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Title: Arthropod Diversity in a Tropical Forest

Authors: Yves Basset,[1, 2, 3*] Lukas Cizek,[2,4] Philippe Cuénoud,[5] Raphael K. Didham,[6] François Guilhaumon,[7] Olivier Missa,[8] Vojtech Novotny,[2,4] Frode Ødegaard,[9] Tomas Roslin,[10] Jürgen Schmidl,[11] Alexey K. Tishechkin,[12] Neville N. Winchester,[13] David W. Roubik,[1] Henri-Pierre Aberlenc,[14] Johannes Bail,[11] Héctor Barrios,[3] Jonathan R. Bridle,[15] Gabriela Castaño-Meneses,[16] Bruno Corbara,[17] Gianfranco Curletti,[18] Wesley Duarte da Rocha,[19] Domir De Bakker,[20] Jacques H. C. Delabie,[19] Alain Dejean,[21] Laura L. Fagan,[6] Andreas Floren,[22] Roger L. Kitching,[23] Enrique Medianero,[3] Scott E. Miller,[24] Evandro Gama de Oliveira,[25] Jérôme Orivel,[26] Marc Pollet,[27] Mathieu Rapp,[28] Sérvio P. Ribeiro,[29] Yves Roisin,[30] Jesper B. Schmidt,[31] Line Sørensen,[31] Maurice Leponce[20]

Affiliations:

[1]Smithsonian Tropical Research Institute, Panama City, Republic of Panama.

[2]University of South Bohemia, 370 05 Ceske Budejovice, Czech Republic.

[3]Universidad de Panamá, Panama City, Republic of Panama.

[4]Czech Academy of Sciences, 370 05 Ceske Budejovice, Czech Republic.

[5]Muséum d'histoire naturelle de la Ville de Genève, 1208 Genève, Switzerland.

[6]The University of Western Australia and CSIRO Ecosystem Sciences, 6009 Perth, Australia.

[7]Universidade de Évora, 7004-516 Évora, Portugal.

[8]University of York,York YO10 5DD, U.K.

[9]Norwegian Institute for Nature Research, 7485 Trondheim, Norway.

[10]University of Helsinki, 00014 Helsinki, Finland.

[11]University of Erlangen-Nuremberg, 91058 Erlangen, Germany.

[12]Santa Barbara Museum of Natural History, Santa Barbara, CA 93105, U.S.A.

[13]University of Victoria, Victoria, BC V8W 2Y2, Canada.

[14]Cirad, 34988 Montferrier-sur-Lez, France.

[15]University of Bristol, Bristol BS8 1TH, U.K.

[16]Universidad Nacional Autónoma de México, México 0510 DF, México.

[17]Université Blaise Pascal, 63000 Clermont-Ferrand, France.

[18]Museo Civico di Storia Naturale, 10022 Carmagnola, Italy.

[19]Centro de Pesquisas do Cacau, 45600-000, Itabuna, & Universidade Estadual de Santa Cruz, 45662-900 Ilhéus-Bahia, Brazil.

[20]Institut Royal des Sciences Naturelles de Belgique, 1000 Brussels, Belgium.

[21]University of Toulouse III, 31062 Toulouse, France.

[22]Universität Würzburg, 97070 Würzburg , Germany.

[23]Griffith University, Nathan QLD 4111, Australia.

[24]National Museum of Natural History, Washington, DC 20008, U.S.A.

[25]Centro Universitário UNA, 30350-540 Belo Horizonte-MG, Brazil.

[26]CNRS, 97379 Kourou, France.

[27]Research Institute for Nature and Forest, 1070 Brussels, Belgium.

[28]Muséum d'histoire naturelle, 2000 Neuchâtel, Switzerland.

[29]Universidade Federal de Ouro Preto, 35400-000 Ouro Preto-MG, Brazil and Universidade dos Açores, 9700-851 Terceira, Portugal.

[30]Université Libre de Bruxelles, 1050 Brussels, Belgium.

[31]Natural History Museum of Denmark, 2100 Copenhagen, Denmark.

*To whom correspondence should be addressed. E-mail: bassety@si.edu

Abstract: Most eukaryotic organisms are arthropods. Yet, their diversity in rich terrestrial ecosystems is still unknown. Here we produce tangible estimates of the total species richness of arthropods in a tropical rainforest. Using a comprehensive range of structured protocols, we sampled the phylogenetic breadth of arthropod taxa from the soil to the forest canopy in the San Lorenzo forest, Panama. We collected 6,144 arthropod species from 0.48 ha and extrapolated total species richness to larger areas based on competing models. The whole 6,000 ha forest reserve most likely sustains 25,000 arthropod species. Remarkably, just 1 ha of rainforest yields > 60% of the arthropod biodiversity held in the wider landscape. Models based on plant diversity fitted the accumulated species richness of both herbivore and non-herbivore taxa exceptionally well. This lends credence to global estimates of arthropod biodiversity developed from plant models.

One Sentence Summary: Total arthropod species richness in a 6,000 ha tropical rainforest, estimated at 25,000 species, can be best predicted by plant diversity.

Main Text:

Most eukaryote species are terrestrial arthropods (*1*), and most terrestrial arthropods occur in tropical rainforests (*2*). However, considerably greater sampling effort is required in tropical arthropod surveys to yield realistic estimates of global species richness (*3-7*). A basic hindrance to estimating global biodiversity lies in a lack of empirical data that establish local biodiversity, which can be scaled up to achieve a global estimate. Although many studies reported species richness for selected groups of well studied insect taxa, no satisfactory estimate of total arthropod species richness exists for a single tropical rainforest location to date.

The unstructured collection and small-scale survey of tropical arthropods cannot yield convincing estimates of total species richness at a specific forest (*7-9*). Most studies either target few arthropod orders or trophic guilds, or use a limited array of sampling methods, or ignore the diverse upper canopy regions of tropical forests (*10-15*). Moreover, sampling protocols have rarely been structured in such a way that, with increased sampling, incomplete data on local diversity (*7*) can be extrapolated to estimate total species richness across multiple spatial scales (*16*). Where such structured estimates are made, it is invariably for insect herbivores on their host plants (*5*). However, species accumulation rates may differ dramatically for non-herbivore guilds, which include more than half of all described arthropod species (*1, 17*). As the degree of host specificity (effective specialisation) of other guilds can be much lower than that of insect herbivores, or may be driven by different factors (*18, 19*), global estimates based on herbivores alone are questionable. Consequently, extensive cross-taxon surveys with structured protocols at reference sites may be the only effective approach towards estimating total arthropod species richness in tropical forests (*3*).

To provide a comprehensive estimate of total arthropod species richness in a tropical rainforest, we established a collaboration involving 102 researchers, with expertise encompassing the full breadth of phylogenies and feeding modes present among arthropods (*20*). This consortium invested a total of 24,354 trap- (or person-) days sampling the San Lorenzo forest (SLPA) in Panama using structured protocols (Fig. S1). We identified 129,494 arthropods representing 6,144 focal species (Fig. 1 and Table S1) from 0.48 ha of intensively sampled mature forest. This allowed us to extrapolate focal arthropod species richness to a larger forest area with unprecedented power, through a series of best-informed species richness estimates derived from six competing models for each of 18 focal data sets. Using taxon ratios to estimate the species richness of non-focal taxa (see Extrapolating results to non-focal taxa in *20*), we then predicted the total species richness of the study area. We also evaluated differences in relative species accumulation rates among arthropod guilds, across spatial scales.

While individual estimators adjusting for different aspects of sampling design offered slightly different estimates (Fig. 1B), the total species richness for the entire San Lorenzo forest (ca 6,000 ha) was consistently quantified at between 18,000 and 44,000 species (including focal and non-focal species). In particular, the most likely lower bound of species richness was estimated to be at least 21,833 species (95% *c.l.* = 18665, 29420; model a1 in Fig. 1B), and the biologically and statistically best-supported estimate of richness (criteria outlined in Table S2) was 25,246 species (95% *c.l.* = 19721, 33181, model B+S in Fig. 1B). According to our estimates, a single hectare of rainforest will be inhabited by an average of 18,439 species (95% *c.l.* = 17234, 18575; Fig. 2B).

A relatively large proportion of the expected species richness of the forest was recovered for most of our focal taxonomic groups (Fig. 2). For example, high proportions of all ant species

and of the parasitoid species targeted in our study were collected from our 12 sites, whereas fungal feeders would require more intensive sampling to achieve adequate coverage (Fig. 2). Beta diversity of all arthropods (in the broad sense of species turnover among sites) increased roughly linearly with cumulative area surveyed ($F_{1,3} = 2422.5$, $P < 0.001$). With increasing sampling effort, sample coverage (an unbiased measure of sample completeness, see *20*) was high and accumulated at different rates across different arthropod orders, guilds and across the various guilds comprised by beetles (Fig. 3With increasing sampling effort, sample coverage (an unbiased measure of sample completeness, see 20) was high and accumulated at significantly different rates across different arthropod orders, guilds and across the various guilds comprised by beetles (Fig. 3). However, despite the high sample coverage values, we cannot discount the possibility that there were some vanishingly rare species that may not have been discovered with the sampling protocols employed in this study.

Despite idiosyncrasies in the rate of increase in sample completeness across insects groups, the high proportion of overall species richness detected at small spatial scales (Figs 2, 3) has a remarkable consequence. Based on a general relationship between species numbers and area we estimate that almost two-thirds (64%) of all species in SLPA occur in a single hectare of rainforest (Fig. 2). Our plant models predicted total arthropod richness in the San Lorenzo forest to a precision of one percent (correlation between richness estimates provided by the plant model and best estimates: $r = 0.992$, $P < 0.0001$, $N = 18$; Fig. 1C). Importantly, small discrepancies between observed arthropod species richness and estimates derived from floristic diversity appeared not to be scale-dependent (Fig. 1D). Hence, even for arthropod guilds other than herbivores, plant diversity seems a powerful predictor of species richness across areas varying in

size (at least within the limits of our study design and given the limited heterogeneity of the study area compared to larger geographical scales).

Because this study targeted the full spectrum of arthropods, it offers a comprehensive test of previous estimates of species richness based only on selected guilds or taxa. Reassuringly, our well-resolved estimates of tropical arthropod species richness are of the same order of magnitude as prior estimates (Table S3), adding credence to recent estimates of tropical arthropod diversity (*5, 21*). While the scope for direct comparison is limited due to regional differences in sampling effort, lowland tropical forest in Panama seems to support 2.1-8.4 times as many arthropod species as observed in temperate forests (Table S3). While this supports the obvious truism that tropical arthropods are indeed more diverse than their temperate counterparts (*22*), the magnitude of that difference is far lower than many previous estimates would suggest (*2*).

The implications of the results observed on a local scale are clear. For every species in the well-known vascular flora (1,294 species), avifauna (306 species) and mammalian fauna (81 species) of SLPA, we estimate there will be a minimum of 17, 71 and 270 arthropod species, respectively (based on lower bound of species richness) and most likely as high as 20, 83 and 312 arthropod species, respectively (Table S3). Based on the dominance of arthropod species in the tropical fauna (Table S3), we may then argue that conservation planning for biodiversity should be largely determined by the spatial scaling of arthropod diversity. In this context, the association between the species richness of plants and arthropods detected across spatial scales suggests that conservation efforts targeted at floristically diverse sites may also serve to conserve arthropod diversity across both taxonomic lineages and trophic guilds. As arthropods are notoriously labour-intensive to survey, such an 'umbrella' approach may be an efficient way forward.

Nonetheless, our findings also suggest that large-scale, region-wide understanding of tropical arthropod richness may actually be more achievable than previously assumed. Our data indicate that a thorough sampling of one ha of rainforest may reveal nearly two-thirds of all arthropod species present in a much larger area (6,000ha in our case; Fig. 2B), consistent with reports of relatively low beta diversity of insect herbivores in tropical rainforests (*23*). Hence, to determine the species diversity of a tropical rainforest, the total area sampled need not be overly large – provided that the sampling design adequately covers both microhabitats and plant species. However, we hasten to add that this does not imply that most arthropod species have self-supporting populations in small forest areas or fragments.

On a global scale, our results have implications for current estimates of total species richness, which have been weakened by the lack of knowledge regarding the strength of association between vascular plant species and non-herbivore guilds (*5*). Based on the close association observed here between floristic diversity and both herbivore and non-herbivore species richness, we tentatively conclude that the most recent estimate of global tropical arthropod species (6.1 million arthropod species, *24*) does not require drastic correction to account for differential scaling relationships of non-herbivore taxa. The robust estimates of local arthropod diversity derived in our study thus offer support for previous estimates of global species richness. They also show how stratified sampling designs and broad scientific co-operation may be developed to formulate efficient estimates of tropical arthropod diversity. Similar initiatives have recently been implemented in other tropical locations around the world, using the current template as a foundation (*25*).

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sorting of the arthropod and plant material. Data (as of 10 May 2012) deposited in the Dryad

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Figure legends

Fig. 1. Number of arthropod species estimated at SLPA (*20*). **(A)** Number of species (closed

bars, log scale) and individuals (open bars, log scale) collected in 0.48 ha for each data set (3-

letter guild code as in Table S1) and number of species estimated in SLPA (best estimate, shaded

boxes). Numbers above bars identify the best model used for calculation (a1-a6, Fig. S2) and the

percentage of singletons. **(B)** Number of arthropod species estimated for SLPA (dots = all focal

taxa, shaded boxes = focal and non-focal taxa, Table S4), as estimated by different methods:

B+S= best estimates, including both biological and statistical arguments (Table S2); B+Sloc = as

B+S but estimates calculated with local instead of global ratios (Fig. S3); S = best estimates,

including only statistical arguments; and models a1 to a5. ? = Optimization algorithms did not

converge to allow calculations of *c.l*. Our estimates are robust to even moderate to large shifts in

taxon ratios, Table S5. **(C)** Plot of the number of species estimated in SLPA with the plant model

against that estimated with the best model, for each data set. Line denotes unity. **(D)** Plot of the

percentage error between all arthropod species observed and estimated by the plant model

against cumulative number of sites. Shaded boxes indicate means and 95% *c.l.*

Fig. 2. Accumulation of species richness with area at SLPA (*20*). For all groups, a high

proportion of overall species richness was detected at small spatial scales. **(A)** Partitioning of

species richness within arthropod guilds at different spatial scales (α: single site of 0.04ha; $\beta3$: 3

sites spaced apart totaling 0.12ha; β6: 6 sites totaling 0.24ha; β12: 12 sites totaling 0.48ha; βha:

1.0ha; βSLPA: 6,000ha; means and s.e.m. are shown for α, β3 and β6). **(B)** Species-area models

for the main arthropod groups and large data sets (for all arthropods, including non-focal species,

values are indicated but the curve not plotted for the sake of clarity). Each curve is characterized

by its function (Ex = Exponential; Lo = Lomolino; Po = Power; We = cumulative Weibull), its

value for one ha (intersection with vertical line, shaded boxes with mean and 95% *c.l.*) and the

percentage of the number of species present in one ha relative to the number of species estimated

to occur in SLPA.

Fig. 3. Average sample coverage (± s.e.m., error bars, see methods, *20*) plotted against the

cumulative number of sites surveyed, for the main (A) arthropod guilds and orders and (B) beetle

guilds. For the sake of clarity, s.e.m. are omitted in (A).