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SYMPOSIUM INTRODUCTION

Measuring Biodiversity and Extinction—Present and Past

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Synopsis How biodiversity is changing in our time represents a major concern for all organismal biologists. Anthropogenic changes to our planet are decreasing species diversity through the negative effects of pollution, habitat destruction, direct extirpation of species, and climate change. But major biotic changes—including those that have both increased and decreased species diversity—have happened before in Earth's history. Biodiversity dynamics in past eras provide important context to understand ecological responses to current environmental change. The work of assessing biodiversity is woven into ecology, environmental science, conservation, paleontology, phylogenetics, evolutionary and developmental biology, and many other disciplines; yet, the absolute foundation of how we measure species diversity depends on taxonomy and systematics. The aspiration of this symposium, and complementary contributed talks, was to promote better understanding of our common goals and encourage future interdisciplinary discussion of biodiversity dynamics. The contributions in this collection of papers bring together a diverse group of speakers to confront several important themes. How can biologists best respond to the urgent need to identify and conserve diversity? How can we better communicate the nature of species across scientific disciplines? Where are the major gaps in knowledge about the diversity of living animal and plant groups, and what are the implications for understanding potential diversity loss? How can we effectively use the fossil record of past diversity and extinction to understand current biodiversity loss?

Introduction

The study of biological diversity is nearly synonymous with the challenge of describing the myriad aspects of the complexity of natural systems. Biodiversity has many dimensions, including taxonomic, functional, and morphological variations, and can therefore encompass energy flow, spatial complexity, trophic linkages, genetic diversity, phylogenetic complexity, and functional traits. Yet, ultimately, all of these components describe the traits of species. Biodiversity describes the diversity of species. But it is not only a list of taxa, nor the distribution of species in space; biodiversity also incorporates temporal variability in the short term (ecological changes) and long term (e.g., reconstructed phylogeny, biogeography, and associated aspects of macroevolution). One critically important underlying question is to what extent are we confident in identifying species, or any other metrics used for quantifying aspects of biodiversity. If there is any potential error in identification, how does that affect different assessments of communities, organisms, or ecosystems in space and time? The papers in this volume address the ways that these issues of species identification, traits, and evolution, underpin cross-cutting questions in organismal biology.

Everyone uses species. Yet, there are several cross-cutting dichotomies that partition our perception of biological diversity and its complexity, and the papers in this volume explore these themes and the

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implications for understanding biodiversity (Table 1). While all biologists are users of species names, specialists in systematics and taxonomy are the makers of names. These name-making disciplines sit at the frontiers of discovery of new species. Species names are shorthand for hypotheses about the identity of evolutionary lineages. Systematists, in articulating these hypotheses, are more concerned than most biologists in defining the boundaries of species identity, and the many layers of accompanying uncertainty. The goal of taxonomy is to use whatever relevant evidence is available to produce a total evidence approach to identify evolutionary lineages that represent species and species groups (Winston 1999); in modern taxonomy, this incorporates a balance of natural history, morphology, and molecular data for living species. The reality of evolution is that species are continuously responding to abiotic and biotic challenges and so may be in flux at any given time (Thompson 1999). Conversely, users of names expect an unambiguous, stable, and useable diagnosis for each species they want to identify.

Another dichotomy, which is perhaps less appreciated but more divisive, is the stark difference between the minority of well-studied taxa and systems (such as birds and mammals, and the flora and fauna of Western Europe), and the overwhelming majority of under-studied systems, organisms, and clades. It is well known that described species represent a small fraction of species that are currently extant (Mora et al. 2011). The problem of undescribed and unrecognized biodiversity is compounded by natural loss through unequal preservation in the fossil record. Among living species, however, some groups really are very well known and well described; nearly all of the estimated 10,000 living bird species have been described and named, as have the majority of mammal species. Nevertheless, as iconic animals, rare discoveries of undescribed terrestrial mammals or birds cause excitement among scientists and the general public. By contrast, there is huge uncertainty about species diversity in fungi: only about 100,000 species have been named, yet global species richness might extend to 1 million, 2.5 million, or 10 million living species (Blackwell 2011). New discoveries of terrestrial insects occupy whole journals. Marine diversity, similarly, has relatively high levels of uncertainty and very high discovery potential. Scientists who work on poorly known groups and systems are familiar with enormous frustrations that come with simply identifying their study species, or responding to comments from peer reviewers who expect an unrealistic resolution of data. For example, there are around 200 species of mammals for which whole genome assemblies have been published (National Center for Biotechnology Information [NCBI] 2018)—a tiny fraction of living diversity, yet a greater level of sampling than any other animal group. In contrast, there are six partial genome assemblies for annelids, a phylum with some 220,000 species of marine, terrestrial, and freshwater annelids (Fig. 1).

The few groups of organisms that are taxonomically "saturated" in the living biota (meaning that the rate of discovery or species accumulation curves have reached a plateau) provide our baseline for assumptions about what species are, how species are diagnosed, and how species lineages evolve. A few model organisms or systems from less well-known clades contribute to understanding evolution (e.g., *Aplysia*, *Caenorhabditis*), but the pervasive dominance of a few groups shape the accepted standards of assessing species diversity, in ways that are often more implicit than explicit (Sigwart and Garbett 2018). Mammals and especially birds are thus uniquely positioned as systematics role models for other less-studied clades (Mayr 1942). Elegant studies of speciation in well-described systems provide aspirational models for examining other clades in which species are less well known. However, it is not at all clear that the evolutionary mechanisms that control lineage dynamics in this small fraction of well-described biological diversity are a good or adequate guide to infer general species dynamics or to capture the beautiful complexity of the whole of organismal life.

Species are the currency of biodiversity

Naming things is intrinsic to humanity, and names form part of our communication from infancy. It is important that we have relevant labels to identify and communicate about other species (Winston 1999). In science, we can differentiate among taxonomy (the science of identifying species) and nomenclature (giving names to lineages and their members) and systematics (categorizing lineages into evolutionary groups or clades). Digital communications have precipitated revolutionary changes in science, including systematics, and in the international codes used in creating and regulating scientific names (Winston 2018).

We face a daunting scientific challenge to understand the diversity of life on Earth, and it seems obvious that we might look to technology to make this problem easier to solve. Molecular data play important roles in taxonomy and phylogenetics, but

Table 1 We identify two primary dichotomies in the study and application of biodiversity: the division between the focus of makers of names, and other users of names, and the division between relatively well-studied groups of organisms or ecosystems and more poorly known groups and systems

	Name makers	Name users
Well known	• Birds and mammals (other vertebrates are close behind) • Some regional floras and faunas (e.g., Western Europe) • Some groups of insects (e.g., butterflies)	• (Macro-) Ecology (keystone and dominant species) • Conservation biology (IUCN Red List species) • Ecotourism • Bird watching • Biogeography • Evolutionary biology • Developmental biology • Agro-ecology and commercial exploitation (e.g., timber, food plants and animals, and aquaculture) • Diseases and vectors • Phylogenetics • Macroevolution • Systematics (are users, too)
Poorly known	• Tropical diversity • Invertebrate animals (including most insect groups) • Marine systems (especially deep sea and polar regions) • Fungi • Microbes • Parasites • Extinct plants and animals • Most micro-organisms not known to be related to human health and disease (algae, bacteria, protists, and unicellular parasites)	• Ecology (knowledge of all species in ecosystems) • Environmental impact assessments • Toxicology • Macro-ecology • Biogeography • Evolutionary biology • Developmental biology • Conservation (majority threatened species) • Commerce/biomimicry (potentially useful, but unknown species) • Pathology and parasitology • Food security • Human health

Most scientists who work on biodiversity have a reference frame from within one of these four panels, which can shape our perspective on how biodiversity and extinction are assessed. The needs and interests of users transcend the limits of available data for organismal groups.

can never replace certain benefits of traditional descriptive work such as field identifications, character level details of evolutionary history, or clues for nature-inspired sustainable solutions to meet human needs (Wheeler 2018). A fusion of taxonomic goals with information science has promise to increase the efficiencies of both creating and using descriptive taxonomic knowledge (Wheeler 2008). Descriptive science is essential to understanding evolution and the development of phenotype, as much as the identification of species *per se*. Additional tools, from DNA to digital instrumentation, contribute both to the establishment of multiple lines of evidence often needed to identify and differentiate species, and digital improved communications can help us to break down the barriers we have identified between different makers and users of species names (Table 1). Species discovery requires the fine details—not just of "charismatic megafauna" but hidden interstitial organisms, microbes, and parasites (Okamura et al. 2018)—and clever evaluation of whether known diversity trends may predict where diversity is hiding.

New large-scale patterns emerge from analyses that are only possible with the resources assembled by digital clearing-house projects that centralize resources for molecular data (e.g., NCBI, GenBank, Barcode of Life Data System) or taxonomic data (Costello et al. 2013; Burgin et al. 2018). Using these kinds of data projects, recent work has shown that there are universal patterns in in the distribution of species among clades, at least at the genus level, and these observed patterns in taxonomy are a predictable outcome of phylogenetic patterns (Sigwart et al. 2018). Species richness of a genus, however,

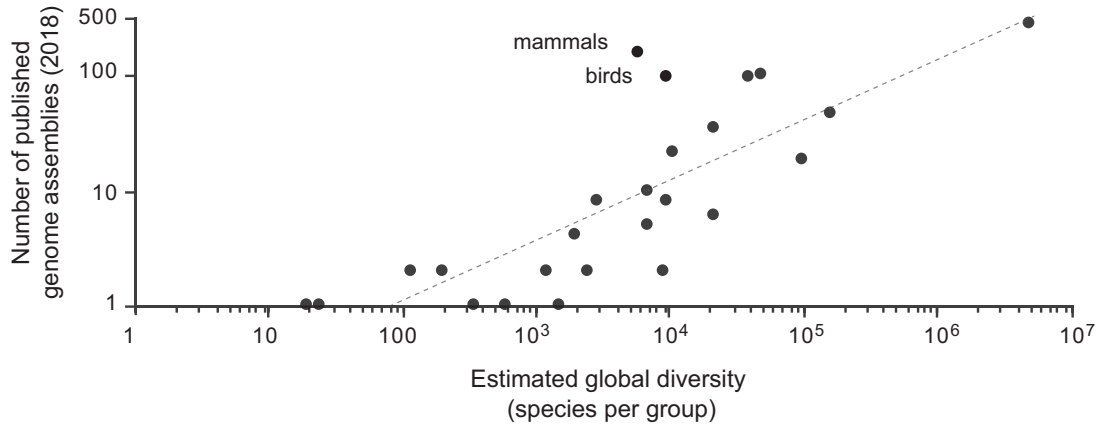

Fig. 1 Comparison of global animal diversity and published genome sequencing efforts to date (data from NCBI 2018). Groups shown include all currently reported genome assemblies for birds ($n = 96$ genomes), mammals (157), amphibians (5), fishes (102), flatworms (platyhelminths; 35), insects (277), reptiles (21), roundworms (nematodes; 93), and those classified by NCBI as "other animals" (116 genomes in total): non-vertebrate Chordata (8), non-insect Arthropoda (45), Annelida (6), Brachiopoda (1), Cephalorhyncha (Scalidophora; 1), Cnidaria (8), Ctenophora (2), Echinodermata (10), Hemichordata (2), Mollusca (18), Myxozoa (4), Nemertea (1), Orthonectida (1), Phoronida (1), Porifera (2), Rotifera (2), and Tardigrada (2). Those that fall below the regression line could be viewed as comparatively under-sampled for genomic data. Well-studied groups, particularly mammals and birds, have dramatically greater availability of genomic data in comparison to their global species richness.

is not connected to genetic diversity in a straightforward way. Genetic "diversity" in taxonomic terms usually means the divergence of sequence fragments used in phylogenetic reconstruction, rather than any more detailed population-level metrics. The divergence of DNA barcode sequences is much more constrained in vertebrates than invertebrate animals (Sigwart and Garbett 2018). This may be a product of differing evolutionary histories, rates of molecular divergence, or different sampling effort, but stark differences between animal groups highlight how well-studied groups may not provide an appropriate null model for expectations of evolution in other clades.

The challenge for understanding diversity and evolutionary history increases with the "data gap" or the level of missing data in the study of a clades or functional groups. Molecular identification of taxa has revealed an increasing number of parasite lineages (Hartikainen et al. 2014, 2016; de Vargas et al. 2015). In many cases, widespread "species" turn out to be a set of separate lineages, with each associated with a specific host organism (Poulin 2014). Parasites contribute substantially to global biodiversity (Okamura et al. 2018) but their diversity is grossly underestimated. Research on parasites is highly biased, mostly focusing on helminths and arthropods in circumscribed regions of the world. Global parasite diversity cannot be approximated by extrapolations based on local diversities of the few relatively well-known taxa in particular regions. Recent demonstration that a previously enigmatic group (the Myxozoa) is major clade of endoparasitic cnidarians (Jiménez-Guri et al. 2007) illustrates how rapid rates of evolution, adaptation to parasitism, and the hidden nature of parasites can obscure appreciating and evaluating parasite biodiversity even at relatively high taxonomic levels within the Metazoa in the present day (Okamura et al. 2018). Accounting for and valuing this parasite diversity is important as parasites substantially contribute to ecosystem dynamics. However, rates of parasite extinction may be particularly high as co-extinction of affiliate (dependent) species is proposed to be the most common form of present and future species loss for these organisms (Dunn et al. 2009).

Extinction threats to living biota are relatively poorly assessed. While the risks to a few iconic species are well known, the majority of named species have never been assessed according to IUCN criteria. Quantitative work on extinction must confront a historical assumption that, for example, small, cryptic land snails are widespread (Yeung and Hayes 2018) and less threatened than their more brightly-colored relatives. Larger, more brightly-colored and conspicuous species are better-studied and their biogeography and dispersal relatively more fully understood, yet better camouflaged species represent the majority proportion of species richness. These data gaps lead to under-estimation of human impacts, which in turn impact the public's perception of, and potential funding for, biodiversity discovery and analysis that are critical for developing conservation strategies (Yeung and Hayes 2018).

The highest diversity in today's terrestrial environments occurs in tropical rainforests, and understanding the origin and geological history of these ecosystems is crucial in order to unravel the long-term controls on the biogeographical evolution of terrestrial biodiversity. One approach is to use molecular clock estimates from phylogeny, which can indicate the origination of clades that are major components of modern tropical rainforests such as in one of the largest orders of flowering plants, the Malpighiales (Davis et al. 2005). However, the presence of particular lineages does not necessarily mean that they were assembled into a forest that looked like (or was functionally equivalent to) an extant tropical rainforest. An alternative method is to use fossils to provide empirical data on ancient vegetation diversity and composition in the tropics. Although estimates of taxonomic, morphological, and functional diversity often disagree (Mander 2018), both plant macrofossils such as leaves and reproductive structures (Wing et al. 2009) and microfossils such as pollen grains (Jaramillo et al. 2006) indicate that tropical vegetation diversity has fluctuated considerably over the last 50 million-years (My), perhaps in association with global temperature (Jaramillo et al. 2006). Fossils highlight that tropical rainforests do not steadily and unfailingly accumulate diversity as time progresses. An on-going challenge is to use data from the fossil record to constrain molecular estimates of extinction rates in the tropics: a vital concern in the context of the present day climate and biodiversity crises.

The best available context for current extinction is comparison with shifts in biodiversity over geologic time, and this has spurred the recognition of the present era by some scientists as a "sixth mass extinction" (Barnosky et al. 2011). The five earlier "mass extinctions" were first identified based on the fossil record of hard-shelled marine invertebrates, considered in terms of family-level taxonomic diversity (Raup and Sepkoski 1982). Ongoing studies have demonstrated that there are clear differences in terrestrial and marine environments during these periods of relatively sudden biodiversity loss. Importantly, there is a background rate of extinction, and the rate of species origination also varies through geologic time. In some cases the loss of diversity is more dependent on lack of speciation than the sudden removal of lineages through extinction. Past "mass extinctions" may be better termed diversity crises (Padian 2018). There are limitations to the comparative potential of past diversity crises and the unprecedented current human-driven extinctions.

Climate and biodiversity have varied both globally and locally through Earth's history, and the extent to which those changes are correlated can inform expectations of biodiversity change under current climate stresses. Through the last 66 My, marine bivalves—one of the hard-shelled marine invertebrate groups that was key to the initial identification of past "mass extinction" events—suffered greater extinction during periods of large absolute changes in temperature and through periods where temperature was changing rapidly (Edie et al. 2018a). The functional variety of bivalves, which is not necessarily linked directly to their taxonomy, also shows climatically-mediated turnover today and through time. Major marine invertebrate mass extinctions, however, dramatically reduce taxonomic diversity but leave functional diversity virtually intact (Edie et al. 2018b)—a scenario that deserves more attention in light of today's compounding climatic and non-climatic factors. Whether the taxonomic and functional consequences of future biotic changes will more closely resemble ancient mass extinctions, or shifts along current diversity gradients, remains an open question.

Changing climate is a dominant issue in current biodiversity studies, yet climatic oscillations on timescales of 20–100 Ky (forced by Earth's orbital variations) are a permanent feature of the planet. Lack of accurate relative and absolute timescales of evolution and environmental change precluded analysis of their interactions until the late 20th century. However, it is now clear that evolutionary radiations of many groups have proceeded independently of fluctuations in climate (Bennett 2013).

Conclusion

The current biodiversity crisis demands urgent attention to identify and conserve diversity. Biologists—including name-users and name-makers—can respond to this need more effectively with diligent attention to species diversity and functional diversity. Understudied species represent the majority of biodiversity; the overlooked may be the most vulnerable or even the most valuable. The major gaps in knowledge about the diversity of living organismal groups are relatively well understood, in that the well-studied groups are mainly terrestrial free-living vertebrates. Most importantly, these well-studied groups comprise a very small and evolutionarily recently-derived portion of the total diversity of species. Although we have some understanding of the geographical, functional, morphological, and genetic patterns in one dominant minority (vertebrates), this provides a lopsided view. We have no

adequate roadmap to make conclusions about the current diversity of organisms, phenotypes, communities, and ecosystems. Large-scale emergent patterns in taxonomic data provide important null models for hypotheses about the distribution of diversity over space and time. The latitudinal diversity gradient—the observation that most diversity occurs at tropical latitudes—is one important guide to where discovery gaps are greatest (Edie et al. 2017). The challenge now is how to expand our horizons and incorporate the many little known, poorly appreciated, non-iconic, and other simply understudied groups to arrive at a more comprehensive view of biodiversity. This is likely to require application of molecular tools, large-scale analyses, quantitative analysis of the fossil record, a focus on representative taxa, and careful extrapolation. Although past changes in biodiversity may not represent a direct proxy for understanding how biodiversity will respond to current global threats, examination of the fossil record during periods of environmental change may enable some understanding of patterns of extinction and diversification that will be informative for evaluating future biodiversity trends and patterns.

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References

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–7.

Bennett KD. 2013. Is the number of species on Earth increasing or decreasing? Time, chaos and the origin of species. Palaeontol 56:1305–25.

Blackwell M. 2011. The fungi: 1, 2, 3... 5.1 million species? Am J Bot 98:426–38.

Burgin CJ, Colella JP, Kahn PL, Upham NS. 2018. How many species of mammals are there? J Mammal 99:1–14.

Costello MJ, Bouchet P, Boxshall G, Fauchald K, Gordon D, Hoeksema BW, Poore GC, van Soest RW, Stöhr S, Walter TC, et al. 2013. Global coordination and standardisation in marine biodiversity through the World Register of Marine Species (WoRMS) and related databases. PLoS One 8:e51629.

Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. Am Nat 165:E36–65.

Dunn RR, Harris NC, Colwell RK, Koh LP, Sodhi NS. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proc Biol Sci 276:3037–45.

Edie SM, Huang S, Collins KS, Roy K, Jablonski D. 2018a. Loss of biodiversity dimensions through shifting climates and ancient mass extinctions. Integr Comp Biol published online.

Edie SM, Jablonski D, Valentine JW. 2018b. Contrasting responses of functional diversity to major losses in taxonomic diversity. Proc Natl Acad Sci U S A 115:732–7.

Edie SM, Smits PD, Jablonski D. 2017. Probabilistic models of species discovery and biodiversity comparisons. Proc Natl Acad Sci U S A 114:3666–71.

Hartikainen H, Ashford OS, Berney C, Okamura B, Feist SW, Baker-Austin C, Stentiford GD, Bass D. 2014. Lineage specific molecular probing reveals novel diversity and ecological partitioning of haplosporidians. ISME J 8:177–86.

Hartikainen H, Bass D, Briscoe AG, Knipe H, Green AJ, Okamura B. 2016. Assessing myxozoan presence and diversity using environmental DNA. Int J Parasitol 46:781–92.

Jaramillo C, Rueda MJ, Mora G. 2006. Cenozoic plant diversity in the Neotropics. Science 311:1893–96.

Jiménez-Guri E, Philippe H, Okamura B, Holland PWH. 2007. *Buddenbrockia* is a cnidarian worm. Science 317:116–8.

Mander L. 2018. The latitudinal distribution of morphological diversity among Holocene angiosperm pollen grains from eastern North America and the Neotropics. Integr Comp Biol published online (doi:10.1093/icb/icy097).

Mayr E. 1942. Systematics and the origin of species, from the viewpoint of a zoologist. Cambridge (MA): Harvard University Press.

Mora C, Tittensor DP, Adl S, Simpson AG, Worm B. 2011. How many species are there on Earth and in the ocean? PLoS Biol 9:e1001127.

National Center for Biotechnology Information [NCBI]. 2018. Genome Information by Organism (ncbi.nlm.nih.gov/genome, retrieved April 2018).

Okamura B, Hartigan A, Naldoni J. 2018. Extensive uncharted biodiversity: the parasite dimension. Integr Comp Biol published online (doi:10.1093/icb/icy039).

Padian K. 2018. Measuring and comparing extinction events: reconsidering diversity crises and concepts. Integr Comp Biol published online (doi:10.1093/icb/icy084).

Poulin R. 2014. Parasite biodiversity revisited: frontiers and constraints. Int J Parasitol 44:581–89.
Raup DM, Sepkoski JJ. 1982. Mass extinctions in the marine fossil record. Science 215:1501–3.
Sigwart JD, Garbett A. 2018. Biodiversity assessment, DNA barcoding, and the minority majority. Integr Comp Biol published online (doi:10.1093/icb/icy076).
Sigwart JD, Sutton MD, Bennett KD. 2018. How big is a genus? Towards a nomothetic systematics. Zool J Linn Soc 183:237–52.
Thompson JN. 1999. Specific hypotheses on the geographic mosaic of coevolution. Am Nat 153:S1–14.
de Vargas C, Audic S, Henry N, Decelle J, Mahé F, Logares R, Lara E, Berney C, Le Bescot N, Probert I, et al. 2015. Eukaryote plankton diversity in the sunlit ocean. Science 348:1261605.
Wheeler QD. 2008. Chapter 10: taxonomic shock and awe. In: Wheeler QD, editor. The new taxonomy. London: Taylor and Francis. p. 211–26.
Wheeler QD. 2018. Blank canvas: the case for descriptive taxonomy. Integr Comp Biol published online (doi:10.1093/icb/icy067).
Wing SL, Herrera F, Jaramillo CA, Gomez-Navarro C, Wilf P, Labandeira CC. 2009. Late Paleocene fossils from the Cerrejon Formation, Colombia, are the earliest record of Neotropical rainforest. Proc Natl Acad Sci U S A 106:18627–32.
Winston JE. 1999. Describing species: practical taxonomic procedure for biologists. New York (NY): Columbia University Press.
Winston JE. 2018. 21st Century biological nomenclature—The enduring power of names. Integr Comp Biol published online (https://doi.org/10.1093/icb/icy060).
Yeung NW, Hayes K. 2018. Biodiversity and extinction of Hawaiian land snails: how many are left now and what must we do to conserve them—a reply to Solem. Integr Comp Biol published online (https://doi.org/10.1093/icb/icy043).