Differential impact of liana colonization on the leaf functional traits of co-occurring deciduous and evergreen trees

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Research Article

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Abstract

The present study was carried out to analyse the leaf functional traits of co-occurring evergreen and deciduous tree species in a tropical dry scrub forest. This study also intended to check whether the species with contrasting leaf habits differ in their leaf trait plasticity, responding to the canopy-infestation by lianas. A total of 12 leaf functional traits were studied for eight tree species with contrasting leaf habits (evergreen and deciduous) and liana-colonization status (Liana+ and Liana−). In the liana-free environment (L−), evergreen trees had significantly higher specific leaf mass (LMA) and leaf dry matter content (LDMC) than the deciduous species. Whereas, the deciduous trees had higher specific leaf area (SLA) and mass-based leaf nitrogen concentration (Nmass). The leaf trait-pair relationship in the present study agreed to the well-established global trait-pair relationships (SLA Vs Nmass, Lth Vs SLA, Nmass Vs Lth, Nmass Vs LDMC, LDMC Vs SLA). There was no significant difference between L+ and L− individuals in any leaf functional traits studied in the deciduous species. However, evergreen species showed marked differences in the total chlorophyll content (Chlt), chlorophyll b (Chlb), SLA, and LMA between L+ and L− individuals of the same species. Deciduous species with the acquisitive strategy can have a competitive advantage over evergreen species in the exposed environment (L−) whereas, evergreen species with shade-tolerant properties were better acclimated to the shaded environments (L+). The result revealed the patterns of convergence and divergence in some of the leaf functional traits between evergreen and deciduous species. The results also showed the differential impact of liana colonization on the host trees with contrasting leaf habits. Therefore, liana colonization can significantly impact the C-fixation strategies of the host trees by altering their light environment. Further, the magnitude of such impact may vary among species of different leaf habits. The increased proliferation of lianas in the tropical forest canopies may pose a severe threat to the whole forest carbon assimilation rates.

Introduction

Lianas with significantly higher stem: leaf ratio often form a dense carpet of leaves over the host trees' crown (Avalos et al. 2007; Van der Heijden et al. 2013; Ichihashi and Tateno 2015), leaving a limited or no light for the trees to perform photosynthesis. Therefore, liana colonization can potentially alter the light environment within host trees' crown, which might affect their photosynthetic performance. However, leaves invariably adapt to the varying light environment through structural and functional plastic responses (Bond et al. 1999; Yoshimura et al. 2010). Therefore, changes in the light levels to which a species acclimated may lead to different physiological responses in its biochemical, anatomical, and growth-related traits (Atroch et al. 2001; Taiz and Zeiger 2006). Several studies have investigated the morphological and physiological acclimation of vascular plant leaves to specific light conditions during their development (Anderson et al. 1995; Kurasova et al. 2002). Plants usually adapt genetically to the prevailing light environment as either sun-requiring or shade-tolerant species at the community level (Larcher 1995; Mathur et al. 2017). However, at the individual level, leaves acclimated to the heterogeneous light environment are found within the canopy (James and Bell 2000) due to self-shading and shading from neighbouring trees (Wyka et al. 2012). The leaves that grow under direct sunlight are typically acclimated for high light environments (sunlit leaves) with a suite of traits favouring their performance under higher irradiance, while leaves growing in the shaded inner canopy adapt to low-light environments (Shade leaves) (Lambers and Poorter 1992). The physiological differences between sunlit and shade leaves are usually due to the differences in leaf structure (Gratani et al. 2006). Leaves growing under shade are relatively thinner than the sunlit leaves due to the under-development of mesophyll tissues (Nobel 1976; Grecco et al. 2014). In addition, sunlit leaves are more productive by means of higher light-saturated photosynthetic capacity (Olsen et al. 2002) than the shade leaves,
that are characterized by innate lower photosynthetic rates, higher total chlorophyll, and lesser chlorophyll a/b ratio (Taiz and Zeiger 2006). Therefore, the decrease in the proportion of sun-shade leaves may decrease the carbon gain per unit leaf area. However, shade-acclimated leaves can be more efficient under low light environments, thanks to their specialized anatomical and physiological adaptations (Givnish 1988; Taiz and Zeiger 2006). Though sun and shade leaves have many physiological and morphological differences, it remains unclear how co-occurring plants with different leaf functional types differ in the magnitude of plastic responses to heterogeneity in the light environment.

The co-occurring evergreen and deciduous species with distinct leaf morphological and functional features (Huang et al. 2015) are ideal candidates to understand such variations in structurally and functionally essential leaf traits and their pattern of co-existence in the same environment. The evergreen leaf habits are associated with lower photosynthetic efficiency compensated by their extended leaf longevity. Whereas deciduous species are short-lived with greater photosynthetic efficiency (Kröber et al. 2014; de Souza et al. 2020). Both these functional types exhibit a trade-off between faster resource acquisition and increased foliar longevity (Jiang et al. 2016; Wright et al. 2004; de Souza et al. 2020). Earlier studies (Givinish 2002; Valladares et al. 2000) have shown that deciduous species with short-lived leaves can have better trait plasticity as a response to light variation than the evergreen species with higher leaf longevity, though such trend may not be universal (Markesteijn 2007). Although much emphasis has been given to plant responses for self-shading and shading from neighbouring trees, the light acclimation responses of host trees to the liana colonization has gained only very little attention. Lianas can significantly reduce the photosynthetically active radiation (PAR) reaching and filtered through the tree crown. Such decline in PAR may affect the photosynthetic efficiency and growth rate of host trees. Thus, altering the whole forest carbon assimilation rates. Although the belowground competition of lianas and trees for water and nutrient uptake is well-studied, the competition for light and its subsequent impact on the leaf-trait configuration of host trees is still poorly understood. Therefore, we undertook this study to analyze the leaf functional traits of co-occurring evergreen and deciduous species and to check whether the host trees with contrasting leaf habits differ in their plastic responses for liana colonization. Since lianas are seemingly increasing in abundance in the tropical forests (Schnitzer and Bongers 2011; Vivek and Parthasarathy 2015), it has become crucial to understand their role in modifying the light environment and its subsequent impact on the host trees' C-fixing abilities.

Materials And Methods

Study area

Leaf functional trait analysis was carried out in situ in a lateritic scrub forest in the West Coast of India (13° 22' 19" N and 74° 47' 00" E) (Fig. 1), dominated by deciduous and evergreen trees. Much of these forests are cleared for cultivation and Acacia plantation, leaving only the remnants (Bhat 2014). The canopy is short (10–12 m) and composed of two to three-layered strata with less to sparse undergrowth. The tree layer comprises Terminalia paniculata, Carea arborea, Olea dioica, Macaranca peltata, and Holigarna arnottiana. The study area also harbours Acacia auriculiformis, either deliberately planted or escaped from the adjoining plantations. Getonia floribunda and Thunbergia grandiflora are the predominant liana species, colonizing most of the trees in the edges, forming a dense carpet of leaves over the host trees' crown. Species including Memecylon edule, Carissa spinarum, and Santalum album dominated the lower canopy. The mean annual rainfall is 2893 mm, with more than 80% of the rainfall received during the South-West monsoon (June – September) with fewer sporadic rains during the late summer (May). The mean annual maximum and minimum temperature corresponds to 33°C and 21°C (Fick and Hijmans 2017, https://worldclim.org/).
Species selection and sample collection

Based on the qualitative woody-species inventory, we selected a total of eight most frequently occurred canopy trees, four each with contrasting leaf habits (Table 1). The individuals of the identified tree species were thoroughly screened for the presence/absence of lianas on the host trees' crown. Lianas colonizing host trees' crown through lateral infestations (secondary host) were also considered along with the primary colonizers through the trunk. *Getonia floribunda*, a deciduous liana species, was a predominant colonizer that infested most of the trees in the study site, followed by *Thunbergia grandiflora*, which colonized most of the trees through the edges. For each tree species, we identified five adult trees (GBH ≥ 60 cm) with their crown homogenously shaded by the lianas (L+ category) and five individuals devoid of lianas (crown exposed to sunlight) on both trunk and crown (L− category). The field collections were made during December-January, 2020-21, i.e., after the rainy season. Leaf functional traits were estimated following Perez-Harguindeguy et al. (2016) and Vivek and Parthasarathy (2018). For each species under both categories, a total of 30 matured (fully-expanded) and healthy leaves (free from folivore damage) were collected using a detachable tree pruner (up to 12 m). For L+ individuals, leaves were collected from the immediate branches beneath the liana layer (fully-shaded). In the case of L− individuals, fully-grown healthy sun leaves (fully-exposed) were collected for further analysis. The collected leaf samples were brought back to the laboratory in an insulated icebox within 30 minutes after the sample collection. The leaf samples were sequentially numbered with unique codes for different species using permanent markers at the abaxial side of the leaf. All the selected species had simple leaf types except *Millettia pinnata*, which had compound leaves. For *M. pinnata*, we collected the largest leaflet for leaf trait analysis following Perez-Harguindeguy et al (2016). For each leaf sample, the petiole was removed, and petiole length (PL, cm) was measured before further processing. The leaf's fresh weight (g) was measured using a top-pan balance (Shimadzu AUX-220, Japan). Leaf thickness (Lth, mm) was measured using a digital micrometer at the intermediate point between the leaf lamina and midrib border, avoiding the secondary veins. Leaf area (one-sided area of a fresh leaf: LA, cm²) was measured using ImageJ software (IJ). The leaf samples were kept in a hot-air oven at 80°C for 48 hours. After measuring the dry weight (g), leaf samples were ground into a fine powder and stored in air-tight containers for further analysis. Leaf nitrogen (Nmass, mg g⁻¹) was analyzed using a CNHS analyzer (Elementar Analysensystem GmbH, Germany). Specific leaf area (SLA, cm² g⁻¹) was calculated as fresh leaf area (cm) / dry weight (g). Specific leaf mass (LMA, mg cm⁻²) was calculated as leaf dry weight (mg) / fresh leaf area (cm). Leaf tissue density (Ltd, g cm⁻³) was calculated as LMA (g cm⁻²) / Lth (cm). Leaf dry matter content (LDMC, mg g⁻¹) was calculated as leaf dry weight (mg) / leaf fresh weight (g). For chlorophyll estimation, 5–10 healthy and fully-grown leaves of similar age were collected from a minimum of two individuals per species. For each species under L+ and L− category, 1g of the fresh leaf was randomly taken from the subsample. Leaf chlorophyll (Chl a – Chlorophyll a and Chl b – Chlorophyll b) was estimated following Arnon (1949) and Brown and Hooker (1977) using UV/Visible Spectrophotometer (Shimadzu UV-1800) at 645 and 663 nm respectively for Chl b and Chl a. The following equations were used for the estimation of Chl a, Chl b and total chlorophyll (Chl t) expressed in mg g⁻¹ in the studied leaf samples:
Table 1
List of tree species selected for the study based on their leaf type and liana colonization status

| Species               | Family            | Leaf form | Leaf type |
|-----------------------|-------------------|-----------|-----------|
| Holigarna arnottiana  | Anacardiaceae     | Simple    | Evergreen |
| Aporosa cardiosperma  | Phyllanthaceae    | Simple    | Evergreen |
| Carallia brachiata    | Rhizophoraceae    | Simple    | Evergreen |
| Olea dioica          | Oleaceae          | Simple    | Evergreen |
| Careya arborea        | Lecythidaceae     | Simple    | Deciduous |
| Terminalia paniculata| Combretaceae      | Simple    | Deciduous |
| Millettia pinnata     | Fabaceae          | Compound  | Deciduous |
| Ziziphus mauritiana   | Rhamnaceae        | Simple    | Deciduous |

Chl_t (mg g\(^{-1}\)) = 20.2 (A\(_{645}\)) + 8.02 (A\(_{663}\)) \times 0.1 (1)

Chl_a (mg g\(^{-1}\)) = 12.7 (A\(_{663}\)) – 2.69 (A\(_{645}\)) \times 0.1 (2)

Chl_b (mg g\(^{-1}\)) = 22.9 (A\(_{645}\)) – 4.68 (A\(_{663}\)) \times 0.1 (3)

Where A\(_{663}\) and A\(_{645}\) are the absorbances at 663 and 645 nm respectively. 0.1 is the conversion factor.

Kruskal-Wallis non-parametric test was used to check whether there is a significant difference in leaf functional traits between evergreen and deciduous species and within L\(^+\) and L\(^-\) individuals of evergreen and deciduous species. Standardized Major Axis (SMA) regression was performed to understand the leaf trait-pair relationship between various leaf functional traits. All the statistical analyses were carried out in R 4.1.0 (R Development Core Team 2021).

Results

Results revealed that evergreen and deciduous leaf habits exhibited contrasting leaf functional strategies. Among evergreen species, A. cardiosperma registered the highest mean SLA and N\(_{\text{mass}}\) in both L\(^+\) and L\(^-\) categories (Table 2). H. arnottiana had the highest mean LA among evergreen species (104.77 ± 4.75 and 117.08 ± 5.23 cm\(^2\)). Among deciduous species, Z. mauritiana had the highest mean SLA and N\(_{\text{mass}}\) and lowest mean LA in both categories (Table 3). C. arborea registered the maximum LA among the deciduous species studied in L\(^+\) and L\(^-\) categories. M. pinnata accounted for the highest Chl_t among the four deciduous species in both L\(^+\) (2.305 mg g\(^{-1}\)) and L\(^-\) (1.182 mg g\(^{-1}\)) categories.
Table 2
Summary of the leaf functional trait analysis of four evergreen species in L⁺ and L⁻ categories. Values presented are mean and the standard error (SE) for 30 leaf samples/species/category. Chlorophyll and N_{mass} values are means of triplicates.

| Leaf trait | Species | Mean (SE) |
|------------|---------|-----------|
|            | Holigama amottiana | Aporosa cardiosperma | Carallia brachiata | Olea dioica |
| L⁻ | L⁺ | L⁻ | L⁺ | L⁻ | L⁺ | L⁻ | L⁺ |
| LA (cm²) | 104.77 (4.75) | 117.08 (5.23) | 49.85 (2.75) | 50.08 (1.92) | 33.66 (0.93) | 48.12 (1.25) | 56.64 (1.69) | 47.4 (2.14) | 61.23 (13.24) | 65.67 (14.85) |
| Lth (mm) | 0.332 (0.01) | 0.194 (0.00) | 0.254 (0.00) | 0.202 (0.00) | 0.347 (0.04) | 0.334 (0.04) | 0.331 (0.00) | 0.152 (0.00) | 0.32 (0.02) | 0.22 (0.03) |
| PL (cm) | 0.4 (0.02) | 0.53 (0.02) | 0.56 (0.01) | 0.57 (0.02) | 0.46 (0.01) | 0.57 (0.01) | 0.22 (0.00) | 0.23 (0.00) | 0.41 (0.06) | 0.48 (0.07) |
| SLA (cm² g⁻¹) | 92.1 (5.28) | 186.7 (5.76) | 109.3 (1.76) | 180.4 (3.00) | 73.3 (1.05) | 106.9 (2.39) | 75.9 (2.15) | 122.3 (2.48) | 87.65 (7.21) | 149.08 (17.49) |
| LMA (mg cm⁻²) | 10.86 (0.56) | 5.36 (0.14) | 9.15 (0.14) | 5.54 (0.09) | 13.64 (0.21) | 9.35 (0.21) | 13.18 (0.34) | 8.18 (0.16) | 11.71 (0.91) | 7.11 (0.85) |
| Ltd (g cm⁻³) | 0.327 (0.02) | 0.277 (0.00) | 0.36 (0.01) | 0.275 (0.00) | 0.393 (0.00) | 0.28 (0.00) | 0.398 (0.01) | 0.539 (0.00) | 0.37 (0.01) | 0.34 (0.06) |
| LDMC (mg g⁻¹) | 469.79 (7.39) | 369.92 (8.04) | 452.41 (4.02) | 328.2 (3.75) | 390.56 (2.55) | 365.79 (4.64) | 504.78 (8.61) | 465.92 (7.90) | 454.39 (20.7) | 382.46 (25.43) |
| CHL_a (mg g⁻¹) | 1.507 (0.14) | 1.339 (0.04) | 0.936 (0.06) | 1.513 (0.12) | 0.812 (0.06) | 1.418 (0.06) | 1.288 (0.06) | 1.544 (0.12) | 1.14 (0.06) | 1.45 (0.04) |
| CHL_b (mg g⁻¹) | 0.536 (0.06) | 0.648 (0.12) | 0.586 (0.06) | 1.25 (0.25) | 0.268 (0.06) | 0.723 (0.06) | 0.566 (0.06) | 1.039 (0.12) | 0.49 (0.06) | 0.92 (0.12) |
| CHL_t (mg g⁻¹) | 2.042 (0.18) | 1.987 (0.18) | 1.522 (0.15) | 2.762 (0.15) | 1.08 (0.18) | 2.201 (0.18) | 1.854 (0.18) | 2.582 (0.15) | 1.62 (0.18) | 2.38 (0.15) |

L⁺ - tree crown colonized by lianas; L⁻ - tree crown free from lianas; LA – one-sided leaf area; Lth – leaf thickness; PL – petiole length; SLA – specific leaf area; LMA – leaf mass per area; Ltd – leaf tissue density; LDMC – leaf dry matter content; CHL_a – chlorophyll a; CHL_b – chlorophyll b; CHL_t – total chlorophyll; CHL_a/b – chlorophyll a/b ratio; N_{mass} – mass-based leaf nitrogen concentration.
| Leaf trait | Species | \( \text{L}^- \) | \( \text{L}^+ \) | \( \text{L}^- \) | \( \text{L}^+ \) | \( \text{L}^- \) | \( \text{L}^+ \) | \( \text{L}^- \) | \( \text{L}^+ \) |
|------------|---------|--------|--------|--------|--------|--------|--------|--------|--------|
| CHL\(_{a/b}\) ratio | *Holigama amottiana* | 2.813 | 2.067 | 1.597 | 1.21 | 3.025 | 1.811 | 2.276 | 1.485 | 2.43 | 1.64 | (0.28) | (0.16) |
| \( \text{N}_{\text{mass}} \) (mg g\(^{-1}\)) | *Holigama amottiana* | 20.004 | 23.93 | 19.732 | 25.43 | 14.614 | 20.05 | 14.032 | 19.89 | 17.10 | 22.33 | (1.39) | (1.21) |

\( \text{L}^+ \) - tree crown colonized by lianas; \( \text{L}^- \) - tree crown free from lianas; LA - one-sided leaf area; \( L_{\text{th}} \) - leaf thickness; PL - petiole length; SLA - specific leaf area; LMA - leaf mass per area; \( L_{\text{td}} \) - leaf tissue density; LDMC - leaf dry matter content; CHL\(_a\) - chlorophyll \( a \); CHL\(_b\) - chlorophyll \( b \); CHL\(_t\) - total chlorophyll; CHL\(_{a/b}\) - chlorophyll \( a/b \) ratio; \( \text{N}_{\text{mass}} \) - mass-based leaf nitrogen concentration.
Table 3
Summary of the leaf functional trait analysis of four deciduous species in L+ and L− categories. Values presented are mean and the standard error for 30 leaf samples/species/category. Chlorophyll and Nmass values are means of triplicates.

| Leaf trait | Species                | Careya arborea | Terminalia paniculata | Millettia pinnata | Ziziphus mauritiana | Mean (S.E) |
|------------|------------------------|----------------|-----------------------|------------------|---------------------|------------|
|            |                        | L−  | L+  | L−  | L+  | L−  | L+  | L−  | L+  | L−  | L+  | L−  | L+  |
| LA (cm²)   |                        | 248.21 | 280.24 | 69.80 | 99.3 | 60.646 | 84.58 | 10.61 | 14.69 | 97.32 | 119.70 |
|            |                        | (7.19) | (12.4) | (6.07) | (2.83) | (3.56) | (3.97) | (0.33) | (0.69) | (44.99) | (49.02) |
| Lth (mm)   |                        | 0.31  | 0.30  | 0.26  | 0.23  | 0.19  | 0.15  | 0.16  | 0.12  | 0.23  | 0.20  |
|            |                        | (0.00) | (0.00) | (0.00) | (0.01) | (0.00) | (0.00) | (0.00) | (0.00) | (0.03) | (0.03) |
| PL (cm)    |                        | 0.97  | 1.696 | 0.397 | 0.701 | 2.35  | 3.894 | 0.26  | 0.623 | 0.99  | 1.73  |
|            |                        | (0.02) | (0.02) | (0.01) | (0.01) | (0.05) | (0.10) | (0.05) | (0.02) | (0.41) | (0.66) |
| SLA (cm² g⁻¹) |                    | 120.26 | 148.27 | 113.12 | 108.67 | 147.70 | 215.53 | 174.01 | 226.0 | 138.77 | 174.62 |
|            |                        | (7.13) | (3.63) | (3.56) | (2.31) | (6.28) | (5.14) | (6.28) | (2.30) | (12.05) | (24.18) |
| LMA (mg cm⁻²) |                    | 8.32  | 6.74  | 8.84  | 9.2   | 6.77  | 4.64  | 5.75  | 4.42  | 7.42  | 6.25  |
|            |                        | (0.29) | (0.2)  | (0.57) | (0.25) | (0.26) | (0.13) | (0.26) | (0.10) | (0.61) | (0.96) |
| Ltd (g cm⁻³) |                    | 0.27  | 0.226 | 0.35  | 0.396 | 0.36  | 0.316 | 0.37  | 0.363 | 0.33  | 0.33  |
|            |                        | (0.00) | (0.01) | (0.02) | (0.01) | (0.01) | (0.01) | (0.01) | (0.00) | (0.02) | (0.03) |
| LDMC (mg g⁻¹) |                   | 281.16 | 294.07 | 318.25 | 418.11 | 377.74 | 410.29 | 279.82 | 269.71 | 314.24 | 348.05 |
|            |                        | (7.66) | (9.39) | (20.36) | (7.73) | (5.83) | (3.06) | (5.83) | (3.28) | (19.89) | (33.39) |
| CHLₐ (mg g⁻¹) |                   | 0.702 | 0.916 | 0.89  | 1.467 | 0.879 | 1.791 | 0.88  | 1.194 | 0.84  | 1.342 |
|            |                        | (0.04) | (0.16) | (0.04) | (0.16) | (0.04) | (0.16) | (0.04) | (0.16) | (0.04) | (0.16) |
| CHLₐ (mg g⁻¹) |                   | 0.197 | 0.316 | 0.143 | 0.413 | 0.303 | 0.514 | 0.179 | 0.43  | 0.20  | 0.418 |
|            |                        | (0.03) | (0.04) | (0.03) | (0.04) | (0.03) | (0.04) | (0.03) | (0.04) | (0.03) | (0.04) |
| CHLₜ (mg g⁻¹) |                   | 0.899 | 1.231 | 1.033 | 1.879 | 1.182 | 2.305 | 1.066 | 1.623 | 1.045 | 1.760 |
|            |                        | (0.05) | (0.20) | (0.05) | (0.20) | (0.05) | (0.20) | (0.05) | (0.20) | (0.05) | (0.20) |

L⁺ - tree crown colonized by lianas; L⁻ - tree crown free from lianas; LA – one-sided leaf area; Lth – leaf thickness; PL – petiole length; SLA – specific leaf area; LMA – leaf mass per area; Ltd – leaf tissue density; LDMC – leaf dry matter content; CHLₐ – chlorophyll a; CHLₐ – chlorophyll b; CHLₜ – total chlorophyll; CHLₐ/ₐ – chlorophyll a/b ratio; Nmass – mass-based leaf nitrogen concentration.
| Leaf trait | Species       | Mean (S.E) |
|------------|---------------|------------|
|            | *Careya arborea* |            |
|            | *Terminalia paniculata* |         |
|            | *Millettia pinnata* |            |
|            | *Ziziphus mauritiana* |           |
| L−         | L+            | L−         | L+       | L−         | L+         | L−         | L+         |
| CHL\(a/b\) ratio | 3.566  | 2.902  | 3.555  | 6.211  | 2.907  | 3.484  | 4.907  | 2.777  | 3.73  | 3.84  |
| \(N_{mass}\) (mg g⁻¹) | 22.982 | 23.41  | 27.652 | 28.55  | 26.96  | 29.35  | 37.24  | 39.77  | 28.71  | 30.27  |

L⁺ - tree crown colonized by lianas; L⁻ - tree crown free from lianas; LA - one-sided leaf area; \(L_{th}\) - leaf thickness; PL - petiole length; SLA - specific leaf area; LMA - leaf mass per area; \(L_{td}\) - leaf tissue density; LDMC - leaf dry matter content; CHL\(a\) - chlorophyll a; CHL\(b\) - chlorophyll b; CHL\(t\) - total chlorophyll; CHL\(a/b\) - chlorophyll a/b ratio; \(N_{mass}\) - mass-based leaf nitrogen concentration.

Within the L⁻ category, deciduous species had significantly higher mean SLA (\(P<0.05\)) and \(N_{mass}\) (\(P<0.05\)) whereas, the evergreen species had significantly higher mean LMA (\(P<0.05\)) and LDMC (\(P<0.05\)) than the deciduous species (Table 4). However, there was no significant difference observed between LA and \(L_{th}\) (\(P>0.05\)).

The leaf chlorophyll content (CHL\(a\), CHL\(b\), and CHL\(t\)) did not vary significantly between the two leaf habits; however, the short-lived deciduous leaves had a considerably higher CHL\(a/b\) ratio than the evergreen species.
Table 4
Results of the Kruskal-Wallis non-parametric test to check for the significant difference in leaf functional traits between evergreen (L$^+$) and deciduous (L$^-$) species.

| Leaf trait | Leaf habit | Mean | SD | SE | $\chi^2$ | $P$ |
|------------|------------|------|----|----|---------|----|
| LA (cm$^2$) | Evergreen  | 61.2 | 26.4 | 13.2 | 0.333  | 0.5637 |
|            | Deciduous  | 97.3 | 89.9 | 44.9 |         |      |
| L$_{th}$ (mm) | Evergreen  | 0.32 | 0.04 | 0.02 | 3.000  | 0.0832 |
|            | Deciduous  | 0.23 | 0.06 | 0.03 |         |      |
| PL (cm)    | Evergreen  | 0.41 | 0.12 | 0.06 | 0.750  | 0.3865 |
|            | Deciduous  | 0.99 | 0.93 | 0.41 |         |      |
| SLA (cm$^2$ g$^{-1}$) | Evergreen  | 87.6 | 14.4 | 7.21 | 5.333  | 0.0209* |
|            | Deciduous  | 138.7| 24.1 | 12.1 |         |      |
| LMA (mg cm$^{-2}$) | Evergreen | 11.7 | 1.82 | 0.91 | 5.333  | 0.0209* |
|            | Deciduous  | 7.42 | 1.23 | 0.61 |         |      |
| L$_{td}$ (g cm$^3$) | Evergreen  | 0.37 | 0.03 | 0.01 | 1.333  | 0.2482 |
|            | Deciduous  | 0.33 | 0.04 | 0.02 |         |      |
| LDMC (mg g$^{-1}$) | Evergreen | 454.3| 41.3 | 20.7 | 5.333  | 0.0209* |
|            | Deciduous  | 314.2| 39.7 | 19.8 |         |      |
| CHL$_a$ (mg g$^{-1}$) | Evergreen | 1.14 | 0.28 | 0.14 | 0.750  | 0.3865 |
|            | Deciduous  | 0.98 | 0.29 | 0.14 |         |      |
| CHL$_b$ (mg g$^{-1}$) | Evergreen | 0.49 | 0.13 | 0.06 | 3.000  | 0.0832 |
|            | Deciduous  | 0.27 | 0.09 | 0.05 |         |      |
| CHL$_t$ (mg g$^{-1}$) | Evergreen | 1.62 | 0.37 | 0.18 | 1.333  | 0.2482 |
|            | Deciduous  | 1.26 | 0.37 | 0.19 |         |      |
| CHL$_{a/b}$ ratio | Evergreen | 2.43 | 0.55 | 0.28 | 4.0833 | 0.0433* |
|            | Deciduous  | 3.73 | 0.73 | 0.36 |         |      |
| N$_{mass}$ (mg g$^{-1}$) | Evergreen | 17.1 | 2.78 | 1.39 | 5.333  | 0.0209* |
|            | Deciduous  | 28.7 | 5.24 | 2.62 |         |      |

*significant at $\alpha = 0.05$ ($P<0.05$); df = 1. SD – standard deviation; SE – standard error ($n = 4$) (abbreviations for leaf traits as in Table 2 and 3).

The evergreen species showed a significant difference in SLA, LMA, Chl$_b$, and Chl$_t$ between L$^+$ and L$^-$ categories (Table 5). However, other structural parameters such as LA, L$_{th}$, L$_{td}$, and LDMC did not show significant variation between the L$^+$ and L$^-$ categories explained by the change in the light environment. Similarly, PL did not show any
marked difference between the two light environments. The deciduous species, on the other hand, did not show significant differences in any of the structural, morphological, and biochemical traits studied ($P \geq 0.05$) between the two categories (Table 6). Though not significant the PL of $L^+$ deciduous leaves were close to two-fold higher values than the $L^-$ category. Although there were no significant variations among the deciduous species in $L^+$ and $L^-$ categories at the community level, there was a significant difference in a few studied parameters at the species level.
Table 5
Results of the Kruskal-Wallis non-parametric test to check for the significant difference in leaf functional traits between L\(^+\) and L\(^-\) categories of evergreen species.

| Leaf trait       | Exposure | Mean   | SD    | SE     | \(\chi^2\) | \(P\) |
|------------------|----------|--------|-------|--------|------------|------|
| LA (cm\(^2\))   | L\(^-\)  | 61.23  | 26.49 | (13.24)| 0.000      | 1.000|
|                  | L\(^+\)  | 65.67  | 29.70 | (14.85)|            |      |
| L\(_{th}\) (mm)  | L\(^-\)  | 0.32   | 0.04  | (0.02) | 2.083      | 0.149|
|                  | L\(^+\)  | 0.22   | 0.07  | (0.03) |            |      |
| PL (cm)          | L\(^-\)  | 0.41   | 0.12  | (0.06) | 1.349      | 0.245|
|                  | L\(^+\)  | 0.48   | 0.14  | (0.07) |            |      |
| SLA (cm\(^2\) g\(^{-1}\)) | L\(^-\) | 87.65  | 14.43 | (7.21) | 4.083      | 0.043|
|                  | L\(^+\)  | 149.08 | 34.97 | (17.49)|            |      |
| LMA (mg cm\(^{-2}\)) | L\(^-\) | 11.71  | 1.81  | (0.91) | 4.083      | 0.043|
|                  | L\(^+\)  | 7.11   | 1.71  | (0.85) |            |      |
| L\(_{td}\) (g cm\(^{-3}\)) | L\(^-\) | 0.37   | 0.03  | (0.01) | 1.333      | 0.248|
|                  | L\(^+\)  | 0.34   | 0.11  | (0.06) |            |      |
| LDMC (mg g\(^{-1}\)) | L\(^-\) | 454.39 | 41.40 | (20.7) | 3.000      | 0.083|
|                  | L\(^+\)  | 382.46 | 50.85 | (25.43)|            |      |
| CHL\(_a\) (mg g\(^{-1}\)) | L\(^-\) | 1.14   | 0.28  | (0.14) | 3.000      | 0.083|
|                  | L\(^+\)  | 1.45   | 0.08  | (0.04) |            |      |
| CHL\(_b\) (mg g\(^{-1}\)) | L\(^-\) | 0.49   | 0.13  | (0.06) | 5.333      | 0.021|
|                  | L\(^+\)  | 0.92   | 0.24  | (0.12) |            |      |
| CHL\(_t\) (mg g\(^{-1}\)) | L\(^-\) | 1.62   | 0.37  | (0.18) | 4.083      | 0.043|
|                  | L\(^+\)  | 2.38   | 0.31  | (0.15) |            |      |
| CHL\(_a/b\) ratio | L\(^-\) | 2.43   | 0.55  | (0.28) | 3.000      | 0.083|
|                  | L\(^+\)  | 1.64   | 0.32  | (0.16) |            |      |
| N\(_{mass}\) (mg g\(^{-1}\)) | L\(^-\) | 17.10  | 2.78  | (1.39) | 4.083      | 0.043|

*significant at \(\alpha = 0.05\) (\(P < 0.05\)); df = 1. SD – standard deviation; SE – standard error (\(n = 4\)) (abbreviations for leaf traits as in Table 2 and 3).
| Leaf trait | Exposure | Mean | SD | SE  | $\chi^2$ | $P$  |
|-----------|----------|------|----|-----|---------|------|
| L$^+$     | 22.33    | 2.41 |    | (1.21) |         |      |

*significant at $\alpha = 0.05 (P < 0.05)$; df = 1. SD – standard deviation; SE – standard error ($n = 4$) (abbreviations for leaf traits as in Table 2 and 3).
Table 6
Results of the Kruskal-Wallis non-parametric test to check for the significant difference in leaf functional traits between \( L^+ \) and \( L^- \) categories of deciduous species.

| Leaf trait     | Exposure | Mean   | SD   | SE   | \( \chi^2 \) | P     |
|----------------|----------|--------|------|------|--------------|-------|
| LA (cm\(^2\)) | \( L^- \) | 97.32  | 89.98| (44.99) | 0.750        | 0.3865|
|                | \( L^+ \) | 119.70 | 98.04| (49.02) |              |       |
| \( L_{th} \) (mm) | \( L^- \) | 0.23   | 0.06 | (0.03) | 0.750        | 0.3865|
|                | \( L^+ \) | 0.20   | 0.07 | (0.03) |              |       |
| PL (cm)        | \( L^- \) | 0.99   | 0.83 | (0.41) | 0.750        | 0.3865|
|                | \( L^+ \) | 1.73   | 1.32 | (0.66) |              |       |
| SLA (cm\(^2\) g\(^{-1}\)) | \( L^- \) | 138.77 | 24.10| (12.05) | 0.750        | 0.3865|
|                | \( L^+ \) | 174.62 | 48.37| (24.18) |              |       |
| LMA (mg cm\(^{-2}\)) | \( L^- \) | 7.42   | 1.23 | (0.61) | 0.750        | 0.3865|
|                | \( L^+ \) | 6.25   | 1.93 | (0.96) |              |       |
| \( L_{td} \) (g cm\(^{-3}\)) | \( L^- \) | 0.33   | 0.04 | (0.02) | 0.000        | 1.0000|
|                | \( L^+ \) | 0.33   | 0.06 | (0.03) |              |       |
| LDMC (mg g\(^{-1}\)) | \( L^- \) | 314.24 | 39.77| (19.89) | 0.333        | 0.5637|
|                | \( L^+ \) | 348.05 | 66.77| (33.39) |              |       |
| \( CHL_a \) (mg g\(^{-1}\)) | \( L^- \) | 0.98   | 0.29 | (0.14) | 2.083        | 0.1489|
|                | \( L^+ \) | 1.20   | 0.36 | (0.18) |              |       |
| \( CHL_b \) (mg g\(^{-1}\)) | \( L^- \) | 0.27   | 0.09 | (0.05) | 0.750        | 0.3865|
|                | \( L^+ \) | 0.35   | 0.14 | (0.07) |              |       |
| \( CHL_t \) (mg g\(^{-1}\)) | \( L^- \) | 1.26   | 0.37 | (0.19) | 0.750        | 0.3865|
|                | \( L^+ \) | 1.55   | 0.49 | (0.24) |              |       |
| \( CHL_{a/b} \) ratio | \( L^- \) | 3.73   | 0.73 | (0.36) | 0.750        | 0.3865|
|                | \( L^+ \) | 3.84   | 1.39 | (0.70) |              |       |
| \( N_{mass} \) (mg g\(^{-1}\)) | \( L^- \) | 28.71  | 5.24 | (2.62) | 0.750        | 0.3865|

*significant at \( \alpha = 0.05 \) \( (P<0.05) \); df = 1. SD – standard deviation; SE – standard error \( (n = 4) \) (abbreviations for leaf traits as in Table 2 and 3).
Leaf trait | Exposure | Mean | SD | SE | $\chi^2$ | $P$ |
--- | --- | --- | --- | --- | --- | --- |
L$^+$ | 30.27 | 5.94 | (2.97) |  |

*significant at $\alpha = 0.05$ ($P < 0.05$); df = 1. SD – standard deviation; SE – standard error ($n = 4$) (abbreviations for leaf traits as in Table 2 and 3).

The leaf trait-pair relationship analysis using the pooled data of L$^+$ and L$^-$ categories revealed that there was a positive correlation between SLA and $N_{mass}$ ($r^2 = 0.66; P < 0.001$) (Table 7, Fig. 2). $L_{th}$ was negatively correlated with $N_{mass}$ ($r^2 = 0.54; P < 0.01$) and SLA ($r^2 = 0.66; P < 0.001$). Similarly, LDMC was negatively correlated with SLA ($r^2 = 0.30; P < 0.05$) and $N_{mass}$ ($r^2 = 0.42; P < 0.001$). There was no correlation observed between $N_{mass}$ and Chl$\alpha$, b, t. Similarly, PL with LA and $L_{th}$ did not show any correlation. SMA results explained similar trend when data analyzed for only L$^-$ categories (Table 7).

Table 7
Summary of the standardized major axis (SMA) regression between different trait-pairs using pooled data of L$^+$ and L$^-$ categories (evergreen and deciduous species) and only L$^-$ category.

| Trait-pair | n | $r^2$ | $P$ | Slope | Elevation |
|---|---|---|---|---|---|
| Pooled data (L$^+$ and L$^-$) | | | | | |
| SLA vs $N_{mass}$ | 16 | 0.665 | 0.0001** | 0.82970 | -0.37994 |
| $L_{th}$ Vs SLA | 16 | 0.666 | 0.0001** | -1.00446 | 1.47081 |
| $N_{mass}$ Vs $L_{th}$ | 16 | 0.547 | 0.001** | -0.83341 | 0.84040 |
| LDMC VS $N_{mass}$ | 16 | 0.423 | 0.006** | -1.40908 | 4.98935 |
| LDMC vs SLA | 16 | 0.302 | 0.027* | -1.69828 | 6.47130 |
| Only L$^-$ | | | | | |
| SLA vs $N_{mass}$ | 8 | 0.897 | 0.0003** | 0.91576 | 0.81011 |
| $L_{th}$ Vs SLA | 8 | 0.826 | 0.0017** | -1.0328 | 1.43692 |
| $N_{mass}$ Vs $L_{th}$ | 8 | 0.727 | 0.007** | -1.1272 | 0.68446 |
| LDMC VS $N_{mass}$ | 8 | 0.549 | 0.035* | -1.4324 | 5.02740 |
| LDMC vs SLA | 8 | 0.459 | 0.064 | -1.3118 | 5.41404 |

*significant at $\alpha = 0.05$ ($P < 0.05$); ** significant at $\alpha = 0.01$ ($P < 0.01$). (abbreviations for leaf traits as in Table 2 and 3).

Discussion
Co-occurrence of evergreen and deciduous species
Interspecific variation in plant functional traits forms the basis of species co-existence in natural ecosystems. The evergreen and deciduous species (L−) in the present study showed contrasting leaf functional strategies for C-assimilation. The deciduous species with higher SLA and N_{mass} coupled with relatively thinner leaves and lower LDMC displayed a set of traits confirming their acquisitive strategy with a shorter leaf lifespan. In contrast, the evergreen species exhibited a conservative plan with relatively thicker leaves, lesser SLA, and N_{mass} in the present study. Our results are consistent with the findings of recent studies, for example, de Souza et al (2020), Ellsworth and Sternberg (2016), and Jiang et al (2016). The deciduous species with a lower leaf lifespan tend to invest more in the active photosynthetic machinery under a high light environment to compensate for the short growing season and sustain higher photosynthetic rates (Niinemets et al. 2004; Wright et al. 2005). Therefore, deciduous species generally exhibit relatively higher potential growth rates and higher photosynthetic rates than evergreen species (Cornelissen et al. 1996; Reich et al. 1992; Worbes et al. 2013). The evergreen species with extended foliar longevity can compensate for their lower photosynthetic efficiencies by assimilating carbon throughout the year (Aerts 1995; Givinish 2002; Baldocchi et al. 2010). Therefore, there is an inevitable trade-off between maximizing the carbon fixation and leaf longevity in evergreen and deciduous species. The shorter leaf life span in deciduous species can be attributed to the strategy to avoid transpiration and favour high tissue leaf water potential (Levitt 1980; Borchert et al. 2002; Markesteijn and Poorter 2009), at least in the seasonally dry tropical forests (SDTFs). In contrast, evergreen species retain their leaves during the entire year across seasons, confirming their ability to compensate for transpiration loss through efficient root hydraulics (Borchert 1994; Ackerly 2004).

There was no significant difference between in L_{th} of the two distinct leaf habits studied, which contrasts the findings of Castro-Diez et al (2000) and Krober et al (2014). However, our results correspond with Burrows (2001), de Souza (2020), who reported a similar trend in the SDTFs. Similarly, PL and LA did not show significant variation between the two leaf habits. However, deciduous species had relatively higher PL and LA than the evergreen species in the studied site. The higher PL and LA can be linked to the strategy for enhanced resource acquisition by maximizing the net photosynthetic area available for light capture and avoiding shade (Yamada et al. 2000; Falster and Westoby 2003; Weijschede et al. 2006). The higher LMA and lower N_{mass} in evergreen species and lower LMA in deciduous species are consistent with the results reported in other studies conducted in the SDTFs (de Souza et al. 2020; Eamus 1999; Ishida et al. 2006; Powers and Tiffin 2010). Overall, in the present study, there was a significant difference between evergreen (L−) and deciduous (L−) species only in the structural traits, and there was no significant difference in the other physiological traits studied, but for the chlorophyll a/b ratio. Our results suggests that both evergreen and deciduous species may diverge in leaf structural traits but may converge in other traits. Westoby and wright (2006) and de Souza (2020) have also reported a similar convergence in leaf traits of species with contrasting leaf habits. The observed convergence in the species traits other than structural traits suggests the role of environmental filtering (Yao et al. 2020), which may favour the taxa that are functionally more similar (Webb 2002), signifying the co-occurrence of evergreen and deciduous leaf habits. Several studies have addressed the advantages of having a longer or shorter leaf life span (Aerts 1995; Chabot and Hicks 1982; Kikuzawa 1991) in co-occurring deciduous and evergreen species. Nonetheless, the functional differences between deciduous and evergreen leaf habits are usually associated with establishing balance between the costs and benefits of leaf construction (Wright et al. 2004; Chabot and Hicks 1982) and growth strategies (Tomlinson et al. 2014). Therefore, despite some differences in the key functional traits, our data (L−) suggests that both deciduous and evergreen functional types are successful strategies in the present study that may only vary significantly in the rate of resource acquisition and patterns of investments into different tissues.
The leaf trait-pair relationship using the pooled data of L+ and L− categories in the present study followed the universal trend with SLA and Nmass correlated positively with each other while negatively correlated with Lth. The Nmass did not correlate with chlα, chlβ, chlτ in the present study, although leaf chlorophyll distribution, in general, is highly correlated with the leaf nitrogen (Daughtry et al. 2000; Yoder and Pettigrew-Crosby 1995) because nitrogen forms one of the major components of the chlorophyll pigments (Filella et al. 1995). Our observation indicates that at higher N-levels, leaf chlorophyll content may not have a linear relationship with Leaf nitrogen concentration (Wood 1993).

Acclimation to liana-mediated shade in evergreen and deciduous species

The present study revealed that the acclimation to liana colonization varied between the evergreen and deciduous species concerning few key functional traits, influencing the photosynthetic potential. Among the evergreen species, the L+ and L− categories showed a significant difference in SLA, LMA, Nmass, and chlorophyll components. The higher SLA and Nmass coupled with lower LMA in the L+ category reflect the shade-tolerant characteristics of the evergreen species that help in maximizing the carbon gain with minimum expenditure. Therefore, the shaded leaves of evergreen species are more efficient under low light conditions with higher SLA coupled with the specialized anatomy of single-layered palisade parenchyma that results in the formation of thin leaves (Lombardini et al. 2009; Givinish 1988). SLA correlates highly with mass-based photosynthesis and respiration rates (Wright et al. 2004). However, Song et al (2020) found a significant correlation between LMA and maximum carboxylation rate (Vmax) for leaves grown under shade. In addition, leaves with higher LMA are physically more robust and less prone to herbivory (Sterck et al. 2006). The present study also reported relatively thinner leaves in the L+ category which, further signifies the importance of conserving carbon in low-light environments. However, the L− leaves with comparatively thicker leaves are associated with well-developed mesophyll tissues, possibly to avoid photo-inhibitory damage as they get exposed to higher light intensities (Taiz and Zeiger 2006). Studies with woody species showed thicker mesophyll tissues with reduced intercellular spaces in plants grown in bright sunlight, compared to plants grown in shade (Nakazono et al. 2001; Piel et al. 2002). The increased Lth at higher irradiance can also enhance the photosynthetic efficiency (Atanasova et al. 2003). PL and LA, both associated with the enhanced light acquisition strategies, did not show any significant variation between L+ and L− categories of evergreen species, which strongly reflects their conservative response in petiole elongation and leaf area expansion.

The leaf chlorophyll is one of the key parameters directly linked to photosynthetic potential and may provide valuable information on the physiological status (Riccardi et al. 2014; Croft et al. 2017). The relatively higher chlorophyll content (a, b, and total chlorophyll) in the L+ leaves is possibly due to a greater level of photooxidation under very high light intensities than at the shaded environments (Kramer and Kozloeski 1979). Ntawuhiganayo et al (2020) also reported the higher chlorophyll content in shade-tolerant species and their ability to increase it further upon shading. According to Dusenge et al (2015), the higher chlorophyll content per unit leaf area in shade-tolerant species did not reflect the quantum yield efficiency. Therefore, the higher chlorophyll content in the L+ evergreen leaves does not necessarily involve enhanced leaf carbon gain. The significantly higher Chlorophyll b in the L+ leaves can be because of the strategy to absorb light in the blue spectrum, which is prevalent in the shaded environments. Therefore, leaves acclimated to the low-light environments tend to have a lesser chlorophyll a/b ratio (Lichtenthaler et al. 2007). The size of the PSII antenna in shaded environments could also be attributed to the lower level of chlorophyll a/b ratio in the L+ leaves of evergreen species (Anderson et al. 1995; Tanaka and Tanaka 2000). Sun leaves have higher chlorophyll a/b ratio than shade leaves, indicating a lower number of light-
harvesting chlorophyll a + b-binding antenna complexes (Anderson et al. 1995). However, few studies have reported the opposite trend (e.g., Zivcak et al. 2014; Falbel et al. 1996), indicating its impact at the species level rather than at the community level.

In contrast to the evergreen species, the deciduous species did not show any plastic variations in the structural traits. However, the PL in deciduous L⁺ categories were close to two-fold-higher than L⁻ leaves. Petiole length plays a dual role by enhancing the leaf light-harvesting efficiencies and influencing the leaf angle (Weijschede et al. 2006). The PL elongation in the L⁺ category should have been beneficial if it leads to enhanced resource acquisition, as petiole length elongation can improve resource acquisition by avoiding the shade (Weijschede et al. 2006). However, in the present study, the petioles of L⁺ category did not reach the better-lit areas, leading to decreased light-harvesting efficiencies despite investing more in the non-photosynthetic throwaway biomass. Therefore, the plastic responses in the petiole length to liana proliferation can be increasingly expensive in biomass investments. In contrast to our observations, Niinemets et al (2004) showed that PL was higher in the exposed areas than in the shaded regions of a dense poplar plantations. Therefore, the other unstudied whole-plant architectural parameters might also play a role in the petiole elongation. L⁺ deciduous species also had a relatively higher leaf area than the L⁻ categories. These plastic responses in PL and LA confirm the shade-intolerant characteristics of deciduous species studied. Shade avoidance responses are induced by the lower amount of photosynthetically active radiation (decreased red: far-red ratio) of the incident light (Schmitt and Wulff 1993; Schmitt et al. 2003). Although the ontogenic changes in PL and LA are known to reduce the negative fitness against shading (Yamada et al. 2000; Takenaka 1994), it was associated only with the resource expenditure in the present study.

Overall, the evergreen species showed plastic variations in the functional traits between L⁺ and L⁻ categories under varying light environments. Such variation in the leaf traits can enhance leaf photosynthesis at a specific irradiance level (Givinish 1988). The deciduous species, however, exhibited a conservative response across the structural and physiological traits. The allocation strategy of evergreen species can be considered successful in the present study concerning the carbon gain under low-light conditions. Ntawuhiganayo et al (2020) found only a minimal decline in growth of the shade-tolerant species under low-light conditions than the shade-intolerant species. Thus, evergreen species showed better acclimation to the liana colonization than the deciduous species' in terms of plastic responses in major traits and better energy allocation between photosynthetic and non-photosynthetic tissue to enhance carbon gain without compromising the structural stability of their leaves. However, deciduous species may have a competitive advantage in L⁻ categories with the legacies of efficient photosynthetic machinery than the evergreen species, given that water is not a constraint factor in the study site.

Liana infestation on host trees' crown may decrease the ratio of the sun: shade leaves and the net amount of leaf area exposed to diffuse and direct sunlight, thus reducing the carbon gain per unit leaf area. Although liana colonization, in general, is considered harmful for the host trees, it may be more detrimental for fast-growing/shade-intolerant species. On the other hand, lianas may be beneficial for some of the shade-tolerant species, allowing them to grow in the shade and protect them from photoinhibition because shade-tolerant species may also be sun-intolerant (Ntawuhiganayo et al. 2020). Nevertheless, this impact of lianas on the leaf functional traits of host trees can have a significant impact on the whole forest carbon assimilation rates, particularly in the tropics where they are abundant.

**Conclusion**
The differences in leaf functional traits between evergreen and deciduous species in the present study supported the well-established trade-off between maximization of C-assimilation and foliar longevity. Interestingly, the leaf habit explained a large proportion of variation in some of the key leaf structural traits studied. Nevertheless, there was a convergence in other leaf functional traits between deciduous and evergreen species, emphasizing their patterns of co-existence. This study also revealed the differential impact of liana infestation on leaf functional traits of the two contrasting leaf habits. In the exposed environment (L⁻), deciduous species can have a competitive advantage in photosynthetic efficiency and relative growth rate, given that water is not a constraint in the study site, thanks to their acquisitive strategies. However, evergreen species with shade-tolerant properties seemingly better adapted to the varying light environment, particularly by optimizing their key structural traits that enhance maximum productivity under the low-light environment (L⁺). Therefore, liana colonization can have a significant impact on the overall photosynthetic efficiencies of the host trees, particularly, it may be detrimental to fast-growing trees with shade-intolerant and acquisitive strategies. Liana infestations are seemingly increasing in tropical forests worldwide, leading to a significant impact on the whole forest carbon assimilation rates. We recommend the need for long-term observational studies to understand the dynamics in canopy occupancy by lianas and its impact on the host trees' productivity.

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**Competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Availability of data and material**

All data generated or analysed during this research work are included in this manuscript

**Code availability**

Not applicable

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Figures
Figure 1

Map showing geographical location of the study area.
Figure 2

Standardized major axis (SMA) regression for trait-pair relationship between different trait-pairs using pooled data of L+ and L- categories (evergreen and deciduous species). Data points are species means with $n = 30$ per species.