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New dimensions of tropical diversity: an inordinate fondness for insect molecules, taxa, and trophic interactions

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Most known insect species are involved in chemically mediated plant–insect multi-trophic interactions, and recent syntheses point to a substantial gap in our understanding of trophic interaction diversity, especially in the tropics. One approach to filling this gap is to examine relationships between genomic, metabolomic, taxonomic, and trophic interaction diversity via quantifying and comparing these dimensions of biodiversity at multiple scales. Innovative approaches to research on the origins and maintenance of tropical insect diversity should merge traditional approaches to natural history and taxonomy with modern measures of interaction diversity, genetic variation, and phytochemical diversity. These approaches will elucidate relationships between plant chemistry, specialization, climate, and different dimensions of biodiversity.

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Introduction

Patterns of tropical diversity at multiple scales constitute a pillar of ecological theory, and the latitudinal gradient in diversity noted by Darwin [1], Wallace [2], and their predecessors has enjoyed a renewed intensity of focus and research [3]. The insects are one great, monophyletic taxon that has contributed spectacularly to this gradient, particularly parasitic insects, in the broad sense, including herbivores and parasitoids. Nevertheless, our understanding of tropical insect diversity is woefully incomplete and is urgently in need of intensified research efforts. There are many powerful new tools for quantifying diversity, including new methods in genomics [4,5•], improved approaches to quantifying phytochemical diversity [6], and improved cyberinfrastructure for traditional taxonomic approaches (e.g., *Encyclopedia of Life*). As we continue to lose hyperdiverse tropical forests [7], it is time to step up efforts to fully characterize tropical insect diversity by integrating new tools with traditional approaches.

Modern science has been extraordinarily successful, yielding technological fruits such as the internet and remote-controlled video cameras on Mars, yet we have still failed to accomplish one simple feat: describing or quantifying Earth's biodiversity. Have we given up on any attempts to finish the job that Linnaeus started several centuries ago? Is taxonomy a thing of the past that has no role in current studies of biodiversity? *Hopefully not.* Here we opine that taxonomy and species counts are still integral to understanding the diversity of multicellular organisms, many of which are insects. However, rather than increasing a focus on molecular barcoding (sequencing a small mtDNA locus) and dumping traditional taxonomy [8], studies of diversity in the tropics will benefit profoundly from an integrated understanding of complex network diversity — 'interaction diversity' — via combining traditional taxonomy with new statistical, genetic, systematic, metabolomic, and ecological network hypotheses and methods. Examining specific interaction networks at small, ecologically relevant scales within sites is not common, but can rapidly increase the understanding of relationships between geographic variation, biodiversity and ecosystem function. Although such interaction diversity is only beginning to be explored, analyses have suggested that components of networks, in particular host specificity of consumers, might differ substantially between different ecosystems and across the geographic ranges of species [9,10••,11,12••]. Recent syntheses and theoretical advances in diversity and ecosystem function research point to a substantial gap in our understanding of trophic interaction diversity and stress the need to include trophic diversity in studies or measures of biodiversity [13,14•]. Among well studied interaction webs, such as plant–pollinator and fruit-disperser networks, plant–herbivore–parasitoid trophic webs are some of the best characterized systems that could be further pursued using new technologies. These interactions include well over half of all known species [15], commonly vary geographically, are often chemically mediated, and are among the most productive and tractable systems for understanding biotic communities [16,17••].

Taxonomic, genetic, and phytochemical diversity of multi-trophic interactions

Interaction diversity

Interaction diversity can be defined as the number of interactions linking species together into dynamic biotic communities [18,19]. The loss of interactions is a poorly studied consequence of extinction, particularly in the complex and hyperdiverse biotic interactions found in tropical ecosystems [19,20]. Theoretical and applied research in ecology and conservation that incorporates measures of taxonomic and genetic diversity should also include interaction diversity metrics [21–24]. Interactions among species are important because they affect attributes such as population dynamics, community stability, primary productivity, and ecosystem services — in fact interaction diversity is more tightly linked to these variables than are other diversity metrics [10••]. For example, the well-studied relationship between diversity and stability of ecological communities is focused on interaction diversity because it deals with the number of trophic links (i.e., connectance), levels of specialization and connectedness, the relative strength of trophic links, and their lateral development [25–28]. Thus, the ecosystem consequences of diversity can be explored by quantifying diversity of community interactions, with a focus on interactions that are more readily quantified.

Taxonomic diversity

Taxonomic diversity is the best studied component of diversity and uses species as the unit of measurement for richness, evenness, relative abundance, and entropy measures within (alpha) and between (beta) habitats. Quantifying taxonomic diversity has slowed down for a number of reasons, but one impediment has been the push for 'transformative' research both from funding agencies (e.g., *United States National Science Foundation*) and journals (e.g., *Ecology Letters*) and traditional taxonomy or natural history are not seen as transformative because supposedly they do not change the way we think about science. But good science includes much more than pumping out myriad new ideas or approaches and needs to incorporate basic building blocks, such as classification of species or feeding habits of immature insects. It is important to document taxonomic diversity in complex tropical ecosystems, and documenting and understanding sympatric multi-trophic interactions is dependent on correct and accurate within-site delineation of genetically cohesive biological groups ('species'). Modern tools are part of documenting taxonomic diversity, since molecular data have revealed high levels of cryptic diversity, especially in tropical ecosystems, changing our view of processes such as host specialization, phenology, within-species behavioral variation, and morphological differentiation among biological species [29,30]. Integration of molecular data with detailed comparative morphology and natural history information provides a more accurate view of taxonomic diversity than any one of these sources of information in isolation [31].

Genetic diversity

Genetic diversity includes diversity from within populations and communities to across the geographic range of species [31,32]. It can be summarized via analysis of DNA sequence variation using tools from population genetics and molecular systematics, and methods that incorporate phylogenetic data and functional traits (e.g., host specificity) into community ecology [33]. Quantification of genetic variation and structure within and among natural populations is important for understanding both historical factors that shape genetic variation across the range of species, communities and ecosystems, as well as metabolic diversity (i.e. metabolites produced as plant defenses, attractants or insect pheromones) and species interactions. This approach is necessary for determining how geographic variation in particulars and outcomes of species interactions shapes genetic structuring across the range of species and vice versa. For example, genetic variation, and associated metabolic variation, in host plants can determine which herbivores will feed on plants at different locations across a geographic mosaic and will reflect adaptation to local selective pressures [34,35••]. Similarly, associated genetic variation in herbivores can mediate the diversity of attacking parasitoids, resulting in more potential interactions at larger geographic scales (as measured by food webs) and fewer realized interactions at smaller, ecologically relevant scales. Analyses of population genetic structure will facilitate an understanding of the extent to which local adaptation may be limited by gene flow, and provide a metric of the potential of geographic variation in species interactions for driving population and species level diversification. In addition, more ancient, stable communities will possibly harbor larger populations, greater genetic diversity and consequently greater interaction diversity. One of the strengths of an integrated approach (Figure 1) is to consider historical processes in the same study design that encompasses indices of interaction and phytochemical diversity.

More specifically, molecular data should be used to address two issues: (1) relationships between genetic variation and multiple measures of diversity (Hypothesis A, Figure 1), and (2) mechanisms of diversification (Hypothesis B, Figure 1), which are fundamental to understanding of all types of diversity. Several general hypotheses stem from previous research on the ecological consequences of genetic diversity, and the effect sizes of host genetic diversity on parasites can be as great as the effects of species diversity on parasites [31]. The distribution of genetic variation within, and genetic differentiation across populations, can now be analyzed in populations of virtually any non-model organism using next-generation Genotyping By Sequencing approaches (GBS) and can be used to understand the influence of