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 hectare and extrapolated total species richness to larger areas on the basis of competing models. The whole 6,000-hectare forest reserve most likely sustains 25,000 arthropod species. Notably, just 1 hectare 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 nonherbivore taxa exceptionally well. This lends credence to global estimates of arthropod biodiversity developed from plant models.

Although 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 (~6,000 ha) was consistently quantified at between 18,000 and 44,000 species (including focal and nonfocal species). In particular, the most likely lower bound of species richness was estimated to be at least 21,833 species [95% confidence level (CL) = 18,665, 29,420; 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% CL = 19,721, 33,181, 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% CL = 17,234, 18,575; 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 (P1,3 = 2422.5, P < 0.001). With increasing sampling effort, sample coverage [an unbiased measure of sample completeness, see (20)] was high and accumulated at significantly different rates across different arthropod orders and guilds, and across the various guilds comprised by beetles (Fig. 3).

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 and 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 1% (correlation between rich-
ness estimates provided by the plant model and best estimates: \( r = 0.992, P < 0.0001, N = 18 \); Fig. 1C). Notably, 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). Although the scope for direct comparison is limited because of regional differences in sampling effort, lowland tropical forest in Panama seems to support 2.1 to 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).

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 (three-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 to a6, fig. S2) and the percentage of singletons. (B) Number of arthropod species estimated for SLPA (dots: all focal taxa; shaded boxes: focal and nonfocal taxa; table S4), as estimated by different methods: B+S: best estimates, including only statistical arguments; and models a1 to a5. ?: optimization algorithms did not converge to allow calculations of CL. 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% CL.
The implications of the results observed on a local scale are clear. For every species in the well-known vascular flora (1294 species), avifauna (306 species), and mammalian fauna (81 species) of SLPA, we estimate that 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 labor-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 1 ha of rainforest may reveal nearly two-thirds of all arthropod species present in a much larger area (6000 ha in our case; Fig. 2B), consistent with

![Species-area models for the main arthropod groups and large data sets (for all arthropods, including nonfocal 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 1 ha (intersection with vertical line, shaded boxes with mean and 95% CL), and the percentage of the number of species present in 1 ha relative to the number of species estimated to occur in SLPA.](image-url)
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, 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 nonherbivore guilds (5). Based on the close association observed here between floristic diversity and both herbivore and nonherbivore 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 nonherbivore taxa. The robust estimates of local arthropod diversity derived in our study thus support previous estimates of global species richness. They also show how stratified sampling designs and broad scientific cooperation 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).

**Fig. 3.** Average sample coverage (+SEM; 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, SEMs are omitted in (A).

**References and Notes**

20. Materials and methods are available as supplementary materials on Science Online.

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**Supplementary Materials**

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Materials and Methods

Supplementary Text

Figs. S1 to S3

Tables S1 to S5

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