



Overview

Mapping and understanding the diversity of insects in the tropics: past achievements and future directions

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Abstract

We still do not know how many insect species there are in tropical forests. The rate of species description peaked a century ago. Unfortunately, taxonomy ceased to be fashionable before it had completed cataloguing insect diversity. Molecular information combined with web-based data dissemination promises to shorten the 20 years it takes on average for insect specimens to be described as new species. Our inability to enumerate tropical species has made estimates of their diversity popular. Plant-based estimates, multiplying the number of plant species by the number of insect species effectively specialized to them, have been used for the past 150 years for global insect diversity estimates and recently also for the first local rainforest diversity estimate of arthropods, at 25 000 species. Why are there so many insect species in tropical forests? Insect diversity may be driven by latitudinal trends in vegetation. The near impossibility of conducting a complete census of complex plant–insect food webs in tropical forests should focus our attention upon the most common species and interactions. Recent studies of trees in Amazonia and herbivores in New Guinea suggest that such reduced food webs may be surprisingly simple and, thus, amenable to study, while still including more than 50% of all plant and insect individuals and their interactions. A pan-tropical network of plots, modelled on the existing network of forest dynamics plots, and potentially utilizing the existing, but rather poorly used, network of canopy cranes, could provide spatially resolved data on plant–insect food webs. The study of food web dynamics requires experimental manipulation, which can range from exclusion or addition of single species to ecosystem-wide manipulation of species composition and habitat fragmentation. Recent progress in molecular taxonomy, proliferation of community phylogenies, improved food web census techniques and an increasing focus on experiments promise an exciting time for tropical entomology.

Key words alpha diversity, beta diversity, DNA barcoding, food web, latitudinal gradient, trophic interaction.

COUNTING SPECIES: TAXONOMIC DIMENSIONS OF DIVERSITY

How many insect species coexist in a tropical forest? This may be the most obvious question asked by an entomologist confronted with tropical biodiversity. The extraordinary diversity of insects has attracted entomologists to the tropics since the early days of biological exploration (Bates 1863; Wallace 1869) and, to this day, tropical entomology remains both blessed and burdened with the diversity of species it purports to study. An insect specimen sampled in the tropics by Henry Bates or Alfred Wallace likely belonged to a new species. The rate of species description for many taxa, including Papua New Guinean (PNG) butterflies, as an example of a well-

known taxon in a tropical region, peaked in the early 20th century (Fig. 1, Gaston *et al.* 1995; Costello *et al.* 2012). Unfortunately, taxonomy ceased to be fashionable science soon afterwards, and well before it could have completed the task of cataloguing the global diversity of tropical insects.

Presently, some of the largest sets of high-quality specimens, often associated with ecological and molecular data, are generated by quantitative ecological studies (Basset *et al.* 2007; Janzen & Hallwachs 2011; Kitching *et al.* 2011). For instance, a comprehensive sampling of 18 focal taxa from a rainforest in Panama produced 130 000 individuals from 6144 species, 62% and 24% of which were assigned to existing genera and species, respectively, after 8 years of analysis by over 100 taxonomists (Basset *et al.* 2012). On average, it takes 20 years for insect specimens to be formally described as new species (Fontaine *et al.* 2012). Ecologists would welcome a somewhat faster pace of taxonomic discovery. A combination

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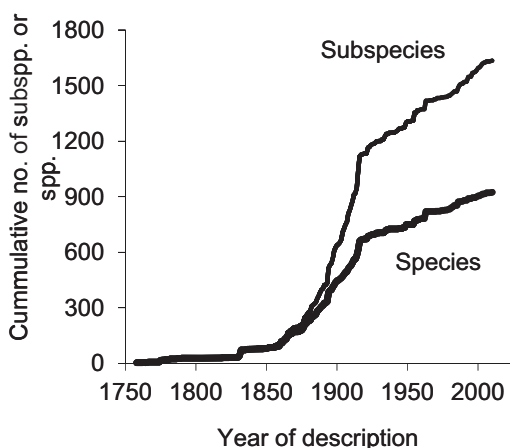


Fig. 1. Cumulative total of currently recognized subspecies and species of butterflies from Papua New Guinea based on their date of taxonomic description. Data from Tennent (2006a,b).

of species definition and recognition based on molecular information, particularly DNA barcodes, with web-based dissemination of data and images promises a radical change in the taxonomy of tropical insects in the near future (Miller 2007). These technologies provide the opportunity to expedite formal descriptions of new species (e.g. Butcher *et al.* 2012; Riedel *et al.* 2013a,b) and also to provide interim taxonomic reference systems that can be used before formal names are available (Schindel & Miller 2010; Ratnasingham & Hebert 2013).

May (1988) noted that we do not know insect diversity even on a local scale, in a ‘representative hectare’ of a tropical forest. A quarter century later, Basset *et al.* (2012) published the first comprehensive assessment of local arthropod diversity in the tropics, estimated at approximately 25 000 arthropod species within 6000 ha of a lowland rainforest in Panama. Only 0.48 ha of the forest and 25% of the predicted species were actually sampled. The plant-based extrapolation of samples to the entire forest, based on the known number of plant species in the forest multiplied by the estimated number of unique (effectively specialized *sensu* May 1990) insect species per plant species, performed best among a range of extrapolation techniques, both for herbivorous and non-herbivorous insect taxa.

Plant-based extrapolation methods also have a long tradition of use in efforts to estimate regional and global diversity of insects. Westwood (1833) multiplied the contemporaneous estimate of 100 000 vascular plant species by four to six insect species per plant, based on his experience from Britain, to estimate the global diversity of insects at 400–600 000 species. The same approach was applied 150 years later by Erwin (1982) to 682 beetle species sampled by insecticidal fogging from canopies of 10 *Luehea seemanii* trees in Panama and, after corrections for host specificity, arthropod taxa other than beetles, and non-canopy species, multiplied by the global estimate of 50 000 tree species to suggest that there were 30 million insect species on the planet.

That paper (Erwin 1982) was especially important in being the first to articulate a set of quantitative assumptions about

insect diversity in a sequence that could be discussed and tested (Miller *et al.* 2002). Several studies re-examined individual parameters of Erwin’s calculation, particularly host specificity, and expanded insect data sets available for calculations (Stork 1988; Thomas 1990; Odegaard *et al.* 2000; Novotny *et al.* 2002; Hamilton *et al.* 2010, 2011, 2013). Global estimates of diversity have subsequently been reduced, usually to below 10 million species, most recently to 6.1 million species (with a 90% confidence interval of 3.6–11.4 million species) (Hamilton *et al.* 2010, 2011). However, none of these estimates is entirely satisfactory as they continue to rely on limited data, mostly on folivorous herbivores from either the Coleoptera or Lepidoptera sampled in a single rainforest community. Few local studies examine an entire insect fauna associated with a particular tree species; Stork (1991) and Basset and Arthington (1992) provide probably the most detailed data for, respectively, tropical and subtropical tree species. Recent discoveries of large rates of cryptic diversity among parasitoids based on molecular data (Smith *et al.* 2008, 2012; Veijalainen *et al.* 2012) may require significant increases in the estimates. Further, even classical taxonomy of some diverse taxa, including Diptera, and guilds, such as soil insects, remain poorly understood (Brown 2005; Wu *et al.* 2011).

A better estimate of overall diversity on regional and global scales could be generated by scaling-up local food web data separately for each guild of herbivores, parasitoids and predators. Individual guilds vary widely in their host specificity and species richness, both in herbivores (Novotny *et al.* 2010) and parasitoids (Lewis *et al.* 2002; Hrcek *et al.* 2013). Interestingly, herbivore host specificity (measured as the ratio of specialists to generalist – see Fig. 2) appears to be negatively correlated with species richness, at least among folivorous guilds (Novotny *et al.* 2012). This means that the most specialized guilds – gallers, miners and cell suckers – are species-poor, typically with less than 10 species on any particular plant species. However, they accumulate species quickly with increasing plant diversity from local to regional scales. The relative species diversity of individual guilds therefore depends on the spatial scale sampled, and hence on the diversity of plants at that scale. Highly specialized guilds should be more prominent in regional species pools than local communities. This prediction is difficult to test because the most specialized guilds are small-bodied and, as such, are particularly poorly known taxonomically (see Gaston 1991 for a correlation between the probability of species description and body size). For instance, we estimated that in the cell-sucking guild, there may be at least 2775 typhlocybina leafhopper species in PNG while, at the same time, there are only 40 species, or less than 0.5% of the total, formally described from that region (Baje *et al.* 2013).

For parasitoids, taxonomic knowledge of species and ecological knowledge of trophic interactions is even poorer than for herbivores (Quicke 2012; Rodriguez *et al.* 2012; Smith *et al.* 2012). For instance, only seven from 119 species of hymenopteran parasitoids reared from caterpillars in PNG (Hrcek *et al.* 2013) were already known taxonomically

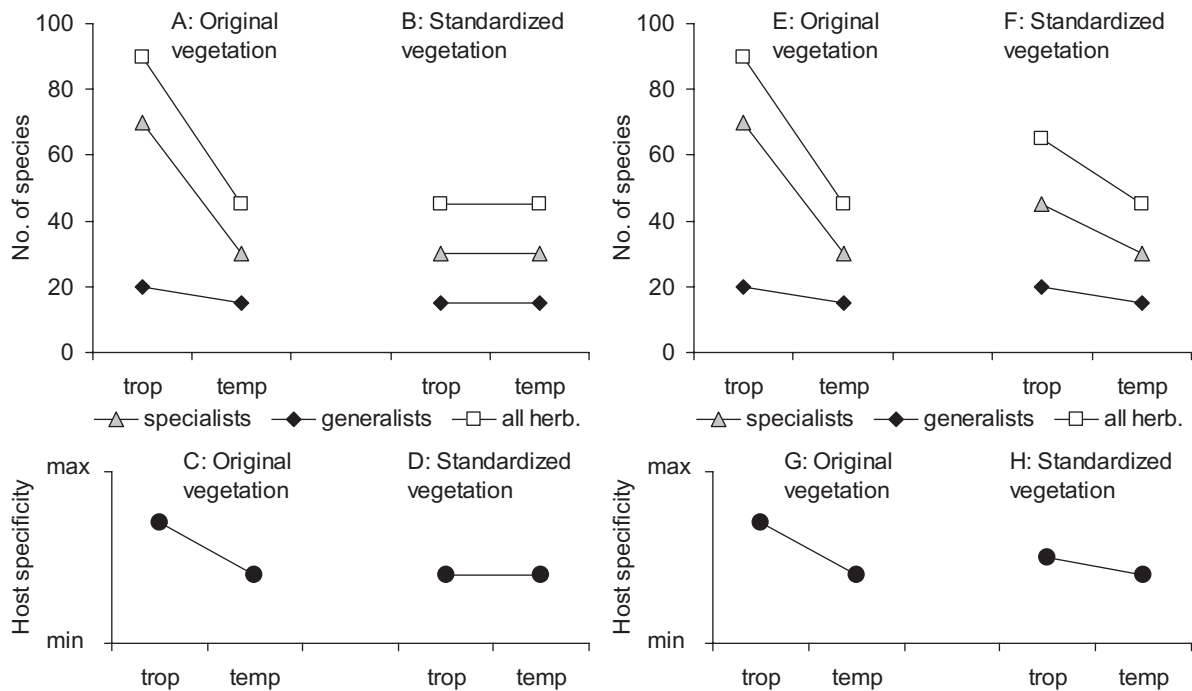


Fig. 2. Hypothetical latitudinal trends (tropical to temperate) in herbivore species richness, steeper in specialists than generalists (A), generated entirely by trends in vegetation composition (B), lead to decreasing host specificity along latitude (C) but only on non-standardized vegetation (D). An alternative (E) where latitudinal trends are only partly explained by vegetation (F), leads to a latitudinal trend in host specificity (G), only partly explained by vegetation (H). In both cases, we assume that latitudinal trends in vegetation affect specialists more than generalists. All herbivores = specialists + generalists.

(J Hrccek pers. comm. 2014). Molecular analysis of parasitoids uncovers more cryptic diversity than in many other insect taxa, including their herbivore hosts (Smith *et al.* 2008). Parasitoid adults can be sampled relatively easily for taxonomic studies, for instance using Malaise traps, but they lack the information on their hosts. Rearing parasitoids is labour-intensive since it is difficult to distinguish parasitized and healthy hosts and focus only on the former. Recent progress in molecular detection of parasitoids in their hosts (Hrccek *et al.* 2011; Jenkins *et al.* 2012) and hosts in their parasitoids (Rougerie *et al.* 2011) may remedy this problem by combining sampling and taxonomic analysis of adult parasitoids with molecular detection of their hosts.

While global estimates of insect diversity may or may not be seen as important (Miller *et al.* 2002; May 2010), the lack of regional, if not global, data on the size and composition of insect faunas is clearly a problem for contemporary tropical entomology. Taxonomically, the field of insect community ecology remains in a pre-Linnaean stage in the tropics, as each research project tends to create its own internal taxonomy, with species that can be well defined morphologically and molecularly, yet are not formally named. This informal taxonomy is adequate for local studies but becomes problematic when data from different studies need to be integrated into larger, regional data sets (but see Ballesteros-Mejia *et al.* 2013). The use of interim taxonomic reference systems based on DNA barcode clusters as implemented in the Barcode of Life Database provides an approach that allows comparison

across studies and sites (Schindel & Miller 2010; Ratnasingham & Hebert 2013). The study of beta diversity and species turnover among communities over large geographic areas (Novotny *et al.* 2007; Beck *et al.* 2012; Baselga *et al.* 2013) or periods of time (Chen *et al.* 2009; Grøtan *et al.* 2012), and the mechanisms of community assembly from regional species pools (Novotny *et al.* 2012; Stone *et al.* 2012), are thus particularly poorly studied in the tropics despite the indication from the classic temperate-zone studies that regional species pools may be the principal determinants of local community composition (Compton *et al.* 1989).

We have a great opportunity for mutual benefit among ecology, evolution and systematics, bringing together morphological, genomic and biological data in a new era of integrative taxonomy that is widely accessible and useful because of new digital tools – a renaissance of taxonomy.

FROM TEMPERATE TO TROPICAL FORESTS: INTERACTION NETWORKS AND LATITUDINAL TRENDS IN DIVERSITY

Why does insect diversity increase from temperate to tropical forests? The simplicity of this question is deceptive because the monotonic increase in species diversity towards the tropics appears to be a complex result of evolutionary history and contemporary ecological interactions (Mittelbach *et al.* 2007;

Schemske *et al.* 2009; Agrawal *et al.* 2010). Phylogenetic studies indicate that the tropics are both the ‘cradle’ and the ‘museum’ of species diversity, i.e. they are characterized by both higher speciation and lower extinction rates than temperate regions (McKenna & Farrell 2006; Condamine *et al.* 2012). These evolutionary dynamics have generated larger, but poorly documented, regional pools of species in the tropics than in the temperate zones.

Understanding how so many species can coexist in a tropical forest requires the study of inter-specific interactions, particularly food webs. The large numbers of herbivore and parasitoid species in tropical relative to temperate forest communities reflect differences in (1) the number of host species (plant species for herbivores and herbivore species for parasitoids); (2) the number of herbivore/parasitoid species per host species, i.e. host vulnerability; and/or (3) the number of host species per herbivore/parasitoid species, i.e. host specificity (Lewinsohn & Roslin 2008). The diversity of herbivores and parasitoids may be maintained by their resources (bottom-up effects) or by their natural enemies, including predators, parasitoids and pathogens (top-down effects) (Denno *et al.* 2005). While the increase in plant diversity towards the tropics is well documented (e.g. there are 5–10 times more plant species per 10 000 km², and six times more woody species per hectare in tropical than temperate areas – Novotny *et al.* 2006; Barthlott *et al.* 2007), our knowledge of latitudinal trends in insect species richness and host specificity, both for herbivores and parasitoids, is surprisingly poor (Stork 2007; Quicke 2012). The number of herbivore species per plant species may be similar in tropical and temperate forests, although we lack a rigorous analysis (Lewinsohn *et al.* 2005; Novotny *et al.* 2006).

The evidence for latitudinal trends in host specificity is controversial (Stork 2007). This is a problem because the role of herbivores as density-dependent mortality agents maintaining plant diversity depends on their specificity (Leigh *et al.* 2004). We found no difference in host specificity between Europe and New Guinea when we compared herbivores feeding on tropical and temperate sets of plant species with comparable phylogenetic diversity (Novotny *et al.* 2006). In contrast, Dyer *et al.* (2007) let the phylogenetic diversity of their study plants vary with latitude and found increasing host specificity towards the tropics in the Americas, i.e. in parallel with increasing plant phylogenetic diversity from temperate to tropical forests.

Contrasting results may reflect biological differences between the studied systems, or different methodological approaches. In particular, each study answers a subtly different question, depending on whether it standardizes for the simplified vegetation in temperate compared with tropical forests. For instance, differences in vegetation structure explained a large part of the differences in ant diversity between primary and secondary rainforests (Klimes *et al.* 2012), and the plant–insect food web structure also changed with simplification of vegetation along a disturbance gradient (Tylianakis *et al.* 2007). The apparently conflicting results between low beta diversity among herbivore communities on conspecific plant species in New

Guinea (Novotny *et al.* 2007) and high beta diversity of geometrid moths on non-standardized vegetation in Borneo (Beck *et al.* 2012) may also reflect different analytical approaches to insect community changes caused by vegetation.

Latitudinal trends in plant species richness, phylogenetic diversity, abundance and biomass may, partially or even completely, explain latitudinal trends in herbivore diversity and host specificity. The null hypothesis is that the rate of increase in herbivore species richness merely reflects increasing diversity of the vegetation from temperate to tropical ecosystems (Fig. 2a) so that herbivore diversity on temperate vegetation equals herbivore diversity on a subset of tropical vegetation matching the temperate vegetation in species and phylogenetic diversity (Fig. 2b). This null hypothesis assumes that herbivores respond more strongly to vegetation changes than generalists (Fig. 2a) so that the latitudinal trend of increasing host specificity towards the tropics (Fig. 2c) is driven solely by vegetation change, particularly by increasing number of rare plant species each hosting its own specialist herbivores (Fig. 2d). An alternative hypothesis (Dyer *et al.* 2007) postulates latitudinal diversity gradient for specialists and generalists (Fig. 2e,f) that may be sensitive to the standardization of vegetation across latitudes (specialists are likely to be more sensitive to reduced plant species richness in temperate forests than generalists), but the standardization does not remove the host specificity trend entirely (Fig. 2g,h). Under this hypothesis, higher herbivore specialization in the tropics would facilitate coexistence by partitioning niche space, thus explaining high tropical diversity independently from latitudinal trends in plant diversity.

The species richness of parasitoids, and their host specificity, probably increases towards the tropics (Stireman *et al.* 2005; Smith *et al.* 2008; Quicke 2012). The null hypothesis is that latitudinal change in herbivorous communities drives latitudinal trends in diversity and host specificity of their parasitoids, which would be an indication that parasitoids do not play an important role in generating high tropical diversity of their hosts (Fig. 3a,b). Alternately, there may be a latitudinal trend in the number of parasitoid species per host species even after vegetation has been standardized (Fig. 3d). This trend may or may not disappear after the assemblage of their herbivore hosts is standardized by subsampling the tropical herbivore community to match the number of species and phylogenetic diversity of the temperate one (Fig. 3e). Recently, Morris *et al.* (2014) found latitudinal trends in parasitoid host specificity present in raw community data, but absent after standardization for latitudinal trends in the diversity of parasitoid hosts.

PLANT–INSECT FOOD WEBS: FROM COUNTING SPECIES TO MAPPING INTERACTIONS

The focus of insect diversity studies is gradually shifting from surveying species to mapping inter-specific interactions, particularly trophic interactions in food webs (Novotny &

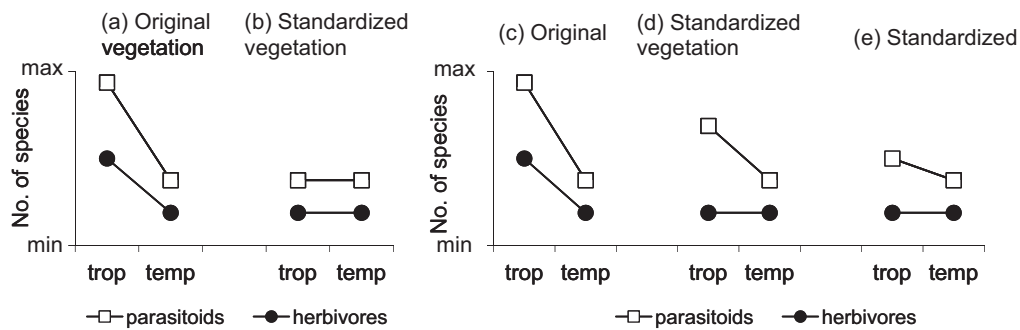


Fig. 3. Two of the many possible outcomes of temperate – tropical standardization in tri-trophic food webs: (1) latitudinal trends (tropical to temperate) in herbivore and parasitoid diversity (a) are driven entirely by change in vegetation (b); (2) latitudinal trend in herbivore diversity (c) is driven by change in vegetation (d) while the latitudinal trend in parasitoid diversity persists even after the standardization of host herbivore communities (e), suggesting a potential for increased parasitoid impact in tropical forests.

Basset 2005; Thompson *et al.* 2012). Unfortunately, documenting trophic interactions is even more difficult, and requires even larger sampling effort, than documenting species. In more than 15 years, we have traced nearly 7000 feeding links between about 200 plants and 1500 insect herbivores from 11 guilds in a lowland rainforest in PNG (Novotny *et al.* 2010). Unfortunately, these figures might represent only 15% of the total herbivore richness and interaction diversity in that lowland forest since we have estimated that there were ~50 000 distinct trophic interactions between ~9600 herbivorous insect species and 200 tree species in that forest (Novotny *et al.* 2010).

This extraordinary complexity of tropical plant–herbivore food webs may stimulate the development of more efficient, particularly molecular, methods for the detection of trophic interactions. However, the near impossibility of conducting complete censuses in plant–insect food webs in tropical forests (Novotny & Basset 2000) should also refocus our attention to targeted studies of species and interactions that are both common and functionally critical, rather than attempting to achieve complete coverage of entire food webs.

Tropical food webs, although extremely complex, are dominated by relatively few interactions (Fig. 4). For instance, 49 597 folivorous herbivores sampled from 38 tree species in PNG represented 865 species, but 50% of all herbivore individuals belonged to the 32 (3.7%) most common species. We documented 3260 distinct trophic interactions between particular plant and folivore species in this food web, but 50% of all individual herbivores were involved in only the 97 (3.0%) most frequent interactions (Novotny *et al.* 2012). There is thus an obvious, but rarely considered, possibility to focus on a few dominant interactions when analyzing complex tropical food webs. Likewise, quantitative samples from tropical insect communities are also dominated by a few species. For instance, only 1–6% of the most common species comprised 50% of all individuals in extensive surveys of butterflies, ants and moths on the Barro Colorado Island (Fig. 5). These common species and interactions could be also used for long-term monitoring of plant–insect dynamics in tropical forests (Basset *et al.* 2013), most feasibly associated with the network

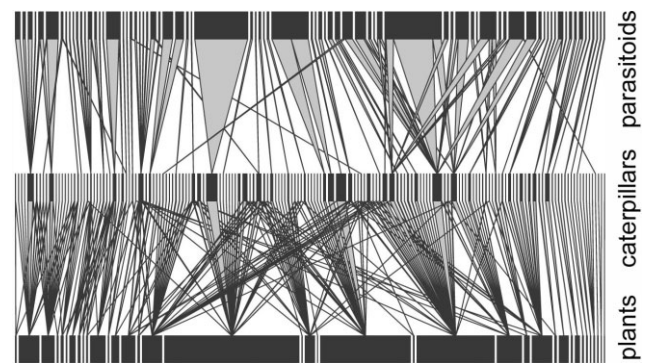


Fig. 4. Quantitative tri-trophic food web for secondary rainforest vegetation in PNG comprising 37 plant species (11.1 m² basal area, representing 70% of basal area from 1 ha), 4803 caterpillars from 154 species (exposed and semi-concealed guilds) and 643 parasitoids from 76 species (mostly Braconidae, Tachinidae and Ichneumonidae) (Hrcek *et al.* 2013).

of forest dynamics plots coordinated by the Center for Tropical Forest Science (Losos & Leigh 2004; Wolf *et al.* 2009).

Recently, ter Steege *et al.* (2013) used this approach to estimate that although Amazonia harbours approximately 16 000 tree species, half of all individual trees belong to just 227 (1.4%) super-abundant tree species. This result suggests that we could perhaps construct a rather simple plant–insect food web for the entire Amazon, combining these super-abundant tree species with the presumably rather limited range of their common herbivore species.

In our PNG study (Novotny *et al.* 2012), each tree species hosted a diverse assemblage of folivorous insects (including adult and larval chewers, miners and mesophyll cell suckers from four insect orders), but 50% of insect individuals feeding on that tree recruited from only 1 to 7 (mean 3.8) species. The total number of folivorous species as well as the number of species comprising 50% of all individuals increased as a power function of the number of plant species included in the food web (Fig. 6). Extrapolation of our data from 38 tree species suggests that the most common 95 folivorous species could include half of all insect individuals in a food web on 227 tree species (the

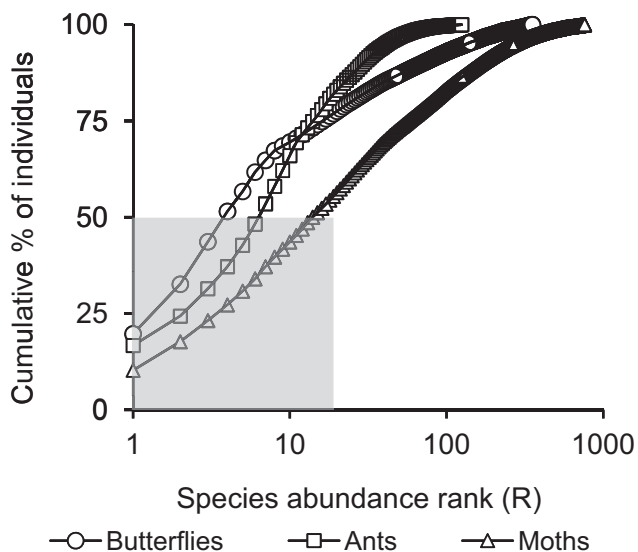


Fig. 5. Cumulative proportion of individuals represented by *R* most common species in quantitative community samples of butterflies, ants and moths (butterflies: surveyed along 500 m transects, $S = 353$ species, $n = 7248$ individuals; ants: Winkler litter extractors, $S = 125$, $n = 10\,938$; moths: light traps, $S = 760$, $n = 26\,636$), from a lowland tropical forest at the Barro Colorado Island. Grey area denotes species representing 50% of all individuals in each sample, represented by respectively 4, 7 and 15 species in butterflies, ants and moths, i.e. 1–6% of all species. Based on unpublished data from Y Basset (pers. comm. 2014).

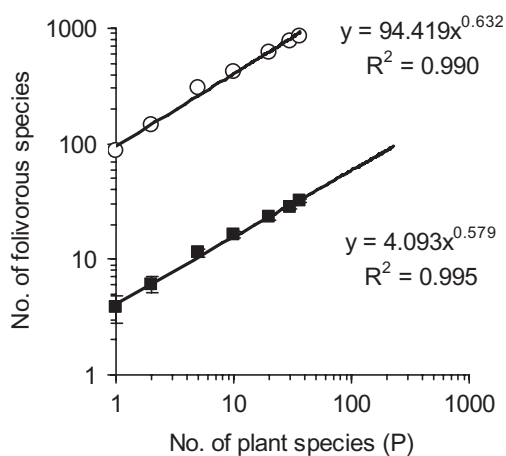


Fig. 6. Accumulation curve for the total number of folivorous herbivores (circles) and the number of common folivorous species comprising 50% of all individuals (squares) with increasing number of plant species (*P*). The curve for common folivorous species is extrapolated to predict diversity for 227 tree species (see text). Individual points represent means for $P = 1$ plant species calculated from the 38 species sampled, 20 random combinations of $P = 2, 5, 10, 20$ and 30 selected from the 38 tree species, and a single data point corresponding to the entire data set of $P = 38$ species. Data are from Novotny *et al.* (2012).

number of super-abundant species from the Amazon; see above). A rather reckless combination of our PNG folivore data with data on Amazon trees suggests that half of all folivorous individuals feeding on 227 super-abundant tree species, which in turn represent half of all individual trees in the Amazon, recruit from merely 95 insect species. In other words, a food web including 227 tree and 95 insect species might comprise 50% of all tree individuals and 25% of the total abundance of folivorous herbivores in the Amazon!

Even a sophisticated description of network structure is unlikely to provide insights into the dynamics of tropical food webs. This is one driver of the current increase in experimental manipulation of tropical food webs, following in the footsteps of classical experiments by Simberloff and Wilson (1969). These include fine-scale manipulation accomplishing removal (Morris *et al.* 2004) or addition (Letourneau & Dyer 1998) of a single insect species, documenting the feasibility of respectively apparent competition and trophic cascades in tropical forest webs. Further, experiments can exclude natural enemies, such as herbivores (Bagchi *et al.* 2010) or predators (Mooney *et al.* 2010; Klimes *et al.* 2011), and/or manipulate plant (Fine *et al.* 2004) or mineral (Kaspari *et al.* 2009) resources. Finally, entire-ecosystem manipulation can include forest fragmentation (Ewers *et al.* 2011) or vegetation assembly, emulating temperate-zone grassland experiments (Hector *et al.* 1999) in a tropical forest environment (Hector *et al.* 2011).

The study of food webs also suffers from some culturally ingrained gaps and biases. In particular, many studies focus either on the species composition, specificity and abundance of herbivores (Dyer *et al.* 2007; Novotny *et al.* 2010), or on the damage caused by herbivores (Kursar & Coley 2003; Lamarre *et al.* 2012), but surprisingly few studies manage to sample insects and measure holes in the leaves at the same time. Further, there are large scientific communities studying either plant–herbivore (Novotny & Basset 2005), or herbivore–parasitoid (Stireman *et al.* 2005) food webs, but very few combining both into tri-trophic food webs (Janzen & Hallwachs 2011), and none, as far as we are aware, including simultaneously parasitoids and predators (but see Van Veen *et al.* 2008 for a temperate food web example). Again, molecular tools provide great opportunities, as shown by recent exploratory studies (García-Robledo *et al.* 2013; Joly *et al.* 2013; Kishimoto-Yamada *et al.* 2013).

TROPICAL ENTOMOLOGY IN 21ST CENTURY

The study of tropical insect ecology did not accomplish as much in the 20th century as it might have. Tropical exploration declined in prominence within the field of biology in the early decades of the century, followed by a long period in which the still immature field of molecular biology had an ambition to dominate the field of biology without offering many useful techniques for insect taxonomy, ecology and phylogenetic studies (Wilson 2006). Last but not least, one of the most publicly visible quests of tropical entomology in the last

century was its efforts to estimate global diversity of insects. The competing estimates ranged by two orders of magnitude, from several million to 100 million species, not inspiring much confidence in the field of tropical insect ecology (Miller *et al.* 2002).

Fortunately, the situation is set to improve in the 21st century. Insect taxonomy is entering a revolution fuelled by molecular techniques including DNA barcoding, combined with internet-based dissemination of information. We can expect our catalogue of insect species, and their ecological traits, to expand significantly in the foreseeable future, thus providing opportunities for macro-ecological studies of insects which are already commonplace in taxonomically better known groups such as tropical vertebrates. Further, ecological studies have greatly benefitted from a robust high-level phylogeny of flowering plants (Bremer *et al.* 2009) and, in the case of birds, phylogenetic relationships resolved to the species level (Jetz *et al.* 2012). The situation in major insect lineages is much less satisfactory, but we can expect rapid progress towards global phylogenies (e.g. Mutanen *et al.* 2010).

While permanent study plots have played a key role in the study of plant diversity in tropical and temperate forests (Hubbell 2013), similar plot-based data on insect communities are lacking despite earlier recommendations to use plant plots for food web studies (Godfray *et al.* 1999). We recommend a focus on building a pan-tropical network of such permanent study plots, surveyed using standardized sets of methods, and modelled perhaps on the network of CTFS forest dynamics plots. The CTFS network could provide botanical information for understanding comprehensive tri-trophic food webs, as well as community phylogenies for plants (Kress *et al.* 2009). Small-scale but detailed, spatially explicit data on plant–insect food webs could be obtained also using the existing network of canopy cranes (Basset *et al.* 2003; Stork 2007) which could also provide a basis for experimental manipulation of food webs in forest canopies. The canopy crane network is presently rather underutilized and its research productivity has been declining, particularly in comparison with some other modern ecological approaches, such as DNA barcoding (Fig. 7). However, it has a potential for coordinated studies with global reach where individual cranes represent replicated data points.

In conclusion, because of the combination of faster taxonomy, robust phylogeny of principal insect taxa, and detailed plot-based food webs subject to experimental manipulation, there is great promise for tropical entomology in 21st century.

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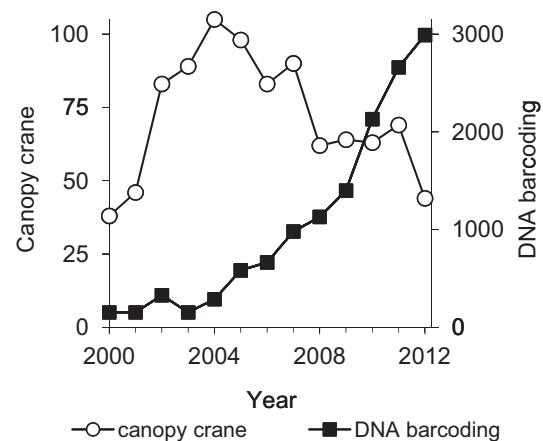


Fig. 7. Number of papers on ‘canopy crane’ and ‘DNA barcoding’ published annually from 2000 to 2012, as reported on Google Scholar (<http://scholar.google.com>), accessed on 22 December 2013.

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