

The Erwin equation of biodiversity: From little steps to quantum leaps in the discovery of tropical insect diversity



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Abstract

Almost 40 years ago, Terry L. Erwin published a seemingly audacious proposition: There may be as many as 30 million species of insects in the world. Here, we translate Erwin's verbal argument into a diversity-ratio model—the Erwin Equation of Biodiversity—and discuss how it has inspired other biodiversity estimates. We categorize, describe the assumptions for, and summarize the most commonly used methods for calculating estimates of global biodiversity. Subsequent diversity-ratio extrapolations have incorporated parameters representing empirical insect specialization ratios, and how insect specialization changes at different spatial scales. Other approaches include macroecological diversity models and diversity curves. For many insect groups with poorly known taxonomies, diversity estimates are based on the opinions of taxonomic experts. We illustrate our current understanding of insect diversity by focusing on the six most speciose insect orders worldwide. For each order, we compiled estimates of the (a) maximum estimated number of species, (b) minimum estimated number of species, and (c) number of currently described species. By integrating these approaches and considering new information, we believe an estimate of 5.5 million species of insects in the world is much too low. New molecular methodologies (e.g., metabarcoding and NGS studies) are revealing daunting numbers of cryptic and previously undescribed species, at the same time increasing our precision but also uncertainty about present estimates. Not until technologies advance and sampling become more comprehensive, especially of tropical biotas, will we be able to make robust estimates of the total number of insect species on Earth.

Abstract in Spanish is available with online material.

KEYWORDS

Diversity estimates, global species richness, host specificity, insect diversity, metabarcoding

1 | INTRODUCTION

In 1981, Terry L. Erwin received a letter from Peter H. Raven asking what seemed to be a very straightforward question: How many species [of insects] are there in one acre of rich tropical forest? Erwin explored Raven's query using his records of canopy insects collected from a tropical rain forest in the Canal Zone of Panama (Erwin & Scott, 1980). To calculate the number of insect species present in the tropics, Erwin estimated the number of host-specific beetle species per trophic guild from his fogging collections found in a single tree species, *Luehea seemannii* (Malvaceae). He extrapolated these estimates by using the proportion of beetles to other insects, the fraction of taxa believed to be restricted to the rainforest canopy, and the number of species of trees in one hectare of tropical forest (see Table 1). Ultimately, he reached an audacious proposition: There may be as many as 30 million species of insects globally (Erwin, 1982).

Here, we translate Erwin's verbal argument into an equation—the Erwin Equation of Biodiversity. Erwin's paper inspired a multitude of subsequent diversity-ratio models and stimulated the development of other methods to estimate biodiversity (May, 1988; Ødegaard, 2000). The Raison d'être of this 50th Anniversary Biotropica paper is to celebrate both Erwin's pioneering work and the subsequent efforts of others to estimate global biodiversity that have taken us closer to a robust estimate of the total number of species on Earth.

Determining how many insect species are in the tropics is a question of paramount relevance in this era of global biodiversity crises. Most metazoan species in the world are insects (May, 1986), and recent studies have demonstrated that insect populations are declining at alarming rates (Hallmann et al., 2017; Janzen & Hallwachs, 2019; Simmons et al., 2019; Wagner, 2019). Quantifying how many insect species exist not only energizes and assists the scientific community in conserving biodiversity, but also fosters a much-needed curiosity and appreciation of biodiversity by the general public.

In this paper, we discuss the connection between the parameters used by Erwin (1982) to estimate the number of insects in the tropics with subsequent diversity models (Hodkinson & Casson, 1991; May, 1990; Ødegaard, 2000; Stork & Gaston, 1990). We also summarize the assumptions of three main approaches used to estimate global arthropod diversity: (a) diversity-ratio models, (b) macroecological models, and (c) taxonomic expert opinions. Finally, we examine the results of the most recent studies evaluating these methodologies to generate current global species richness estimates for six major groups of insects. Many of the subsequent studies have provided “quantum leaps” in our understanding of arthropod biodiversity, since the publication of Erwin's (1982) thought-provoking seminal paper.

2 | METHODS AND RESULTS

To determine similarities and underlying assumptions of different methods to estimate insect species richness, we selected

publications after 1982 that represent major theoretical advances to estimate the number of species on earth. For each model, we standardized the notation of all equations sharing homologous parameters (see description of all parameters in Table 1).

We also illustrate our current understanding of insect diversity by focusing on the six most speciose insect orders worldwide (Figure 1). For each order, we compiled estimates of the (a) maximum estimated number of species, (b) minimum estimated number of species, and (c) number of currently described species. A detailed description of the methodologies and assumptions associated with each species estimate are included in the supplementary material (Table S1).

2.1 | The Erwin equation and other diversity-ratio models

Based on Erwin's, 1982 publication, and further discussions with Terry L. Erwin, we translated Erwin's argument into a diversity-ratio model, the Erwin Equation of Biodiversity (Table 1). The Erwin Equation describes the number of specialized beetles per guild feeding on a particular plant species (B) and assumes that taxon abundance and specialization ratios are similar among tree species. Therefore, the number of insect species can be calculated by multiplying such ratios by the number of tree taxa (species or genus-group lineages) in the tropics (T , Table 1).

Erwin's assumptions have been explored in later estimates (Table 1). The one which has received the most attention is the assumption of insect specialization ranging from strict specialization on one to multiple related plant species. Relaxing this assumption has been a focus of many subsequent diversity-ratio models. Eight years after Erwin's seminal publication, May (1990) proposed a second model, which assumes that insect specialization ratios represent empirical values specific to each host plant species (May Equation, parameter $p(i)$, Table 1).

Both Erwin and May's equations assume that species compositions of plants and insects do not change at different spatial scales. This limitation was noticed by Ødegaard (2000), who proposed that diversity-ratio models should include empirical estimates of insect and host plant turnover across geographic ranges (parameters β_1 and β_2 in Ødegaard Equation, Table 1). While neither β_1 nor β_2 have been quantified for many systems, the values reported by Ødegaard are nearly equal.

A third assumption of the Erwin Equation is that the fraction of known insects that are beetles (B_K/I_K) is the same as the fraction of all insects that are beetles. However, large-bodied, morphologically diverse organisms have long been recognized to be better described than smaller, less distinctive insects (May, 1988). This would lead one to believe that species diversity estimates based on beetles or other large-bodied insect taxa are likely underestimates of total insect diversity.

For diversity-ratio models, including estimates of insect habitat specialization (Erwin and May Equations, Table 1), there is very

TABLE 1 Estimates of tropical insect diversity. Although some estimates were originally proposed as estimates of arthropod diversity, for simplicity we have standardized them to estimate insect diversity. Whenever possible, methods are expressed as equations to aid comparisons of their mechanisms and assumptions

Estimate	Method ^a	Assumptions ^b	References
Diversity-ratios			
Host specificity		<ul style="list-style-type: none"> All assumptions associated with taxon ratios (see below) 	Reviewed by Hamilton et al. (2010)
Erwin equation	$I_T = \frac{(B_{SH} \times H_{spec} + B_{SP} \times P_{spec} + B_{SF} \times F_{spec} + B_{SS} \times S_{spec}) \times T_T}{C \times B_K / I_K}$	<ul style="list-style-type: none"> Specialization ratios Geographic homogeneity A uniform proportion of canopy species 	Erwin (1982)
May equation	$I_T = \frac{(B_{SH} + B_{SP} + B_{SF} + B_{SS}) \times \sum_{i=1}^M \frac{1}{i} p(i) \times T_T}{C \times B_K / I_K}$	<ul style="list-style-type: none"> Similar to Erwin equation. May also analyzes the sensitivity of the estimate to changes in each parameter 	May (1990)
Ødegaard equation	$I_T = \frac{B_{CT} \times T_{TC} + B_{CL} \times L_{TC} + B_{CE} \times E_{TC}}{\beta_1 \times P_H \times \beta_2 \times C \times B_K / I_K}$	<ul style="list-style-type: none"> Accurate estimate of the proportion of herbivorous beetles Uniform interaction turnover across the ranges of plant (β_1) and arthropod (β_2) species for different taxa and ecosystems 	Ødegaard (2000)
Taxon ratios	$I_T = \text{Taxon}_S \times (I_K / \text{Taxon}_K)$	<ul style="list-style-type: none"> Number of species in the focal taxon is globally well-known Equivalent sampling of focal and non-focal arthropod taxa Global A_K / Taxon_K ratio scales equally with any Taxon_S 	Stork (1993), Stork and Gaston (1990), Stork et al. (2015) and Basset et al. (2012)
Known-unknown ratios	$I_T = \text{Taxon}_S / \text{Taxon}_{SU} \times (I_K / \text{Taxon}_K)$	<ul style="list-style-type: none"> Known-unknown ratios for the focal taxon are uniformly distributed in space Equivalent sampling of focal and non-focal arthropod taxa Global I_K / Taxon_K ratio scales equally with any Taxon_S sample 	Hodkinson and Casson (1991)
Macroecology			
Body size	$\log(A_T) = \int_{\min(L_T)}^{\max(L_T)} \log(L_T)^k$	<ul style="list-style-type: none"> Uniform species-body size scaling Uniform body size distributions among taxa 	May (1988)
Species-space relationships	Species rarefaction curves estimate increasing species richness with increasing sampling (number of sites, area, and/or distance sampled), then extrapolate the local estimate to the desired scale using taxon ratios	<ul style="list-style-type: none"> Species turnover within samples is equivalent to turnover throughout the larger region Sampling intensity is sufficient to generate asymptotic rarefaction curves 	Basset et al. (2012)
Biogeography	$I_T = I_G \times P_{trop}$	<ul style="list-style-type: none"> Proportion of tropical species can be accurately estimated and is uniform across taxa 	Dolphin and Quicke (2001) (Braconidae only) and Stork (2018)
Taxonomic experience			
Discovery curves	Curves estimating rates of species discovery relative to time, body size, or author activity	<ul style="list-style-type: none"> Enough taxon members have been described to generate asymptotic curves Consistent relationships between species discovery and the variable of interest within the taxon 	Time: Dolphin and Quicke (2001); body size: Stork et al. (2015); author activity: Dolphin and Quicke (2001)
Expert estimates	Surveys of taxonomic experts	<ul style="list-style-type: none"> Experts give accurate and independent estimates 	Gaston (1991)

(Continues)

TABLE 1 (Continued)

Estimate	Method ^a	Assumptions ^b	References
Higher taxon approach	Curves estimating discovery rates of different taxonomic ranks over time were used to parameterize regression models estimating the species richness of different higher taxa	<ul style="list-style-type: none"> • Taxonomic ranks are equivalent across taxonomic subdisciplines • The higher taxonomy of a kingdom or domain has stabilized 	Mora et al. (2011)

^aVariables: B_{CE} = sampled herbivorous beetle species associated with canopy epiphytes; B_{CL} = sampled herbivorous beetle species associated with lianas; B_{CT} = sampled herbivorous beetle species associated with canopy trees; B_K = known beetle species; B_{SF} = number of sampled fungivorous beetle species; B_{SH} = number of sampled herbivorous beetle species; B_{SP} = number of sampled predatory beetle species; B_{SS} = number of sampled scavenger beetle species; C = fraction of sampled species that are canopy specialists; E_{TC} = tropical canopy epiphyte species; F_{spec} : fraction of fungivores specialized on the focal tree species; H_{spec} : fraction of herbivores specialized on the focal tree species; I_G = global estimate of insect species richness; I_K = known insect species; I_T = estimated number of tropical insect species; k = a scaling constant, May (1988) suggests $-3 \leq k \leq -1.5$; L_T = length in meters of tropical arthropods; L_{TC} = tropical canopy liana species; M = total number of regional tree species; $p(i)$ = proportion of sampled insect species found on a total of i tree species; P_H = proportion of known beetle species that are herbivorous; P_{spec} : fraction of predators specialized on the focal tree species; P_{trop} = the proportion of tropical species; S_{spec} : fraction of scavengers specialized on the focal tree species; $Taxon_K$ = globally known species richness of a taxon; $Taxon_S$ = locally sampled species richness of a taxon; $Taxon_{SU}$ = number of locally sampled species that are undescribed; T_T = number of tropical tree species; T_{TC} = tropical canopy tree species; β_1 = mean fraction of herbivorous beetles locally associated with a host species relative to the number of herbivorous beetle species associated with the host throughout its range; β_2 = mean number of plant species that one member of a specialized group uses throughout its range.

^bAll of these methods share an assumption that the estimators can accurately identify clearly delimited species according to the estimators' criteria, regardless of what those criteria are (e.g., non-synonymous species names, morphological species, molecular operational taxonomic units).

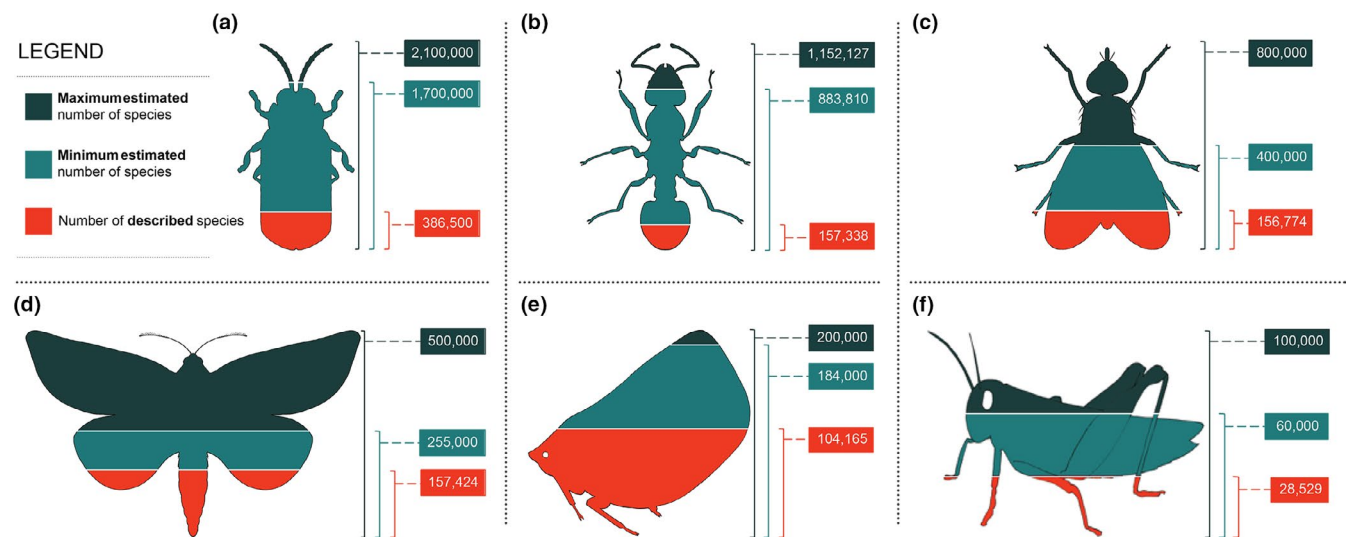


FIGURE 1 Filled insect silhouettes for the six most speciose hexapod orders, in descending order of maximum estimated species richness. The maximum estimated number of species in each order is represented in dark blue, filling the entire outline of the order's representative silhouette. Minimum estimated number of species in each order is shown in lighter teal blue. The most current number of described species is represented in red (from Stork, 2018). Brackets to the right of each organism display the actual numbers associated with the proportions represented in each silhouette. Data were collected from: (a) Coleoptera maximum and minimum species number estimates: (Stork, McBroom, Gely, & Hamilton, 2015); described number of species: (Stork, 2018). (b) Hymenoptera maximum and minimum species number estimates: (Forbes et al., 2018); described number of species: (Klopfstein, Vilhelmsen, Heraty, Sharkey, & Ronquist, 2013). (c) Diptera maximum and minimum species number estimates: S. Marshall (pers. comm.); described number of species: (Zhang, 2013). (d) Lepidoptera maximum species number estimate: (Kristensen, Scoble, & Karsholt, 2007); minimum species number estimate: (Heppner, 1998); described number of species: (Stork, 2018). (e) Hemiptera maximum species number estimate: (Capinera, 2004); minimum species number estimate: (Gaston, 1991); described number of species: (Zhang, 2013). (f) Orthoptera maximum and minimum species number estimates: A. Hochkirch C. Nufio and D. Rentz (pers. comm.), described species number estimate: (Cigliano, Braun, Eades, & Otte, 2019). The methodology used to obtain each species estimate is described in Table S1. Illustrations by E. K. Kuprewicz

limited information on habitat use for most tropical insects. For example, the assumption that 2/3 of all tropical insects is canopy specialists originated from Erwin's initial observations. However, the

accuracy of this proportion has not been thoroughly investigated. In all cases, a single value was used even though relative canopy size differs among forest types (Parameter C in Erwin and May

Equations, Table 1). Forests with 30 and 10 m canopies are unlikely to have the same proportions of canopy specialists. The parameter *C* could also vary depending on how much of the understory consists of unique understory plant species and to what degree mature and immature individuals of canopy trees host different insect communities. Unfortunately, even when intensive canopy and understory sampling are undertaken at the same site (e.g., Basset et al., 2012), the data are rarely analyzed or presented in ways that allow *C* to be estimated.

2.2 | Macroecological diversity models

A second approach to estimate the number of species on Earth is to use macroecological patterns such as arthropod body size distributions (May, 1988), rarefaction curves of arthropod communities at different spatial scales (Basset et al., 2012), or biogeographic methods, which calculate the proportion of tropical taxa from global diversity estimates (Dolphin & Quicke, 2001; Stork, 2018; Table 1). Each macroecological diversity method has its unique set of assumptions (Table 1). For example, body size-distribution methods assume uniform species-body size scaling and size distributions among taxa (Table 1). Rarefaction curves assume that species turnover is equivalent at both local and regional scales (Table 1). Biogeography methods assume that the proportion of temperate versus tropical species is uniform across taxa (Table 1).

2.3 | Diversity curves and expert opinions

Another method used to estimate the number of species in a particular taxon is to generate diversity curves, that is, accumulation curves of species discovered over time (Table 1). Although diversity curves can generate reliable estimates of the potential number of species for well-studied taxa, this method becomes increasingly unreliable for hyper-diverse and poorly studied taxonomic groups. For taxa with nascent taxonomy, estimates have been traditionally based on the opinions of taxonomic authorities (Table 1).

2.4 | How many insects are there?

To illustrate our current understanding of this diversity, we visually represented the (a) maximum estimated number of species, (b) minimum estimated number of species, and (c) number of currently described species for the six most speciose hexapod orders (Figure 1). To assign numerical values to each insect order, we used a combination of the most recent primary literature and the opinions of taxonomic experts (Figure 1).

Coleoptera has the most described species, followed by Lepidoptera, Hymenoptera, Diptera, Hemiptera, and Orthoptera (Figure 1). We estimate that only 20%–28% of the species in these six insect orders have been described at this time (Figure 1). These

estimates suggest that there are between 3,482,810 and 4,852,127 insect species in these orders alone. If the host/ parasitoid wasp ratios proposed by Forbes, Bagley, Beer, Hippee, and Widmayer (2018) are applied to estimated host species numbers rather than described species numbers (an estimate of 5,144,479 hymenopteran species), there could be at least 8,800,000 species in these six orders, and perhaps many more.

3 | DISCUSSION

Knowing how many species are on Earth is a fundamental question to determine the processes generating biodiversity and to understand how humans fit into the web of life (Mora, Tittensor, Adl, Simpson, & Worm, 2011). Stork (2018) reviewed the current ordinal estimates for global insect diversity and noted how more recent approaches for estimating global insect diversity have converged on estimates between 5 and 10 million insect species (his figure 2). Despite this growing consensus, there remains much uncertainty about tropical species richness. Based on the taxonomic knowledge of better-known taxa, Stork (2018) estimates that 85% of global insect diversity occurs in the tropics and southern hemisphere. But how much of this tropical diversity is specialized on single hosts or is geographically restricted remains unknown. There are also uncertainties globally regarding the species richness within the four megadiverse holometabolous orders: Coleoptera, Diptera, Hymenoptera, and Lepidoptera. For these orders, the uncertainty is anchored within the “microtaxa,” where more is unknown than known, especially for the microdiptera and microhymenoptera (Forbes et al., 2018).

The first area of uncertainty is how specialized tropical insects are. The case has frequently been made that the niches of tropical organisms are more fine-grained than those of temperate species, due to greater biotic pressures within and across trophic levels in the tropics (Coley & Kursar, 2014; Dobzhansky, 1950; Forister et al., 2015; Janzen, 1973; MacArthur, 1972; Roslin et al., 2017; Sedio, Parker, McMahon, & Wright, 2018). In this scenario, because specialization begets species diversification, tropical diversity might be an emerging property of such specialized symbiotic relationships.

Biodiversity estimates assume high specialization in the tropics. However, the possibility of greater tropical niche specialization due to elevated species interactions remains much contested with considerable contrary data (e.g., Moles, Bonser, Poore, Wallis, & Foley, 2011; Moles & Ollerton, 2016; Novotny et al., 2006). Regardless of the answer, the question is not a trivial one. In the best-characterized insect fauna, 68% of British insects are herbivores and parasitoids (Price, 1980) and therefore require hosts. This means that a general understanding of diet breadths of tropical insects is a critical element for making diversity extrapolations. Burgeoning molecular data sets, and in particular molecular estimates of both taxonomic diversity and diet/host breadths, promise to reveal much-needed data about the specificity of tropical communities.

The second area of uncertainty is how tropical species are geographically distributed. The tropical regions, particularly the

Neotropics, are geographically diverse. South America is the earth's largest equatorial land mass and possesses tremendous topographic diversity in regions such as the Andes and the Guiana Shield. These features are additional multipliers for species richness. Alpha and, especially, beta diversities for Neotropical insects are largely unquantified, even for groups as familiar as butterflies, giant silk moths, and dragonflies. For instance, a single 65-km transect on the east slope of Andes in Peru has already yielded 2,500 butterfly species, with 500 more species estimated to be present (Lamas, 2017). This equates to 15% of the known global butterfly fauna and four times the number found north of Mexico. As it seems very unlikely that 15% of the global fauna would occur along a single 40-km transect, many more butterfly species likely remain to be discovered. Stated differently, there is still much we do not know about the alpha and beta diversity of the world's tropics, even for butterflies, the most well-studied insects. Without beta diversity estimates for Neotropical plant–insect interactions, it is difficult to correct the second assumption of the Erwin Equation—that geographic turnover of insects and host plants is constant—using the Ødegaard Equation.

The third area of uncertainty is whether beetles are truly the largest insect order. Diversity estimates through Stork's (2018) treatment hold to this traditional view. However, there is increasing evidence that both Hymenoptera and Diptera are more diverse. In Britain, both Hymenoptera and Diptera (Chandler, 1998; Kloet & Hincks, 1945) outnumber beetles. A canopy fogging study of 10 trees at a lowland forest in Borneo yielded greatest richness for Hymenoptera, followed by Coleoptera and Diptera (Stork, 1991). A recent assessment of hymenopteran species diversity based on the host specificity of well-studied hymenopteran parasitoid communities estimated that there could be 2.5–3.2 hymenopterans for every beetle species (Forbes et al., 2018).

Recent large-scale insect inventories, especially those that employ DNA barcoding identification methods, further support the hypothesis that Coleoptera is not the most speciose order. Haplotype diversity for 1 million insects from Malaise trap samples from across Canada was substantially greater for Hymenoptera and Diptera than for beetles—the former two orders taken together accounted for two-thirds of all insect BINs (barcode index numbers, a type of molecular operational taxonomic unit, or operational species unit) recovered from the traps (Hebert et al., 2016). Hymenopteran haplotype BINs were 2–3 times more diverse than those of beetles, while dipteran BINs were 7–8 times more diverse than those for beetle. Staggering Cecidomyiidae (gall fly) haplotype diversity was discovered—projections suggested that more than 16,000 gall fly species would be found in Canada and that the global fauna of gall flies may approach two million species. A similar study in Germany found that Diptera accounted for just over half (51.6%) of all the insect BINs recovered (Geiger et al., 2016). While comparable numbers for tropical systems are not yet available, preliminary Malaise trap samples from Costa Rica are yielding staggering numbers of unique dipteran and hymenopteran BINs (D. Janzen and W. Hallwachs personal communication).

All three of these unknowns can be addressed with widespread insect diversity inventories using DNA barcoding with BINing

(Ratnasingham & Hebert, 2013). This method provides a rapid and economical means of objectively identifying and estimating insect species diversity. Barcoding inventories from Malaise trap samples provide substantial evidence that Hymenoptera and Diptera may be more diverse than Coleoptera (Geiger et al., 2016; Hebert et al., 2016). In addition to providing diversity estimates that are independent of taxonomic nomenclature and availability of taxonomic expertise, barcodes and other molecular data have tremendous potential to increase the accuracy of several of the insect diversity estimate methodologies, including those based on host specificity, known-to-unknown ratios, portion of new species in samples, and discovery curves (see Stork, 2018, Table 1 of this paper). Given present resources for taxonomy, the rapidly decreasing costs of DNA methodologies, and sheer diversity of tropical biotas, molecular data—especially once nuclear markers are included—promise to revolutionize biotic inventory and species discovery. While some tropical DNA barcoding inventories are ongoing at well-characterized sites (e.g., Area de Conservación Guanacaste and the New Guinea Binatang Research Center), additional large-scale inventories are needed. For instance, in 2019, the government of Costa Rica committed to DNA barcoding its national biodiversity over the next ten years. If similar efforts are undertaken in other tropical areas, they will substantially improve our biodiversity estimates.

We are moving ever closer to a robust estimate of global insect richness thanks to the efforts of many scientists combining multiple methods to estimate biodiversity on Earth. Because most species on Earth are insects, enumerating the planet's insect biodiversity would allow us to better (a) identify what eco-evolutionary factors promote diversification, (b) estimate absolute rates of species extinction and speciation, (c) direct support for most-needed taxonomic efforts, (d) delineate geographic areas of extraordinary diversity and endemism, (e) employ insects in ecological and evolutionary studies, and far more.

A better understanding of insect diversity and how it is distributed across the planet can inform conservation planning and help guide stewardship actions needed for the protection of the planet's insect fauna. It is a pity that at a time of widespread reports of global insect decline (Hallmann et al., 2017; Janzen & Hallwachs, 2019; Simmons et al., 2019; Wagner, 2019), we lack the fundamental data on insect richness necessary to ascertain the geographic scope, magnitude, and time scale of insect declines. We cannot even know if the more extreme claims insect losses (e.g., Sánchez-Bayo & Wyckhuys, 2019) are overstated or understated. How many taxa are at risk? What lineages or ecological guilds might be in steepest decline? From first principles, parasites and their hyperparasites, being apex predators, will be among the first to fail under biotic and abiotic pressures in the Anthropocene (Shaw & Hochberg, 2001). Likewise, entomophagous predators, such as ground beetles and wasps, might also be expected to experience steeper rates of declines as their prey species' abundances diminish (Hassell & May, 1986). To guide effective conservation efforts, we desperately need to know how many species inhabit our planet.

Since Erwin first estimated insect species richness, there has been an exponential increase in the resources available for

documenting and identifying insects. Molecular techniques such as CO1 barcoding, BINing, eDNA prospecting, and metabarcoding, especially when coupled to high-throughput and third generation sequencing technologies, are revolutionizing taxonomic delimitation and discovery (Joly et al., 2014; Kennedy et al., 2020; Kress, García-Robledo, Uriarte, & Erickson, 2015). Furthermore, with the proliferation of the internet, smartphone applications, and online open-access databases curated by taxonomic experts, we have the unprecedented ability to gather data and connect scientists and non-scientists around the globe in species identification and monitoring efforts. Comprehensive open-access online databases (e.g., iNaturalist, International Barcode of Life, Global Biodiversity Information Facility, Encyclopedia of Life) curated by expert taxonomists and populated by data from scientists and amateur naturalists have the potential to provide expansive global records of biodiversity at scales impossible before now (Chandler et al., 2017; Schmeller et al., 2017). These new technologies and resources promise to greatly accelerate our abilities to categorize, describe, curate knowledge, and quantify the number of insect species on Earth.

While Erwin's estimate of 30 million insects has been abandoned for decades, it is far too early to regard it as dead. Molecular methods, combined with global insect surveys, are unveiling vast cryptic diversity. Microdipterans and wasps alone have the potential to push global insect diversity well beyond our upper limit of 8.8 million, perhaps to 20 million or beyond.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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