforest. *Ecol. Applic.* **7**, 1263–1277.

Longino, J., Colwell, R. K. & Coddington, J. A. 2002 The ant fauna of a tropical rainforest: estimating species richness three different ways. *Ecology* **83**, 689–702.

Losos, J. B. 1996 Phylogenetic perspectives on community ecology. *Ecology* **77**, 1344–1354.

Losos, J. B., Jackman, T. R., Larson, A., De Queiroz, K. & Rodriguez-Schettino, L. 1998 Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118.

Lucas, J. R. & Stange, L. A. 1981 Key and descriptions to the Myrmeleon larvae of Florida (Neuroptera: Myrmeleontidae). *Florida Entomol.* **64**, 208–216.

Lyons, S. K. & Willig, M. R. 1999 A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* **80**, 2483–2491.

McPeek, M. A. & Miller, T. E. 1996 Evolutionary biology and community ecology. *Ecology* **77**, 1319–1320.

Magurran, A. E. 2003 *Measuring biological diversity*. Oxford: Blackwell Press.

Mallet, J. & Willmott, K. 2003 Taxonomy: renaissance or Tower of Babel? *Trends Ecol. Evol.* **18**, 57–59.

Morin, P. J. 1999 *Community ecology*. Malden, MA: Blackwell Science.

Olmstead, R. G., DePamphilis, C. W., Wolfe, A. D., Young, N. D., Elisons, W. J. & Reeves, P. A. 2001 Disintegration of the Scrophulariaceae. *Am. J. Bot.* **88**, 348–361.

Paine, R. T. 1994 *Marine rocky shores and community ecology: an experimentalist's perspective.* Excellence in ecology series (ed. O. Kinne), book 4. Luhe, Germany: International Ecology Institute.

Palmer, M. W. 1990 The estimation of species richness by extrapolation. *Ecology* **71**, 1195–1198.

Parmesan, C. (and 12 others) 1999 Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583.

Peet, R. K. 1974 The measurement of species diversity. *A. Rev. Ecol. Syst.* **5**, 285–307.

Peterson, A. T., Ortega-Huerta, M. A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R. H. & Stockwell, D. R. B. 2002*a* Future projections for Mexican faunas under global climate change scenarios. *Nature* **416**, 626–629.

Peterson, A. T., Stockwell, D. R. B. & Kluza, D. A. 2002*b* Distributional prediction based on ecological niche modeling of primary occurrence data. In *Predicting species occurrences: issues of accuracy and scale* (ed. J. Michael Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall & F. B. Samson), pp. 617–623. Washington, DC: Island Press.

Pineda, J. & Caswell, H. 1998 Bathymetric species-diversity patterns and boundary constraints on vertical range distributions. *Deep Sea Res. II* **45**, 83–101.

Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. 1999 Biological response to climate change on a tropical mountain. *Nature* **398**, 611–615.

Rahbek, C. 1995 The elevational gradient of species richness: a uniform pattern? *Ecography* **18**, 200–205.

Rahbek, C. & Graves, G. R. 2000 Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proc. R. Soc. Lond.* B **267**, 2259–2265. (DOI 10.1098/rspb.2000.1277.)

Ricklefs, R. E. & Bermingham, E. 2002 The concept of the taxon cycle in biogeography. *Global Ecol. Biogeogr.* **11**, 353–361.

Ricklefs, R. E. & Schluter, D. (eds) 1993 *Species diversity in ecological communities*. University of Chicago Press.

Ricklefs, R. E. & Starck, J. M. 1996 Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* **77**, 167–172.

Ricklefs, R. E., Latham, R. E. & Qian, H. 1999 Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos* **86**, 369–373.

Rohde, K. 1992 Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweigk, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60.

Rosenzweig, M. L. 1995 *Species diversity in space and time*. New York: Cambridge University Press.

Roy, K., Jablonski, D., Valentine, J. W. & Rosenberg, G. 1998 Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl Acad. Sci. USA* **95**, 3699–3702.

Sagarin, R. D., Berry, J. P., Gilman, S. E. & Baxter, C. H. 1999 Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.* **69**, 465–490.

Sanders, H. 1968 Marine benthic diversity: a comparative study. *Am. Nat.* **102**, 243–282.

Schluter, D. 2000 *The ecology of adaptive radiation*. Oxford University Press.

Sharrock, J. T. R. 1976 *The atlas of breeding birds in Britain and Ireland*. Berkhamsted: Poyser.

Shen, T.-J., Chao, A. & Lin, C.-F. 2003 Predicting the number of new species in further taxonomic sampling. *Ecology* **84**, 798–804.

Simberloff, D. 1970 Taxonomic diversity of island biotas. *Evolution* **24**, 23–47.

Smith, G. F., Steenkamp, Y., Klopper, R. R., Siebert, S. J. & Arnold, T. H. 2003 The price of collecting life. *Nature* **422**, 375–376.

Soberón, J. & Peterson, A. T. 2004 Biodiversity informatics: managing and applying primary biodiversity data. *Phil. Trans. R. Soc. Lond.* B **359**, 689–698. (DOI 10.1098/rstb.2003.1439.)

Sokal, R. R. & Rohlf, F. J. 1995 *Biometry*, 3rd edn. New York: Freeman.

Struder-Kypke, M. C. & Montagnes, D. J. S. 2002 Development of web-based guides to planktonic protists. *Aquatic Microbial Ecol.* **27**, 203–207.

Thiele, K. & Yeates, D. 2002 Tension arises from duality at the heart of taxonomy. *Nature* **419**, 337.

Thomas, C. D. & Lennon, J. J. 1999 Birds extend their ranges northward. *Nature* **399**, 213.

Tipper, J. C. 1979 Rarefaction and rarefiction—the use and abuse of a method in paleoecology. *Paleobiology* **5**, 423–434.

Tofts, R. & Silvertown, J. 2000 A phylogenetic approach to community assembly from a local species pool. *Proc. R. Soc. Lond.* B **267**, 363–369. (DOI 10.1098/rspb.2000.1010.)

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P. & Parmenter, R. 1999 The relationship between productivity and species richness. *A. Rev. Ecol. Syst.* **30**, 257–300.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395.

Webb, C. 2000 Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* **156**, 145–155.

Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. 2002 Phylogenies and community ecology. *A. Rev. Ecol. Syst.* **33**, 475–505.

Westoby, M., Leishman, M. R. & Lord, J. M. 1995 On misinterpreting the 'phylogenetic correction'. *J. Ecol.* **83**, 531–534.

Wiens, J. A. 1989 *The ecology of bird communities*. Cambridge studies in ecology series (ed. R. S. K. Barnes, H. J. B. Birks, E. F. Connor & R. T. Paine). Cambridge University Press.

Williams, C. B. 1964 *Patterns in the balance of nature*. New York: Academic.

Williamson, M., Gaston, K. J. & Lonsdale, W. M. 2001 The species-area relationship does not have an asymptote! *J. Biogeogr.* **28**, 827–830.

Wilson, E. 2000 O. 2000 A global biodiversity map. *Science* **28**, 2279.

GLOSSARY

ITIS: Integrated Taxonomic Information System

MCZ: Museum of Comparative Zoology (Harvard University)