

Seeing beyond the trees: a comparison of tropical and temperate plant growth forms and their vertical distribution

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Abstract. Forests are the most diverse and productive terrestrial ecosystems on Earth, so sustainably managing them for the future is a major global challenge. Yet, our understanding of forest diversity relies almost exclusively on the study of trees. Here, we demonstrate unequivocally that other growth forms (shrubs, lianas, herbs, epiphytes) make up the majority of vascular plant species in both tropical and temperate forests. By comparing the relative distribution of species richness among plant growth forms for over 3,400 species in 18 forests in the Americas, we construct the first high-resolution quantification of plant growth form diversity across two ecologically important regions at a near-continental scale. We also quantify the physical distribution of plant species among forest layers, that is, where among the vertical strata plants ultimately live their adult lives, and show that plants are strongly downshifted in temperate forests vs. tropical forests. Our data illustrate a previously unquantified fundamental difference between tropical and temperate forests: *what* plant growth forms are most speciose, and *where* they ultimately live in the forest. Recognizing these differences requires that we re-focus ecological research and forest management plans to encompass a broader suite of plant growth forms. This more holistic perspective is essential to conserve global biodiversity.

Key words: biodiversity; diversity distributions; epiphytes; forest strata; growth form; herbaceous plants; legacy data sets; lianas; physiognomy; temperate forests; trees; tropical forests.

INTRODUCTION

Forest ecology has been strongly biased towards the study of trees, because this growth form contributes the most to carbon sequestration, plant biomass, and economic value (Braun 1950, Richards 1952, Spurr and Barnes 1973, Condit 1995, Lewis et al. 2009, Linares-Palomino et al. 2009, Muller 2014, Lutz et al. 2018). This selective view of forest ecology is inimical to diversity conservation because it overlooks plant growth forms that significantly contribute to biodiversity, faunal habitat, and forest function (Johansson 1974, Gentry and Dodson 1987, Schnitzer and Carson 2000, Gilliam 2014, Thrippleton et al. 2016, Landuyt et al. 2019). Epiphytes, for instance, are particularly diverse in montane forests, where they can comprise as much as 50% of the flora, and may be particularly vulnerable to both anthropogenic and natural canopy disturbances (Kelly et al. 1994, Foster 2001, Nadkarni and Solano 2002, Woods and DeWalt 2013). Including non-tree vegetation in ecological studies can also change our understanding of fundamental ecological processes. Research on lianas (woody vines), a once-overlooked growth form,

demonstrates that lianas regulate gap dynamics, water relations, and canopy to canopy connectivity in Neotropical forests (Schnitzer and Carson 2010, Ledo and Schnitzer 2014, Adams et al. 2017, Schnitzer 2018). A systemic bias towards trees means we are missing key components of forest function, rendering it difficult to identify the processes that promote and maintain biodiversity of all growth forms.

Our understanding of forest *structure* is also biased, likely because of the limitation of ground-based censuses. Forest spatial ecology has focused on the two-dimensional distribution of plant diversity, despite the long-standing importance of three-dimensional structure for biodiversity and ecosystem processes (MacArthur and MacArthur 1961, Smith 1973, Terborgh 1985). Overlapping forest layers create strong vertical abiotic and biotic gradients, ranging from the exposed, disturbance-prone canopy, to the deeply shaded, microbially rich understory (Parker 1995, Schnitzer and Carson 1999, Gilbert and Reynolds 2005, Griffin et al. 2017, Gora et al. 2019); this complexity maintains high faunal diversity (MacArthur and MacArthur 1961, Smith 1973). Given the long history of studying the vertical niche partitioning of both plants (Johansson 1974) and animals (MacArthur and MacArthur 1961), it is surprising that studies that map forest habitats rarely explicitly incorporate a three-dimensional component. While the

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field of forest physiognomy has long recognized the categorical structural differences among biomes (Richards 1939, 1952, Kuchler 1949, Beard 1955, Webb 1959), there have been few studies that rigorously quantify these physiognomic differences, which no doubt underlie major forest structure-function links. Comparisons of vertical structuring of diversity among ecosystems across the world are needed to identify biodiversity priorities and create biome-wide yet region-specific management plans.

Here, we test the idea that the three-dimensional distribution of plant species represents an intuitive, yet thus far unquantified, intrinsic difference between tropical and temperate forests. Specifically, we hypothesize that tropical and temperate forests differ in which plant *growth forms*, and which *vertical strata*, are most speciose, what we term the Forest Physiognomy Concept (Fig. 1). We make two predictions that characterize this difference. First, in Neotropical forests, the majority of plant species will reach reproductive maturity in the overstory due to the structurally dependent growth forms of epiphytes and lianas. Second, in temperate forests, the majority of plant species will reach reproductive maturity in the understory, due to a spring ephemeral niche and thus species-rich terrestrial herbaceous and shrub growth forms. These predictions, although not explicitly rooted in classical ecological theory, are drawn from some of the earliest comparisons of tropical and temperate forests, which noted the unique diversity of tropical plants inhabiting the canopy (Hartwig 1863, von Humboldt 1873, Wallace 1878).

To test our hypothesis, we build off of classification schemes that use plant traits (e.g., woodiness) to characterize forest types and profiles among diverse habitats (Raunkiaer 1934, Richards 1952, Beard 1955, 1978, Baker and Wilson 2000, reviewed in Loidi 2018). Specifically, we collected data on the growth form and ultimate stratum for 3,456 plant species from nine tropical and nine temperate sites. We define *ultimate stratum* as the location in the vertical forest profile where a plant species typically spends its adult life and becomes reproductive. Our 18 sites spanned a wide variety of latitudes, elevations, and ecological habitats throughout the Americas (Appendix S1: Fig. S1, Table S1). Our data illustrate a previously unquantified fundamental difference between tropical and temperate forests: *what* plant growth forms are most speciose and *where* they ultimately live in the forest. Recognizing these differences requires that we broaden our focus in conservation biology and plant ecology to non-arborescent plant growth forms. This more holistic perspective is essential to conserve global biodiversity.

METHODS

Site selection

We selected a total of 18 primarily closed-canopy mature forest research sites that had open-access

vascular plant species lists, published species lists in downloadable form, or were data from our collaborators (Appendix S1: Fig. S1, Table S1). All sites are primarily old-growth or uncut forest, but many have younger or disturbed forest as part of their landscape matrix. Our focal forests varied in size (112–400,000 ha), elevation (35–3,450 m above sea level), land use history, and life zone categorization, spreading across the Americas from Canada to Brazil (see Appendix S1: Table S1 for details). Sites spanned a total latitudinal range of 62° from the northernmost part of the eastern deciduous forest (46.8° N) to the southern end of the tropical forest in the Americas (15.2° S). We selected nine sites throughout each of these two major temperate and tropical forest regions (Braun 1950, Holdridge 1967). Although these sites are nonrandomly distributed, our approach is robust because we selected high-resolution, site-level data, amassed over many decades, representing all vascular plant growth forms at each site.

Because the species lists commonly contained more than 500 species long (range: 244–2,086), we randomly subsampled 20% of the species to characterize growth form and strata of species within each forest. This subsampling was necessary for feasibility; we systematically read through dozens of herbarium specimen descriptions per species and per site, which was often necessary to obtain our two key response variables (i.e., growth form and strata). In total, we examined more than 100,000 records (see *Physiognomic data collection*). Although this approach limited our taxonomic scope (how many total species we studied), it holds one advantage over automated data extraction and collection: specific search terms were not preselected. Thus, descriptions with misspellings, synonyms, and multiple languages were included, which would be quite difficult with an automated approach. Nonetheless, to verify that a 20% subsample accurately reflected the true relative proportion of each forest growth form and ultimate stratum distribution, we evaluated the entire species list from one temperate and one tropical site (Allegheny National Forest Region with 244 species and La Planada in Colombia with 893). Our analysis confirmed that 20% subsamples accurately represent the population of growth form and ultimate strata distributions (see Appendix S1: Fig. S2; Statistical analysis). We only included plants that were identified to species in data collection and removed strictly aquatic (submerged) plant species from both temperate and tropical sites. Had we included these, herbs would likely have been even more proportionally diverse than we report.

Physiognomic data collection

For each selected species, we used the USDA PLANTS database and TROPICOS herbarium database to identify the growth form (tree, shrub, liana, terrestrial herb, or epiphyte) and maximum height in the forest strata where the plant was observed as a reproductive

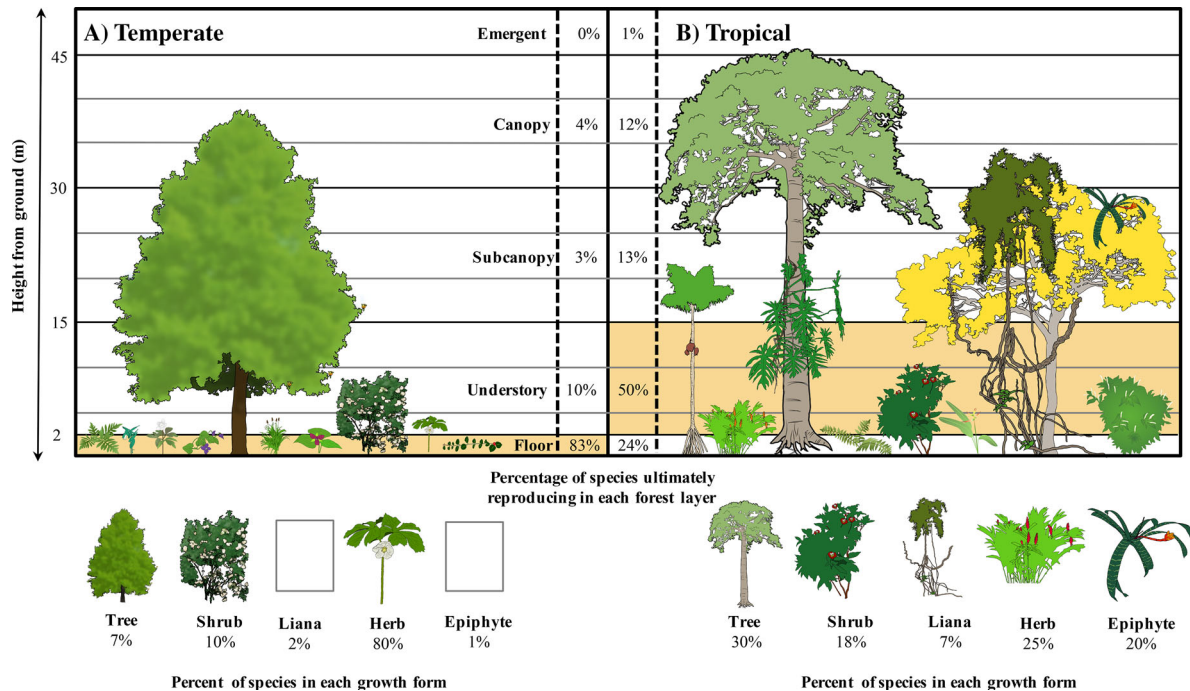


FIG. 1. The Frest Psiognomy Concept. A comparison of how species are allocated to growth forms and strata between temperate vs. tropical forests. (A) Temperate forests are dominated by herbs concentrated on the forest floor. In contrast, (B) species in Neotropical forests are more evenly distributed among growth forms and strata. Growth forms that make up <2% of species are indicated by blank boxes (bottom panel). The relative contribution of each plant growth form to total species richness is accurately represented by the different number of species depicted for each growth form. Plants are distributed within their appropriate ultimate strata across the forest profile, although true heights (y-axis) may vary among forests. The orange shading depicts the ultimate stratum with maximum relative species richness.

adult. Ultimate stratum categorizations (forest floor, understory, subcanopy, canopy, or emergent) were made via explicit statements in the annotated descriptions of the databases (e.g., “liana reaches canopy,” “understory tree,” “forest floor herb”). We collected data on reproductive specimens by checking their annotated descriptions for key words (e.g., “flowering,” “fruiting,” “fertile,” “adult,” etc.). If a categorical maximum height was not explicitly stated for a given species, but the collector specified the height of the species, we identified the appropriate stratum of that species using strata described in Terborgh (1985) and Richards (1952). In this case, we categorized the strata as the forest floor (0–2 m), understory (2–15 m), subcanopy (15–30 m), canopy (30–45 m), and emergent layer (>45 m). Note that we report only the categorical strata heights; we do not compare continuous height data because not all maximum canopy heights are the same (e.g., montane forests are shorter overall than lowland forests). Whenever TROPICOS had more than 100 specimens for any given species, we collected data from at least 50 records and noted the maximum height of all 50 records. We categorized each species into one of five major growth forms: tree, shrub, liana, herb, or epiphyte. Due to continued debate over hemiepiphyte classifications (Zotz 2013), we classified all of the following aerial or climbing

plants into a single broad “epiphyte” category: holoepiphytes, primary hemiepiphytes, secondary hemiepiphytes, nomadic vines (sensu Moffett 2000), suffrutescent climbers, and herbaceous vines. When species information was not available on either TROPICOS or PLANTS, we used published literature via Google Scholar searches with the scientific name to gather our two response metrics (growth form and ultimate stratum).

We often found that the ultimate stratum data were limited for epiphytic species relative to data on other growth forms. Specimens collected opportunistically may lack height data (and therefore are not included in the ultimate stratum), or are more likely to be from individuals that occur low in the forest profile. Because climbing into the canopy to survey arboreal plants is difficult, expensive, and dangerous, epiphyte collections are frequently serendipitous, and only contain those individuals (and species) that can be reached by an outstretched hand (under 2 m in height). Although many epiphyte species do have wide ranges of suitable substrate heights (Johansson 1974, Zotz and Schultz 2008, Woods et al. 2015), we suspect the maximum height we report for epiphytes are substantial underestimates because they remain less frequently sampled or seen high in the canopy. Thus, we would expect the up-shift in tropical

species to be even more striking (see Results) if we had more accurate epiphyte height data.

To explore the spring ephemeral niche as a possible mechanism for differences in plant species allocations between temperate and tropical forests, we collected phenology data for all of the temperate forest floor herbs included in the main analysis (854 species). We used online databases such as the Missouri Botanical Garden, Efloras, and the University of Texas Austin's wildflower.org to categorize each species into "true ephemerals," "spring blooms," or "other." We defined spring blooms as plants that bloomed between March and May and true ephemerals as spring blooms that senesced before 1 July; most of the spring bloom species are perennials.

Statistical analysis

To test our hypothesis that plant species richness is concentrated in different forest layers between tropical and temperate forests, we ran five separate generalized linear models for each of the forest strata, with forest type (temperate or tropical) predicting relative species richness in the strata. Our statistical approach was conservative, because we interpreted the resulting P values with a Bonferroni correction to account for the inherent dependency among the proportions ($\alpha_{\text{Bonferroni}} = 0.05/5 = 0.01$). We similarly used five Bonferroni-corrected generalized linear models to analyze whether forest type predicts relative species richness for each growth form, to test the hypothesis that vascular plant growth form composition differs between tropical and temperate forests. For both sets of GLMs, the response variable was the proportion of species in each growth form or strata, weighted by the total number of species studied (specified with the *weights* function in the *stats* package; Zuur et al. 2009). We modeled the response variable (proportion of plant species richness in each site) with a quasibinomial distribution, which is particularly appropriate for overdispersed proportional data (Bolker 2008). To test whether overall herbaceous plant relative species richness was higher in tropical or temperate forests, we re-grouped the species in each site to be either woody (trees, shrubs, lianas, and woody epiphytes) or herbaceous (graminoids, ferns, forbs, and herbaceous epiphytes). We then use the same type of binomial GLM to test whether the proportion of total species that were herbaceous plants (response variable) differed between the two forest types (predictor variable). All analyses were run with R version 3.6.0 (R Core Development Team 2019) in R Studio version 1.0.153 (RStudio Team 2016).

To confirm that using 20% of the species was a sufficient subsample and characteristic of the data set, we used a bootstrap approach to characterize the random sampling error of two sites where we collected growth form and ultimate strata data on *all* species (Allegheny National Forest Region, with 244 species, and La

Planada, with 893 species). We iteratively sampled 20% of each full data set 1,000 times for both growth form and strata distributions. The patterns we observed in the iterative approach match the overall patterns of all subsampled data sets; almost all categories of growth form and strata from the full samples overlap the overall (among-site) subsamples (Appendix S1: Fig. S2).

RESULTS

Our results clearly demonstrate that tropical and temperate forests contrast sharply in growth form composition (Fig. 2A; Appendix S1: Table S1). In temperate forests, herbs are the predominant growth form (80%) and trees represent a mere 7% of plant species. Although terrestrial herbs are the majority of temperate forest species, only 4% are true spring ephemeral species (Appendix S1: Fig. S3). In tropical forests, conversely, trees are the most species-rich group (30%) and species are relatively evenly allocated among the five growth forms (Fig. 2A, Appendix S1: Table S1). Lianas and epiphytes are a characteristic and speciose part of tropical forests (27% of plant species), but are depauperate in temperate forests (<3% of species). Woody species (trees, shrubs, lianas, and woody epiphytes) are predominant in tropical forests (63% of species) but in temperate forests, only 19% of species are woody ($N = 18$, $t = -9.875$, $P < 0.0001$; Appendix S1: Fig. S4).

Tropical forests also differ strongly from temperate forests in how species are distributed throughout the vertical forest profile (Fig. 2B; Appendix S1: Table S1). The vast majority of plant species in temperate forests (83%) are downshifted, reaching reproductive maturity near the forest floor (0–2 m). Conversely, while plant species in tropical forests are distributed more evenly among forest layers, they are also up-shifted, reaching peak species richness (50%) in the understory stratum (2–15 m).

DISCUSSION

Several mechanisms likely contributed to the stark differences we demonstrated between tropical and temperate forests (Figs. 1, 2) in both growth forms and strata. The vertical up-shift in the forest profile for tropical species may be more pronounced than reported here because many plant species inventories are biased in favor of plants rooted in the soil. We also did not consider bryophytes, a highly diverse and abundant nonvascular epiphyte group in many Neotropical and temperate rainforests. Moreover, even extensive vascular plant lists may be missing many species from high in the diverse, yet poorly studied, forest canopy (Nakamura et al. 2017).

The overwhelming preponderance of herbs in temperate forests may be due to a spring ephemeral niche, which does not occur in evergreen or asynchronous deciduous tropical forests (Lapointe 2001). If the vast majority of temperate herb species were spring

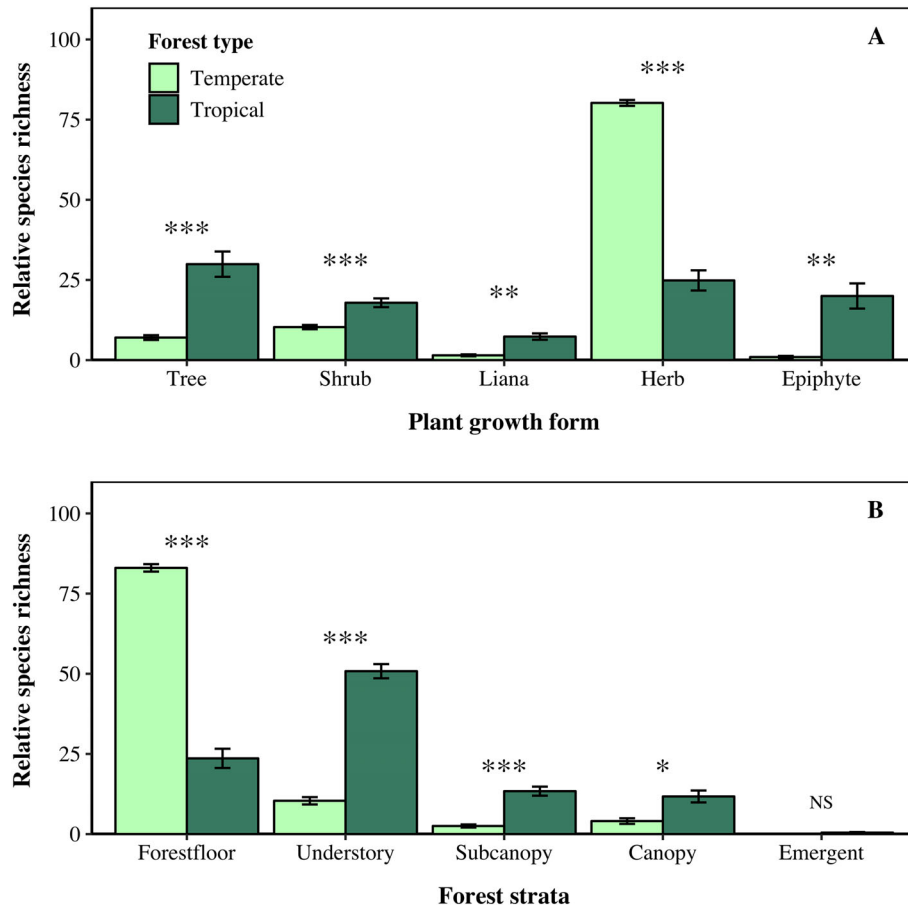


FIG. 2. Two physiognomic differences between tropical and temperate forests. Within-site relative species richness (per site; mean \pm SE) among (A) the five major vascular plant growth forms and (B) the five ultimate strata, comparing temperate (light green bars) and tropical (dark green bars) forests in the Americas. Ultimate strata represent the maximum height in the forest layers where species typically reach reproductive maturity. Asterisks indicate Bonferroni-corrected statistical differences from generalized linear models ($N = 18$; * $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$; NS, not significant).

ephemerals, this would have supported the hypothesis that synchronized deciduousness facilitates a downshift in plant diversity. However, we found that very few species of temperate herbs are limited to periods with high light availability during the early spring (only 4%; Appendix S1: Fig. S3). To truly test whether there exists a window of ephemerals in tropical forests, we would need data from seasonal light increases during the dry season in semi-deciduous tropical forests. Because these data were limited, we did not gather or statistically analyze any tropical ephemeral information. Instead, we provide the quantitative measure of ephemeralism in temperate forests, and encourage future research to test whether this process could drive differences in species allocations between tropical and temperate forests. Moreover, there are likely other mechanisms that more parsimoniously explain the overrepresentation of forest floor herbs in temperate forests. For example, phylogenetic and biogeographic histories undoubtedly contribute to the high relative species richness of some

growth forms, particularly herbs in temperate forests and bromeliads in the Neotropics (Guo and Ricklefs 2000, Givnish et al. 2011, Christenhusz and Chase 2013). Physiological constraints restrict structurally dependent growth forms (epiphytes, lianas) to primarily lower latitudes, because traits such as succulent leaves and efficient vascular systems would be subject to freeze-thaw embolism in temperate zones (Zotz 2016, Schnitzer 2018). The low relative abundance of herbs in tropical forests may be partly due to two ecological factors: deep shade and abundant enemies. Light availability at the forest floor is much lower in tropical forests vs. temperate forests (Leigh 1975, Chazdon and Fetcher 1984, Terborgh 1985, Canham et al. 1990, Schnitzer and Carson 1999), and soil pathogens cause extensive plant mortality (Gilbert 2002, Mangan et al. 2010, Barry and Schnitzer 2016). Enemies may contribute to the high relative abundance of epiphytes in tropical forests, because the evolution of an aerial growth habit would allow escape from terrestrial soil-dwelling pathogens. We term

this potential explanation the Epiphyte Enemy Escape Hypothesis, but it remains to be tested. The mechanisms for the *proportional* differences in growth form distributions in tropical vs. temperate forests remain speculative.

Our findings should be broadly applicable across much of the world. European temperate forests are even less speciose than North American ones, and are frequently dominated by only a few tree species (Röhrig and Ulrich. 1991, Gilliam 2014). Thus, European herbaceous plants likely make up an even higher proportion of temperate vascular plant diversity. In tropical forests in China, trees represent 35–58% of all plant species, herbs 7–26%, lianas 9–19%, and shrubs 9–10%, and a higher proportion of east Asian forest species are woody than in North American temperate forests (Guo and Ricklefs 2000, Zhu et al. 2005). These proportions resemble our Neotropical forest findings, though epiphytes were not quantified. Notably, epiphytes make up a smaller proportion of the vascular plant diversity in Eurasia and Africa vs. the Neotropics, but epiphytes are more speciose in tropical vs. temperate forests (Johansson 1974, Zotz 2005, 2016). Australian tropical forests appear to be even more dominated by woody growth forms (>75% of species) than Neotropical forests (Russell-Smith 2006). Overall, more quantitative comparisons are needed to test the extent to which the Forest Physiognomy Concept applies globally.

Our results have critical implications for biodiversity conservation and management. Because tropical plant species are up-shifted in the vertical strata (Figs. 1,2B), the forest structure is more complex and the plants more interdependent. Logging of tropical forests not only removes trees, but also impacts the epiphytes and lianas that are structurally dependent on trees (together, 57% of tropical species). While lianas appear to do well following disturbance or logging, epiphytes often require nearby propagule sources to recolonize and are usually slow to redevelop diverse assemblages (Nadkarni 2000, Schnitzer et al. 2004, Woods and DeWalt 2013, Reid et al. 2016). Consequently, even small-scale harvesting will substantially reduce overall biodiversity. Moreover, the complex architecture of large old trees is known to create vital hotspots of diversity and should be a renewed priority in tropical conservation (Díaz et al. 2010, Woods and DeWalt 2013, Lindenmayer and Laurance 2017, Lutz et al. 2018). In contrast, temperate forests may be more resilient to small-scale logging, because 93% of temperate forest species never reach the canopy. Logging does not target these diverse herb and shrubs on the forest floor, and sometimes these communities recover quickly (Roberts 2004, Spicer et al. 2018). In temperate forests, the most pernicious threats to the understory may lie elsewhere. Indeed, overbrowsing by large ungulates and fire suppression collapses temperate biodiversity and causes the formation of persistent depauperate understory communities across vast spatial scales (Côté et al. 2004, Nuttle et al. 2013). These depauperate and open forest understories may subsequently

become inundated with invasive species (Knight et al. 2009, Wavrek et al. 2017). We suggest that these pressures on temperate forest understories, which have already caused plant diversity collapses, should become conservation priorities by forest managers. Instead, forest management (in both tropical and temperate regions) focuses almost exclusively on trees, because trees generate revenue and sequester the most carbon dioxide. To illustrate this oversight, we reviewed two prominent forest ecology journals and found that 92% of temperate-plant-related publications focused on trees (Appendix S1: Fig. S5; see Supplemental Methods).

Understudied plant growth forms and forest strata provide numerous ecosystem services, reinforcing their high conservation value. For instance, while controversial, there is now growing evidence of a worldwide and dramatic decline in insect diversity and abundance (Sánchez-Bayo and Wyckhuys 2019). The retention of species-rich temperate understory layers, particularly in fragmented forests or refugia (Carson et al. 2005, Comisky et al. 2005), can provide pollinator refugia that may help mitigate declines in insect communities, especially in pollinator deserts characteristic of agricultural landscapes (Brockhoff et al. 2017, Landuyt et al. 2019). A diverse temperate understory layer can also aid in nutrient retention and mediate water dynamics during flooding events (Peterson and Rolfe 1982, Muller 2014, Landuyt et al. 2019). These ecosystem services will only become more valuable in the future, as recent changes in climate have increased the frequency and intensity of storm events in temperate areas (Gilliam 2014, Brockhoff et al. 2017). A complex and diverse tropical canopy structure, replete with epiphytes and lianas, provides floral and fruit resources to herbivores, frugivores, and pollinators alike (Zotz 2016, Schnitzer 2018). Epiphytes modify their host tree microenvironment and mediate ecosystem processes (Díaz et al. 2010, Angelini and Silliman 2014, Zotz 2016). Indeed, epiphytes can contribute more foliar biomass to litterfall than their host trees and intercept >20% of rainfall (Nadkarni 1984, Hofstede et al. 1993, Van Stan and Pypker 2015). Lianas uptake carbon even during droughts and long dry seasons when trees are relatively stagnant (Schnitzer 2018, Schnitzer and van der Heijden 2019).

CONCLUSIONS

A bias in favor of trees in ecological field studies impedes a comprehensive understanding of forest diversity. Herbs, shrubs, lianas, and epiphytes comprise the vast majority of both tropical and temperate forest plant species, and are vital components of ecosystem processes. Only by expanding our view of the forest, to include these understudied plant growth forms and forest strata, can we tailor conservation and management plans to sustain a more diverse, productive, and resilient plant community. We make the following recommendations to address some of the conservation concerns we

have described. (1) Explicitly incorporate non-tree plant groups into long-term forest monitoring research, with standardized protocols for measurement (e.g., CTFSS-ForestGEO, Forest Inventory and Analysis). (2) Include non-tree plant groups in forest management plans and urban planning (e.g., creating city parks with native understory plants underneath trees instead of non-native grasses). (3) Test the generality of classic ecological theories in plant growth forms other than trees (Dyer et al. 2010, Schnitzer 2018). (4) Routinely quantify the responses of herbs at the species level to both natural and anthropogenic disturbances (cf. Royo et al. 2016). (5) Contribute non-tree data to open-source databases to identify global patterns and processes (e.g., Map of Life, GBIF). (6) Study hard-to-access strata such as the canopy. (7) Shift education and science communication to include non-trees in the public understanding of the value of forests and natural spaces.

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