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Can Functional Traits Explain Plant Coexistence? A Case Study with Tropical Lianas and Trees

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Abstract: Organisms are adapted to their environment through a suite of anatomical, morphological, and physiological traits. These functional traits are commonly thought to determine an organism's tolerance to environmental conditions. However, the differences in functional traits among co-occurring species, and whether trait differences mediate competition and coexistence is still poorly understood. Here we review studies comparing functional traits in two co-occurring tropical woody plant guilds, lianas and trees, to understand whether competing plant guilds differ in functional traits and how these differences may help to explain tropical woody plant coexistence. We examined 36 separate studies that compared a total of 140 different functional traits of co-occurring lianas and trees. We conducted a meta-analysis for ten of these functional traits, those that were present in at least five studies. We found that the mean trait value between lianas and trees differed significantly in four of the ten functional traits. Lianas differed from trees mainly in functional traits related to a faster resource acquisition life history strategy. However, the lack of difference in the remaining six functional traits indicates that lianas are not restricted to the fast end of the plant life–history continuum. Differences in functional traits between lianas and trees suggest these plant guilds may coexist in tropical forests by specializing in different life–history strategies, but there is still a significant overlap in the life–history strategies between these two competing guilds.

Keywords: functional traits; coexistence; competition; lianas; meta-analysis; trees; tropical forests

1. Introduction

Plant and animal species are uniquely adapted to both the abiotic and biotic components of their environment. Many of these adaptations are known as “functional traits” and are specific anatomical, morphological, and physiological characteristics that define species' performance and fitness, and may ultimately determine species' coexistence [1,2]. Functional traits may explain how species tolerate their environment and utilize resources, as well as compete with co-occurring species [2]. Over the past two decades, there has been a surge of research on functional traits, which has advanced our understanding of plant life–history strategies and the ecological differences among species [3–6].

One of the ultimate goals of the functional trait approach is to provide a mechanistic explanation for how species are adapted to their environment and for species coexistence in ecological communities [2,7]. Theoretically, differences in functional traits can explain species coexistence if these differences allow species to partition resources to limit competition and prevent competitive exclusion [7,8]. For example, species with functional traits related to efficient uptake and utilization of one set of resources may

coexist with species that have functional traits that allow them to efficiently uptake and utilize another set of resources. Because both species acquire resources in different ways and are able to uptake enough essential resources, theoretically they can coexist [8]. How variation in functional traits among species mediates competition and, thus, competitive exclusion remains poorly understood [7,9].

The first step in assessing how functional traits may explain species coexistence is to quantify the degree to which coexisting species differ in their functional attributes. Indeed, numerous studies have documented differences in functional traits among co-occurring species [1–10]. For example, Wright et al. [4] showed that tropical trees vary considerably in functional traits, with some traits, such as wood density, predicting clear differences in species life–history strategies. Functional traits related to leaf tissue construction are also able to predict plant life–history strategies. For example, plants that invest more in leaf construction typically have lower growth rates [10]. Thus, there is compelling evidence that species differ in their functional traits.

The second step is to show that the differences in functional traits sufficiently reduce resource use overlap and competition, and ultimately mediate species coexistence [5,7]. Currently, the link to differences in functional traits allowing species to coexist remains tenuous [11,12]. The range in functional traits within a community may be constrained between the similarities in traits that allow species to tolerate local environmental conditions, and the differences in traits among species that allow them to avoid competitive exclusion [11,12]. Thus, while the functional trait approach is promising, it remains unclear whether functional traits actually explain species coexistence [11–13]. The functional trait approach is especially challenging to explain species coexistence in complex ecosystems with thousands of co-occurring plant species, such as tropical forests, given the constraints in the range of trait differences necessary to withstand and thrive in local environmental conditions [3–6].

An alternative approach to determine whether functional traits can explain plant coexistence in highly diverse ecosystems is to simplify the comparison by dividing species into broad functional guilds that have direct competitive effects on each other [14,15]. In tropical forests, lianas and trees are two guilds of woody plants that compete strongly for the same suite of resources and seem to differ significantly in some functional traits [16]. Lianas climb their host trees to reach the high light environment at the top of the forest’s canopy [15]. Numerous experimental studies have shown strong negative effects of lianas on many aspects of tree performance, including growth, survival, and reproduction [17–21]. Furthermore, lianas and trees appear to diverge in patterns of growth and abundance, with lianas having higher diametric growth during dry seasons and higher abundance in more seasonal forests [22,23]. Therefore, differences in how lianas and trees use resources and tolerate environmental conditions in the presence of competition may be reflected in differences in functional traits that reduce competition, and thus competitive exclusion, between these two plant guilds. Studies comparing liana and tree functional traits have shown differences in functional traits related to nutrient uptake, hydraulic and photosynthetic rates [24]. Nonetheless, few studies have compared functional traits of co-occurring lianas and trees at a pan-tropical scale or considered the extent that such differences in functional traits explain liana and tree coexistence.

We used a meta-analysis to test the hypotheses that: (1) lianas and trees differ in functional traits; and (2) these functional differences may explain liana–tree coexistence. We examined mean functional trait differences between lianas and trees and, for each mean functional trait value that differed between the two plant guilds, we examined the association between that particular trait and resource uptake. We then considered how these differences could be related to the coexistence of lianas and trees in tropical forests.

2. Methods

2.1. Study Selection

We created our liana–tree functional trait database by assembling studies that explicitly compared functional traits in co-occurring tropical liana and tree species. On 18 September 2020, we searched for

studies on Web of Science and Google Scholar using the key search terms “tree”, “liana” and “functional trait”. The Web of Science search retrieved 76 studies in total. The Google Scholar search retrieved 1210 results and included all of the search results that we found on Web of Science. Using the three key terms in combination with additional terms did not improve the total number of studies comparing liana and tree functional traits retrieved by the search engines. We also included two additional studies that compared functional traits between lianas and trees that were present in the LianaEcologyProject.com database, but that were missed by the other two search engines [25,26]. We restricted our selection to studies that measured functional traits in co-occurring species of both lianas and trees in tropical forests. We compiled all the traits measured in each study into our database (Table 1 and Table S1). We restricted our analyses to the functional traits that were measured (and thus served as replicates) in at least five separate studies, which was our minimum level for comparisons between the two growth forms (including single studies that measured functional traits in more than one environment). Thus, our database included a total of 36 studies that compared a total of 140 different functional traits of co-occurring lianas and trees (Table 1 and Table S1).

Table 1. Studies that explicitly compared liana and tree functional traits. The table includes the citation of the published study, location and country of the study, forest type, mean annual rainfall and wet season months for the site, and the number of liana and tree species included.

Study Citation	Site Country	Forest Type	Mean Annual Precipitation Wet Season Period	Liana and Tree Species Sampling
Apagua et al. 2016 [27]	Daintree Rainforest Observatory Australia	Lowland Tropical Rainforest	4900 mm	15 lianas and 45 trees
Avalos et al. 1999 [28]	Parque Metropolitano Panama	Tropical Dry Forest	1740 mm	12 lianas and 7 trees
Buckton et al. 2019 [29]	Cape Tribulation Australia	Lowland Tropical Rainforest	4207 mm December–April	7 lianas and 11 trees
Castellanos et al. 1989 [25]	Chamela field station Mexico	Tropical Deciduous Forest	748 mm July–October	41 lianas (no information about tree sampling)
Castellanos-Castro & Newton 2015 [30]	Totumo region, Caribbean coast Colombia	Tropical dry forest	900 mm April–December	14 lianas and 94 trees
Cernusak et al. 2008 [31]	Gamboa Panama	Tropical Moist Forest	Not informed	4 lianas and 9 trees
Cai et al. 2007 [32]	Xishuanbanna China	Tropical Seasonal Forest	1539 mm May–October	3 lianas and 2 trees
Cai et al. 2009 [33]	Xishuanbanna China	Tropical Seasonal Forest	1559 mm May–October	18 lianas and 16 trees
Chen et al. 2014 [34]	Xishuanbanna China	Karst forest; Tropical Seasonal Forest; Flood Plain Forest	1560 mm May–October	Karst forest-6 lianas and 10 trees; TSF-9 lianas and 12 trees; FPF-5 lianas and 11 trees
Collins et al. 2016 [35]	Barro Colorado Island Panama	Tropical Moist Forest	2600 mm May–December	6 lianas and 6 trees
Dias et al. 2020 [36]	Ribeirão Cachoeira Brazil	Tropical Seasonal Semi-deciduous forest	1409 mm October–March	16 lianas and 15 trees
Dias et al. 2019 [37]	Paraná forest Brazil	Seasonally Dry Forest	1409 mm September–March	The most abundant lianas and trees
De Guzman et al. 2016 [38]	Parque Metropolitano Panama	Lowland Tropical Rainforest	1865 mm May–November	6 lianas and 6 trees

Table 1. Cont.

Study Citation	Site Country	Forest Type	Mean Annual Precipitation Wet Season Period	Liana and Tree Species Sampling
De Guzman et al. 2020 [39]	Fuerte de San Lorenzo Panama	Lowland Tropical Rainforest	3300 mm April–December	3 lianas and 6 trees
Domingues et al. 2007 [40]	Flona Tapajós, Santarém Brazil	Amazonian terra-firme tropical Rainforest	2000 mm December–June	6 lianas and 11 trees
Han et al. 2010 [41]	Xishuanbanna China	Lowland Tropical Rainforest	1500 mm May–October	14 lianas and 16 trees (SF); 18 lianas and 18 trees (MF)
Johnson et al. 2013 [26]	Parque Metropolitano Panama	Lowland Tropical Rainforest	1865 mm May–October	2 lianas and 1 tree
Kazda & Salzer 2000 [42]	Makandé Gabon	Lowland Tropical Rainforest	1753 mm October–December and March–May	49 lianas and 42 trees
Kazda et al. 2009 [43]	Masoala National Park Madagascar	Dense subequatorial humid forest	3500 mm November–April	57 samples of lianas and trees (species per life form not mentioned)
Liu et al. 2012 [44]	Yunnan Province China	Monsoon evergreen broad-leaved forests	1547.6 mm May–October	91 species (liana and tree species not mentioned)
Marechaux et al. 2017 [45]	Nouragues French Guiana	Lowland Tropical Rainforest	3000 mm December–July	11 botanical families of lianas and 71 trees
Marechaux et al. 2019 [46]	Nouragues French Guiana	Lowland Tropical Rainforest	3000 mm December–July	11 botanical families of lianas and 10 trees
Rios et al. 2014 [47]	Multiple sites and countries	Forest Ecosystems	Multiple sites	63 lianas and 71 trees
Sánchez-Asofeifa et al. 2009 [48]	Fuerte de San Lorenzo and Parque Metropolitano Panama	Tropical Wet and Tropical Dry	3300 mm May–December 1740 mm May–December	35 lianas and 18 trees
Santiago & Wright 2007 [16]	Fuerte de San Lorenzo Panama	Lowland Tropical Rainforest	3100 mm April–December	11 lianas and 21 trees
Slot et al. 2013 [49]	Parque Metropolitano Panama	Tropical Dry Forest	1740 mm May–December	13 lianas and 13 trees
Slot et al. 2014 [50]	Parque Metropolitano Panama	Tropical Dry Forest	1865 mm May–December	14 lianas and 14 trees
Smith-Martin et al. 2019 [51]	Canal zone–Summit Panama	Tropical Moist Forest	2226 mm May–December	6 lianas and 6 trees
van der Sande et al. 2013 [52]	Parque Soberania Panama	Lowland Tropical Rainforest	2400 mm April–December	11 lianas and 13 trees
van der Sande et al. 2019 [53]	Fuerte de San Lorenzo and Parque Soberania Panama	Tropical Moist Forest and Wet Forest	3203 mm April–December 2311 mm May–November	13 lianas and 13 trees
Vivek & Parthasarathy 2018 [54]	Coromandel Coast India	Tropical Dry Evergreen Forest	1141mm October–December	10 lianas and 10 trees
Werden et al. 2017 [55]	Guanacaste Costa Rica	Seasonally Dry Forest	880–3030 mm May–Decemebr	7 lianas and 14 trees

Table 1. Cont.

Study Citation	Site Country	Forest Type	Mean Annual Precipitation Wet Season Period	Liana and Tree Species Sampling
Zhang et al. 2019 [56]	Xishuanbanna China	Lowland Tropical Rainforest	1493mm May–October	12 lianas and 10 trees
Zhu et al. 2017 [57]	Xishuanbanna China	Lowland Tropical Rainforest	1600 mm May–October	Karst forest- 2 lianas and 8 trees; Non-karst forest–3 lianas and 10 trees
Zhu & Cao 2010 [58]	Xishuanbanna China	Tropical Seasonal Forest	1500 mm May–October	18 lianas and 19 trees
Zhu & Cao 2009 [59]	Xishuanbanna China	Tropical Seasonal Forest	1379 mm May–October	3 lianas and 3 trees

2.2. Data Collection and Analyses

We compiled the mean trait values for 10 functional traits that met our study selection criteria. (1) Specific leaf area (SLA); (2) maximum area-based net photosynthetic rate (A_{\max}); (3) stomatal conductance (gs); (4) mass-based nitrogen concentration (N_{mass}); (5) mass-based phosphorus concentration (P_{mass}); (6) sapwood specific conductivity (K_s); (7) wood density (WD); (8) leaf turgor loss point (π_{tlp}); (9) carbon isotopic composition ($\delta^{13}\text{C}$); and (10) water potential at 50 percent loss of conductivity (P50). We recorded the mean trait value for different forest types (wet, dry, flood plain or karst forest), successional stage (secondary, mature) and season (wet and dry) analyzed in single studies [34,37,41,48]. In some cases (4 studies), we digitally measured the mean trait values directly from the published figures [32,37,42,52]. We could not retrieve stomatal conductance (gs) data from four studies [26,31,46,55], limiting our analysis of gs to seven studies. We were also unable to retrieve SLA data from one study [31], A_{\max} from two studies [31,46]; and K_s from one study [53]. The functional trait K_s from [39] was not included due to discrepancies in the value range with the other study values.

Some studies reported leaf mass per area (LMA) instead of specific leaf area (SLA) [29,34,39,41–43,46,48,50] and one study [25] measured specific leaf weight (SLW). SLA, SLW and LMA are related traits that represent ratios of area per mass and mass per area, respectively. Since SLA is the inverse of LMA, we transformed leaf mass per area (LMA), including specific leaf weight (SLW), to specific leaf area (SLA) using the equation $\text{SLA} = 1/\text{LMA}$ and compared SLA between the plant guilds for all studies that measured such ratios. In the studies that we included in our analysis, wood density was calculated as the ratio of dry mass to the fresh volume of a stem segment. Even though other studies have used the term “wood specific gravity”, which seems appropriate for the methods that were used [60], we chose to be consistent with the cited literature and thus we use the term “wood density” hereafter. Santiago and Wright [16] measured net photosynthetic rate on a mass basis (A_{mass}); we converted this measurement to a net photosynthetic rate per area basis (hereafter, A_{\max}) by dividing SLA by A_{mass} [47]. Finally, to determine if functional traits between lianas and trees differed significantly, we performed a Student’s t-test for paired data for each functional trait (10 traits). We performed the statistical analysis using R [61] and created the figures using Python [62,63].

3. Results

We assembled a total of 140 different functional traits for tropical lianas and trees from 36 separate studies (Table 1). The studies were conducted in eleven countries: thirteen of the studies were from forests of Panama, nine were from China, three from Brazil, two from French Guiana and two from Australia, and one study from each of the following: Colombia, Costa Rica, Gabon, India, Madagascar and Mexico. One of the studies, Rios et al. [47], included data from multiple studies, and we used the data that they compiled for four of the studies in China [32,33,58,59].

The 36 tree–liana functional trait studies in our database were conducted in forests that varied widely in annual precipitation and seasonality (Table 1). Chamela, in Jalisco, Mexico, was the driest site with 748 mm of annual precipitation [25] and Daintree rainforest observatory, Australia, was the wettest site, with 4900 mm of annual precipitation [27]. Most of the studies were conducted in seasonal lowland tropical forests, with dry season lengths varying from 3 months in the wet forests of San Lorenzo, Panama, to 6–8 months in the dry-evergreen forest of Coromandel Coast, India and the dry forest of Chamela, Mexico [16,25,48,53,54]. Nineteen studies measured functional traits during the wet season, six studies measured traits during the dry season [26,27,39,52,53,55], and five studies measured traits in both seasons [31,33,34,45,55]. Six studies omitted information on the season when the data were collected [25,36,40,41,44,47].

Of the 140 functional traits, ten traits were measured in five or more different studies. Specific leaf area (SLA) was the most commonly measured trait in the assembled literature, and it was present in 15 studies. Ten studies measured leaf mass per area (LMA), which we converted to SLA, resulting in a total of 25 studies that measured the ratios of leaf area/mass or mass/area. Fourteen studies measured maximum net photosynthetic rates (A_{\max}); thirteen studies measured mass-based nitrogen concentration (N_{mass}); eleven studies measured stomatal conductance (g_s); twelve studies measured wood density (WD); eight studies measured carbon isotopic composition ($\delta^{13}\text{C}$); seven studies measured sapwood specific conductivity (K_s) and water potential at 50 percent loss of conductivity (P50); and finally, six studies measured leaf turgor loss point (τ_{tlp}); and mass-based phosphorus concentration (P_{mass}). Interestingly, most of the functional traits used in these studies were physiological traits or traits of considerable measurement complexity rather than the simple and easy to measure traits like SLA and WD [64].

From the 10 functional traits that we analyzed, four showed significant differences between lianas and trees. The mean SLA was significantly greater for lianas than trees (Table 2). Lianas had higher mean values of SLA than trees in twenty of the twenty-four comparisons (Figure 1A). Both N_{mass} and P_{mass} were significantly greater for lianas than trees (Table 2). Lianas had higher mean values of N_{mass} than trees in ten of the twelve comparisons (Figure 1B), and higher values of P_{mass} in all six comparisons (Figure 1C). The functional trait K_s was significantly greater for lianas than trees (Table 2) and all five studies supported this conclusion. The mean values of A_{\max} did not differ significantly between lianas and trees; values of A_{\max} were higher for lianas in 8 of the 13 comparisons (Figure 2A). The five remaining traits showed no significant difference between growth forms (Table 2, Figure 2).

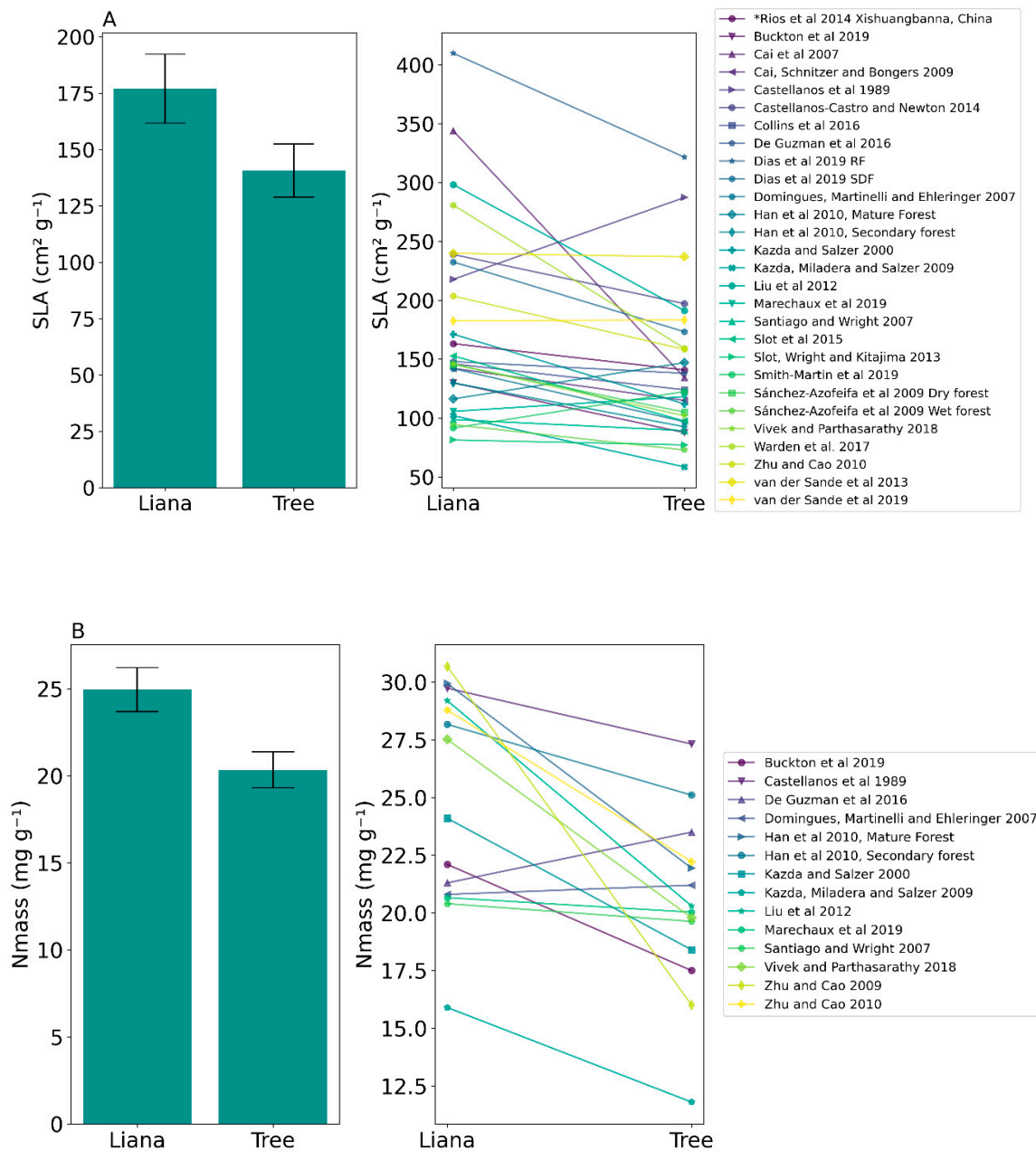


Figure 1. Cont.

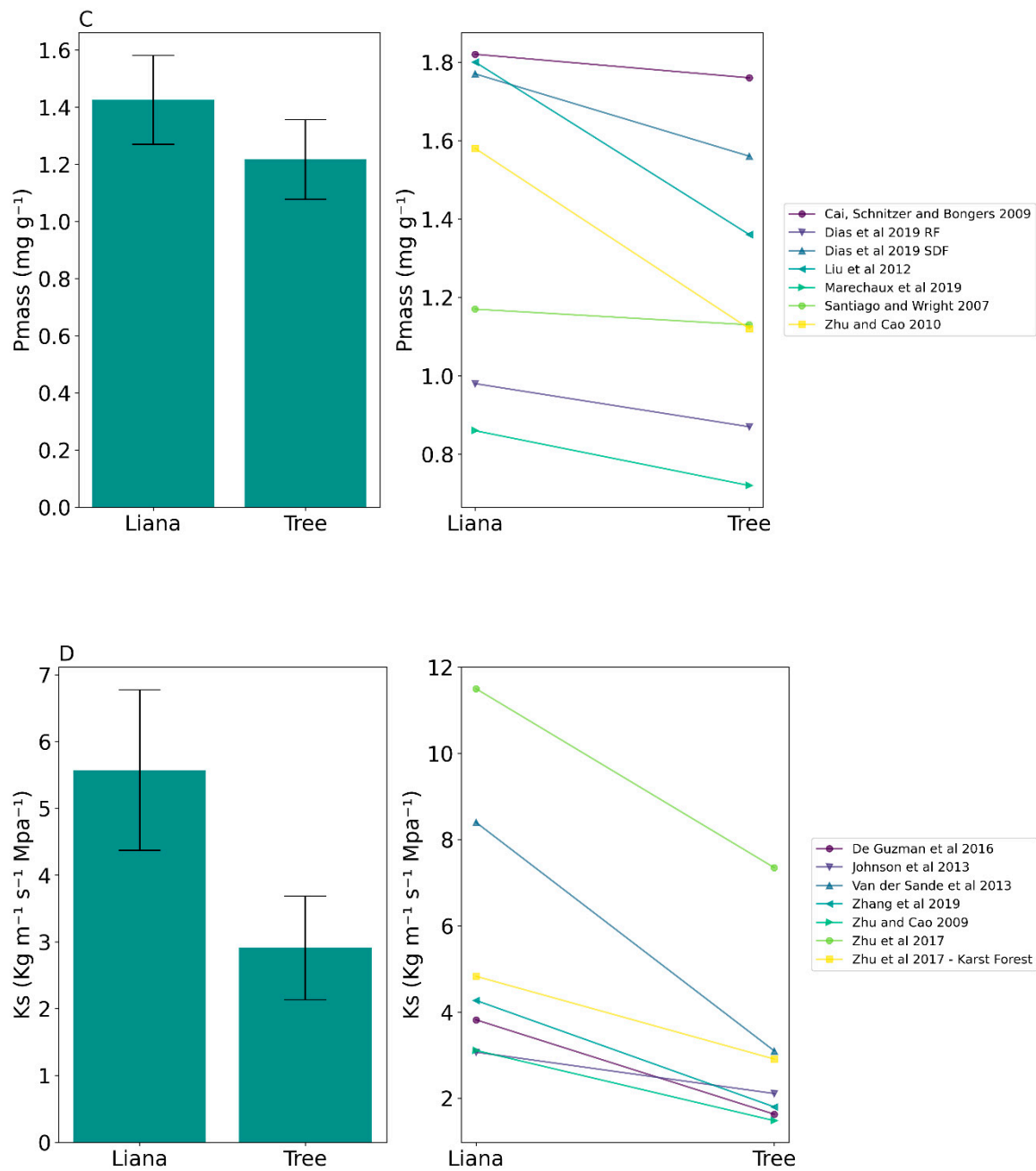


Figure 1. Differences in mean functional trait value for (A) specific leaf area—SLA; (B) mass-based nitrogen concentration— N_{mass} , (C) mass-based phosphorus concentration— P_{mass} , and (D) sapwood specific conductivity— K_s . On the right side of each panel are the slopes for the mean trait values between lianas and trees. Each slope represents one study, except for Dias et al. [37], Han et al. [41], Sánchez-Azofeifa et al. [48], and Zhu et al. [57], which measured functional traits in more than one environmental condition. Error bars represent standard errors.

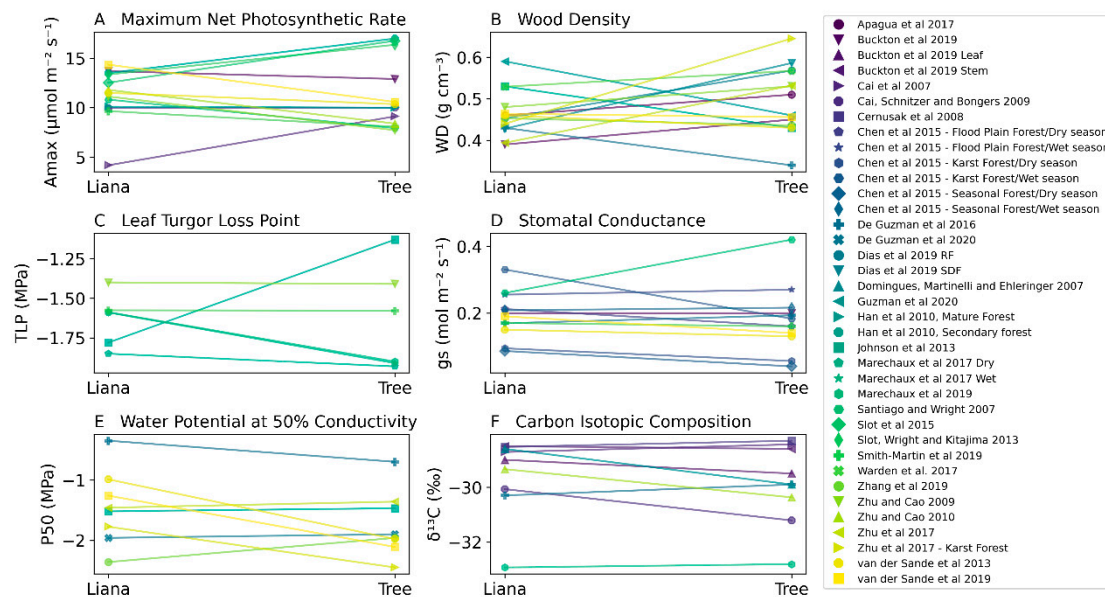


Figure 2. Slopes for the differences in mean trait values for the six functional traits with no statistically significant differences between lianas and trees. The traits are (A)-maximum area-based net photosynthetic rate (A_{max}); (B)-wood density (WD); (C)-leaf turgor loss point ($\pi_{t_{lp}}$); (D)-stomatal conductance (g_s); (E)-water potential at 50 percent loss of conductivity (P_{50}); and (F)-carbon isotopic composition (δ_{13C}). Each slope represents one study, except for Dias et al. [37], Han et al. [41], Chen et al. [34], Buckton et al. [29] Marechaux et al. [45], and Zhu et al. [57], which measured functional traits in more than one environmental condition or in other parts of the plant.

Table 2. Results of the statistical test for differences in liana and tree mean trait values. Traits were measured in at least five separate studies. Asterisks indicate significant differences.

Functional Trait	Liana Mean Trait Value	Tree Mean Trait Value	t-Test Statistic and p-Value
Specific Leaf Area (SLA)	176.98 ± 80.77 SD	140.70 ± 62.41 SD	t(27) = 3.64, p = 0.001 *
Mass-based nitrogen concentration (N_{mass})	24.95 ± 4.73 SD	20.34 ± 3.85 SD	t(13) = 3.89, p = 0.002 *
Mass-based phosphorus concentration (P_{mass})	1.43 ± 0.41 SD	1.22 ± 0.4 SD	t(6) = 3.17, p = 0.02 *
Sapwood specific conductivity (K_s)	5.57 ± 3.18 SD	2.91 ± 2.05 SD	t(6) = 4.62, p = 0.004 *
Maximum area-based net photosynthetic rate (A_{max})	11.28 ± 2.63 SD	11.17 ± 3.45 SD	t(12) = 0.12, p = 0.9
Carbon isotopic composition (δ_{13C})	-29.55 ± 1.43 SD	-29.9 ± 1.46 SD	t(8) = 1.51, p = 0.17
Wood density (WD)	0.46 ± 0.05 SD	0.5 ± 0.08 SD	t(13) = -1.16, p = 0.26
Leaf Turgor Loss Point ($\pi_{t_{lp}}$)	-1.63 ± 0.16 SD	-1.64 ± 0.33 SD	t(5) = 0.09, p = 0.93
Stomatal conductance (g_s)	0.19 ± 0.07 SD	0.18 ± 0.1 SD	t(6) = -0.18, p = 0.86
Water potential at 50 percent loss of conductivity (P50)	-1.46 ± 0.62 SD	-1.74 ± 0.54 SD	t(7) = 1.56, p = 0.16

4. Discussion

We found an impressive total number of functional traits (140) in the 36 published comparisons of lianas and trees, which illustrates that ecologists are now measuring a wide variety of liana functional traits. Liana traits have been measured at the leaf, stem, root, and whole-plant levels (Table S1). The majority of these measured traits were at the leaf level, and included anatomical, morphological,

and physiological measurements. There were also many functional trait measurements at the stem level, with the majority focused on stem anatomy and morphology. There were far fewer traits measured at the root level—attesting the difficulty in harvesting plants for roots measurements (e.g., [51]). Even with 140 total traits measured in our collection of 36 published studies, only 10 traits were replicated sufficiently for us to use them in our liana–tree comparisons.

Lianas had significantly higher mean trait values than trees for four of the 10 traits that we examined (SLA, N_{mass} , P_{mass} , K_s). Species with high values for these four traits often have a “fast” life–history strategy, characterized by light-demanding species with quick growth and poor survival, that can dominate recruitment sites in treefall gaps or in the early stages of succession after land abandonment [3–6]. For example, high values of SLA indicate a lower investment in leaf structural tissues and secondary compounds for defense in exchange for a larger leaf surface area with a higher photosynthetic capacity [4,65,66]. Moreover, high values of leaf nutrient traits such as N_{mass} and P_{mass} are also characteristic of species with higher photosynthesis and a “fast” life–history strategy [3,67]. Photosynthesis is often limited by the foliar concentrations of nitrogen and n-rich compounds (e.g., rubisco), thus nitrogen seems to be less limited for lianas than for trees. In turn, leaf phosphorus content can regulate photosynthetic rates indirectly for a given nitrogen concentration [67]. Functional traits such as SLA, N_{mass} and P_{mass} , all of which were higher for lianas, often show positive correlations with A_{max} values [3]. Therefore, we had expected that lianas would have higher photosynthetic rates by acquiring and using greater quantities of both nitrogen and phosphorus compared to trees [65,67]. However, mean A_{max} values were not significantly different between plant guilds, and lianas had higher A_{max} than trees in only eight of the thirteen comparisons. Nonetheless, higher values of SLA, N_{mass} , and P_{mass} , suggest that lianas tend to reside more towards the “fast” life–history strategy compared to co-occurring trees; a conclusion that would have been stronger had A_{max} also been higher in lianas.

Lianas have significantly higher sapwood specific conductivity (K_s) than trees, demonstrating that lianas can move more water per stem diameter. This striking difference in K_s between lianas and trees was also observed in a recent global study where lianas had the highest K_s values, on average, compared to other plant functional types [68]. The greater values of K_s in lianas are attributed to the presence of remarkably large xylem vessels. Lianas throughout the tropics have a wide range of vessel diameters and lumen sizes, incorporating a combination of both large and small vessels in their stems [69,70]. The large vessels within a liana stem, however, have been shown to contribute the most to plant-level hydraulic conductivity [15,71]. In addition, lianas may have a suite of anatomical functional traits that increase their hydraulic efficiency and, ultimately their hydraulic conductivity, such as low wood density, very long vessel elements, and modified perforation plates on their vessel elements [15].

The higher capacity for lianas to move water would suggest a decrease in hydraulic safety, as suggested by the efficiency–safety trade-off that is evident in most tree species [33,72,73]. Paradoxically, lianas can grow particularly well during dry periods [22] and are also more abundant in drier and highly seasonal forests [23,74,75]. This unusual pattern of high liana abundance in highly seasonal forests, combined with wider vessels in lianas compared to trees [37], seems to contradict the efficiency–safety trade-off. That is, as K_s increases, plants can move more water; however, plants also face a higher risk of embolism and cavitation in drier conditions, particularly for plants with large vessels that have wide lumens [14,22,74]. One way that lianas may resolve this paradox is by avoiding embolism and cavitation by carefully controlling the amount of time they open their stomata, and by conducting more photosynthesis early in the day when vapor pressure deficit is low (the fast and furious hypothesis [14]). At some level, all plants, including lianas, must adhere to the efficiency–safety trade-off. Nonetheless, these clear differences between lianas and trees in their capacity to move water may explain their coexistence and relative abundance if each group differs in their ability to exploit resources seasonally, as well as their vulnerability to low levels of these resources [8,22].

The alignment of functional traits along the slow-to-fast life–history continuum may also explain tree–liana coexistence in tropical forests. Both lianas and trees have a range of shade-tolerance and each plant guild includes species that span the fast–slow life–history strategy axis [76,77]. However, our meta-analysis suggests that lianas tend to have a “faster” strategy compared to trees. The relatively high values of K_s , SLA, N_{mass} , and P_{mass} shared by lianas are consistent with a “fast” life–history strategy [26,32,37,38,51,53,59]. Indeed, in a comparison of lianas and trees on Barro Colorado Island Panama, the majority of the liana species were associated with disturbance, and treefall gaps appeared to maintain liana diversity, whereas only a small proportion of tree species were maintained by gaps and the vast majority of trees were shade-tolerant [77–79]. These differences between lianas and trees along the slow–fast life–history continuum, expressed by their mean trait values, could be enough, theoretically, to allow lianas and trees to coexist.

Plant functional traits such as $\delta^{13}C$, g_s , P50, and π_{tlp} , which are proxies for hydraulic efficiency and drought tolerance, did not differ between lianas and trees in our analyses. The lack of significant differences for these traits indicates that lianas and trees have considerable overlap in hydraulic life–history strategies. These trait similarities may reflect adaptations to the environmental constraints that co-occurring lianas and trees share. Alternatively, it is possible that the similarities between lianas and trees are biased by the season in which the trait was measured. For instance, Maréchaux et al. [45] observed a seasonal difference in the drought tolerance related trait turgor loss point (π_{tlp}) for lianas but not for trees, suggesting a seasonal adjustment of this functional trait in lianas. Moreover, Cai et al. [33] also observed a seasonal dependence of the differences in leaf N and P contents between lianas and trees, with meaningful differences only during the dry season but not during the wet season (see also [51]). Thus, measuring functional traits of lianas and trees within and across seasons may further elucidate underlying differences in life–history strategies between these two plant guilds. Additional studies are necessary to evaluate the importance of functional traits such as $\delta^{13}C$, g_s , P50, and π_{tlp} to explain the coexistence of tropical lianas and trees.

Another dimension in which lianas and trees differ in their life–history strategies, which may explain their coexistence, is the “high leaf efficiency hypothesis”. This hypothesis proposes that lianas invest in leaves that are inexpensive and easy to replace but have high photosynthetic efficiency [43,46,50]. Thus, lianas may invest in leaves with an increased surface area for light interception relative to its mass (high SLA) and high leaf nitrogen (N) and phosphorus (P) content to increase photosynthetic rates (A). In fact, the high values of SLA, N_{mass} , P_{mass} , and K_s for lianas support the high leaf efficiency hypothesis. By contrast, the mean trait values of tree leaves suggest more investment in structure and defense, which confers longer leaf lifespans [66,77]. Thus, trees appear to have less photosynthetically efficient leaves when compared to lianas, but their leaves are better defended and last much longer [77]. Thus, the tradeoff between leaf cost, leaf efficiency and leaf life span is another way by which lianas and trees differ along the fast-slow life–history continuum.

High leaf efficiency, while beneficial in terms of photosynthetic gain, may leave lianas at a disadvantage compared to trees if lianas are more vulnerable to herbivory [80]. Lianas tend to invest less than co-occurring trees in chemical defenses of their leaves [76]. However, lianas may overcome this increased vulnerability to herbivory by investing in non-chemical traits that are involved in herbivory defense [80]. For instance, Schupp and Feener [81] observed that lianas of Barro Colorado Island, in Panama, have more extra-floral nectaries and other ant-defense mechanisms compared to trees, which could provide an important non-chemical defense strategy. Herbivory may decrease the competitive advantage that lianas have over trees at the leaf level and may facilitate liana–tree coexistence [81]. Additional studies are necessary for a more complete understanding of how trade-offs and ecological interactions differ in liana and tree life–history strategies and how these differences mediate plant coexistence in tropical forests.

In summary, functional traits may explain liana–tree coexistence. Four functional traits (SLA, N_{mass} , P_{mass} , and K_s) were particularly important in defining differences between the two plant guilds. These differences suggest that lianas have a tendency for a “fast” life–history strategy compared to

trees, with lianas likely realizing faster growth rates and the capacity to more rapidly capitalize on available resources. Additional studies that directly compare functional traits between lianas and trees in different seasons and environmental conditions may further our understanding of the differences between these two important plant guilds and how they coexist in tropical forests.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1424-2818/12/10/397/s1>, Table S1: List of functional traits measured in the 36 studies comparing co-occurring trees and lianas.

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