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COMMENTARY

Evaluating Tropical Biodiversity: Do We Need a More Refined Approach?

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ABSTRACT

The exceptional biodiversity of tropical forests inspired the earliest ecologists such as H. W. Bates. Today we still strive to quantify and understand this diversity. Drawing on our own experience of Mamirauá reserve in Amazonas, which is located in an area that Bates explored, we argue that the emphasis of research in tropical ecosystems should shift away from species richness as an end in itself, and focus instead on other fundamental, but more tractable, questions that will increase our ecological understanding of these systems, support conservation management, and appeal to policy makers and society in general.

Key words: rarefaction; species estimation statistics; species richness.

> *The neighbourhood of Pará is rich in insects. I do not speak of the quantity of insects, which is probably less than one meets with, excepting ants and termites, in summer days in temperate latitudes; but the variety, or in other words the number of species is very great. It will convey some idea of the diversity of butterflies when I mention that about 700 species of that tribe are found within an hour's walk of the town; whilst the total number found in the British Isles does not exceed 66, and the whole of Europe supports only 390.*
> H. W. Bates. 1863. *A naturalist on the river Amazons.* John Murray, London, UK.

FOR MANY ECOLOGISTS the words 'tropical' and 'biodiversity' form a natural pair. This is not just because tropical ecosystems are unusually rich, but also due to the fact that natural history books written by Victorian naturalists and explorers played an influential role in establishing the discipline that we now call ecology. These pioneering scientists include Charles Darwin who, though best known for his contributions to evolutionary biology, made many insightful observations on species abundances and distributions, Alfred Russell Wallace, who along with Darwin recognized the role of natural selection in evolutionary change, but was also the first to write about beta diversity, and Henry Walter Bates, who documented many new species during his time in the Amazon and developed a theory of mimicry that is sill used today.

Bates spent four and a half years at Ega, now called Tefé, on the Solimões (Upper Amazon). During this time he recorded over 7000 species of insects, including 550 species of butterflies and made many notes on other taxa. Today Tefé is the base for an ambitious conservation initiative, the Mamirauá Institute for Sustainable Development that was established by Marcio Ayres in 1990 and hosts around 100 researchers working on a wide range of topics (see http://www.mamiraua.org.br). The Mamirauá reserve covers 1,124,000 ha of *varzea* (flooded forest) habitat. Amanã reserve, which extends over a further 2,350,000 ha of terra firme, *varzea* and *igapó* forest, is also managed by the Mamirauá Institute. Although it is over 150 yr since Bates left Ega to travel home to England, there is still much to be learnt about this ecosystem and still many challenges involved in documenting its biodiversity. We discuss these challenges and recognize that they are common to nearly all evaluations of tropical biodiversity (or indeed any investigations of diverse but poorly catalogued systems). In particular, we highlight the need to focus on tractable problems that take advantage of recent developments in biodiversity research and assessment.

The first question that people almost always ask is 'how many species are there?' This is not just a desire to document and describe the world around us, but also reflects the widely held view that species richness is the most natural—and seemingly the simplest—measure of biodiversity. However, as Lawton *et al.* (1998) recognized, the time and resources needed to identify and collate information on biodiversity in tropical habitats means that a few well-studied groups apart, comprehensive lists of species may be unachievable. The data for the Mamirauá reserve bear this out. There are approximately 330 species of bird and 520 species of tree in the area, and these figures are unlikely to change substantially. The fish are also fairly well documented. There are over 300 species of fish inside Mamirauá alone (this rises to about 660 species, if we include Amanã reserve and Tefé lake). Terrestrial mammals are also well-known: there are 69 species, some of which are described in detail by Bates. Bats, on the other hand, have not, as yet, been thoroughly investigated. For other taxa the picture is even less clear. Bates's inventory of insect species still stands as one of the most complete, and very little is known about the biodiversity of other invertebrate groups. Although we can be confident

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that the invertebrate fauna is far richer than anything we see in temperate regions we cannot put an accurate figure on the magnitude of this richness, particularly because it can be tricky to make inferences about patterns of biodiversity in understudied groups using data from other, better known 'surrogate' taxa (Gardner *et al.* 2007).

Species richness estimation is one technique that seems to offer an appealing solution to the problem of knowing how much diversity there is. There has been a rapid development of species estimation statistics over the last two decades, building on Anne Chao's innovative work (Chao 1984, Colwell & Coddington 1994, Chao *et al.* 2009, Gotelli & Colwell 2010). These measures use information about the abundance or occurrence of species, particularly rare species, to generate a minimum estimate of species richness. These methods can also be used to devise a stopping rule, that is a guide to how big a sample must be to include all species in an assemblage. The problem of course is that many tropical assemblages are characterized by high numbers of rare species. For example, Coddington *et al.* (2009) examined 71 of largest and most ambitious tropical arthropod surveys and found that on average 32 percent of species were singletons. The presence of high numbers of singletons means that any estimate of species richness will have very wide confidence limits. It also implies that extensive sampling may be needed to be reasonably sure that all species have been included in the inventory. The stopping rule mentioned above argues that no further species will be found if all the species already sampled are represented by at least two individuals (or are found in at least two samples) (Chao *et al.* 2009, Gotelli & Colwell 2010). Coddington *et al.* (2009) suggested that the log normal distribution might be a viable alternative approach to estimating species richness. The idea here is that an undersampled assemblage produces a truncated log normal distribution, and that total species richness can be inferred by unveiling this distribution (Preston 1948, Pielou 1975). Unfortunately, species abundance distributions can take on a variety of forms (McGill *et al.* 2007) and even those that resemble log normal distributions will not necessarily unveil to reveal the symmetrical distribution that Preston envisaged (Nee *et al.* 1991, Williamson & Gaston 2005). Another difficulty is that the number of species recorded (and predicted) will creep ever upwards if samples are taken at different times or in different places (Magurran 2010).

In light of these difficulties what should researchers at Mamirauá and elsewhere do? We suggest that asking 'how many species are there?' may be the wrong question, at least where poorly documented taxa are involved. Species lists can become an end in themselves, and do not necessarily help us solve fundamental questions in biodiversity research or improve conservation management. Instead, we can potentially learn more about the structure and function of tropical biodiversity by approaching it in different ways. For example, we know that tropical habitats are species-rich relative to temperate ones but what form does this difference take? If we use the same sampling and effort—in so far as that is possible—in our different habitats (and these could of course also be different tropical localities), we can ask whether we are getting more species because there is a higher density of individuals, or as a result of the fact that most species are indeed rarer in the tropical habitats as Bates implied in the opening quotation. Rarefaction is a technique that allows the investigator to make fair comparisons in analyses such as these (Gotelli & Colwell 2010).

Similarly, one might use species time curves to quantify temporal turnover, examine the equivalence between these and species area curves, and then ask if they behave differently to the patterns already documented in temperate regions (Rosenzweig 1995, White *et al.* 2006). Continuing the same theme, tracking temporal change in the diversity of ecologically coherent groups of organisms is not only feasible, but also increasingly important given the emphasis now being placed on reducing biodiversity loss. A reduction in the rate of biodiversity loss is the focus of the 2010 target established by the Convention for Biological Diversity (http://www.cbd.int/2010-target/) and of the UN's International Year of Biodiversity. To quantify biodiversity loss, we need good data on the background rate of change in ecological communities, particularly tropical ones.

Another approach might be to examine the patterns of abundance that emerge when species importance is assessed using different currencies, such as biomass and numerical abundance (Morlon *et al.* 2009, Henderson & Magurran 2010), and use these observations to make predictions about the relative extent of biodiversity in different groups or habitats. These ideas have yet to be fully explored but are tractable in tropical systems. Additional potentially informative avenues include tracking the abundance (or rank) of labeled species in space and/or time (MacNally 2007, Collins *et al.* 2008), partitioning the assemblage in various ways (McGill *et al.* 2007), for example by phylogeny (Vellend *et al.* 2010), function or traits (Weiher 2010), or according to whether species are core or occasional members of the community (Magurran & Henderson 2003, Ulrich & Zalewski 2006). These partitions may help us understand why some systems are richer than others, and how they might respond to or recover from disturbance. There are many more possibilities.

In conclusion, we suggest that because the biodiversity of the tropics awes us, as it did Darwin, Wallace, and Bates, we too can be overwhelmed by the challenges involved in documenting it. But although we may still be some way from knowing the extent of this diversity, or from attaching names to all the organisms that live in the tropics, we can make significant progress toward understanding how, and why, tropical communities are diverse. Indeed, as we have argued, there is a case for setting aside the traditional goal of assessing species richness in favor of more realistic aims. It may also be wise from a strategic perspective to shift the focus away from species richness as an end in itself. Assessment of species richness, combined with the compilation of species lists, has been used extensively to justify research projects and conservation initiatives. We believe that funders, policy makers and society in general will increasingly demand a more innovative approach and will ask us to continually refine our research goals. As we have tried to show, tropical ecosystems offer rich opportunities for biodiversity research that can meet this demand and that will, in turn, support the conservation needed to secure the future of these irreplaceable habitats.

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