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Effects of host size and substrate types on the distribution of accidental and obligate epiphytes in a temperate forest of Japan

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Abstract

In a forest, the distribution of vascular epiphytes depends on host tree size and substrate type. However, previous studies have mainly focused on tropical forests, despite the growing interest in temperate forests with a high diversity of epiphytes and the frequent occurrence of accidental epiphytism in terrestrial species. This study examined the distribution of accidental and obligate epiphytes on 8 *Cercidiphyllum japonicum* (Cercidiphyllaceae) trees in a Japanese temperate forest based on the observation of 1,301 epiphyte individuals belonging to 49 species. The hypothesis that the number of total epiphyte species and individuals increased significantly and exponentially with increasing tree size were supported. As predicted, the proportion of accidental epiphyte species would increase with tree size but that of obligate epiphytes would decrease. In agreement with our hypothesis, the major rooting substrate types of accidental and obligate epiphyte assemblages were different. Accidental epiphytes depended mainly on arboreal soil and, to a lesser extent, on moss; however, they were absent on the bark. By contrast, obligate epiphytes were most frequently found on moss, followed by bark and arboreal soil. These results highlight the greater impact of host tree size on the diversity of accidental epiphytes compared to obligate epiphytes, suggesting that there are differential effects of host tree size on accidental and obligate epiphytes in temperate forests. Additionally, the thick accumulation of organic matter is crucial for the establishment and growth of accidental epiphytes.

Introduction

Epiphytism, where plants grow on other plants without parasitizing them, has evolved in various phylogenetically independent vascular plant taxa. Approximately 10% of all vascular plant species worldwide are epiphytic (Zotz et al. 2021). Vascular epiphytes generally colonize trees, and on the “host trees,” they provide various arboreal organisms with essential habitats and food sources (Díaz et al. 2012; Nadkarni and Matelson 1989; Scheffers et al. 2014). Moreover, they are important nutrient- and water-cycling components in arboreal ecosystems (Hargis et al. 2019; Nadkarni et al. 2004).

Given the contribution of epiphytes to biodiversity and material cycling in arboreal ecosystems, understanding the habitats of each epiphytic species is important. First, on an individual host tree scale, the size of the host tree is a major factor that affects the entire epiphyte assemblage on the tree. Specifically, the number of epiphyte species and individuals on a tree is often higher on larger trees than on small trees (Taylor and Burns 2015; Flores-Palacios and García-Franco 2006; Hattori et al. 2009; Komada et al. 2022; Wagner and Zotz 2020; Woods et al. 2015), resulting in a significant difference in the species composition of epiphyte assemblages (Wagner and Zotz 2020; Woods et al. 2015). This phenomenon has been attributed to the large surface area of the habitats on large trees (Taylor and Burns 2015; Wagner and Zotz 2020; Woods et al. 2015) and the protracted availability of the habitats (Flores-Palacios and García-Franco 2006). In addition, large trees generally have highly complex tree architecture and habitats with considerable environmental variation, enabling many epiphyte species with different microhabitat preferences to co-occur (Woods et al. 2015; Woods et al. 2019).

Second, in a single host tree crown, the distribution of each epiphyte species is influenced by various micro-environmental factors. One is the nature of the substrate around the epiphyte rooting point. Arboreal soil (sometimes referred to as canopy soil, canopy humus, and suspended soils), moss, and bark are known to influence epiphyte establishment and growth (Hoeber and Zotz 2022; Ishii et al. 2018; Woods et al. 2019). For instance, Harrison et al. (2003) found that epiphytic seedlings of *Ficus* spp. (Moraceae) in a Bornean lowland forest required microhabitats with arboreal soil deposition for their establishment. In Costa Rican tropical forests, Woods et al. (2015) found that the presence of certain epiphytic species is determined by the presence of arboreal soil or bark. Johansson (1974) summarizes the substrate types, including arboreal soil, moss, and bark, in which each epiphyte species grows. This pattern is considered to be related to the differences in the capacity of such microhabitats to retain water and nutrients (Hoeber et al. 2019; Hoeber et al. 2020; Hoeber and Zotz 2022; Ishii et al. 2018; Sillett 1999), and the water content has been shown to be higher in thick substrates than in thin substrates (Sillett and Pelt 2007; Tatsumi et al. 2021).

On a global scale, the number of studies clarifying the within-forest distribution of epiphytes is strongly biased toward tropical regions. Although some temperate forests harbor rich epiphyte floras, and the diversity of epiphytes in the forests is comparable to that of the tropics (Zotz 2005), few studies have targeted temperate forest epiphytes. Temperate forests are characterized by a high diversity of accidental epiphytes, which are plant species that generally grow on the ground and do not necessarily occur in arboreal habitats (Azuma et al. 2022; Hoeber et al. 2019; Ishii et al. 2018). In addition, accidental epiphytes may account for more than 90% of the total number of epiphyte species in temperate forests (Hoeber and Zotz 2022). In contrast, the epiphytic flora of tropical forests is generally composed of obligate epiphytes, which almost always occur on trees (Hoeber and Zotz 2022; Nieder et al. 2000). While numerous obligate epiphyte species manage to establish themselves on bare bark by acquiring drought-resistant traits such as Crassulacean acid metabolism (CAM) photosynthesis (Zotz 2016), the establishment of accidental epiphytes is restricted to specific microhabitats rich in organic matter, such as arboreal soil or moss (Hoeber et al. 2019; Hoeber et al. 2020; Hoeber and Zotz 2022; Ishii et al. 2018; Sillett 1999). Although the precise distribution of accidental and obligate epiphytes within temperate forests remains poorly understood, their distributions likely different from one another. This distinction arises from the greater prevalence of microhabitats with arboreal soil or moss on large, old trees compared to smaller, younger trees (Hoeber and Zotz 2022; Ishii et al. 2018; Woods et al. 2019). Additionally, the number of obligate epiphyte species in a forest is lower than that of co-occurring terrestrial species (Taylor et al. 2022). Consequently, if accidental epiphytism frequently occurs among numerous terrestrial species within a forest, the proportion of accidental epiphyte species and individuals would likely increase with increasing tree size. However, the proportion of obligate epiphytes would decrease as a result of the different species-pool-sizes of accidental and obligate epiphytes.

Among temperate forest areas, those in Japan harbor relatively rich epiphytic flora(Hattori et al. 2009; Zotz 2005). In an old-growth forest in western Japan, approximately 5% of vascular plant species is occurring as obligate epiphytes (Sakaguchi et al. 2008). In addition, a single large individual of *Cercidiphyllum japonicum* Siebold, and Zucc. (Cercidiphyllaceae) in this forest has been shown to host

39 plant species, including 32 accidental and 7 obligate epiphyte species (Azuma et al. 2022). Therefore, this forest is a suitable site for the investigation of distribution patterns of accidental and obligate epiphytes in temperate regions.

Here, within the forest, based on the census of epiphytes on eight different-sized *Cercidiphyllum* trees, we aimed to investigate the effects of host tree size on the number of species, number of individuals, and species composition of epiphyte assemblages. In addition, we aimed to identify which microhabitats with three different substrate types (i.e., arboreal soil, moss, and bark) each accidental/obligate epiphyte species preferred in a temperate forest. To this end, on each host tree, we recorded the number of individuals of each epiphyte species and the substrate types of each epiphyte individual. We hypothesized that:

1. The number of epiphyte species and individuals would increase with increasing tree size.
2. The proportion of accidental epiphyte species and individuals would increase with increasing tree size, but those of obligate epiphytes would decrease.
3. The major establishing substrate type differs between accidental and obligate epiphyte assemblages, and the former are more strictly dependent on water and nutrient-rich arboreal soil or moss than obligate epiphytes.

Material and methods

Study site and targeted host trees

All field surveys were conducted in the Ashiu Research Forest of Kyoto University (35°18'N, 135°43'E; 355–959 m a.s.l.) in northeastern Kyoto Prefecture, Japan. The area is part of Kyoto Tamba Kogen Quasi-National Park, and more than half of the vegetation is old-growth forest. The forest is located in the transition zone between cool-temperate and warm-temperate, with snowfall ranging from 1–3 m and mean monthly temperatures ranging from − 0.4 ºC in January to 24.0 ºC in August. The mean annual precipitation was 2280 mm at a forest weather station at 640 m a.s.l. from 2000–2015.

We targeted eight Cercidiphyllum japonicum trees in a riverine forest at the study site because large individuals of the species in the Ashiu Research Forest have been confirmed to host many epiphyte individuals. This tree is one of the most common species in the riparian forests at the study site, where it generally occurs sympatrically with *Aesculus turbinata* Blume (Sapindaceae) and *Pterocarya rhoifolia* Siebold and Zucc. (Juglandaceae) (Yamanaka et al. 1993). We measured the size of each tree, that is, girth at breast height (GBH) and tree height, using a measuring tape and a razor rangefinder (TruPulse 360; Lasor Technology, Inc.). The eight trees differed in their GBH and tree height, and the data are summarized in Table 1. The physiognomy of the host tree architecture is shown in Fig. S1. The largest individual tree is the same as that targeted in Azuma et al. (2022) and Tatsumi et al. (2021).

Field survey

We conducted a field census of epiphytes from 2018–2021 (early summer to autumn) using single- and double-rope climbing techniques with the aid of binoculars. First, on each targeted tree, we checked almost all epiphyte individuals and recorded their species names, the position of each epiphyte individual on the tree, and the proximal aboveground height at which each epiphyte individual occurred. Rhizomatous epiphytes were difficult to distinguish from one another. Therefore, to count the approximate number of individuals for these species, we regarded a patch that were clearly separated from another individual as one plant. Second, from 2020–2021, we recorded the substrate types around the rooting points of epiphyte individuals. Based on preliminary observations, we classified the epiphyte substrates into three types: arboreal soil, moss, and bark. The arboreal soil was defined as a substrate with accumulated organic matter of ≥ 2 cm depth, regardless of the presence of bryophyte and lichen; moss was the substrate with bryophyte and/or lichen cover of < 2 cm depth, often accompanied by the frequent accumulation of organic matter beneath it; and bark was the substrate without any arboreal soil, moss, or lichen cover. Figure 1 summarizes the physiognomy of substrate types. Epiphytes whose roots were confirmed to reach the ground were unclassified and excluded from the analysis. For subsequent taxonomic identification, voucher specimens were created for all epiphyte species.

Classification of epiphyte species

Taxonomic classification of the recorded epiphytes was performed based on our previous work (Azuma et al. 2022) and examination of herbarium specimens stored at the Ashiu Research Forest of Kyoto University. Each epiphyte species was classified according to its epiphyte type, i.e., obligate or accidental, based on reliable literature. We defined obligate epiphytes as species that occur almost always on trees and do not generally grow on ground soil, and accidental epiphytes as species that generally grow terrestrially on ground soil. Root-climbing liana species (e.g., *Hydrangea* spp.) were also censused, as were epiphyte individuals, but were excluded from the analyses. However, some individuals of these species germinate and grow on trees without contact with the ground soil (authors, pers. obs.) It is often difficult to distinguish epiphytic individuals from those connected to ground soil by their roots and/or stems. Seedlings of epiphytic individuals with stem lengths less than 5 cm and without adult leaf stages were not recorded to avoid misidentification due to their scant morphological characteristics.

Statistical analysis

All analyses were performed using the R software version 4.0.5 (R Core Team 2021), with a significance of < 5 %. To analyze te effects of tree size on epiphyte assemblages, we used GBH as an indicator of tree size. Then, to analyze the relationship between the number of epiphyte species or individuals on a tree and tree size, we used generalized linear models (GLMs) with a Poisson distribution and a log-link function, and a quasi-Poisson distribution and a log-link function. The number of species or individuals of all epiphytes on each target tree was the response variable, and GBH was the explanatory variable. We then calculated the McFadden pseudo-R^2 (McFadden 1974) to measure the goodness of fit. Linear models (LMs) were used to examine the changes in the composition of obligate and accidental epiphytes along the GBH. The response variable was the percentage of obligate or accidental epiphyte species out of the total number of epiphyte species on a tree, and GBH was the explanatory variable. We calculated

the Shannon–Wiener diversity index (H') (Shannon 1948) for each host tree to compare species richness based on evenness. Regarding the analyses of substrate types, epiphyte individuals whose establishing substrates were unclassified were excluded from the calculation. Differences in the proportion of epiphytes distributed among the established substrate types were identified using Kruskal–Wallis test, followed by Steel–Dwass multiple comparison tests. Due to the small sample size, the Kruskal–Wallis and Steel-Dwass test calculations were performed based on Monte Carlo resampling procedures. Proportional changes in substrate types relative to GBH were analyzed using GLMs, with the proportion of arboreal soil, moss, or bark as a response variable and GBH as an explanatory variable.

Results

Overall epiphyte assemblages on Cercidiphyllum trees

A total of 1,301 epiphytes belonging to 49 species were found in 7 of 8 *Cercidiphyllum* trees (Table 2). The Polypodiaceae and Rosaceae were the most species-rich families, with five epiphyte species. Of the total epiphyte species, 38 (77.6%) were accidental, and 11 (22.4%) were obligate (Table 2). In terms of abundance, accidental epiphytes comprised 17.5% of the total number of individuals, and obligate epiphytes accounted for approximately 82.5%.

The most abundant species was *Crepidomanes minutum* (Blume) K. Iwats. (Hymenophyllaceae), with 609 individuals, accounting for 47.2% of the total number of recorded epiphytes (Table 2). The most abundant species were *Polypodium fauriei* Christ (Polypodiaceae, 198 ind., 15.3%), *Davallia mariesii* T. Moore ex Baker (Davalliaceae, 112 ind., 8.7%), *Oxalis nipponica* S. Aoki et J. Murata ssp. *nipponica* (Oxalidaceae, 85 ind., 6.53%), and *Lepisorus annuifrons* (Makino) Ching (Polypodiaceae, 51 ind., 3.9%). Of these abundant species, only *O. nipponica* is an accidental epiphyte. In contrast, rare species with only one or two individuals were predominantly accidental (95.5%). The variations in epiphyte species composition among host tree individuals are summarized in Fig. 2. Among the epiphyte species with a recorded number of individuals, five or more occurred in more than two host trees (Table 2, Fig. 2). In particular, *P. fauriei* and *O. nipponica* subsp. *nipponica* were found on seven and six host trees, respectively (Table 2, Fig. 2). However, 35 epiphyte species (71.4% of the total number of species) occurred only on the largest individual tree (Table 2 and Fig. 2).

Effects of host tree size on the distribution of epiphyte assemblages

The number of epiphyte species on a tree significantly and exponentially increased with greater GBH (pseudo $R^2 = 0.92$, $P < 0.001$; Fig. 3a). The same trend was also observed for the number of epiphytes per tree (pseudo $R^2 = 0.95$, $P < 0.001$, Fig. 3b).

Regarding the proportional changes in species richness and the abundance of accidental and obligate epiphytes with GBH, there was, in part, a significant correlation. For species richness, the proportion of

accidental epiphytes significantly increased as GBH increased (R^2 = 0.50, P < 0.05) and that of obligate epiphytes decreased (R^2 = 0.50, P < 0.05) (Fig. 4a). Regarding abundance, proportional changes were not significantly correlated with GBH, both in terms of accidental and obligate epiphytes (R^2 = -0.1, P = 0.60) (Fig. 4b).

Relationship between epiphyte type and substrate type

We found that the epiphytes occurred on a variety of substrates (Figs. 5 and 6). Among all epiphyte individuals investigated, the substrate most commonly used by epiphytes was moss (1,046 ind., 80.4% of the total), followed by arboreal soil (176 ind., 13.5%) and bark (74 ind., 5.7%) (Fig. 5). At the species level, 38 species were found to establish on arboreal soil, which was c. 78% of the total number of epiphyte species recorded in this study. Moss was colonized by 22 species (approximately 45%), and 3 species were found on the bark, accounting for 6%.

The abundances of both accidental and obligate epiphyte assemblages were markedly different among the substrate types (Kruskal–Wallis test, P < 0.001; Fig. 5). Steel–Dwass multiple comparisons revealed a significant difference in the abundance of accidental epiphyte assemblages among the three substrate types (Fig. 5), which were primarily dependent on arboreal soil (58.7% of the total number of accidental epiphytes), followed by moss (41.3%), and absent on bark. The abundance of obligate epiphytes was the highest in the moss substrate, and 88% of the total number of obligate epiphytes was found there (Fig. 5). The number of individuals on moss was significantly different from that on the other two substrates, bark (established by 6.9% abundance) and arboreal soil (4.2%) (Fig. 5). At the epiphyte species level, the type of substrate on which each epiphyte species mainly occurred varied depending on the species (Fig. 6). Although epiphyte species predominantly established in the arboreal soil or moss were abundant, no species were established mainly on the bark (Fig. 6).

Discussion

Overall epiphyte assemblages on Cercidiphyllum trees

Our results, namely, the epiphyte species composition and the fact that nearly 80% of the species were accidental epiphytes, were similar to those presented in our previous work, which investigated a large *Cercidiphyllum* tree in this forest (Azuma et al. 2022). A higher percentage of accidental epiphytes than obligate epiphytes among the total epiphyte diversity in a forest has been reported from some temperate forests in North America and Western and Central Europe; however, this trend is uncommon in tropical regions(Hoeber and Zotz 2022). Although the mechanisms underlying the high diversity of accidental epiphytes in temperate forests remain to be elucidated, they may be related to climatic factors such as temperature, precipitation, or competition between accidental and obligate epiphytes. Nadkarni and Solano (2002) suggested that terrestrial species germinate after obligate epiphytes die, suggesting potential competition between them.

The dominance of certain epiphytic species, such as *C. minutum*, *P. fauriei*, *D. mariesii*, *O. nipponica* ssp. *nipponica*, and *Lepisorus annuifrons* can be attributed to the specific ecological characteristics that enable them to thrive in arboreal habitats. *Crepidomanes minutum* and *P. fauriei* have poikilohydric leaves that are drought resistant, which allows these species to withstand periods of water scarcity (Cea et al., 2014; Zotz, 2016). Additionally, *P. fauriei*, *D. mariesii*, *O. nipponica* ssp. *nipponica*, and *L. annuifrons* possess fleshy rhizomes that may contribute to water storage. *Davallia mariesii*, in particular, has high water-use efficiency (Azuma et al., 2022). Moreover, all five species reproduce clonally through their rhizomes. This strategy allows them to expand their populations and occupy larger areas within arboreal habitats. Seven out of eleven obligate epiphyte species were belonging to Orchidaceae or Polypodiaceae, it can be attributed to the possession of CAM photosynthesis that enhances their drought tolerance, which is advantageous for arboreal environments (Zotz 2016) of these two families. *Oxalis nipponica* ssp. *nipponica*, has been regarded as a terrestrial species. Oxalidaceae has not been recorded as major epiphyte taxa (Komada et al. 2022; Zotz et al. 2021). In addition, only a few studies have observed epiphytism in Oxalidaceae (Komada et al. 2020; Nadkarni 1984); therefore, high frequency of epiphytic occurrence of the species in the present study is intriguing. Although the ecological mechanisms enabling terrestrial species to grow abundantly on trees are not fully understood, the above-mentioned characteristics may help to elucidate the frequent epiphytic occurrence of this species and clarify the evolutionary pathway of epiphytism of terrestrial lineages.

Effects of host tree size on epiphyte assemblage distribution

As hypothesized, species richness and abundance increased significantly with increasing tree size (Fig. 3), reflecting global trends (Taylor and Burns 2015; Flores-Palacios and García-Franco 2006; Hattori et al. 2009; Komada et al. 2022; Wagner and Zotz 2020; Woods et al. 2015). These positive correlations could be attributed to the large habitat area (Taylor and Burns 2015; Wagner and Zotz 2020; Woods et al. 2015), extended habitat availability (Flores-Palacios and García-Franco 2006), and more complex architecture (Hietz and Hietz-Seifert 1995; Woods et al. 2015) of large trees compared to small trees. In addition, because tree height increases with tree size, vertical changes in the habitat within a tree are expected to be greater for large trees than for small trees. For example, the water content of substrates (Tatsumi et al. 2021), temperature (Azuma et al. 2022), and light intensity (data not shown) change along a height gradient within a single tree. Thus, our results may be explained by the greater environmental variation in large trees than in small trees. In contrast, the smallest *Cercidiphyllum* trees selected in this study had no epiphytes, suggesting that they may not yet have reached a size that can provide adequate habitat, time, and environment for epiphytes.

In line with the second hypothesis, the proportion of accidental epiphyte species significantly increased as the trees got bigger, replacing the obligate epiphytes (Fig. 4a). This suggests that in this forest, accidental epiphytes are mainly responsible for the larger trees than obligate epiphytes, and the accidental epiphytism frequently occurs among numerous terrestrial species within this forest. Our hypothesis was not supported in terms of the positive relationships between the percentage of number of

individuals of accidental epiphytes and tree size (Fig. 4b), partly because of the high abundance of specific obligate epiphytes such as *C. minutum*, *P. fauriei*, *D. mariesii*, and *L. annuifrons* in large trees (Table 2, Fig. 2). However, the increase in the number of epiphyte individuals was significant even when only the data for accidental epiphytes were used in calculations, indicating that large *Cercidiphyllum* trees contributed to the high abundance of accidental epiphytes as well as obligate epiphytes. In addition, this suggests that each of the accidental and obligate epiphytes is differently affected by host tree size in the temperate forest; that is, the species richness of accidental epiphytes is influenced by tree size more strongly than that of obligate epiphytes, as the increment in the Shannon–Wiener diversity index (H') along with host tree size (Fig. S2) was more pronounced in the accidental epiphytes when the tree GBH was at its maximum (Fig. S2). Our results suggest that the larger *Cercidiphyllum* trees in this forest are the chief contributors to the maintenance of epiphyte diversity.

Epiphytes and substrate type

As predicted, the major substrate types for each epiphyte species differed between the accidental and obligate epiphyte assemblages (Figs. 5 & 6). Accidental epiphyte species had a stronger preference for thicker substrates, that is, arboreal soil, than obligate epiphytes, which again agreed with our hypothesis (Figs. 5 & 6). The greater abundance of epiphytes on substrates with accumulated organic matter, such as moss and arboreal soil, than on bark was similar to that reported in other studies (Hoeber et al. 2019; Hoeber and Zotz 2022; Ingram and Nadkarni 1993; Nakanishi et al. 2013; Ter Steege and Cornelissen 1989). The high epiphyte abundance on the accumulation of organic matter is related to the high capacity of these habitats to retain water and nutrients (Hoeber et al. 2019; Hoeber et al. 2020; Hoeber and Zotz 2022; Ishii et al. 2018; Sillett 1999). In addition, it has been found that moss-covered substrates promote the establishment of epiphytes by trapping their diaspores (Ingram and Nadkarni 1993; Mizuno et al. 2012) and that the water content is higher in thick than in thin substrates (Sillett and Pelt 2007; Tatsumi et al. 2021).

Studies that have attempted to clarify the differences in substrate types or depths favoring the establishment of accidental and obligate epiphytes are scarce. However, some scholars have demonstrated that accidental epiphytes are restricted to habitats where organic matter accumulates (Hoeber et al. 2019; Ishii et al. 2018), which is congruent with our results. In addition, we showed that accidental epiphytes were more dependent on arboreal soil than obligate epiphytes (Fig. 5). This can be attributed to the fact that the water content in thick substrates, i.e., arboreal soil, is higher than in moss-covered thin arboreal soil (Tatsumi et al. 2021). Moreover, the majority of conspecifics of accidental epiphytes grow in terrestrial habitats with a lower frequency and degree of drought stress than in the arboreal habitats that obligate epiphytes generally inhabit, and obligate epiphytes generally have drought-tolerant traits (as discussed above).

Furthermore, the nutrient levels in arboreal habitats can be similar to (Tatsumi et al. 2021) or even higher than those of the ground soil (Hoeber and Zotz 2021). Therefore, as Hoeber et al. (2020) suggested, if the water supply and rooting area are sufficient for growth, arboreal habitats with an accumulation of organic matter may not limit accidental epiphytism. Our results showed that the increase in diversity of accidental

epiphytes with host tree size was greater than the diversity increase in obligate epiphytes (Fig. S2). This might be partly explained by the different degrees of dependence on thickly accumulated organic matter discussed here because the number of habitats with thick organic matter deposition is greater on large and old trees than on small and young trees (Hoeber and Zotz 2022; Ishii et al. 2018; Woods et al. 2019). Additionally, we showed that some species were almost always established on arboreal soil or moss, but no species were established predominantly on bark (Fig. 6). In addition, although the number of epiphytes in the arboreal soil and moss significantly increased with tree size, the number of individuals on the bark was not significantly correlated with tree size (Fig. S3). Considering these results, in our study site, arboreal habitats without organic matter were harsh environments for both accidental and obligate epiphyte species, independent of host tree size.

Lianas on host trees may assist the establishment and growth of epiphytes. We found that the obligate epiphyte *P. fauriei* was mainly found on substrates with moss, but nearly 30% of the individuals were found on bare bark (Fig. 6). Furthermore, we found that of these bark-established individuals, 40% were rooted around areas where the bark surface was appressed by woody stems of *Hydrangea* spp. (Fig. 1d). Whether the presence of liana stems assists the establishment or growth of these individuals is unclear and requires clarification. However, it is plausible that once bare bark is covered by the stems of lianas, the habitat will improve, promoting the establishment and growth of certain epiphyte species. This notable phenomenon was also found at our study site in other epiphyte and host tree species (Authors, pers. obs.). Consequently, lianas may positively affect epiphytes' establishment and subsequent growth and can be considered an example of ecosystem engineering or habitat cascading effects. Figure S4 summarizes the vertical distribution of epiphytes and shows the occurrence of lianas.

Suggestions for future studies

Although we found a clear pattern in the effects of tree size and substrate type on the distribution of accidental and obligate epiphytes, the sample size in this study was small, and a more intensive census targeting a large number of host-tree individuals is needed for future studies. In addition, the host tree species affect epiphyte assemblages on a tree and their substrate type differently because different host species offer different environments, such as tree architecture, physicochemical traits on bark, and growth rate, and affect the epiphyte species composition (Adhikari et al. 2012; Mehltreter et al. 2005; Wagner and Zotz 2020; Wolf 1994; Woods et al. 2015; Valencia-Díaz et al. 2013). Thus, a forest stand-scale census of various sympatric host tree species is needed to detect further characteristic distributional patterns related to host tree size and substrate types of epiphyte assemblages in the temperate forests of Japan.

Cercidiphyllum japonicum is characterized by multiple reiterated trunks with basal resprouting (Kubo and Sakio 2020), resulting in many crotches or large horizontal areas on the basal part of the tree trunk with organic matters (Fig. S1d). Such habitats are known to be favorable for accidental epiphytes (Azuma et al. 2022; Hoeber et al. 2019; Ishii et al. 2018). Therefore, the occurrence of many accidental epiphytes in the lower parts of larger trees in this study (Fig. S4) may be attributed to the characteristic architecture of this tree species. In addition, we have observed that many individuals of accidental epiphyte species in

this study site flower and fruit for several years (Authors, unpublished). As suggested in Azuma et al. (2022), large-sized *C. japonicum* with characteristic multiple trunk reiterations can be important for future re-colonization of accidental epiphyte species on the ground because the regeneration of terrestrial species in this forest has been negatively affected by deer overbrowsing, (Fujii 2010) and long-term overbrowsing is known to decrease the number of viable seeds in the soil (Tamura 2016). Our findings contribute to a better understanding and assessment of the impact of large trees on the re-colonization of ground habitats by accidental epiphyte species, that are their original growth environments. We have demonstrated that many terrestrial species and individuals can grow epiphytically. Considering the potential of any terrestrial species to acclimatize an epiphytic lifestyle given the availability of suitable microhabitats and successful dispersal (Hoeber and Zotz 2022), a comparative analysis of ecological characteristics related to microhabitats and seed dispersal of accidental epiphytes, their terrestrial conspecifics, and obligate epiphytes will contribute to the understanding of the limiting factors and evolutionary trajectory of epiphytism.

Declarations

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Conflict of interest

None

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Tables

Tables 1-2 is available in the Supplementary Files section.

Figures

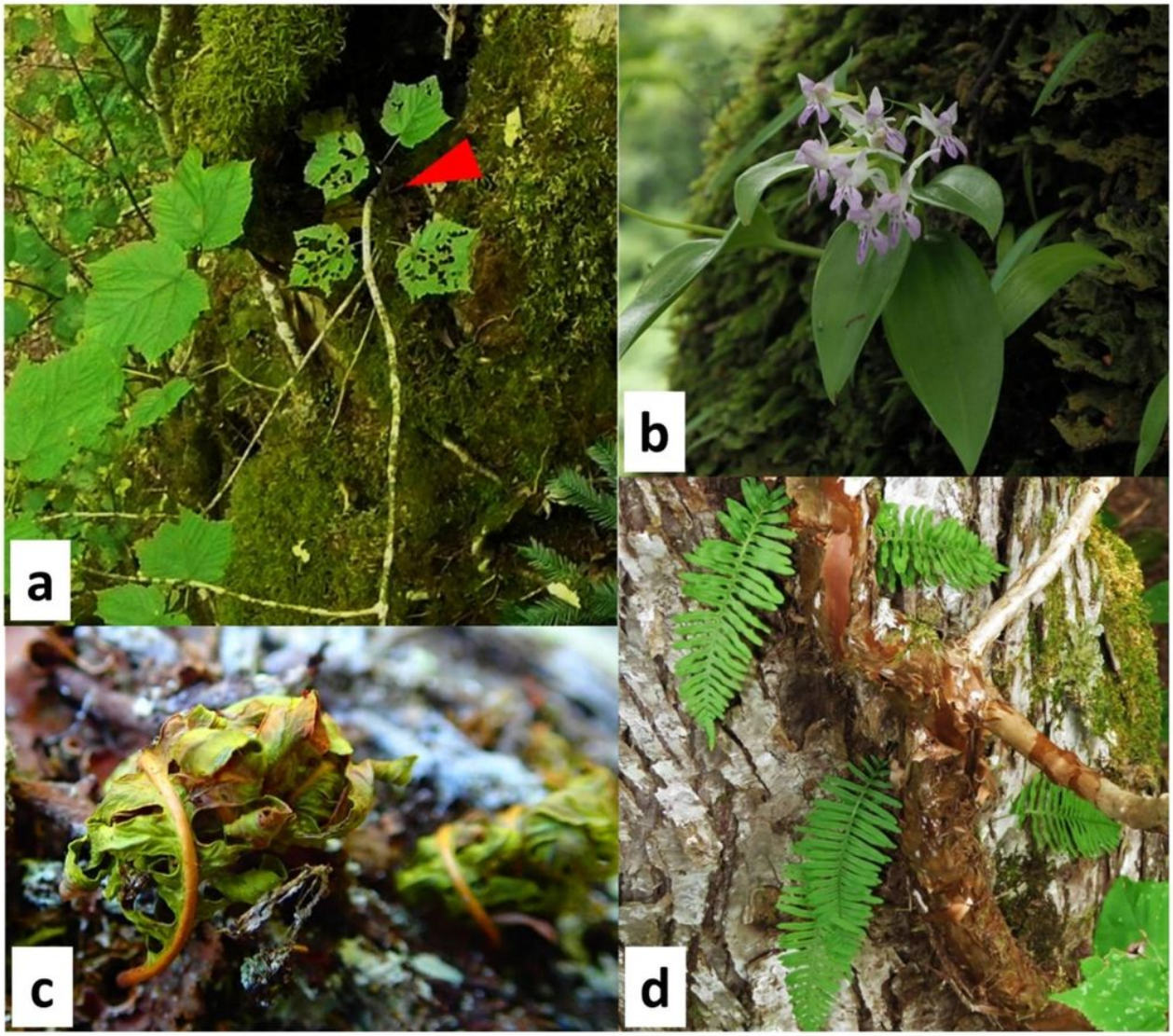


Fig. 1. Examples of habitats of epiphytes. A juvenile of *Acer rufinerve* Siebold et Zucc. rooting in arboreal soil accumulated in a hollow, red arrow indicates basal part of the stem (a), *Hemipilia chhidori* growing with bryophytes and lichens (b), and *Polypodium fauriei* growing on bark (c), and *P. fauriei* on bark aside of a stem of *Hydrangea petiolaris* (d).

Figure 1

See image above for figure legend.

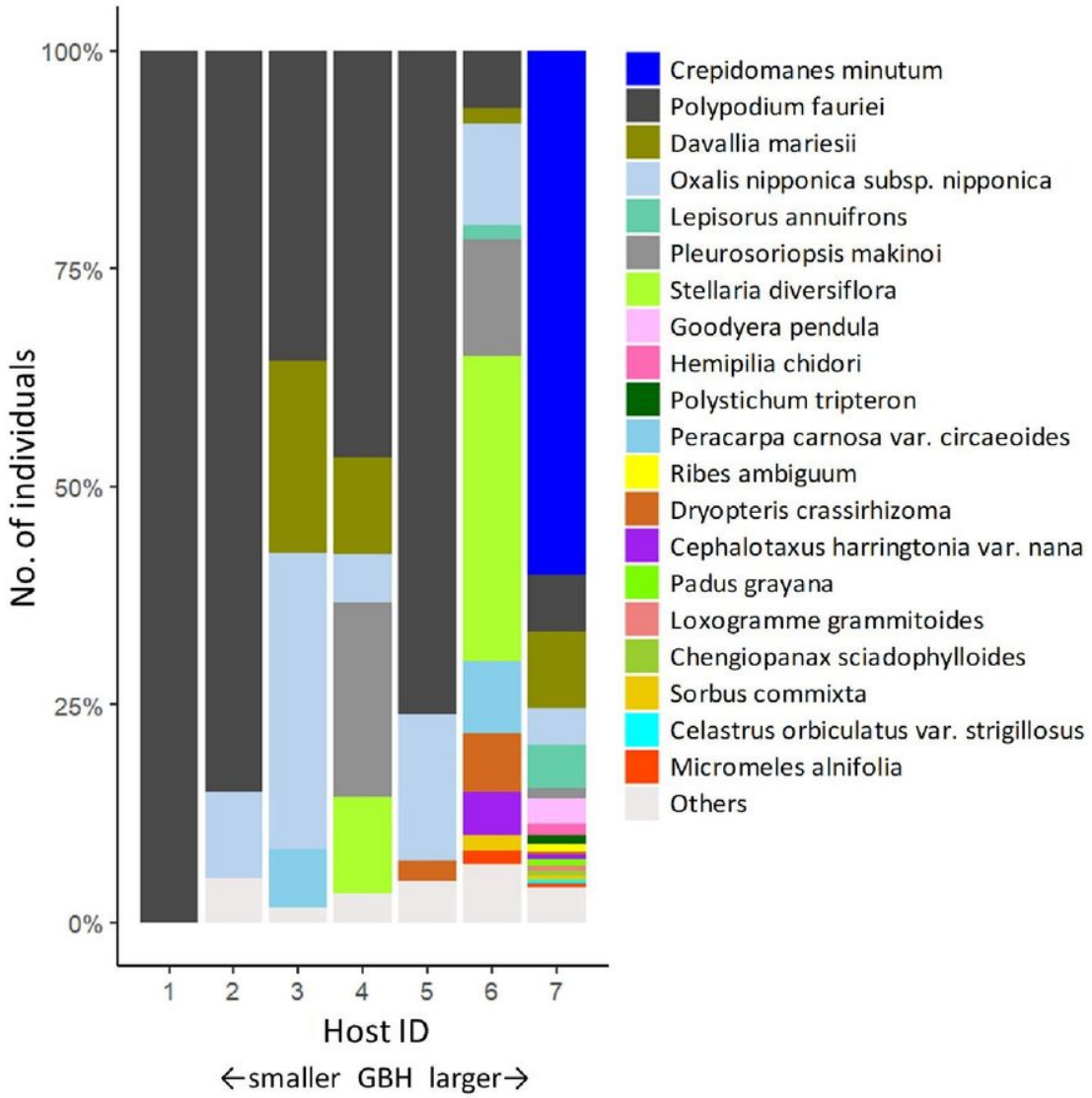


Fig. 2. Relative abundances (%) of each epiphyte species among host tree individuals. Epiphyte species whose number of individuals were less than five were lumped as others.

Figure 2

See image above for figure legend.

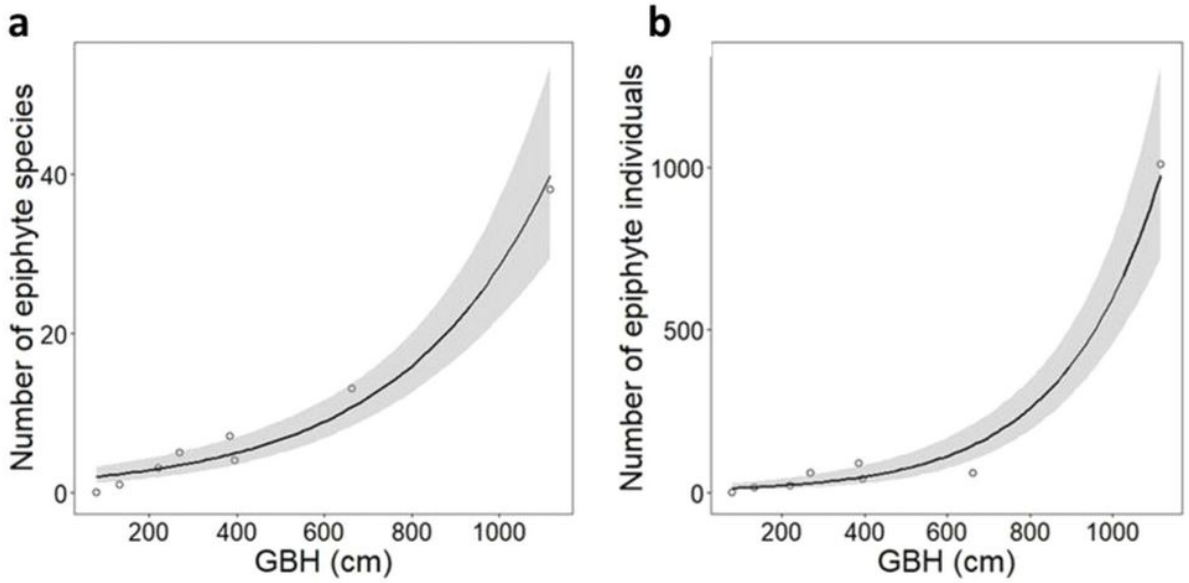


Fig. 3. (a) Relationships between GBH and epiphyte species richness on a tree. The regression line was obtained through a Poisson GLM (y = exp (0.447 + 0.003 x), pseudo R^2 = 0.92, P <0.001). The shaded band indicates the 95% confidence interval. (b) Relationships between GBH and epiphyte abundance on a tree. The regression line was obtained through a quasi-Poisson GLM (y = exp (2.205 + 0.004 x), pseudo R^2 = 0.95, P <0.001). The shaded band indicates the 95% confidence interval.

Figure 3

See image above for figure legend.

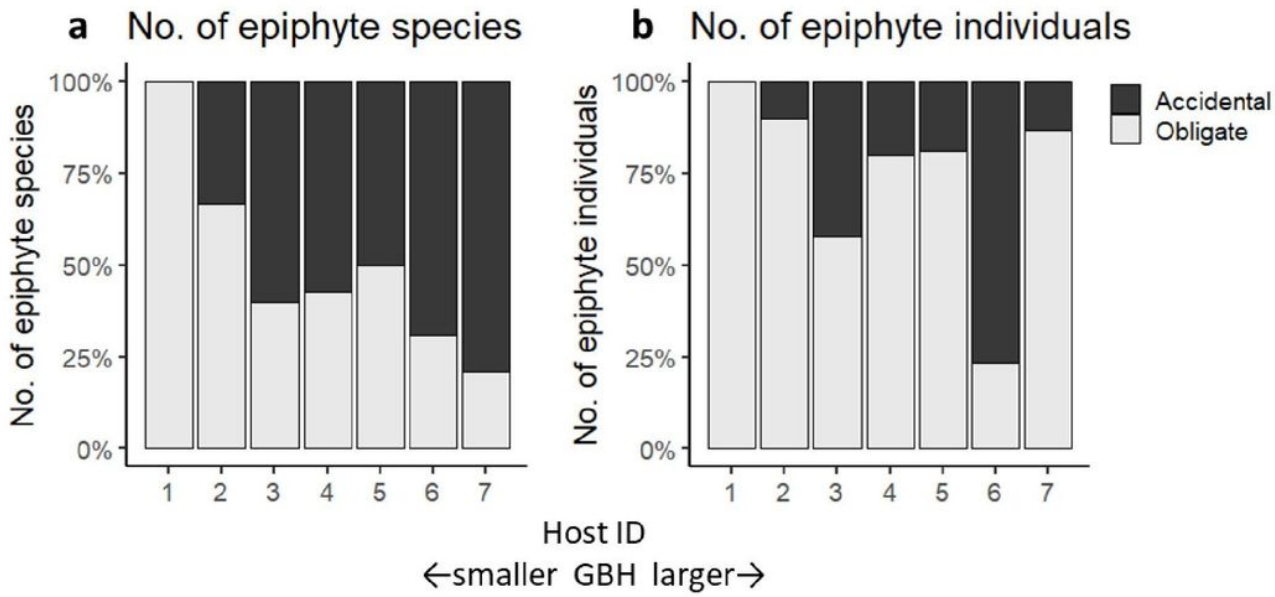


Fig. 4. Proportional changes of number of epiphyte species (a) or individuals (b) of obligate and accidental epiphytes along with host tree GBH.

Figure 4

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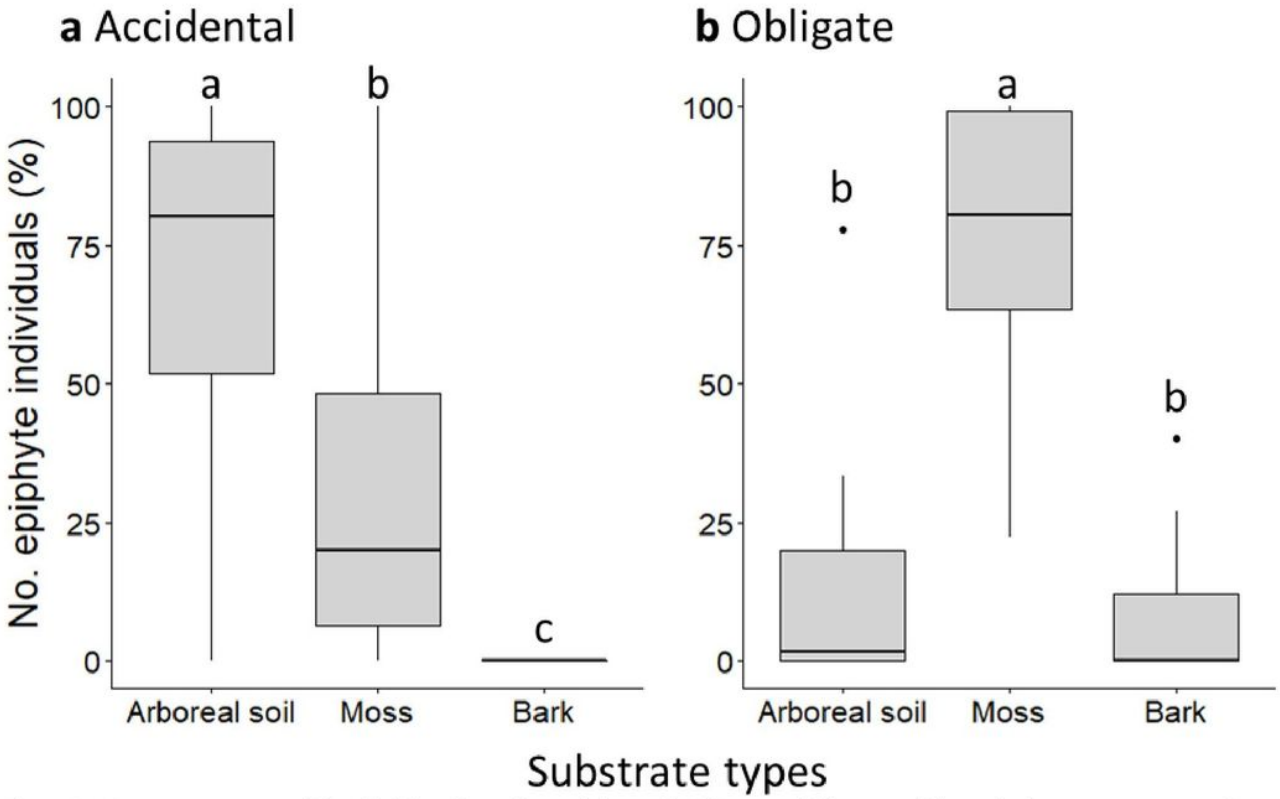


Fig. 5. Percentages of individuals of accidental (a) or obligate (b) epiphytes among three substrate types. Results of statistical analyses as follows. For accidental epiphytes, Kruskal-Wallis test ($P < 0.001$) and Steel-Dwass test ($P < 0.05$ in arboreal soil and moss, $P < 0.01$ in arboreal soil and bark, $P < 0.001$ in moss and bark). For obligate epiphytes, Kruskal-Wallis test ($P < 0.001$) and Steel-Dwass test ($P < 0.001$ in arboreal soil and moss, n.s. in arboreals soil and bark, $P < 0.001$ in moss and bark). Data on epiphyte individuals whose substrate types were unclassified were excluded.

Figure 5

See image above for figure legend.

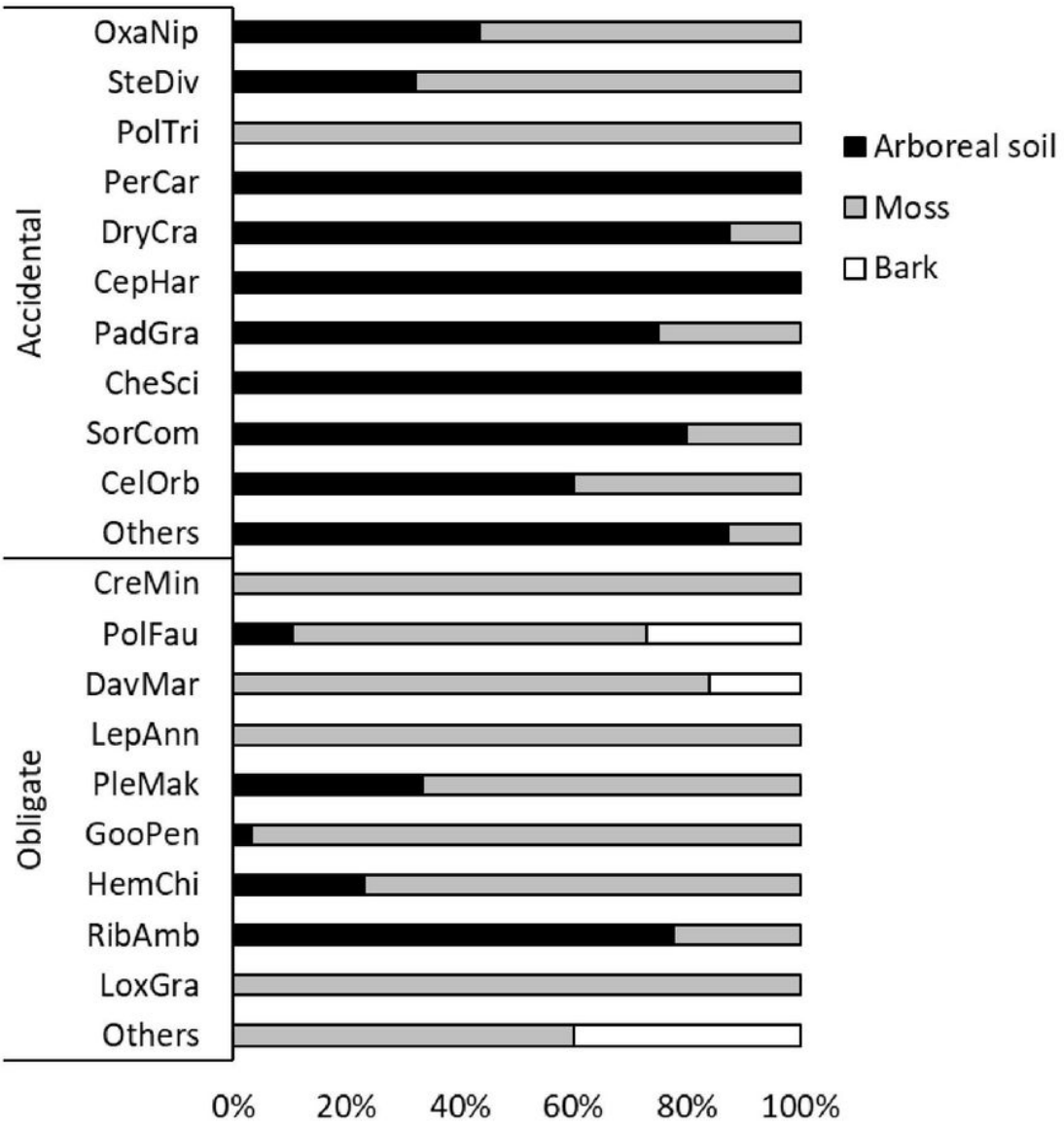


Fig. 6. Relative composition of substrate types of each epiphyte species. Epiphyte species whose number of individuals were less than five were lumped as others. The relationships of species codes in the figures and scientific names of epiphytes are same as those presented in Figure 2.

Figure 6

See image above for figure legend.

Supplementary Files

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- Komadaetal.TablesandFigures.pdf
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