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COMMENTARY

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Invertebrates and the complexity of tropical ecosystems

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Abstract

It has been estimated that there are seven million terrestrial arthropod species on Earth consisting of 6.1 million species of insects, 1.5 million of which are beetles. Tropical forests hold a majority of these species, yet few such places have been adequately sampled for alpha diversity, and there remains even more uncertainty about beta diversity. From an ecological point of view, it is the functional role of organisms within ecosystems that is the particular focus. It has been customary to classify invertebrates within ecosystems in terms of their trophic roles, but it is also useful to consider their roles in networks. In broad terms, we can classify these networks on the grounds of their basal resources. Those based directly on the photosynthetic products of plants are so-called "green" food webs, and those based on dead and dying plant material are "brown" food webs. Here, we principally discuss the diversity and functional roles of the invertebrates in tropical terrestrial ecosystems. New sampling and analytical techniques, an expanded set of focal taxa, and an enhanced concern with interactions and processes hold the promise of a productive future for invertebrate studies in the tropics. These will not only add to general understanding of the dynamics of tropical ecosystems but will also provide powerful tools for monitoring and responding to environmental change.

KEYWORDS

food webs, invertebrates, tropical ecosystems

> *There is, however, one natural feature of this country, the interest and grandeur of which may be fully appreciated in a single walk: it is the "virgin forest"[…] Here no one who has any feeling of the magnificent and the sublime can be disappointed. These, and many other novel features […] taken altogether surpass description, and produce feelings in the beholder of admiration and awe.*
>
> *Wallace, Letter to Members of the Mechanics Institute (1849)*

> *…… contemplate an entangled bank, clothed with many plants of different kinds, with birds singing in the bushes, with various insects flitting about, and with worms crawling through the damp earth […] reflect that these elaborately constructed forms, so different from each other, […] dependent on each other in so complex a manner have all been produced by laws acting around us.*
>
> *Darwin, Origin of Species (1859)*

Tropical rain forests are truly complex places exhibiting a very high diversity of life in virtually all terrestrial taxa. From an ecological viewpoint, this means that these form eye-wateringly complex networks of species–species interactions at spatial scales varying from the local to the continental. As our attention moves from rain forests to drier forests, scrublands and grasslands, this complexity diminishes but is still of a very high order.

As both Wallace and Darwin recognized, the principal multicelled players in this ecological drama are the invertebrates, particularly the arthropods and predominantly the insects. This dominance reflects not just diversity but also functional importance leading Edward O. Wilson to suggest they were *"The Little Things that Run the World"* (Wilson, 1987).

In this special issue of *Biotropica*, we showcase some of the latest research on invertebrates in tropical ecosystems and speculate on the future of invertebrate studies in tropical forests. Historically, of course, some taxa and their ecological roles have received attention from researchers throughout the period in which "Tropical Ecology" has been an acknowledged sub-discipline. A browse through the early issues of *Biotropica* supports this assertion. The first rather slim issue of the journal in 1969, nevertheless, contained work on tropical cockroaches (Willis, 1969), and the first of many papers on tropical butterflies appeared in volume 2 (Cook, Frank, & Brower, 1970).

The papers included in the present issue present less familiar model taxa (such as the Auchenorrhyncha), exploring innovative methods and responses to elevation gradients. Other contributions examine complexity and mapping approaches to understanding responses of invertebrates to human-modified landscapes, and some examine the functional roles of invertebrates in tropical ecosystems. In this introduction, we focus principally on the diversity and functional roles of the arthropods.

1 | THE CONTEXT

1.1 | Global diversity

Even by 1988 (May, 1988), there were well over a million described species of arthropods, followed (in the terrestrial biota) by the nematodes (10^3–10^4 species), the molluscs (10^3–10^4), and the annelids (10^3–10^4). Of the 10^5 plus described species of terrestrial arthropods, an overwhelming majority were insects. Stimulated by Erwin's (1982) initial estimates of global arthropod diversity, a vigorous debate on the "how many species?" question has challenged entomologists for over 40 years. Recent estimates have tended to converge on the more modest (but still impressively large) average of about 7 million species of terrestrial arthropods of which 6.1 million are insects and 1.5 million beetles (Stork, 2018). It is noteworthy that these may include about a million species of mites. Overall, it is estimated that perhaps 80% of these species remain to be described. Stork (2018) repeatedly stresses the preponderance of the tropical fauna in these assessments across all biogeographical realms.

1.2 | Local diversity

Substantial fractions of the arthropod biodiversity of tropical rain forests have been assessed in very few locations globally (Basset et al., 2012). Comprehensive surveys necessarily target a wide range of taxa and use multiple survey methodologies. While we recognize that knowledge about the identities, roles, and uses of many invertebrates were, and remain, known to the original human populations of tropical regions, the Centenary Expedition of the Royal Entomological Society of London to northern Sulawesi in 1985 was one of the first modern quantitative attempts at such an assessment (Knight & Holloway, 1990). Resulting from that work, Hammond (1990) summarized the results from a core area of about 500 ha of lowland forest based on a sampling of several million insect specimens. He focussed down on the Coleoptera estimating somewhat more than 6,000 species from among the 1.17 million specimens sampled. The Sulawesi study was ground-breaking, but Hammond's report did not use extrapolation methods to estimate total diversity. The "IBISCA Panama" study (Basset et al., 2007, 2012), subsequently, did use such methods. Working on multitaxon, multiple methods surveys of the 6,000 ha lowland San Lorenzo Forest, Basset et al. (2012) estimated the presence of about 25,000 species of arthropod of which about 60% might be found in a single hectare. Other local studies in the tropics have focussed either on particular host plants, particular taxa or particular trophic groups (e.g. Basset & Novotny, 1999; Dahlsjö et al., 2014; Novotny et al., 2004; Prinzing & Woas, 2003).

Exciting and instructive (not to say challenging) as these local estimates (alpha diversity) have been, it is place to place taxonomic turnover—beta diversity—that generates the immense regional values for species richness characteristic of the tropics. Few places have been adequately sampled for alpha diversity, and there remains even more uncertainty about beta diversity (Bell, Heard, Manion, Ferrier, & Klinken, 2013).

There is evidence that suggests that the magnitude of spatial turnover may be taxon-specific, reflecting the dispersive abilities of the organisms concerned. When termites are assessed using standard transects, for example, Davies's , Eggleton, Jones, Gathorne-Hardy, and Hernández (2003) cross-continental comparisons show low beta diversity within biogeographical areas, but almost complete turnover across biogeographical boundaries (Eggleton et al., 1997, 1996). Novotny showed that beta diversity is relatively low in New Guinea herbivores (Novotny et al., 2007). Other, more dispersive groups such as moths show higher rates of turnover especially when this is assessed to include relative abundance (Beck & Khen, 2007; Kitching, Ashton, Nakamura, Whitaker, & Khey, 2013).

An underlying problem, especially when turnover is assessed using species presence or absence, is undersampling, which is common in tropical studies (Coddington, Agnarsson, Miller, Kuntner, & Hormiga, 2009) producing the appearance of turnover that inflate estimates of beta diversity. Carefully designed comparative studies which incorporate relative abundance can show patterns of turnover even when the entire fauna cannot be realistically sampled. When it comes to identifying general patterns, however, the jury is still out.

2 | ECOLOGICAL ROLES

From an ecological point of view, of course, it is the functional role of organisms within ecosystems which is the particular focus. It has been customary to classify invertebrates within ecosystems in terms of their trophic roles—the herbivores, decomposers, predators, parasites, and so on. In an ecosystem context, it is also useful to consider their roles in networks. In broad terms, we can classify these networks on the grounds of their basal resources. Those based directly on the living photosynthetic products of plants (or their subsequent biochemically transformed derivatives) are so-called "green" food webs; those based on dead and dying plant material are "brown" food webs (Kaspari & Yanoviak, 2009; Swift, Heal, & Anderson, 1979). These detritus-based "brown" webs are, of course, multitrophic including microbial decomposers, animal cadavers, and wastes, as well as non-living products based entirely on plant material. Table 1 summarizes the principal trophic roles within each of these types of food webs and some examples of arthropod groups that fit within these categories.

2.1 | The green food web

Constructing a "green" food web generally begins by assessing the species diversity of plants in any location. In tropical systems, this seldom goes beyond an estimation of the number of woody plants in surveyed plots although some of the best work on tropical plant–herbivore connections has focused on herbaceous plants (e.g. Morris, Lewis, & Godfray, 2004) or woody seedlings and saplings (e.g. Maunsell, Kitching, Burwell, & Morris, 2015). Leaf miners have been a focus of attention principally because host–plant identity is firmly established by the existence of the leaf mine. Establishing and quantifying host–plant associations in the case of free-living herbivores is considerably more challenging and is best done by large teams of collectors followed by large-scale rearing programmes (e.g. Basset & Novotny, 1999). Rearing programmes have the additional advantage of quantifying the level of parasitoidism within the food web.

Within tropical systems, other forms of living-plant herbivory—such as feeding on pollen, flowers, seeds, fruits, bark or wood, or on basal plants and lichens in general, are relatively little studied at the community level. This represents a major knowledge gap.

Among the arthropods, several higher-level taxa are almost exclusively herbivorous. The orders, Lepidoptera and Phasmida together with very large sections of the Orthoptera and Hemiptera, are cases in point. Among the vast order Coleoptera, the large families Chrysomelidae and Curculionidae are dominant herbivores. Other players may make up in mass action what they lack in species diversity—canopy scale insects, herbivorous grasshoppers, and leaf-cutting ants are striking examples.

Defining trophic levels above that of primary consumers (herbivores in the case of green webs) presents a challenge. Hymenopteran, dipteran, and other parasitoids are generally supposed to be restricted in their host ranges and, accordingly, can often be assigned confidently to particular food webs. For other predators, web specificity is less common. Free-living predators such as spiders, odonates, predatory flies, and the like no doubt participate across many webs regardless of the resource base involved. Indeed, in this respect, they are likely to play important roles in forming the "meta-web" which exists within the entire ecosystem regardless of the basal resource involved (Devoto, Bailey, & Memmott, 2014; Pocock, Evans, & Memmott, 2012).

Vertebrate dung, cadavers, and other produce may also be regarded as an adjunct to the traditional idea of green food webs, although whether or not the generators of these resources are or are not primary herbivores or their predators makes this placement open to interpretation. In any case, these resources maintain specialist sets of invertebrate necrophages, coprophages, keratinophages, nest commensals, and so forth.

2.2 | The brown food web

Plant detritus in its many forms constitutes the resource base of "brown" food webs often through the intermediary actions of fungi or saprophagous micro-organisms. Taxa generally assumed to form the base of saprophagous food webs include the Termitoidea, Isopoda, Diplopoda, and Collembola. Few arthropods, however, appear to feed directly on dead plant material without the assistance of microbes either externally or internally. Fungi are crucial in this regard: In fact, just as herbivores release the photosynthetic energy synthesized by plants to the wider green food web, so fungi process dead and dying plant material making it available to the wider participants in the brown food web.

In terrestrial systems, brown food webs have received much less attention by ecologists than their green counterparts perhaps because of this "fungal wall" to understanding. Just as green plants offer roles for many different feeding guilds, so fungi are also far from an homogenous resource. Lawrence and Milner (1996) offer one of the few reviews of the manifest roles of fungi as resources for arthropods. The categories presented in Table 1 are condensed from their detailed treatment.

2.3 | The importance of vertebrates?

There are probably, globally, about 53,000 species of terrestrial vertebrates. This liberal estimate allows all Amphibia to be honorary "terrestrials." This maximum accepts the substantial increases for birds (Barrowclough, Cracraft, Klicka, & Zink, 2016) and mammals (Burgin, Colella, Kahn, & Upham, 2018) recently proposed based, in part at least, on untested assumptions about cryptic species expected to arise from further molecular analyses. Undoubtedly, more species will be described but it is reasonable to assume that this figure represents a substantial proportion of all extant terrestrial vertebrates. These vertebrates comprise a complete sub-phylum of the Chordata with all the classes, orders, and families contained within this clade. In contrast, recent estimates

TABLE 1 Arthropods in terrestrial food webs: roles, examples[a]

	Coleoptera	Lepidoptera	Diptera	Hymenoptera	Others
The "green" food web—basal resource: Direct products of plant photosynthesis					
Herbivores—Chewers	Chrysomelidae, Curculionidae	Geometridae	—	Symphyta; Formicidae:Attinae (as fungal substrate)	Orthoptera, Phasmida
Herbivores—Suckers	—	—	—	—	Hemiptera
Herbivores—Gallers	Anthribidae, Curculionidae, Buprestidae, Cerambycidae	Gelechiidae, Tortricidae, Elacchistidae	Agromyzidae, Cecidomyiidae, Trupaneidae	Cynipidae, Tenthredinidae	Eriophyidae (Acarina), Psyllidae, Eriosomatidae, Adelgidae (Hemiptera)
Herbivores—Lignophages	Cerambycidae, Belidae	Cossidae, Hepialidae	—	Siricidae	Termitoidea
Herbivores—Anthophages	Cetoniinae, many Chrysomelidae	Lycaenidae	some Drosophilidae	—	Thysanoptera
Herbivores—Pollenophages	Melyridae	Heliconinae	—	Apidae	Thysanoptera
Herbivores—Nectarivores	Many adults	Majority of adults	Many adults	Many Adults	Many species
Herbivores—Frugivores	Curculionidae, Anthribidae	some Lycaenidae, Erebidae	Tephritidae, Drosophilidae	—	Dermaptera
Herbivores—Granivores	Bruchidae, Curculionidae, Ptiliidae	some species of many families including Carposinidae, Oecophoridae, Tortricidae, Gelechiidae	some Chloropidae	Eurytomidae, some Formicidae	Pentatomidae
THE "brown" food web—basal resource: Dead and dying products of plant photosynthesis and animal waste					
Detritivores	Salpigidae. Scirtidae	Tineidae, Oecophorinae	Tipulidae, Chironomidae,	—	Isopoda, Termitoidea, Diplopoda
Fungivores—Fruiting bodies	Leiodidae, Anobiidae, Cryptophagidae, Endomychidae, Erotylidae, Lathridiidae etc	Scardiinae	Mycetophilidae, Drosophilidae	—	Termitoidea
Fungivores—Leaf litter	Many taxa of unspecified exact feeding habits				
Fungivores—Rotten wood	Passalidae, Lucanidae, Buprestidae etc	Nematopogininae, Scardiinae	Tipulidae, Mycetophilidae	Siricidae, Xiphydriidae	Acarina, Aradidae, Collembola
Fungivores—Ambrosia feeders	Scolytinae, Platypodinae, Limexylidae	—	—	—	—
Fungivores—Myxomycota	Leiodinae, Camiarinae, Sphindidae, Lathridiidae	—	Sciaridae, Scatopsidae, Drosophilidae, Lonchaeidae, Muscidae, Sepsidae	—	Collembola (Tomoceridae, Neanuridae)

(Continues)

TABLE 1 (Continued)

	Coleoptera	Lepidoptera	Diptera	Hymenoptera	Others
Fungivores—Slime fluxes	Derodontidae, Nosodendridae, Nitidulidae	—	Ceratopogonidae, Sciaridae, Psychodidae, Scatopsidae, Drosophilidae	—	—
Fungivores—Spore masses	Nitidulidae, Cryptophagidae, Anobiidae, Endomychidae	—	Phoridae (*Megaselia*)	—	—
Fungivores—Sporocarps	Leiodidae, Geotrupiudae, Nitidulidae,	—	Heleomyzidae	—	—
Fungivores—Stromatia and sclerotia	Phalacridae, Monotomidae, Laemophloeidae. Cryptophagidae, BiPhyllidae	—	—	—	—
Fungivores—Hyphae and spores	Derodontidae, Phloeostichidae, Phalacridae, Languriidae	—	Myxetophilidae, Heleomyzidae, Drosophilidae	Formicidae: Attinae	Psocoptera, Acarona (Laelapidae, Acaridae, Ceratozelidae)
Fungivores—Hymenial surfaces	Erotylidae, Endomychidae, Leiodidae, Staphylinidae: Gyrophaenina	—	—	—	—
Fungivores—Pore tubes	Ptilliidae: Nonosellinae, Corylophidae	—	—	—	Ascidae, Acaridae (Acarina)
Fungivores—Context tissues	Endecatomidae, Anobiidae, Trogossitidae, Lamngtoniidae, Erotylidae etc	some	some	—	—
Fungivores—Lichens	Colydiidae, Antheribidae, Tenebrionidae	Psychidae, Lipteninae	Terrestrial Chironomidae	—	Acarina, Collembola, Archaeognatha, Psocoptera,
Secondary consumers and de composers—may participate in either class of food web					
Predators—Free—living	Carabidae, Histeridae, Staphylininae	Liphyrinae, other selected genera	Empidae, Asilidae, Dolichopodidae	Vespidae, Formicidae	Odonata, Neuroptera, Mantodea, Araneida
Predators—Ectoparasites	—	Epipyropidae	Calliphoridae,	—	Siphonaptera, Phthiraptera
Predators—Endoparasites	—	—	Gasterophilidae	—	—
Predators—Parasitoids	Ripiphoridae	—	Tachinidae	Hymenoptera-Parasitica	—
Predators—Haematophages	—	Some Calpinae (*Calyptra*)	Culicidae, Glossinidae, Ceratopogindae, Carnidae	—	Triatomidae, Cimicidae
Top Predators	Carabidae	—	Asilidae	Formicidae	Odonata, Araneida
Necrophages	Silphidae, Necrophoridae	—	Calliphoridae, Muscidae, Sarcophagidae	Formicidae: *Technimyrmex*; Apidae: Meliponinae	—

(Continues)

TABLE 1 (Continued)

	Coleoptera	Lepidoptera	Diptera	Hymenoptera	Others
Commensals (Bird and mammal nest dwellers)	Trogidae, Cavognathidae, Dermestidae	Some Tineidae, Oecophoridae	Anthomyiidae, Fanniidae, Muscidae, Calliphoridae, Heleomyzidae, Sphaeroceridae, Sepsidae Stratiomyiidae	Formicidae	Many Acarina: Glycyphagidae, Chortopglyphidae, Pyroglyphidae, Acaridae; Juliidae
Keratinophages	—	Some Tineinae, some Pyralidae	—	—	—
Coprophages	Scarabaeidae,	—	—	—	—
Hyper-parasites	Some Ripiphoridae	—	Bombyliidae, Conopidae	Many Chalcidoidea, selected other families	—

[a] Many families may differ in adult versus larval feeding habits and, even within these stadia, not all members of each taxon have the same feeding habits. Wherever a family name is given here, it should almost always be prefaced by "some." Examples given here are of well-known feeding modes that are dominant within at least one stadium of that family. Sources of information include Dauphin (2012), Kitching, Bickel, and Boulter (2005), Scoble (1992), Lawrence and Milner (1996), and Lawrence and Slipinski (2013). These sources include many more examples.

suggest that the single family of true weevils (the Curculionidae), within the Order Coleoptera, itself contains 53,000 *described* species (Lawrence & Slipinski, 2013). Zimmerman (1994) quotes Marshall's estimate that there may be anywhere between 200,000 and 250,000 species of weevils globally, most still awaiting description.

Nevertheless, although comparisons of species richness of vertebrates with terrestrial arthropods may be "no-contests," it can be argued that in places with an intact megafauna—like some African savannahs—the vertebrates make up for their modest species richness by their large biomass. Here, again data are sparse, and it may well be that the termites alone are comparable to the vertebrates in sheer mass (Bell, 1982; Ferrar, 1982; Tuma, Eggleton, & Fayle, 2019).

Vertebrates participate directly, mostly in green food webs as herbivores, predators, and top predators. Their invertebrate ecto and endoparasitic loads add a further trophic level to these green webs as do blood feeders such as mosquitoes. Endoparasites such as nematodes and platyhelminths are ubiquitous and usually host-specific. Arthropods dominate the ectoparasitic load through a range of taxa from gasterophilid flies to ticks, fleas to arixeniine Dermaptera. The non-living products of vertebrates—their cadavers, dung, skin debris, nesting material, and so forth—are further resources within the forest ecosystem. A well-known set of arthropods play major roles as necrophiles feeding on the cadavers of vertebrates. The beetle families Silphidae and Necrophoridae together with a range of higher fly taxa are among the best-known of these. Dung feeders include scarab and staphylinine beetles, muscid, and calliphorid flies. A further set of taxa feed on sloughed keratin within the living or dead pelts of vertebrates. Finally, there is a range of commensal feeders from specialists that infest the nests of vertebrates through to those that benefit from the grazing or browsing activities of their "hosts." The presence of an intact vertebrate fauna, accordingly, is vitally important in maintaining arthropod and other invertebrate diversity. Their presence, in addition, is important in maintaining soil nutrients and seed dispersal with flow-on effects for forest structure—and the complex of resources these present to the invertebrates (Doughty *et al*., 2013). There is some evidence that invertebrates decline with defaunation of megafauna due to the impact on understory vegetation and resource availability (Lamperty, Zhu, Poulsen, & Dunham, 2019) but more broadly based work is needed. The "empty forest syndrome" (Redford, 1992) may not be just a conservation disaster for hunted vertebrates, and it may well have knock-on effects upon the entire forest fauna.

3 | CONCLUSIONS AND THE NEXT 50 YEARS

Through these complexes, ubiquitous and inter-connected food webs the invertebrates, particularly the arthropods, clearly play key roles in energy transformation and nutrient flows within ecosystems. There remain far more data gaps, some of which we have mentioned above, especially in tropical systems, than well-sampled locations. Nevertheless, there is considerable justification for E. O. Wilson's (1987) prognosis that these are "the little things that run the world."

The contributions in this issue add weight to this contention and indicate exciting new directions for future work. We touch on several such directions here.

1. Well-designed comparative approaches comparing ecological patterns across ecological gradients and boundaries produce new and more general insights (see Chatelain, Elias, Guilbert, & Soulier-Perkins, 2019; Mottl, Fayle, Yombai, Novotný, & Klimeš, 2019; Rabl, Gottsberger, Brehm, Hofhansl, & Fiedler, 2019; Raine, Slade, & Lewis, 2019, all available in this issue).
2. Expanding attention into a wider spread of invertebrate taxa adds insights as a wider range of ecosystem functions is encompassed (see Chatelain et al., 2019, Drinkwater, Williamson, Clare, & Rossiter, 2019, Luke, 2019 and Phillips, Chung, Edgecombe, & Ellwood, 2019, all available in this issue).
3. Using the rapid response times of invertebrates in terrestrial ecosystems allows us to evaluate impacts of and recovery from environmental transformations due to natural and human actions (see Franca et al. 2019, Luke et al., 2019, Stone, Shoo, Stork, Sheldon, & Catterall, 2019, Torppa, Wirta, & Hanski, 2019, all available in this issue).
4. The availability of effectively limitless computing power potentially allows the enormous complexity of tropical food webs and distribution maps (see Scriven et al., 2019, this issue) to be modeled realistically: Interpreting very complex model systems of course may be as challenging as contemplating the real thing (McLane, Semeniuk, Mcdermid, & Marceau, 2011).
5. Aligning pattern and process: Does tropical biodiversity matter beyond its intrinsic value? Can ecosystem processes and service survive a massive decline in invertebrate species and density? (see Dahlsjö et al., 2019, this issue)?

These and other developments paint an exciting picture for invertebrate biologists working in the tropics over the next 50 years. Novel methods and approaches, of course, do not invalidate the more traditional approaches and the gradual accrual of natural historical information on tropical systems. *Biotropica* and other outlets will continue to be a conduit for this fundamental information as well as championing novelty and innovation—as it has done for the last 50 years.

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