





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 (2002) 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.

### ( ) *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; McPeck & Miller 1996; Webb 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 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 1998), adaptive radiation (Schluter 2000) and coevolution (Janz 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 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 2003), and comparative methods no longer imply a simplistic partitioning of variation into phylogenetic and ecological components (Ackerly & Donoghue 1995; Harvey 1995). To test historical and evolutionary hypotheses, community ecologists ideally need fully resolved phylogenies, preferably with estimates of branch lengths (Harvey 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.

#### ( ) *Taxonomic keys*

We need well-written taxonomic keys based on morpho-



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.

#### ( ) *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 1997), the ecologist John Wiens provided designations of ecological guilds of closely related species, based on the species lists in Blakers (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 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 Com3efFdivftZo042 ali803 sn1 (27f)7(USAilief)-8bef7.5(more)]TJ0-1.204210.9(2e,)-380vasregat2

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 biogeograph-

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.





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.

( ) ***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



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## GLOSSARY

- ITIS: Integrated Taxonomic Information System  
MCZ: Museum of Comparative Zoology (Harvard University)