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

Natsuki Komada[1,2] · **Wakana A. Azuma**[3] · **Yuya Ogawa**[3] · **Chikae Tatsumi**[4]

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Abstract

In forests, the distribution of vascular epiphytes is controlled by various environmental factors such as host tree size and substrate type. However, a few studies focused on temperate forests, despite the growing interest in temperate forests with high diversity of accidental epiphytes. This study examined the distribution of accidental and obligate epiphytes on 8 *Cercidiphyllum japonicum* (Cercidiphyllaceae) trees in a Japanese temperate forest based on observations of 1,301 epiphyte individuals belonging to 49 species. As predicted, the number of species and individuals of accidental and obligate epiphytes increased with host tree size. While the percentage of accidental epiphyte species increased with the host tree size, the percentage of obligate epiphyte species decreased; however, these changes were not significant for the number of individuals. Consistent with our hypothesis, the major rooting substrates of accidental and obligate epiphytes was different. Accidental epiphytes primarily depend on arboreal soil and, to a lesser extent, on moss, but are absent on tree bark. Contrastingly, obligate epiphytes were most frequently found on moss, followed by bark and arboreal soil. These results highlight the impact of host tree size on the diversity of accidental epiphytes compared to obligate epiphytes, suggesting that the host tree size effects are different between accidental and obligate epiphytes in temperate forests. Additionally, a thick accumulation of arboreal soil is crucial for the establishment of accidental epiphytes.

Keywords Arboreal soil · Canopy ecosystems · *Cercidiphyllum japonicum* tree · East Asia · Spatial distribution

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 epiphytes is important. First, on an individual host tree scale, the size of the host tree is a major factor that affects the 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 (Flores-Palacios

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✉ Natsuki Komada
caerulea2818@gmail.com

✉ Wakana A. Azuma
wakana@port.kobe-u.ac.jp

[1] Graduate School of Global Environmental Studies, Kyoto University, Yoshida Nihonmatsu-Cho, Sakyo, Kyoto 606-8501, Japan

[2] Graduate School of Advanced Science and Engineering, Hiroshima University, Kagamiyama, Higashihiroshima, Hiroshima 739-0046, Japan

[3] Graduate School of Agricultural Science, Kobe University, Rokkodaicho, Nada Ward, Kobe, Hyogo 657-0013, Japan

[4] Research Faculty of Agriculture, Hokkaido University, Jonishi, Kita Ward, Sapporo, Hokkaido 060-0809, Japan

and García-Franco 2006; Hattori et al. 2009; Komada et al. 2022a; Taylor and Burns 2015; 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, 2019).

Second, in a single host tree crown, the distribution of 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, 2020; Hoeber and Zotz 2022; Ishii et al. 2018; Sillett 1999) and the water content has been shown to be increased with the thickness of arboreal soil (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 plants that occasionally grow on trees as epiphytes but usually spend their entire lives as ground-rooted plants (Azuma et al. 2022; Hoeber et al. 2019; Ishii et al. 2018). Globally, the diversity of accidental epiphytes tends to be higher than that of obligate epiphytes in temperate forests, with the percentage of accidental epiphytes among the total number of epiphyte species in a forest sometimes exceeding 80% (Hoeber and Zotz 2022). In contrast, the epiphyte flora of tropical forests is generally composed of obligate epiphytes, which almost always occur on trees (Hoeber and Zotz 2022; Nieder et al. 2000), and their diversity and abundance decrease with increasing latitude (Zotz 2016; Taylor et al. 2022). While many 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, 2020; Hoeber and Zotz 2022; Ishii et al. 2018; Sillett 1999). Considering the difference of major substrates between accidental and obligate epiphytes, the distributions of their assemblage within a forest are likely to differ. Moreover, since microhabitats with arboreal soil or moss are more prevalent on large, old trees than on small, young ones (Hoeber and Zotz 2022; Ishii et al. 2018; Woods et al. 2019), the host size necessary for accidental epiphytes to establish is likely larger than that for obligate epiphytes. Furthermore, given the higher diversity of accidental epiphytes in temperate forests, large-sized trees are likely more colonized by accidental epiphyte species than by obligate ones. This may be reflected in the differing patterns of proportional changes in species and individuals along with host tree size between 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 species and individuals of accidental and obligate epiphytes would increase with increasing host tree size.
(2) The proportion of the number of species and individuals for accidental epiphytes on a tree would increase with increasing host 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 the latter.

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 to 3 m and mean monthly temperatures ranging from − 0.4 °C in January to 24.0 °C in August. The mean annual precipitation was 2280 mm at a forest weather station at 640 m a.s.l. from 2000 to 2015.

We targeted eight *Cercidiphyllum japonicum* trees in a riparian 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 common species in the forest 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 girth at breast height (GBH) of and height of each tree, using a measuring tape and a razor rangefinder (TruPulse 360; Lasor Technology, Inc.), and recorded the data (Table 1). The physiognomy of the host tree architecture was illustrated (Fig. S1). The largest tree is the same as that targeted in Azuma et al. (2022) and Tatsumi et al. (2021). We selected the other seven trees based on the feasibility of safe tree climbing and observation, and consideration of sampling a wide range of tree sizes. All eight trees were located in a forest along the same stream. Hemispherical photographs were taken at nine points from ground to the upper crown in the tree with largest GBH and analyzed using Gap Light Analyzer ver. 3.0 (Simon Frazer University, Burnaby, BC, Canada) to quantify vertical changes in the light environment as canopy openness.

Table 1 Individual ID and size of each *Cercidiphyllum* tree targeted in this study

Host ID	GBH (cm)	Height (m)
0	81	18.2
1	134	25.7
2	221	30.6
3	271	30.8
4	386	34.1
5	395	30.7
6	663	23.0
7	1116	37.8

Field survey

We conducted a field census of epiphytes from 2018 to 2021 (early summer to autumn) using single- and double-rope climbing techniques with the aid of binoculars. First, on each targeted tree, we checked all observed epiphyte individuals and recorded their species names. 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 to 2021, we recorded the substrate types around the rooting points of epiphyte individuals. Based on preliminary observations of arboreal organic matter and the our previous study (Tatsumi et al. 2021), we classified the epiphyte substrates into three depth categories: substrate ≥ 2 cm in depth was defined as arboreal soil (Fig. 1a), and was composed of accumulated organic matter; substrate < 2 cm in depth was defined as moss (Fig. 1b), and was deposited on the underside of mosses; and substrate without any organic matter or bryophyte and lichen cover was considered as bark (Fig. 1c–d). The substrate depths were measured by inserting a metal ruler into the substrate. Epiphytes with indeterminate rooting substrates were defined as unclassified and were 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., accidental or obligate, based on reliable literature (Ohashi et al. 2015; Flora of China 2023). 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 included in the census as epiphyte individuals, but were excluded from the analyses. It is because, some individuals of these species germinate and grow on trees without contact with the ground soil (authors, pers. obs.), but often difficult to distinguish epiphytic individuals from those connected to ground soil by their roots and stems. Seedlings of epiphytic individuals with stem lengths less than 5 cm and without adult leaf

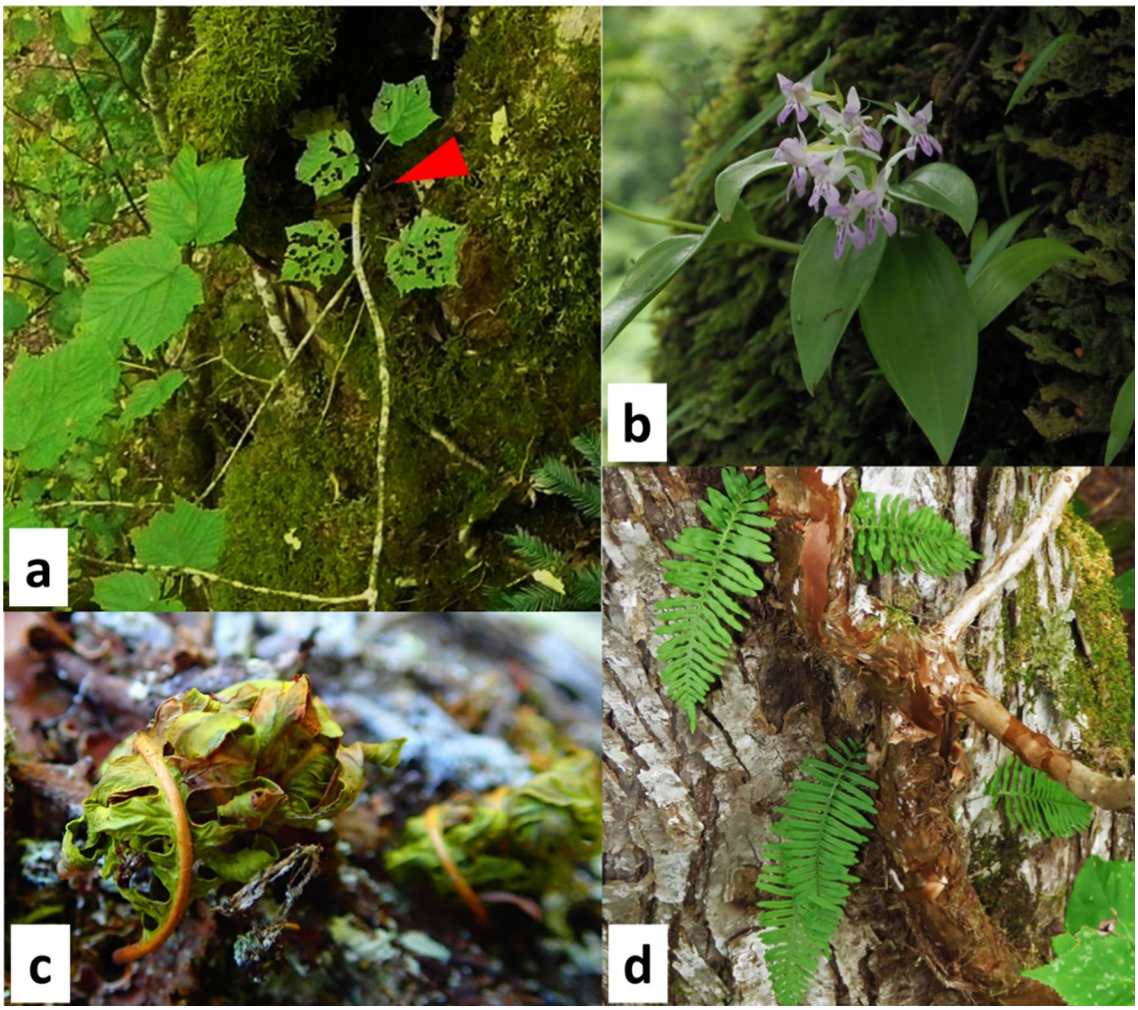


Fig. 1 Examples of habitats of epiphytes. A juvenile of *Acer rufinerve* Siebold et Zucc. rooting in arboreal soil accumulated in a hollow, red arrow indicates basal part of the stem (**a**), *Hemipilia chhidori* growing with bryophytes and lichens (**b**), and *Polypodium fauriei* growing on bark (**c**),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

stages were not recorded to avoid misidentification due to their scant morphological characteristics.

Statistical analysis

To analyze the relationships between the number of accidental and obligate epiphyte species and individuals and tree size, we performed generalized linear models (GLMs) with log-link function using a Poisson distribution or quasi-Poisson distribution. We set the number of species and individuals of epiphytes on each target tree as the response variable. We defined GBH as the tree size and set it as the explanatory variable. Both variables were assumed to be continuous. 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 proportion 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 examine the changes in species richness based on evenness along tree size. Regarding the analyses of substrate types, we excluded the records of epiphytes whose establishing substrates were unclassified. 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 limited sample size, these 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 a continuous explanatory variable. All analyses were performed using

the R software version 4.0.5 (R Core Team 2024), with a significance of < 5%.

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). Since the smallest tree (Host ID is 0) did not host any epiphytes, we excluded the tree from the analyses concerning the distribution of accidental and obligate epiphytes. The Polypodiaceae and Rosaceae were the most species-rich families, with five epiphyte species respectively. 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., with 609 individuals, accounting for 46.8% of the total number of epiphyte individuals (Table 2). The second most abundant species were *Polypodium fauriei* Christ (Polypodiaceae, 199 ind., 15.3%), followed by *Davallia mariesii* T. Moore ex Baker (Davalliaceae, 112 ind., 8.7%), *Oxalis nipponica* S. Aoki et J. Murata (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%). As a whole, major part of the epiphyte species (35 spp., 71.4% of the total number of species) occurred only on the largest tree (Table 2, Fig. 2). In addition, there is no epiphyte species occurred on the all individuals of targeted trees, however, *P. fauriei* and *O. nipponica* were found on seven and six host trees, respectively.

Effects of host tree size on the distribution of epiphyte assemblages

For both accidental and obligate epiphytes, the number of species on a tree significantly increased with increasing GBH, and this increase was more pronounced for accidental epiphytes than for obligate epiphytes (Fig. 3a). Similarly, the number of individuals of accidental and obligate epiphytes on a tree also increased with increasing GBH, but the increase was smaller for accidental epiphytes than for obligate epiphytes(Fig. 3b).

Regarding the proportional changes in the number of species and individuals 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

Epiphytes occurred on a variety of substrates (Figs. 5 and 6), and substrate preferences vary more in obligate epiphytes than in accidental epiphytes (Fig. 6). Among all epiphyte species, 14 species (28.6%) occurred on more than one substrate type (Table 2). 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%) (Table 2). 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 (45%), and 3 species were found on the bark, accounting for 6% (Table 2).

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. 5a), 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. 5b). The number of individuals on moss was significantly different from that on the other two substrates, bark (6.9%) and arboreal soil (4.2%) (Fig. 5). At the epiphyte species level, the type of substrate on which each epiphyte species primarily occurred varied depending on the species, with most epiphyte species predominantly established in the arboreal soil or moss, and no species found exclusively on 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 congruent with those presented in our previous work, which investigated a large *Cercidiphyllum* tree in this forest (Azuma et al. 2022). A higher percentage of

Table 2 List of epiphyte species with number of individuals of each host tree individual and number of individuals on each substrate type (A = arboreal soil, M = moss, B = bark, and U = unclassified), and types of epiphytism (white circle and black circle denote accidental epiphytes and obligate epiphytes, respectively). Asterisk shown after the species name indicates that any signs of maturity such as flowering or fruiting were observed for the species

Species name and taxonomic group	No. of ind. on each host tree							No. of ind. of each substrate type				Epiphytic type
	1	2	3	4	5	6	7	A	M	B	U	
Eudicots												
Actinidiaceae												
Actinidia polygama (Siebold et Zucc.) Planch. Ex Maxim	0	0	1	0	0	0	1	2	0	0	0	○
Alangiaceae												
Alangium platanifolium (Siebold et Zucc.) Harms var. *platanifolium*	0	0	0	0	0	0	3	3	0	0	0	○
Alnaceae												
Corylus sieboldiana Blume var. *sieboldiana*	0	0	0	0	0	0	1	0	1	0	0	○
Anacardiaceae												
Rhus javanica L. var. *chinensis* (Mill.) T.Yamaz	0	0	0	0	0	0	2	0	2	0	0	○
Toxicodendron trichocarpum (Miq.) Kuntze	0	0	0	0	0	0	3	3	0	0	0	○
Aquifoliaceae												
Ilex macropoda Miq	0	0	0	0	0	0	1	1	0	0	0	○
Araliaceae												
Aralia elata (Miq.) Seem	0	0	0	1	0	0	1	2	0	0	0	○
Kalopanax septemlobus (Thunb.) Koidz	0	0	0	0	0	3	0	3	0	0	0	○
Chengiopanax sciadophylloides (Franch. et Sav.) C.B.Shang et J.Y.Huang	0	0	0	0	0	0	6	6	0	0	0	○
Campanulaceae												
Peracarpa carnosa (Wall.) Hook.f. et Thomson*	0	0	4	0	0	5	0	9	0	0	0	○
Caryophyllaceae												
Stellaria diversiflora Maxim.*	0	0	0	10	0	21	0	10	21	0	0	○
Celastraceae												
Euonymus sieboldianus Blume var. *sanguineus* Nakai	0	0	0	0	0	0	1	1	0	0	0	○
Euonymus alatus (Thunb.) Siebold var. *alatus* f. *striatus* (Thunb.) Makino*	0	0	0	0	0	0	4	4	0	0	0	○
Celastrus orbiculatus Thunb. Var. *strigillosus* (Nakai) H.Hara	0	0	0	0	0	0	5	3	2	0	0	○
Clethraceae												
Clethra barbinervis Siebold et Zucc	0	0	0	0	0	0	2	2	0	0	0	○
Ericaceae												
Vaccinium smallii A. Gray var. *versicolor* (Koidz.) T.Yamaz	0	0	0	0	0	0	1	1	0	0	0	○
Lyonia ovalifolia (Wall.) Drude var. *elliptica* (Siebold et Zucc.) Hand.-Mazz	0	0	0	0	0	0	1	1	0	0	0	○
Fagaceae												
Quercus crispula Blume var. *crispula*	0	0	0	0	0	0	1	1	0	0	0	○
Gentianaceae												

Table 2 (continued)

Species name and taxonomic group		No. of ind. on each host tree							No. of ind. of each substrate type				Epiphytic type
		1	2	3	4	5	6	7	A	M	B	U	
	Gentiana zollingeri Fawc.*	0	0	0	2	0	0	0	2	0	0	0	○
Grossulariaceae													
	Ribes ambiguum Maxim.*	0	0	0	0	0	0	9	7	2	0	0	●
Helwingiaceae													
	Helwingia japonica (Thunb.) F.Dietr.*	0	0	0	0	0	0	1	1	0	0	0	○
Lamiaceae													
	Callicarpa japonica Thunb.*	0	0	0	0	0	0	1	1	0	0	0	○
Oxalidaceae													
	Oxalis nipponica S.Aoki et J.Murata*	0	2	20	5	7	7	44	37	48	0	0	○
Rosaceae													
	Cerasus incisa (Thunb.) Loisel. var. kinkiensis (Koidz.) H.Ohba	0	0	0	0	0	0	1	1	0	0	0	○
	Cerasus jamasakura (Siebold ex Koidz.) H.Ohba*	0	0	0	0	0	0	1	0	0	0	1	○
	Micromeles alnifolia (Siebold et Zucc.) Koehne*	0	0	0	0	0	1	4	1	2	0	2	○
	Sorbus commixta Hedl.*	0	0	0	0	0	1	4	4	1	0	0	○
	Padus grayana (Maxim.) C.K.Schneid	0	0	0	0	0	0	8	6	2	0	0	○
Sapindaceae													
	Acer palmatum Thunb	0	0	0	0	0	0	1	1	0	0	0	○
	Acer sieboldianum Miq.*	0	0	0	0	0	1	0	0	0	0	1	○
	Acer rufinerve Siebold et Zucc	0	0	0	0	0	0	2	2	0	0	0	○
Thymelaeaceae													
	Daphne miyabeana Makino	0	0	0	0	0	0	1	0	1	0	0	○
Trochodendraceae													
	Trochodendron aralioides Siebold et Zucc.*	0	0	0	0	0	0	1	0	0	0	1	○
Pteridophytes													
Davalliaceae													
	Davallia mariesii T.Moore ex Baker*	0	0	13	10	0	1	88	0	94	18	0	●
Dryopteridaceae													
	Arachniodes standishii (T.Moore) Ohwi*	0	0	0	0	0	0	3	3	0	0	0	○
	Dryopteris crassirhizoma Nakai*	0	0	0	0	1	4	3	7	1	0	0	○
	Polystichum tripteron (Kunze) C.Presl*	0	0	0	0	0	0	11	0	11	0	0	○
Hymenophyllaceae													
	Crepidomanes minutum (Blume) K.Iwats.*	0	0	0	0	0	0	609	0	609	0	0	●
Polypodiaceae													
	Lepisorus annuifrons (Makino) Ching*	0	0	0	0	0	1	50	0	51	0	0	●

Table 2 (continued)

Species name and taxonomic group		No. of ind. on each host tree							No. of ind. of each substrate type				Epiphytic type
		1	2	3	4	5	6	7	A	M	B	U	
	Lepisorus thunbergianus (Kaulf.) Ching*	0	1	0	0	2	0	0	0	1	2	0	●
	Loxogramme grammitoides (Baker) C.Chr.*	0	0	0	0	0	0	6	0	6	0	0	●
	Pleurosoriopsis makinoi (Maxim. Ex Makino) Fomin*	0	0	0	20	0	8	11	13	26	0	0	●
	Polypodium fauriei Christ*	16	17	21	42	32	4	67	21	124	54	0	●
Monocots													
Cyperaceae													
	Carex *foliosissima* F.Schmidt*	0	0	0	0	0	0	4	4	0	0	0	○
Orchidaceae													
	Hemipilia chidori (Makino) Y.Tang, H.Peng et T.Yukawa*	0	0	0	0	0	0	13	3	10	0	0	●
	Goodyera pendula Maxim.*	0	0	0	0	0	0	30	1	29	0	0	●
Poaceae													
	Poa sp.	0	0	0	0	0	0	1	1	0	0	0	○
Lycophytes													
Huperziaceae													
	Phlegmariurus cryptomerinus (Maxim.) Satou*	0	0	0	0	0	0	2	0	2	0	0	●
Gymnosperms													
Taxaceae													
	Cephalotaxus harringtonia (Knight ex Forbes) K.Koch var. *nana* (Nakai) Rehder	0	0	0	0	0	3	5	8	0	0	0	○
	Total	16	20	59	90	42	60	1014	176	1046	74	5	0

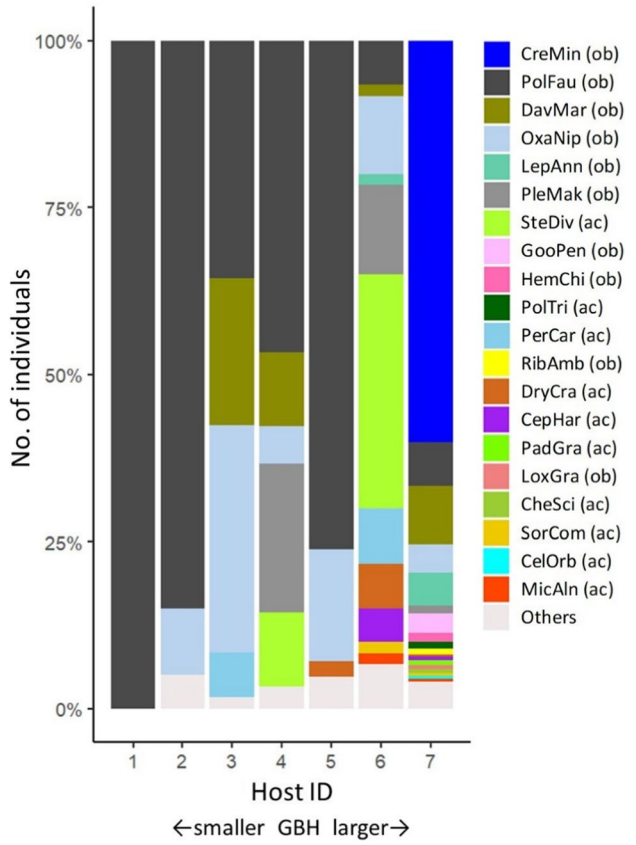


Fig. 2 Relative abundances (%) of each epiphyte species among host tree individuals. Epiphyte species whose number of individuals were less than five were lumped as others. The species codes in the figure correspond to the following scientific names: CreMin = *Crepidomanes minutum*; PolFau = *Polypodium fauriei*; DavMar = *Davallia mariesii*; OxaNip = *Oxalis nipponica* subsp. *nipponica*; LepAnn = *Lepisorus annuifrons*; PleMak = *Pleurosoriopsis makinoi*; SteDiv = *Stellaria diversiflora*; GooPen = *Goodyera pendula*; HemChi = *Hemipilia chidori*; PolTri = *Polystichum tripteron*; PerCar = *Peracarpa carnosa* var. *circaeoides*; RibAmb = *Ribes ambiguum*; DryCra = *Dryopteris crassirhizoma*; CepHar = *Cephalotaxus harringtonia* var. *nana*; PadGra = *Padus grayana*; LoxGra = *Loxogramme grammitoides*; CheSci = *Chengiopanax sciadophylloides*; SorCom = *Sorbus commixta*; CelOrb = *Celastrus orbiculatus* var. *strigillosus*; MicAln = *Micromeles alnifolia*. Accidental and obligate epiphytes were indicated as "ac" and "ob" respectively in the parenthesis at the end of the species codes

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 remain to be elucidated, climatic attributes (e.g., temperature and precipitation) and disturbance are considered as possible factors (Hoeber and Zotz 2022). Among eleven recorded species of obligate epiphytes (Table 2), seven species were belonging to Orchidaceae or Polypodiaceae. As these families are known to have CAM photosynthesis that enhances drought tolerance and is advantageous for arboreal environments (Zotz 2016), acquisition of some extent of drought tolerance might be needed for obligate epiphytism in this forest.

The dominance of certain species such as *C. minutum*, *P. fauriei*, *D. mariesii*, *O. nipponica*, and *L. annuifrons* can be attributed to the specific ecological characteristics that enable them to thrive in arboreal habitats. For instance, the poikilohydric leaves of *C. minutum* and *P. fauriei* allow them to withstand periods of water scarcity (Cea et al. 2014; Zotz 2016). In addition, Azuma et al. (2022) showed that the leaves of *D. mariesii* have high water-use efficiency. The rhizomes of *P. fauriei*, *D. mariesii*, *O. nipponica*, and *L. annuifrons* are fleshy, and may contribute to water storage. Moreover, all the above five species reproduce clonally via rhizomes; this strategy allows them to expand their populations and occupy large areas within arboreal habitats. However, the relatively high abundance of an accidental epiphyte species, *O. nipponica* (Table 2), is intriguing; this species generally occurs as a terrestrial plant, and Oxalidaceae, the family which this species belongs to, is not a major epiphyte taxa (Komada et al. 2022b; Zotz et al. 2021). To date, only a few studies have reported epiphytism for this family (Hoeber and Zotz 2021a, b; Komada et al. 2020; Nadkarni 1984). The mechanisms enabling terrestrial species to grow abundantly on trees are still yet to be fully understood, and the characteristics of the species discussed above may help to clarify the background of epiphytic occurrence of this family.

Effects of host tree size on epiphyte assemblage distribution

As we expected, the number of species and individuals of accidental and obligate epiphytes increased significantly with increasing tree size (Fig. 3). Although the studies that separately analyzed the trends between these two epiphyte types is limited, the positive correlations between tree size and the number of epiphyte species, and between the number of epiphyte individuals are known as global trends (Flores-Palacios and García-Franco 2006; Hattori et al. 2009; Komada et al. 2022a; Taylor and Burns 2015; Wagner and Zotz 2020; Woods et al. 2015). These correlations have been attributed to the large habitat area (Taylor and Burns 2015; Wagner and Zotz 2020; Woods et al. 2015), extended habitat availability, and an increased chance that diaspores of epiphytes reach (Flores-Palacios and García-Franco 2006), as well as the more complex architecture (Hietz and Hietz-Seifert 1995; Woods et al. 2015) of large trees compared to small trees. In fact, the substrate water content (Tatsumi et al. 2021), temperature (Azuma et al. 2022), and light intensity (Fig. S2) for the largest tree targeted in this study changed along a height gradient from the ground to the crown. These environmental

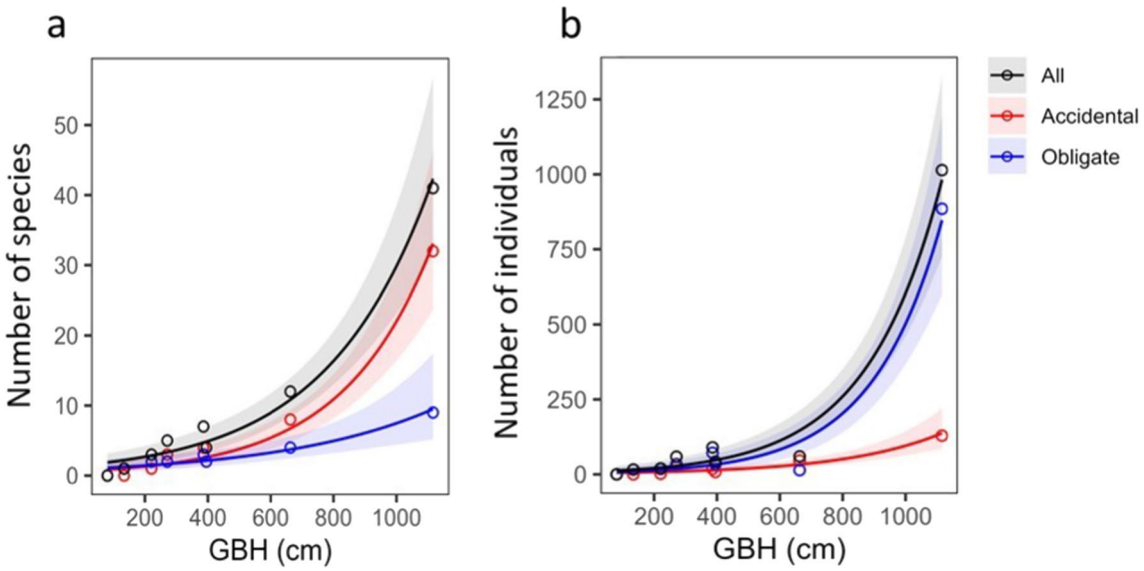


Fig. 3 **a** Relationships between GBH and number of epiphyte species on a tree. The regression lines were obtained through a Poisson GLMs: y = exp (0.387 + 0.003 x), pseudo $R^2 = 0.94$, $P < 0.001$ for all epiphytes (accidental and obligate); y = exp (-0.426 + 0.004 x), pseudo $R^2 = 0.936$, $P < 0.001$ for accidental epiphytes; y = exp (-0.052 + 0.002 x), pseudo $R^2 = 0.83$, $P < 0.001$ for obligate epiphytes. The shaded band indicates the 95% confidence interval. **b** Relationships between GBH and epiphyte individuals on a tree. The regression line was obtained through a quasi-Poisson GLMs: y = exp (2.198 + 0.004 x), pseudo $R^2 = 0.95$, $P < 0.001$ for all epiphytes (accidental and obligate); y = exp (1.418 + 0.003x), pseudo $R^2 = 0.85$, $P = 0.001$ for accidental epiphytes; y = exp (1.711 + 0.005x), pseudo $R^2 = 0.93$, $P < 0.001$ for obligate epiphytes. The shaded band indicates the 95% confidence interval

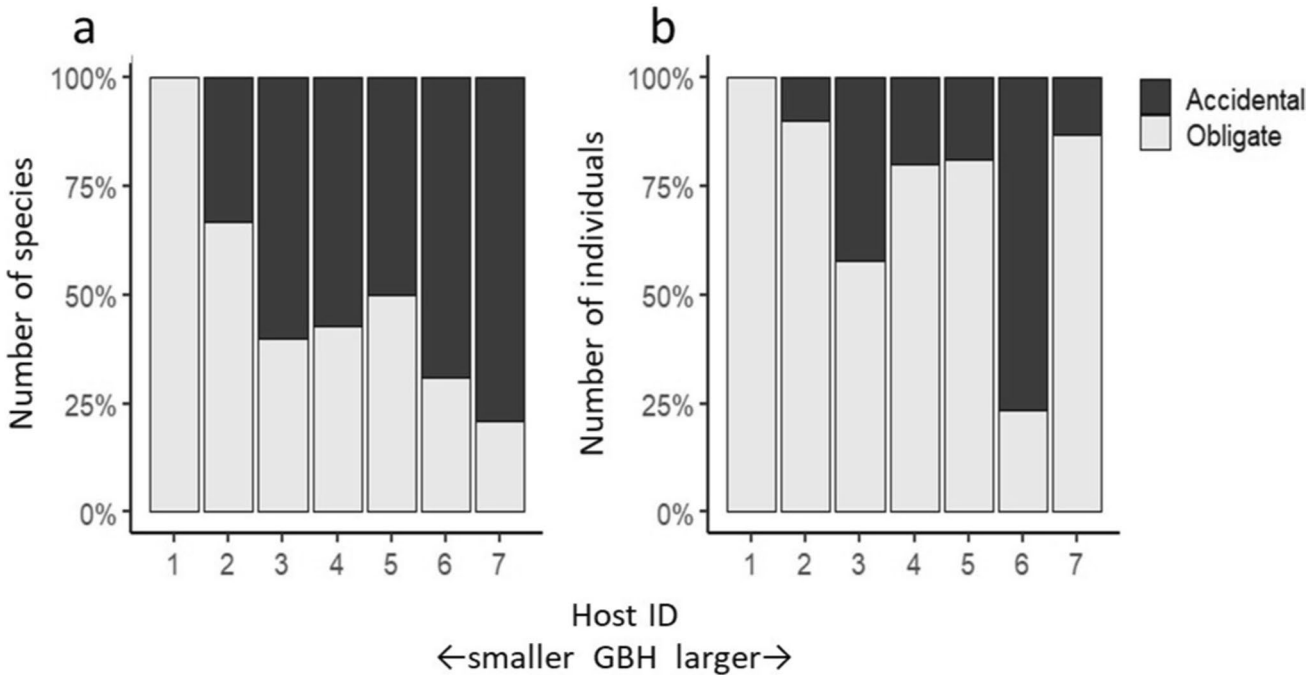


Fig. 4 Proportional changes of number of epiphyte species **a** or individuals **b** of obligate and accidental epiphytes along with host tree GBH

factors are likely to be more varied for larger and taller trees than for smaller and shorter trees, providing more diverse habitats. Since the smallest *Cercidiphyllum* tree had no epiphytes, this suggests that the tree may not yet have reached a size that can provide an adequate environment for epiphyte growth. Although we were only able to

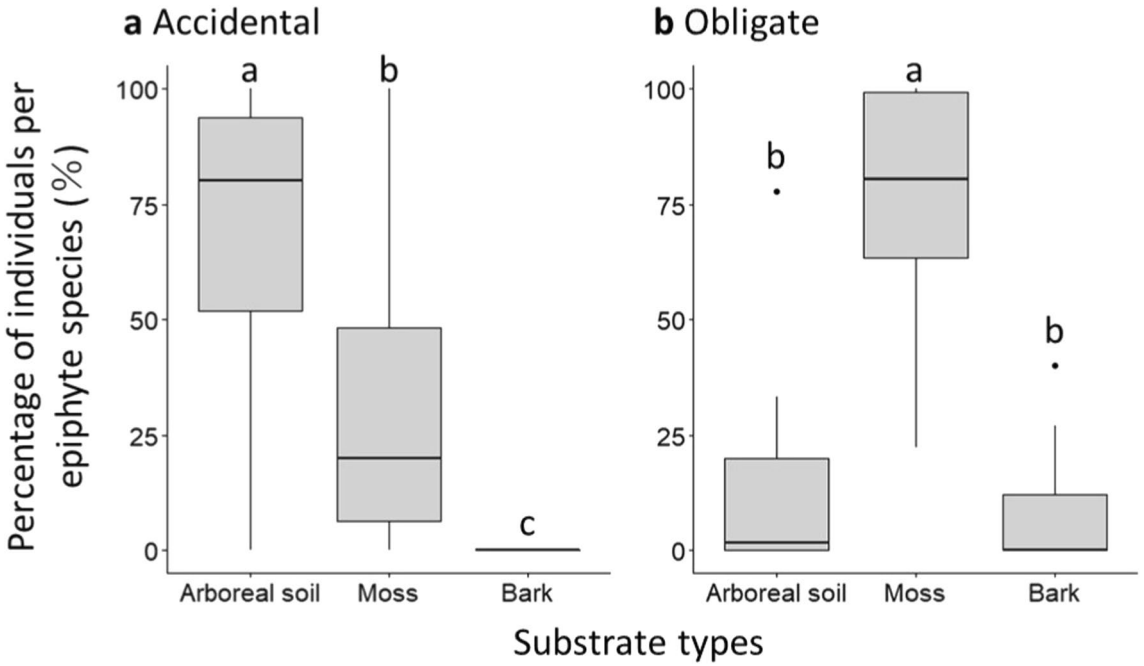


Fig. 5 Percentages of individuals per accidental epiphyte species (**a**) or obligate epiphyte species (**b**) among three substrate types. Results of statistical analyses as follows. For accidental epiphytes, Kruskal–Wallis test ($P < 0.001$) and Steel–Dwass test ($P < 0.05$ in arboreal soil and moss, $P < 0.01$ 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

thoroughly examine a single tree of this size, we observed that conspecifics of similar or smaller size generally had few or no epiphytes.

The patterns of increase in the number of species and individuals with increasing host tree size differed between the two types of epiphytes. Specifically, the large increase in the number of accidental epiphyte species relative to obligate epiphyte species (Fig. 3a) was reflected in the proportion of accidental epiphyte species significantly increasing as the host tree size increased, surpassing that of obligate epiphytes (Fig. 4a). This trend aligns with our hypothesis, and was further supported by changes in the Shannon–Wiener diversity index (H') with tree size (Fig. S3); the incremental change in the index value was more pronounced in accidental epiphytes than in obligate epiphytes, especially when the GBH was at its maximum. These results can be attributed to the relatively low diversity of obligate epiphytes in this area (approximately 13 species, Komada et al., unpublished), which is lower compared to many tropical forests. This number is notably smaller than the overall diversity of accidental epiphytes in this forest, as evidenced by the occurrence of 38 accidental epiphyte species on a single large tree (Table 2). These findings suggest that, with increasing host tree size, the maximum number of epiphyte species is reached earlier in obligate than in accidental epiphytes. In this forest, accidental epiphytes primarily depend on larger trees compared to obligate epiphytes, and accidental epiphytism frequently occurs among terrestrial species.

By contrast, the increment of the number of individuals was greater in the obligate epiphytes than in the accidental epiphytes (Fig. 3b). This finding, contrary to our hypothesis, indicated that the percentage of accidental epiphyte individuals did not increase with tree size (Fig. 4b). These can be attributed to the occurrence of abundantly found obligate epiphytes including *C. minutum*, *P. fauriei*, *D. mariesii*, and *L. annuifrons* (Fig. 2), and their ability to clonal reproduction as discussed above. In addition, unlike those obligate epiphytes, most individuals of accidental epiphytes did not show signs of clonal reproduction, and their main source of diaspore might be from terrestrial individuals. However, since the probability that diaspores of a species reach the canopy and succeed to establish on a tree increases through time, large *Cercidiphyllum* trees would certainly contribute to the high abundance of accidental epiphytes as well as obligate epiphytes. Further investigations involving more host tree species and individuals are needed to robustly determine how the diversity of accidental and obligate epiphytes is differentially affected by host tree size.

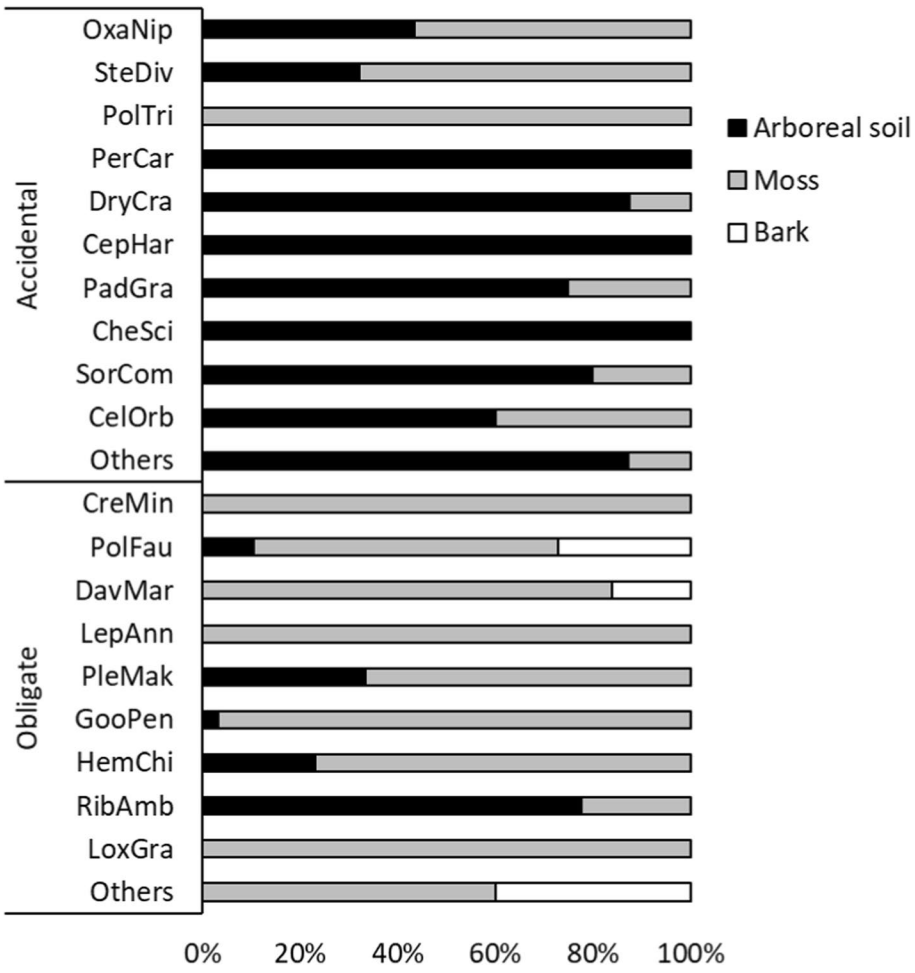


Fig. 6 Relative composition of substrate types of each epiphyte species. Epiphyte species whose number of individuals were less than five were lumped as others. The relationships of species codes in the figures and scientific names of epiphytes are same as those presented in Fig. 2

Epiphytes and substrate type

As predicted, the major substrate types for each epiphyte species differed between the accidental and obligate epiphyte assemblages (Figs. 5 and 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 and 6). The greater epiphyte abundance on substrates with accumulated organic matter, such as moss and arboreal soil, than on bark has previously been reported (Hoeber et al. 2019; Hoeber and Zotz 2022; Ingram and Nadkarni 1993; Nakanishi et al. 2013; Ter Steege and Cornelissen 1989). This trend is considered to be related to the high water- and nutrient-retaining capacities of moss and arboreal soil (Hoeber et al. 2019, 2020; Hoeber and Zotz 2022; Ishii et al. 2018; Sillett 1999), and water content is higher in thick than in thin substrates (Sillett and Pelt 2007; Tatsumi et al. 2021). In addition, substrates with moss promote the establishment of epiphytes by trapping their diaspores (Ingram and Nadkarni 1993; Mizuno et al. 2012). In contrast, bark may not be a good habitat for many epiphyte species in our study sites. We showed that there were some species that are frequently found on arboreal soil or moss, however, we did not find any species that occurred predominantly on bark (Fig. 6). Further, the number of epiphyte individuals on arboreal soil and moss were positively correlated with tree size, but the relationships between epiphytes on bark and tree size was insignificant (Fig. S4). Thus, at our study site, bark likely produces a harsh environment for both accidental and obligate epiphyte species.

Studies that characterize the differences in substrate type between obligate and accidental epiphytes are scarce. Recently, a few studies have reported that accidental epiphytes are restricted to habitats where arboreal soil accumulates (Hoeber et al. 2019; Ishii et al. 2018), and this was consistent with our results. In this study, we showed that accidental epiphytes were more dependent on arboreal soil than obligate epiphytes (Fig. 5). These findings likely resulted from the lower drought tolerance in the accidental epiphytes than in the obligate epiphytes, and higher water content in thick substrates than in thin substrates. As discussed above, we showed that the proportion of accidental epiphyte species increased with tree size, surpassing the obligate epiphyte population (Fig. 4a). This can be explained

by the fact that the accumulation of organic matter is more abundant on large and old trees than on small and young trees (Hoeber and Zotz 2022; Ishii et al. 2018; Woods et al. 2019), and our results demonstrated that the occurrence of accidental epiphytes was more restricted to environments with thick organic matter contents than obligate epiphytes.

Because of the scarcity of studies on the ecology of accidental epiphytes, the fate of terrestrial plants after their germination or establishment on trees is unclear. If they grow until maturity and reproduce diaspores, their colonization on arboreal habitats may be beneficial in maintaining and expanding the population size and genetic diversity. Several studies have reported that arboreal habitats are not as stressful for terrestrial plants, and that the nutrition levels in arboreal habitats can be similar to Tatsumi et al. (2021) or even higher than those of the ground soil (Hoeber and Zotz 2021a, b). In addition, Hoeber et al. (2020) suggested that if the water supply and rooting area are sufficient for growth, arboreal habitats with accumulated organic matter may not limit accidental epiphytism. The present study recorded 38 accidental epiphyte species. Of these, we found that at least 16 species (42%) can grow until maturity, as we observed flowers, fruits, or sori on epiphytic individuals of those species (Table 2). We observed that accidental epiphytic individuals of tree species targeted in this study, such as *Callicarpa japonica* Thunb., *Cerasus jamasakura* (Siebold ex Koidz.) H.Ohba, and *Micromeles alnifolia* (Siebold et Zucc.) Koehne, can flower and fruit for more than five years. In addition, we observed that seedlings of herbaceous accidental epiphytes such as *Oxalis nipponica* S.Aoki et J.Murata subsp. *nipponica,* and *Stellaria diversiflora* can grow sporadically near putative mother epiphytic individuals. Although further quantitative surveys are needed to evaluate the adaptation of these terrestrial species to accidental epiphytism, our observations suggest that the arboreal habitats in our study site are not necessarily harsh environments, at least for those terrestrial species.

Although not included as a substrate type in this study, lianas on host trees may provide further research on their potential to assist the establishment and growth of epiphytes. We found that the obligate epiphyte *P. fauriei* was mainly found on substrates with moss, but about 30% of the individuals were found on bare bark (Fig. 6). Furthermore, we found that among the bark-established individuals, 40% were rooted around areas where the bark surface was appressed by stems of lianas (*Hydrangea* spp.) (Fig. 1d). Although whether the liana stems really assist epiphyte establishment is unclear, it is plausible that once bare bark is covered by the stems of lianas, the habitat condition in relation to water availability will improve, promoting the epiphyte establishment. We also observed this phenomenon in other epiphytic species in our study site; mature epiphytic individuals of *Hosta* sp. and *Calanthe* sp., and *O. nipponica* were found aside liana stems on several *Aesculus turbinata* trees (Authors, pers. obs.). Although further research is needed, this phenomenon may be considered an example of ecosystem engineering or habitat cascading effect, because the distributions of epiphytes and root climbing liana on trees were often similar at our study site (distribution of epiphytes and lianas on targeted trees are summarized in Fig S5).

Suggestions for future studies

We reported that the distribution of accidental and obligate epiphytes can be influenced by the tree size, however, the sample size in this study was limited, and a more intensive census targeting a large number of host trees is needed for future studies. That would help to know the variability of epiphyte distribution among same size classes. 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. S5) may be attributed to the characteristic architecture of this tree species. 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.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by, Natsuki Komada, Wakana A Azuma, Yuya Ogawa, and Chikae Tatsumi. The first draft of the manuscript was written by Natsuki Komada and Wakana A Azuma, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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