ISRAEL JOURNAL OF ECOLOGY & EVOLUTION, Vol. 55, 2009, pp. 91–97
DOI: 10.1560/IJEE.55.2.91

IJEE Soapbox: A MEDITATION ON SPECIES AS STORIES

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Embedded in every species is a story with many levels—from the broad drama of its origin, spatial spread, and ultimate fate, to the daily dramas, squabbles, and stratagems of the organisms that make it up. And when we lose that species to habitat loss, or climate change, or overexploitation, or some other facet of environmental degradation, we lose its story as well—its slice in the narrative of life.

Earlier this year, when teaching an undergraduate course in ecology, I tried to pull together a lecture on the topic of biodiversity and conservation, and in so doing to think of a fresh angle of conveying to students (or anyone) how difficult it really is to get one's head around this topic. This difficulty is greatly aggravated by the fact that many university students, at least in my experience, have scant knowledge of even rudimentary natural history, such as the names of the trees, birds, and butterflies that surround them every day as they walk across campus. According to the Oxford English Dictionary, a largely obsolete usage of the word "history" is a "story or narrative" (as in the French "histoire"). So if we think of natural history as the grand "story of nature", then each species has its own subplot, its own specific story in this larger overall story of life on Earth. But before one can make a start on unveiling a species' stories, one has to know what species are, in general; who that species is, i.e., put a name on it; and, preferably, have a sense of where it hangs on the tree of life. To get a sense of how many distinctive stories may be out there, one has to at least quantify the number of species.

The diversity of life is truly staggering. I think there are real conceptual issues in our fully grasping the great unplumbed richnesses of biodiversity, having to do with our own cognitive limitations. To connect this issue of the daunting magnitude of biodiversity to something the undergraduate student might be able to readily relate to, and also to provide a possibly more familiar metric for gauging the expanse of the problem, I thought about the issue of the constrained capacity of our own memory, with respect to

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Robert D. Holt is our first invited ***IJEE Soapbox*** essayist. Bob is Professor of Biology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

the number of words used in our own language, and even for knowing and appreciating other human beings *qua* individuals. So I rummaged on the Web a bit to find relevant facts on these themes. Before presenting those, it is useful to get some more general and necessary observations about the nature of species out of the way.

Knowing what species are, and how they are related, genealogically and in other ways, is essential to delineating their stories (Brooks and McLennan, 2002). There is of course a huge literature on species concepts, which raise a wide range of conceptual and methodological challenges. Most of these details are not all that relevant to the theme of this essay. MacLaurin and Sterelny (2008), to my eye, cogently argue that some variant of G.G. Simpson and E.O. Wiley's "evolutionary species concept" is particularly useful for characterizing biological diversity. An evolutionary species is defined to be a lineage of organisms with "their own evolutionary tendencies and historical fate" (Wiley, 1978, see also Wiley and Mayden, 2000), so one measure of biodiversity is the number of distinct evolutionary species that are found, say, in a geographical region. In practice, reproductive isolation (the key element of Mayr's biological species concept, e.g., Mayr, 1969) is often needed for an evolutionary species to retain its identity over time, which is necessary if evolution is to capture locally unique and favorable traits in the face of the homogenizing effects of mating and gene flow (Futuyma, 1987).

Viewing species as individuated lineages with extensions through time and across space, and thus edges (fuzzy at times), is particularly apt if we think of species as having stories. Stories by their very nature are narratives that unfold in time, with a start, an ending, many salient details along the way, and a bounded domain of action. *Alice's Adventures in Wonderland* begin on an English stream bank one afternoon, and end there the same afternoon, with perambulations down a rabbit hole in between. A major part of each species' story is likewise describing at a broad scale how it arose, spread, spawned daughter species, and maybe eventually declined to end in extinction, and how it affected and was affected by the world around it along the way, including interactions with other species. Embedded in each species' story are the multiple life-tales of those individuals who comprise the species, whose multifarious adaptive and non-adaptive traits—ranging from the details of their chromosomal arrangements, to anatomical structures, to tolerances to abiotic conditions, to reproductive behaviors—reflect the history of their lineage and the environments through which that lineage has passed (Brooks and McLennan, 2002; Dawkins, 2004).

Understanding biodiversity is much more than just counting species, but getting a handle on the numbers is at least a place to start. E.O. Wilson (1992, p. 43) recounts the famous story about how Ernst Mayr, in visiting the Arfak Mountains of New Guinea, found essentially the same number of bird species as recognized by the local people. A few years ago when visiting New Guinea, I experienced this depth of local knowledge about the avifauna first-hand myself, when I hired Mr. Daniel Wakra, a professional bird guide, to take me to Virarita National Park outside of Port Moresby. Daniel had a truly amazing knowledge of the local birds, identifying every chirp and twitter more or less instantly, and knowing where to hunt for particular species. The word "hunt" was quite appropriate. In talking to Daniel about his background, he told a tale of how he had grown up in the highlands, where from an early age to support his family he had to snare, lure, dart, and otherwise catch any bird that moved in the forest, because birds were their main source of protein. So he had a strong practical motivation to learn the microhabitats and behavioral traits of all bird species in the forest, from the smallest mouse-warbler morsel to the largest (and so very desirable for the pot) cassowary and crowned pigeon—because that was knowledge that was needed to put food on the table. Wilson remarks that in his own visit to the Saruwaget Mountains of New Guinea, he queried the local people about ants, and in his words, to them "an ant was an ant was an ant". So for most of us, our knowledge of diversity is driven by "need to know", rather than curiosity.

Some individuals can of course learn to identify and name a very large number of species. Wilson mentions shamans in Amazonia who have known a thousand or more plants, and tropical botanists such as Robin Foster and Al Gentry can perform similar feats in identifying several thousand species of tropical trees without the aid of keys or field guides (R. Foster, pers. comm.). I have known birders such as Ted Parker and Scott Robinson who can quite capably identify from sight or song some thousands of bird species (S. Robinson, pers. comm.). Yet even the best of us can grasp only a tiny fraction of the diversity of life.

One measure of our cognitive capacity is the size of our standard speaking vocabulary. Typical estimates of the number of words in the vocabulary of a typical speaker of English range from 20,000 (Nation and Waring, 1997) to about 50,000 (Pinker, 2007, p. 90). Of these, in a typical week, however, only about 2000 words might actually be used (Nation and Waring, 1997; Rob Waring, pers. comm.). In making these estimates, there are methodological issues in what counts as a word, with pronounced differences between estimates provided by "splitters" and "lumpers"; the estimate of 20,000 was for lumped "word families", consisting of a base word, inflections, and various minor deviations. The total size of the language, of course, is vast, and indeed rather hard to define. The Oxford English Dictionary has around 600,000 definitions, and by some counts there are now over 1,000,000 words (http://en.wikipedia.org/wiki/English_language). Like a gene pool, languages collectively contain much more information than is represented by any single "carrier" of the language.

Humans are social animals, and another apt measure of our cognitive limitations that might be more relevant to appreciating biodiversity is how many individuals we come to know, in terms of their own personalities, habits, histories, social standing, and so forth. Unlike ants for the Saruwaget people, we humans take pride in our individuality (as well as our association with different groups, which also helps define who we "are"), and resent being treated as just a number. How many people does the average person know, either reasonably well—in terms of their habits and peculiarities—or even just as a name with a few factoids about them (e.g., in the sense that I "know" that George Washington was the first president of the United States, William Shakespeare wrote Hamlet, Julius Caesar crossed the Rubicon, etc.)? To "know" a person is to know something about her, not merely her name—i.e., it is to know her "story". It is not easy to find an answer to this question, but the anthropologist Robin Dunbar (1992, 1996) has suggested that there are hard-wired cognitive limitations in the human brain that make it difficult for most folk to interact meaningfully with more than about 150 individuals at a time (e.g., within a year). There are doubtless some gregarious politicians and social mavens who go well beyond this limit (or at least have the social skills to give the illusion that they do; my father B.D. Holt once met Bill Clinton, who, after a few minutes of social chat, made my dad feel that Bill had known him his whole life). But it is doubtful that this upper bound would be more than an order-of-magnitude or so larger than the "Dunbar number". I have not been able to find estimates as to the number of proper names that the typical person knows, not just as a cipher, but with some factual information associated with them. My guess is that it might be several thousands (but that is really just a guess). My well-read research associate Mike Barfield visited a biographical website that said it had over 25,000 entries, and of the sample he scanned, he recognized about 20% (there were other cases in which he recognized a name, but had only a very vague idea who the person was). So if we double the Dunbar number and multiply by ten or a bit more, that would be a "recognition set" of about 3–5,000 names. So we can "really know" (i.e., as a friend or family member) several hundreds of individuals, and "slightly know" (i.e., as a name and a bit more) several thousands of individuals.

We live in a world that is increasingly urbanized and connected, which means that there is a larger and larger pool of human beings with whom we might potentially interact. This expansion in our social world (via Facebook and like technologies) is alas likely to come at the cost of degradation of our (often already meager) knowledge of the natural world. A story I heard many years ago from another student, about the limitations of human memory for proper names, involved the first president of Stanford, David Starr Jordan—an ichthyologist renowned in his time for his encyclopedic knowledge of fish. The version of the story I remember is that at a cocktail party, Jordan was amiably talking with a woman, who after some minutes of conversation said to him, with indignation in her voice, words along the following lines: "President Jordan, I have met you before, on several occasions, and I could swear you do not even know my name." Jordan replied, in effect, "Madame, every time I learn the name of a person, I forget the name of a fish." It would appear that the story is not entirely apocryphal and has some basis in truth, although it probably had to do with Jordan's explanation for his inability to remember the names of all the students at Stanford (Hubbs, 1964; I still like my version better). So the more people we connect with on the Web, or at work, or in our neighborhood, the harder it may be to retain a deeply-based, reticulate knowledge of nature in our own heads.

There are about 250,000 named vascular plant species, and Raven and Crane (2007) estimate that there may be up to 100,000 species of trees alone (including undescribed species; Damon Little, pers. comm.). There are roughly 1,000,000 named insect species, and estimates of the actual number range from 5 to 80 million (Millenium Ecosystem Assessment, 2005)! Professor Klaus Rohde has argued that some particular groups and habitats, such as meiofauna in subtidal coastal areas, nematodes in the deep sea, and parasites across the globe, are vastly undersampled, and so it is hard to even make sensible guesstimates of the number of undescribed species present (Rohde, 2002, 2009, pers. comm.).

But even if one accepts quite conservative estimates of these numbers, there is one thing we can know for sure—the number of organic species sharing the planet with us is a really, *really* big number, particularly when one recalls the fact that all these species are distinct entities with their own histories and properties (or they wouldn't be individual species), which makes them quite different from the notion of "bigness" appropriate to, say, a million dollars or widgets (all of which are identical to each other and interchangeable for the purpose of making a purchase, or handing out a loan, or conducting a business in widgets).

I think it is difficult for any of us, even seasoned (to jaded) professional biologists, to claim that we have an understanding of more than a tiny sliver of biodiversity, even at the bare bones level of knowing the names of taxa. And of course, the "story" implicitly denoted by species identity is vastly richer than just having a name. Even the best-known species continue to produce surprises. For instance, *E. coli* must be the most thoroughly documented organism on the planet, in terms of its molecular biology, but recently scientists at The Weizmann Institute of Science learned an intriguing new factoid about it (Mitchell et al., 2009). *E. coli* lives (among other places) in the human gut, where during digestion the sugar lactose appears prior to the sugar maltose. Exposure of the microbe to lactose triggers genes that produce enzymes for metabolizing lactose, which is immediately useful, and also genes that permit the bacterium to utilize maltose, which will only be useful in the future. As Amir Mitchell, a scientist involved in the study, noted in an interview, it is as if the bacteria can anticipate the future (Bland, 2009). As another example out of the vastly diverse sea that could be mentioned, and at the other end of the taxonomic spectrum, recent studies (Raby et al., 2007) show that the Western Scrub Jay (*Aphelocoma californica*) also plans for the future, both by differentially placing cached food one day in locations where they know they will be foraging the next day, and by putting food in places where that food will not be available the next day.

Given the number of species that exist on Earth, and the wealth of specific information that abides in each, it is clearly impossible to grok* the "whole thing" of biodiversity. One of the advantages of living in the modern world is that we can "out-source" much of our memory bank to external devices such as research articles, books, photographs, computer disks, and iPods. One other way to deal with the gargantuan volume of information that is implicit in the term "biodiversity" is to search for general patterns, which indeed is at the core of much of the scientific enterprise (MacArthur, 1972). As a strategy for aiming towards such generality, a close scrutiny of the detailed stories of many species widely dispersed across the tree of life, and across biomes and geographical domains, is essential, not just continued detailed analyses of a handful of model organisms. We can indirectly gain a sense of the whole story by aiming for generalities, for instance, by focusing closely on small pieces that can be extrapolated or scaled up, or by seeking cross-cutting patterns that we can then use to see major themes across the whole (as in the research program of the metabolic theory of ecology, Brown et al., 2004). Knowledge is not merely an accumulation of factoids, or even of numerous separate stories,

*The useful word "grok" was coined by the science fiction writer Robert Heinlein in *Stranger in a Strange Land*, and is defined by the OED as "To understand intuitively or by empathy; to establish rapport with".

but more of a web of interconnected tales (Quine and Ullian 1978). The meaning of any one tale about the world emerges in substantial measure from the other tales about the world that it informs, and that inform it. One of the vital contributions of phylogenetic systematics is that it can provide a kind of roadmap to the web of knowledge represented by the diversity of life (E.O. Wiley, pers. comm.), a hierarchically structured guide to the shared and divergent story lines of species. And the most important repository of information about the story of life, and the many plot lines of the vast number of species that comprise this larger story, is still inside human brains, in particular those of skilled taxonomists and systematists who "really know their organisms". No one brain can do it, but our communal brains maybe can. There is a robust ongoing debate about how best to maintain this community of scholars (Godfray et al., 2007; Carvalho et al., 2007), but there should be no doubt as to the importance of this vital task.

ACKNOWLEDGMENTS

I thank my friend Ed Wiley for many illuminating and robust conversations over the years related to the theme of this essay (and for using the word "grok"). Thanks also, to Robin Foster, Mike Barfield, Rob Waring, Leon Blaustein, Klaus Rohde, Scott Robinson, and Damon Little for thoughtful comments on the content of the essay; to my father Dan Holt, for the story about Bill Clinton; and to the University of Florida Foundation for its support.

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