

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

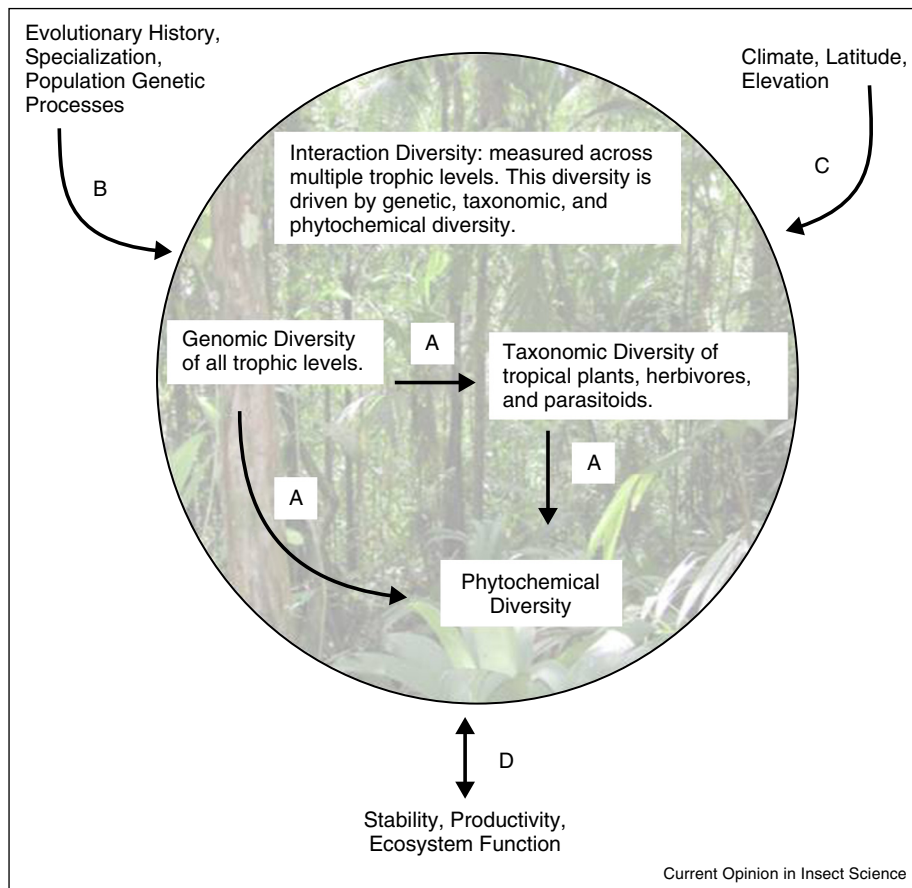
taxonomic diversity than any one of these sources of information in isolation [31].

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 particular 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

Figure 1



Hypotheses related to multidimensional diversity of insects in the tropics. The hypotheses (A–D) correspond to relationships that are labeled as path coefficients in the diagram. The diagram assumes sampling within diverse ecosystems at small, ecologically relevant scales (e.g., 10 m² plots randomly sampled across an entire ecosystem) for plant–insect interactions; the hypotheses would change for larger scales. (A) We hypothesize that the local (plot-scale) diversity of multi-trophic interactions is a consequence of the combined contributions of genetic, phytochemical, and taxonomic diversity: with greater diversity of interactors (either variants within a species or different species) there is greater opportunity for the evolution and persistence of unique interactions between species. Furthermore, we predict deviations from positive correlations between genetic and taxonomic diversity will be explained by phytochemical diversity and the degree of consumer specialization (e.g., more generalists and lower plant toxicity cause lower taxonomic–genetic correlations between sites and plots). Interaction diversity is best measured at small, ecologically relevant scales [9], since full food webs are impossible to fully characterize, thus interaction diversity predictions are different from those derived from food-web parameters that are based on all possible interactions across the range of a focal group. For example, an increase in consumer specialization (i.e., fewer linkages with resources across sites) does not decrease interaction diversity within a small to medium-sized plot when specialists have higher abundances in a community than generalists, because species with higher densities are more likely to be represented at smaller scales. In this case an increase in phytochemical diversity can mediate this positive association between specialization and interaction diversity by favoring adapted specialists. (B) For tropical ecosystems, we predict that genetic variation and biodiversity are generated and maintained by multiple factors, including resource specialization and geographic barriers to gene flow. Studies on the origins of diversity, both within and between species, are frequently conducted within the conceptual framework of speciation research, which is often divorced from a community context. A more synthetic approach should investigate drivers of diversity in a sampling design that encompasses geographic variation in genetic structure and diversity, species interactions, community structure, and ecosystem processes — latitudinal and altitudinal gradients are perfect for such an approach. Quantifying population genetic variation within and among populations of host plants, herbivores, and parasitoids allows for tests of the hypothesis that host plant genetic variation predicts genetic, taxonomic, and interaction diversity across trophic levels as well as the associated hypothesis that levels of differentiation across host plant populations predict the genetic diversity and structure of interacting species at multiple trophic levels [51,52]. (C) Tropical trophic interaction diversity is characterized by unique, predictable patterns of variation across latitudinal, elevational, climatic, and disturbance gradients. Relationships between different measurements of diversity will also change across these gradients. For example, at higher elevations, we predict larger effect sizes for associations between phytochemical diversity, taxonomic diversity, and interaction diversity. Typically, diversity of chemical defenses is lower and generalist herbivores are more common at higher elevations. Any increases in plant chemical diversity at higher elevations are more likely to have strong negative effects on taxonomic diversity of herbivores, since generalists can be more susceptible to increases in phytochemical diversity [53,54]. Such changes in chemically mediated interactions between plants and herbivores can in turn affect genetic structure across the elevational gradient. (D) Interaction diversity is a multidimensional measure of diversity that is an important determinant of productivity and ecosystem function, and is a more measurable and reliable indicator than classic food-web parameters.

multiple factors on population differentiation [4,5,36^{*}]. As population genomic data sets are now uncovering previously unrecognized population structure [37^{*},38], the payoff of these approaches for diversity studies will be great. It is now possible to analyze genomic variation at incredibly fine scales to detect regions of the genome involved in local adaptation, and to detect previously undetected patterns of geographic population structure. These genomic analyses will be relevant for understanding the consequences of host use variation for population-level differentiation and speciation [39]. The genetic diversity approaches that we advocate are rarely utilized in rich, tropical communities, particularly with the kind of statistical power afforded by genomic technologies, which have only recently become available for non-model organisms [40]. In addition to addressing mechanisms of diversification (Figure 1), genomic data can provide a useful check on molecular identification methods (barcoding), which have proliferated and are extremely useful but not infallible [41]. Specifically, markers from genomic analyses can be used to understand genetic differentiation and admixture across populations and species and to generate multi-locus phylogenies to corroborate specific assignments from molecular identification [42]. With the rapid decline in the cost of DNA sequencing and its ability to uncover patterns of genetic variation at a far higher resolution than barcoding approaches (which assay variation at only a minute portion of organellar genomes), barcoding is quickly becoming obsolete and thus not worth increases in time and monetary investments.

Phytochemical diversity

Phytochemical diversity can be defined as the richness and relative abundance of secondary metabolites within a plant species, and like species diversity, it can be decomposed into richness, evenness, and abundance of individual compounds. It has rarely been quantified, but new methods in metabolomics make this an appealing and tractable measure of tropical diversity. Variance in metabolic diversity, which is further downstream than transcriptome or proteome diversity, reflects variation in responses to a diversity of plant enemies, including insect herbivores. Furthermore, phytochemistry is one of the most relevant phenotypes to measure when determining functional roles of plants in natural and managed communities. One general hypothesis that should drive research on tropical insect diversity is that there is a geographic mosaic [34] of chemically mediated specialization of herbivorous insects and their parasitoids on particular host taxa, with considerable variation in the associations between plant chemistry, specialization, and diversity across trophic levels. Since taxonomic diversity, phytochemistry, and specialization are among the most important determinants of trophic interaction diversity [9], one should be able to predict how interaction diversity varies across the landscape based on taxonomic and phytochemical diversity. Similarly, population genetic

variation within focal taxa may reflect the extent of geographic variation in species interactions, and predict diversity structure across trophic levels. Finally, population genomic level data, when coupled with metabolomic data, may facilitate the mapping of genetic regions influencing plant phenotypes [43^{*},44].

The causes and consequences of diverse mixtures of natural products within a single plant remains a subject of debate. In many cases, individual compounds do not demonstrate potent biological activities [6,45], leaving questions regarding the evolution of plant natural product diversity [46,47]. One hypothesis is that mixtures of secondary metabolites have evolved because each compound functions to defend against each different parasite. An alternative hypothesis is that defensive mixtures often result in synergistic effects against a variety of plant parasites [48]. Nonetheless, experimental studies of secondary metabolite mixtures have largely been constrained due to the lack of approaches that rapidly and accurately quantify chemical diversity across thousands of samples [49]. Unfortunately, these limitations have led ecologists to make broad, and perhaps misleading conclusions regarding evolution and consequences of phytochemical diversity based upon weakly quantitative and overly simplified chemical data [49]. Modern approaches to chemical ecology can overcome these obstacles by uniting the tools of organic synthesis, metabolomics, ecology, and statistics to provide a comprehensive understanding of the causes and consequences of phytochemical diversity and how it mediates plant–insect interactions [50^{*}].

Goals for insect science and hypotheses for studying tropical diversity

Tropical entomologists should apply novel methods and protocols to well-protected sites along tropical latitudinal and altitudinal gradients in diverse and threatened ecosystems to examine how different measures of biodiversity are affected by biotic and abiotic gradients and by specialization across a geographic mosaic of trophic interaction diversity. New tools should allow insect biologists to determine how taxonomic, genetic, phytochemical, and interaction dimensions of biodiversity are associated, as well as how interaction diversity affects ecosystem function, as measured by ecosystem productivity and resistance to natural or experimental changes in climate or extreme weather events. Ecologists should explore and dissect these relationships with very thorough natural history data sets [12^{**}], large-scale experiments, population genomic data, and metabolomics data [39]. The general relationships depicted by Figure 1 are related to potentially useful hypotheses and predictions regarding determinants of multidimensional biodiversity across environmental gradients.

Recent syntheses point to a substantial gap in our understanding of tropical trophic interaction diversity and

stress the need to include trophic diversity in studies or measures of biodiversity. Testing the hypotheses we have proposed is best accomplished via a combination of analytical, simulation, and statistical models that guide collection of observational and experimental empirical data. The tools now exist to examine relationships between taxonomic, genetic, functional, and interaction diversity as well as other variables, such as specialization, temperature, incidence of extreme weather events, disturbance, and elevation. For example: How do degrees of specialization and levels of interaction diversity vary between plants with different diversities of chemical defense? Do extreme weather events affect specialized parasitoids more than generalists, and what are the consequences for interaction diversity? Addressing these questions will facilitate novel hypothesis tests and will spur developments in ecological theory and understanding tropical insect diversity. Tropical entomologists are poised to rapidly increase our understanding of diversity and to uncover relationships between biodiversity and ecosystem function.

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