

A new approach to an old problem: how to categorize the habit of ferns and lycophytes

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- **Background and Aims** Substrate preferences are often treated as species traits and are used to distinguish different habits, i.e. an epiphytic, lithophytic or terrestrial habit. Such a categorization, however, ignores substantial intraspecific variation. An approach that takes biological variability within a species into account is needed.
- **Methods** We focused on four large genera of ferns and lycophytes and found relevant information in >500 sources, such as online databases, checklists, floras and species descriptions. Translating textual information into a quantitative index, we quantified the propensity to grow on either substrate as a continuous trait for 1475 species.
- **Key Results** Only a minority of species exhibited strict substrate fidelity, but a majority of them showed clear habitat preferences. The relative frequencies of intermediates between strict lithophytes, epiphytes and terrestrials does not support the frequent notion of ecological similarity of the lithophytic and epiphytic habitat.
- **Conclusions** The compiled data are useful immediately for ecological and evolutionary studies with the focal taxa. More importantly, we propose the replacement of the concept of distinct habits with one of gradual differences. This should have a profound impact on any such study with plants in general.

Key words: *Asplenium*, *Elaphoglossum*, ferns, habit, habitat generalist, habitat specialist, hemiepiphyte, *Hymenophyllum*, interspecific variation, intraspecific variation, lycophytes, *Phlegmariurus*.

INTRODUCTION

There are numerous schemes to categorize plant diversity, using differences in phenology (evergreen vs. deciduous), life history (annuals vs. perennials), stature (free-standing vs. climbing), photosynthetic pathway (C₃ vs. C₄ or CAM plants), tolerance against particular stressors (e.g. halophytes vs. glycophytes), habit (epiphytic vs. lithophytic vs. terrestrial) and many more to define different groups of plants. However, in many of these cases there are fundamental doubts concerning whether such categorizations capture natural variation appropriately and do not obscure more gradual differences. For example, [Ogburn and Edwards \(2010\)](#) crisply state that ‘succulence is not a binary trait’, although it is often used in that sense by scientists, as indicated by titles such as ‘succulent plants’ ([Griffiths and Males, 2017](#)). A similar case is the common practice of labelling species as ‘epiphytic’, ‘lithophytic’ or ‘terrestrial’. Are these genuinely distinct groups of vascular land plants?

Most land plants root in soil, i.e. they are terrestrials. An epiphyte, in turn, is defined as a non-parasitic plant that grows on another plant throughout its life, without contact with the ground ([Zotz, 2016](#)). Lithophytes (also called saxicolous or epipetric plants) are defined as plants ‘that grow on rock and derive their nourishment chiefly from the atmosphere’ ([Barnhart, 2005](#)). Lithophytes and epiphytes share growth on a largely impenetrable substrate, with resulting problems of anchorage and procurement of water and nutrients. However, in both cases the

growing conditions can be increasingly similar to those of terrestrial plants, e.g. in montane tropical forests with substantial accumulations of organic material on the branches of trees or when rocks are densely covered with moss. Although application of these definitions to an individual plant can work rather well in most cases, it is impossible to show that all individuals of a given species use the same substrate in all but the exceptional case. Hence, there is some inevitable ambiguity in the terms ‘epiphytic species’, ‘lithophytic species’ or ‘terrestrial species’.

Previous work has emphasized interspecific differences, whereas intraspecific variation has been largely ignored. For example, we have recently compiled a global list of epiphyte species, EpiList 1.0 ([Zotz et al., 2021b](#)). For each species, at least one reference was given to justify its inclusion. However, such a list undoubtedly lumps species with very different degrees of fidelity to the epiphytic habitat, and additional information will lead to the exclusion of some species and the addition of others. To acknowledge this problem, these authors called their list a compilation of ‘31,000 hypotheses’.

More recently, we presented a literature-based approach to tackle the question of the degree of fidelity to epiphytic, lithophytic or terrestrial growth for the family Hymenophyllaceae ([Zotz and Einzmann, 2023](#)). We showed that the literature is a rich source for information on intraspecific variation in growing sites, which was used to arrive at a much more realistic picture of habitat preferences in that family than any previous work.

The present study applies this approach in a larger taxonomic context. Specifically, we picked the four globally distributed genera with the largest absolute numbers of epiphytic species in Epilist 1.0 (Zotz et al., 2021b), namely *Asplenium*, *Elaphoglossum* and *Hymenophyllum* among ferns with ~250–450 epiphytic taxa each, and *Phlegmariurus* among lycophytes with >100 epiphytic taxa. We quantified the propensity of epiphytic, lithophytic or terrestrial growth in these four genera as a continuous variable with a numerical approach.

Fawcett et al. (2022) have recently emphasized the importance of making information that is hidden in taxonomic treatments, printed floras and other scientific literature available in digital, accessible form. We did this, with the presentation of data of 1475 species from >500 publications. We believe that our data will be a rich resource for future ecological and phylogenetic studies with these four genera and will also help to arrive at a more realistic view of epiphytic, lithophytic and terrestrial growth in the plant kingdom at large.

MATERIALS AND METHODS

The present study follows the approach presented by Zotz and Einzmann (2023). We augmented the data set on *Hymenophyllum* used in that study with 120 additional entries and seven additional species. For the other three genera (*Asplenium*, *Elaphoglossum* and *Phlegmariurus*), we obtained information on growing sites of almost 1300 species from the taxonomic literature (species descriptions, checklists and floras), the ecological literature (community studies and vegetation descriptions) and numerous online data bases and other web sites, e.g. *Brazilian Flora 2020 in construction (continuously updated)* or *eFloras (2020)*. An important criterion to decide whether to accept a source for our purpose was that the source acknowledged that a species might occur on different substrates. This was mostly not stated explicitly in a publication, but we considered it to be given implicitly when species lists included at least one species, e.g. as growing both as an epiphyte or lithophyte. Thus, all studies with an exclusive focus on vascular epiphytes (e.g. Hietz and Hietz-Seifert, 1995; Benavides et al., 2005; Einzmann et al., 2015) were excluded, unless the authors included accidental or facultative epiphytes (e.g. Werner et al., 2005; Francisco et al., 2023). Likewise excluded were all checklists that assigned all species to a single category (e.g. Freitas et al., 2016; Kipkoech et al., 2019; Jiménez López et al., 2023). Although one misses potentially valid information with this conservative approach, the inclusion of such studies would bias our data set to extreme values of habitat preference.

The final number of sources that was used for this study was 542 (Supplementary Data Table S1). All species names were standardized against the check list of Hassler (2004–2022), but the names used in the original publications can still be found in the Supplementary Data (Table S1).

A quantification of epiphytic, lithophytic or terrestrial occurrences of the individual plants of a given species in a study is exceedingly rare (e.g. Acuña-Tarazona et al., 2022). Thus, in almost all cases we had to translate literal descriptions of epiphytic, lithophytic or terrestrial occurrences of a given species in proportions, as detailed in Table 1.

This approach yielded three values per entry, an epiphyte value (EV), a lithophyte value (LV) and a terrestrial value (TV), which sum to unity (100 %). We are fully aware that it is unlikely that, e.g. the description ‘epiphytic and lithophytic’ is really meant to indicate the exact same number of 50 % epiphytic and 50 % lithophytic occurrences. Moreover, one cannot assume that different authors use a term such as ‘occasionally’ in a consistent way, and inevitably, the translation of vague descriptions such as ‘mostly terrestrial’ or ‘rarely epiphytic’ in a numerical system can only be arbitrary. However, our approach allows a coarse ranking of preferences for epiphytic, lithophytic and terrestrial growth and is a clear improvement on the typical practice of simple categorical assignments (e.g. Zotz et al., 2021b). Moreover, our approach is transparent and flexible, in that the criteria given in Table 1 can be adjusted in any future analysis by other researchers.

For the majority of species (about two-thirds), information from several sources was available. We considered all sources as equivalent and calculated the simple average of EV, LV and TV for each species (Supplementary Data Table S2). A large number of sources should improve the quality of the final estimate. This study provides data for 1475 species (~53–76 % per genus; see Supplementary Data Tables S1 and S2), with an average number of four sources with occurrence information per species (range: 1–54 entries per species).

As already discussed by Zotz and Einzmann (2023), any number can be seen only as a rough estimate, and the interpretation for a particular species is not straightforward. For example, an entry of 50 % epiphyte/50 % lithophyte for a species in the final results (Supplementary Data Table S2) can be for a number of reasons: (1) there might be a single source available that describes the species as, e.g. ‘growing on tree trunks and rocks’; or (2) there might be two or more studies,

TABLE 1. Numerical translation of literal descriptions of species occurrences in the original sources as epiphytes (E), lithophytes (L) or terrestrials (T) used in the large majority of all sources. There are a few special cases, such as Bidin (1987), with explicit information on the habit of specimens, where we used the proportions, or Acuña-Tarazona et al. (2022), where the individual counts of a census were available.

Verbal information	Percentage epiphytic occurrence (= EV)
Epiphyte and lithophyte (50 % to L)/epiphyte or terrestrial/facultative epiphyte (50 % to T)	50
Epiphyte, lithophyte or terrestrial (33/34 % to L and T)	33
Holoepiphyte/hemiepiphyte/epiphyte	100
Obligatory epiphyte	100
Rarely/seldom	5
Very rarely/accidental epiphyte/exceptionally	1
Also as/sometimes/occasionally/uncommonly	15
Commonly/generally/mainly/mostly/preferentially/primarily/usually	85
Often/frequently/most frequently	67
Less frequently	33

half of which describe the species as ‘growing epiphytically’, the others as ‘lithophyte’, or other possible combinations. Such differences could reflect true biological diversity when sources describe regional differences in occurrence patterns as reported, e.g. for the bromeliad *Aechmea distichantha* (Barberis *et al.*, 2021), but there might also be erroneous entries in some sources. By presenting all this information in the [Supplementary Data](#), we expose such differences to future analyses and provide a starting point to study the underlying reasons.

We performed three types of numerical analyses with our data set. First, we produced a histogram of epiphytic (EV) vs. non-epiphytic (LV + TV) occurrences and compared these distributions with uniform distributions with a χ^2 test. A second type of analysis took advantage of the fact that the EV, LV and TV of each species sum to unity. This allows us to show the distribution of the species of the four genera in the epiphyte–lithophyte–terrestrial space (Zotz and Einzmann, 2023). For these ordinations, we used the `plotrix` library v.3.8-1 (Lemon, 2006) in R v.4.2.0 (R Core Team, 2022). In a third analysis, we quantified the number of species between two extremes (i.e. species located on the edges of the triangles) by, e.g. counting the number of facultative epiphyte/lithophyte species, which are defined by $TV < 1\%$, $LV < 95\%$ and $EV < 95\%$. In an analogous way, we determined the number of facultative epiphyte/terrestrials and facultative lithophyte/terrestrials.

RESULTS

Our analyses are based on >6000 entries, covering almost 1500 species (Table 2). In a first analysis, we lumped terrestrials and lithophytes as non-epiphytes and quantified the degree of epiphytism of each species. The bins of the histogram should not differ much in frequency if the propensity to grow as an epiphyte were a continuous trait (scenario 1). Alternatively, if there were strong preferences for growth on trees, or not, we would expect a pronounced bimodal distribution (scenario 2). Support for the scenario 1 was not found in any case (Fig. 1). Invariably, the distribution deviated significantly from uniformity (χ^2 tests, d.f. = 9, $P < 0.001$). Scenario 2 was observed only in *Phlegmariurus*, where the two extreme bins held >80% of all species. In the other genera, the terrestrial/lithophytic

extreme (*Asplenium*) or the epiphytic extreme (*Elaphoglossum* and *Hymenophyllum*) held the highest number of species. The existence of a possible third peak of ‘facultative’ epiphytes in *Hymenophyllum* and *Elaphoglossum* is doubtful, because a large proportion of the species that fell into the category of even probability to occur epiphytically or not were single-entry cases.

Triangular ordinations (Fig. 2) allowed us to include preferences for epiphytic, lithophytic and terrestrial growth in a single analysis. There were clear differences between the genera in terms of habitat preferences. Specialists, i.e. species that occur (almost) exclusively in one habitat (species in which EV, LV or TV was >95%) were a minority in all genera but *Phlegmariurus*. In contrast, a preference (species in which EV, LV or TV was >50%) was found in the large majority of species in all genera.

Habitat specialists were most common in *Phlegmariurus*, where 67% of all taxa occurred almost exclusively as epiphytes, lithophytes or terrestrials, whereas the proportion of such specialists was lowest in *Asplenium*, where only about half that value (36%) was reached. In *Elaphoglossum*, most of the 46% specialists were restricted to growth on trees, although by far the highest proportion of obligatory epiphytes was found in *Hymenophyllum*.

Apart from depicting specialists, the ordination could be used to visualize and quantify a preference to grow on trees, rocks or in soil. Although a position in the central small triangle of the ordination in Fig. 2 identifies generalists, the occurrence in one of the other three small triangles in Fig. 2 indicates a clear preference for one of the three habitat types (Fig. 3). In agreement with the large proportion of obligatory epiphytes in *Hymenophyllum*, >80% of the filmy ferns grew primarily as epiphytes, i.e. species values were found in the lower left triangle of the epiphyte–lithophyte–terrestrial space, where EV was $\geq 50\%$. A strong preference for epiphytic growth could also be observed in *Elaphoglossum*, whereas the genus *Phlegmariurus* was characterized by either epiphytic or terrestrial growth, with a similar number of species in both groups. The most even use of the epiphyte–lithophyte–terrestrial space was found among *Asplenium* species. The number of *Asplenium* species with a preference for each of the three habitats was virtually identical, with ~30% of the total, with the remaining 8% of species not showing a preference.

TABLE 2. Proportion of species in the four genera with a preference ($EV \geq 50\%$) or specialization ($EV > 95\%$) for epiphytic growth, the number of species in the present analysis, and the proportion of epiphyte species per genus in *EpiList 1.0* (Zotz *et al.*, 2021b) and total number of species given by Hassler (2004–2022). Life form description follows Kubitzki (1990) for *Asplenium*, *Elaphoglossum* and *Phlegmariurus* and Ebihara *et al.* (2006) for *Hymenophyllum*. Note that the values of the first three data columns are derived from the set of sampled species in this study (number of species), whereas the percentage of epiphytes in *EpiList 1.0* was calculated relative to the total number of species per genus in world flora online.

Genus	Life forms	EV ≥ 50 %	EV > 95 %	Number of species	Percentage of epiphytes in <i>EpiList</i>	Number of species
<i>Asplenium</i>	Terrestrial, epilithic or epiphytic	30	9	440	36	830
<i>Elaphoglossum</i>	Epiphytic or epilithic, less often terrestrial	65	36	584	57	764
<i>Hymenophyllum</i>	Usually, low to middle epiphytes on tree trunks; sometimes, canopy sun epiphytes; occasionally, epilithic or terrestrial	81	38	237	89	319
<i>Phlegmariurus</i>	Epiphytic or terrestrial (<i>Huperzia</i>)	51	35	214	35	308

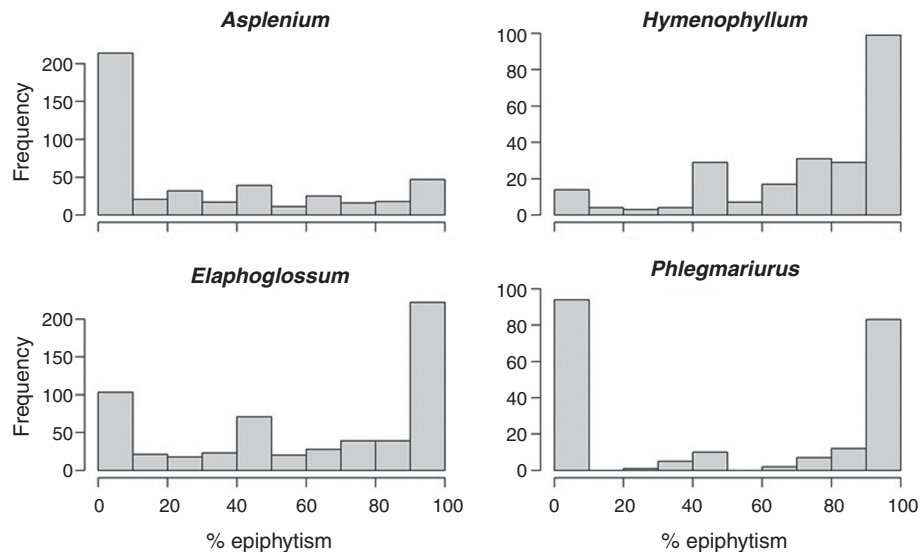


FIG. 1. Histogram showing the tendency of *Asplenium*, *Elaphoglossum*, *Hymenophyllum* and *Phlegmariurus* species to occur epiphytically.

From both ecological and evolutionary perspectives, it is instructive to analyse which of the three possible transitions (epiphyte–lithophyte, epiphyte–terrestrial or lithophyte–terrestrial) is more common. The four genera differ strongly in that regard. In *Hymenophyllum*, the genus with the strongest trend to epiphytic growth, the facultative epiphytic/lithophytic growth exceeds facultative epiphytic/terrestrial growth by a factor of three (48 species vs. 16 species). Only two species (*Hymenophyllum macrosorum* and *Hymenophyllum nahuelhuapiense*) seem to grow facultatively on rock or terrestrially. In contrast, in *Elaphoglossum*, which can also be described as a primarily epiphytic genus, the number of facultatively epiphytic/terrestrial species is twice as large as that of facultatively epiphytic/lithophytic species (91 vs. 44 species), with a smaller number of species along the lithophyte–terrestrial axis (31 species). In *Asplenium*, the number of facultatively epiphytic/lithophytic and facultatively epiphytic/terrestrial species was almost identical (37 vs. 34 species), whereas owing to the large proportion of habitat specialists in *Phlegmariurus* there are few facultative epiphyte/lithophyte/terrestrials in general.

DISCUSSION

How many ‘epiphyte species’ are there in the focal genera?

We compared the proportion of epiphytic species as listed in EpiList 1.0 (Zotz et al., 2021b) with the respective number of species with a preference for epiphytic growth (EV > 50%) or the number of obligate epiphytes (EV > 95%) (Table 2). With the exception of *Phlegmariurus*, the number of ‘epiphyte species’ in EpiList 1.0 is always substantially higher than the estimated proportion of obligate epiphytes in the present study (EV > 95%). This has a clear methodological reason. EpiList 1.0 included any species with at least one reference in the scientific literature describing it as epiphytic or primarily epiphytic. In contrast, the present study quantified habitat preference using as many

sources as possible. For example, *Elaphoglossum angulatum*, *Asplenium mucronatum* or *Hymenophyllum nephrophyllum* were included in EpiList 1.0 because of their description as ‘epiphytes’ by Steyermark et al. (1995), Labiak and Prado (1998) and Hennequin et al. (2008), respectively. The present analysis, based on numerous sources, now suggests that their propensity for epiphytic growth varies substantially (EV = 67%, EV = 99% and EV = 43%, respectively). However, this discrepancy between EpiList 1.0 and the present data set largely disappears in all genera when an ‘epiphyte species’ is defined as a species with a preference for epiphytic growth, i.e. where EV ≥ 50% (Table 2).

Producing any such species list is ‘work in progress’. With the revision of additional literature for the present study, we found evidence for a number of species that certainly should have been included, but were missed, in EpiList 1.0. For example, *Phlegmariurus balansae* (Cerneaux et al., 1990), *Phlegmariurus nutans* (Cerneaux et al., 1990) and *Phlegmariurus vanuatuensis* (Field, 2018) or *Elaphoglossum alvaradoanum* (Matos et al., 2021) and *Elaphoglossum moyeri* (Tryon et al., 1991) all seem to be obligate epiphytes (Supplementary Data Table S1). Consequently, a future version of EpiList will both exclude now doubtful entries, such as *H. nephrophyllum*, and include additional species, such as those mentioned in the previous sentence.

Interestingly, the problem with defining an ‘epiphytic species’ resembles that of defining a ‘CAM species’. Plants using crassulacean acid metabolism show a highly variable proportion of nocturnal and diurnal CO₂ uptake (Zotz et al., 2023), and calling every species with some measurable nocturnal acidification a ‘CAM species’ would inflate their number in a similar fashion to calling any species with occasional epiphytic occurrence an ‘epiphyte species’. Although admittedly arbitrary, Winter (2019) defined ‘CAM species’ as those that obtain the majority of their carbon through the CAM pathway throughout their lives, typically deduced from a δ¹³C values of leaf tissue of >–20‰. Using this rationale as a model for how to deal with the observed continuous variation in habitat

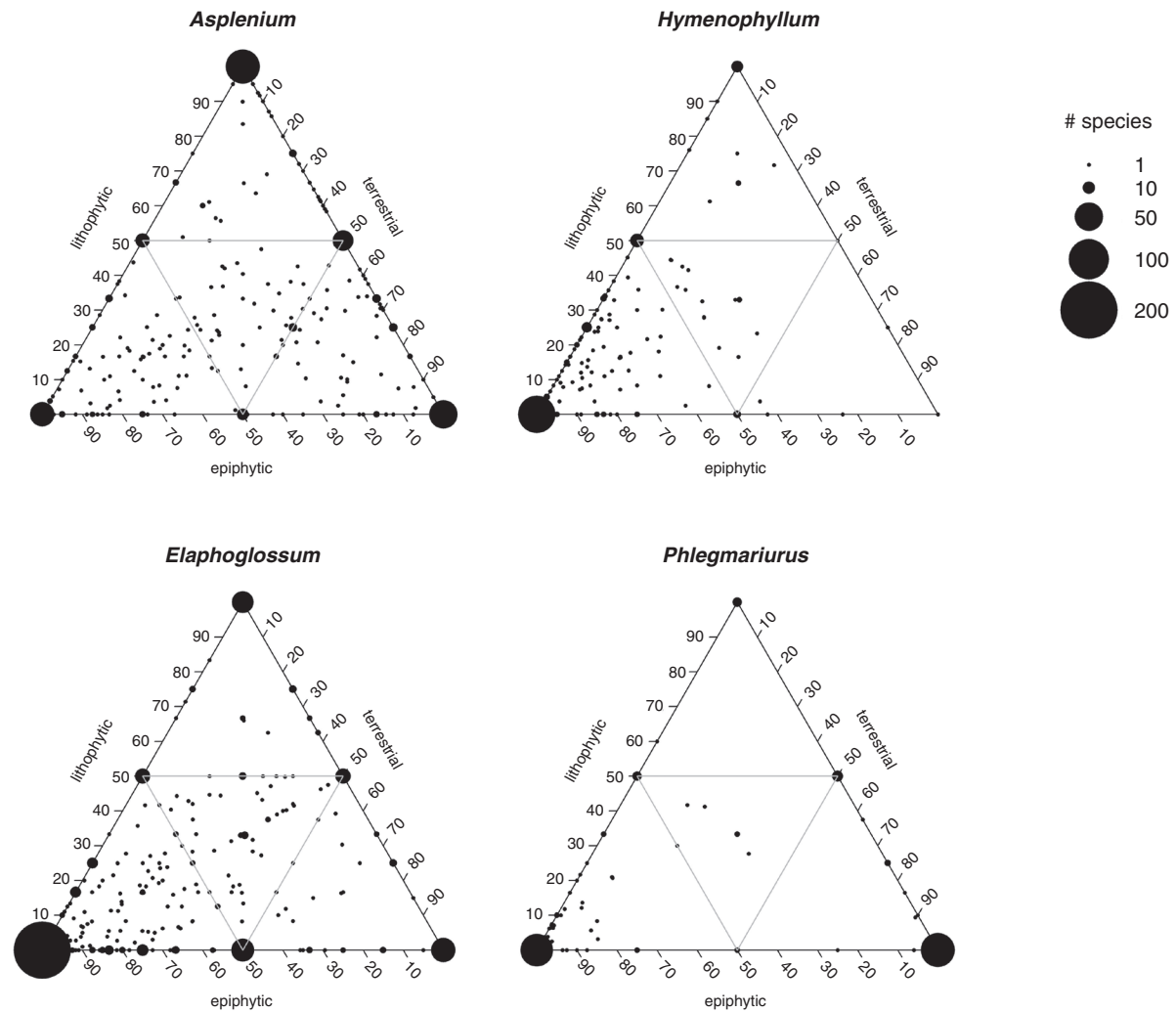


FIG. 2. Distribution of 440 *Asplenium*, 584 *Elaphoglossum*, 237 *Hymenophyllum* and 214 *Phlegmariurus* species in the epiphyte–lithophyte–terrestrial space. Symbol size varies according to the number of species with the same values of EV, LV and TV. The thin grey lines separate three zones of preference for epiphytic, lithophytic or terrestrial growth, with the central triangle being occupied by generalists. Individual species values are based on 1–54 sources. The full data set is given in the [Supplementary Data \(Tables S1 and S2\)](#).

preference in vascular plants, we suggest that ‘epiphyte species’ should be defined as those species that occur primarily in tree crowns. Within the epiphyte–lithophyte–terrestrial space, this would be equivalent to all species in the lower left of the four triangles (Fig. 2).

Intraspecific variation in habitat preference: overestimated or underestimated?

A fundamental goal of this study was to capture natural intraspecific and interspecific variation in habitat use in four large fern and lycophyte genera with a numerical approach. This goal faces many challenges. In many cases, information is very limited, e.g. when data are available only from the type or from very few specimens from one or a few locations. This is true, e.g. for *Asplenium dayi* (Proctor, 1985), *Asplenium merapohense* (Jaman et al., 2017) or *Hymenophyllum chamaecyparicola* (Chang et al., 2022), which might potentially lead to an

underestimation of intraspecific variation in such cases. In turn, lumping several taxa with distinct ecology in one species might lead to an overestimation of intraspecific variation. Recently, Gonzatti et al. (2023) analysed the *Hymenophyllum polyanthos* complex in the Brazilian Atlantic Forest Domain: taxa such as *Hymenophyllum schomburgkii* or *Hymenophyllum viridissimum*, which are treated as synonymous in the check list of Hassler (2004–2022), differ in their habitat preferences from *H. polyanthos*, which might increase the variation documented for that species. Similar problems are likely in the *Asplenium nidus* complex (Yatabe and Murakami, 2003). There are numerous other examples, in which different species concepts influence the outcome of such an analysis, and variation might thus be interpreted as either intraspecific or interspecific. For example, Kramer (1978) distinguishes *Elaphoglossum schomburgkii* and *Elaphoglossum luridum* (with different preferences: terrestrial and epiphytic vs. epiphytic), but Hassler (2004–2022) treats them as synonyms, or an epiphytic form of *H. polyanthos* with pendulous fronds has been treated as a

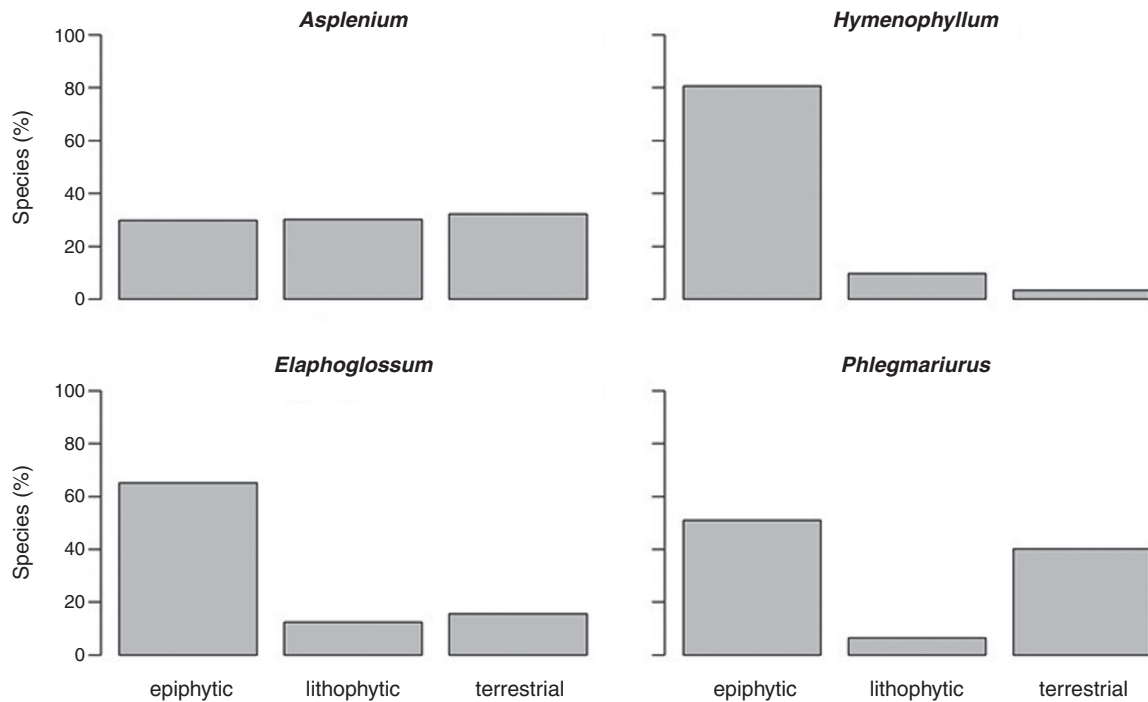


FIG. 3. Preference for epiphytic, lithophytic or terrestrial growth in four genera of ferns and lycophytes. Preference is defined by species values of EV, LV or TV $\geq 50\%$. For species at the border, e.g. EV = LV = 50%, we assigned half of them to E and half to L. The numbers do not sum to 100% because, in a small number of species, neither EV nor LV nor TV reaches 50% (central triangle in Fig. 2).

species, *Hymenophyllum blumeanum*, or can be seen as a variety (Sledge, 1982). As a final example, variants of several *Asplenium* species vary in preferences, e.g. *Asplenium radicans* var. *cirrhatum* is ‘usually on mossy tree trunks and shaded banks’, whereas the three other variants occur only terrestrially (Proctor, 1985).

Besides taxonomic ambiguities, inconsistent use of terminology is another major problem. For example, in the species description of *Phlegmariurus loefgrenianus*, Ølgaard and Windisch (2019) initially described it as ‘epiphytic’, but later as ‘epiphytic or epilithic’. In the same paper, *Phlegmariurus itambensis* is initially described as ‘terrestrial’ and later as ‘epilith growing in some of the driest harshest quartzitic rock conditions’. The second example is probably indicative of a larger issue: many authors probably do not distinguish consistently between ‘terrestrial’ and ‘lithophytic’.

Apart from such inconsistencies, there seems to be a tendency among many researchers to prefer neat categories over ‘noise’. As a case in point, Mellado-Mansilla *et al.* (2018) state that at their site a large proportion of the species described as ‘epiphytes’ by Moreno *et al.* (2013) for the region were found primarily on rocks or slopes of river beds. Yet, they still classified them as epiphytes as ‘the most common growth form’ in the region. Such an approach produces neat categories but obviously conceals true biological variation. Being mentioned explicitly by Mellado-Mansilla *et al.* (2018), we could at least reject that data set for our analysis. An unknown number of studies might have taken a similar approach and included the ‘typical’ habit from other sources without mentioning it. There is no way to exclude this potential source of error from our analysis.

As discussed in detail by Zotz and Einzmann (2023), our numerical approach has some issues of its own. First, different researchers will not have had the same numerical equivalent in mind when using terms such as ‘commonly’, ‘less frequently’ or ‘rarely’. Second, to assign a 50% preference for epiphytic and lithophytic growth for a statement such as ‘on trees and rocks’ vs. ‘on rocks and trees’ was simply the most parsimonious approach for want of a more convincing alternative; it remains unclear whether such an order reflects a real difference in preference. Third, we used a single species average for epiphytic, lithophytic or terrestrial growth in our analysis. Intermediate values can reflect local variation in substrate use or geographical variation of a rather strict growing site preference, as mentioned by Tryon *et al.* (1993) for numerous *Asplenium* species. It was outside the scope of the present study to tackle this question, but the detailed compilation of information in the Supplementary Data can be the starting point for future investigations.

Towards a more realistic view of habitat preferences?

The correct assessment of the growing sites of a species represents an important part of the description of its biology. It is even indispensable when trying to understand its ecology. Unfortunately, species are often assigned rather coarsely to one of several types, ignoring the true complexity as evidenced in the present study. The notion that lithophytic, terrestrial and epiphytic habitats are inherently distinct (e.g. Watts and Watkins, 2021) is clearly an oversimplification, because arguably, the growth conditions among ‘epiphytes’ or ‘lithophytes’ can vary almost as much as between them. For instance,

compare the vastly different growth conditions of an epiphyte in the moist understorey of a rainforest with those of an epiphyte in the outermost parts of a tree crown in a dry forest or those of a lithophyte on a fully exposed boulder vs. those of one on a shaded rock near a creek. In contrast, the growth conditions on the lower portions of a moss-covered tree trunk might hardly differ from those on a moss-covered rock in the understorey; growth in thick moss cushions might be more important than the subjacent substrate rock, soil or bark. Likewise, we recently showed that an epiphyte growing in a detritus-filled crotch can enjoy similar or even better growth conditions than a terrestrial conspecific in the immediate vicinity on the ground (Hoerber and Zotz, 2021).

Overall, however, there is the frequent notion that lithophytic and epiphytic growth conditions are more similar than conditions of plants rooting in soil. This can be an implicit assumption, e.g. by Holtum and Winter (1999) or by Dittrich *et al.* (2005), or stated explicitly. For example, Seifriz (1943) states that ‘epiphytic aroids ... on rocks ... are still epiphytes, physiologically considered’, Tsutsumi and Kato (2006) claim that ‘obligate epiphytes also occur on rocks’, Weston *et al.* (2005) write that ‘many epiphytes also grow on rocks’ or Couto *et al.* (2023) stress that growth in trees and on rocks ‘requires similar adaptations’. The claimed ecological similarity also suggests evolutionary scenarios. With this in mind, Zotz (2016) speculated that evolutionary transitions from lithophyte to epiphyte and vice versa might have been more common than those from the terrestrial habit to either of the two. Our analysis does not provide strong support for this notion (Fig. 2). Although the facultative use of the epiphytic and lithophytic habitats was indeed much more common than the two alternatives in *Hymenophyllum*, this was not the case in *Elaphoglossum*: species of this genus that occur both terrestrially and epiphytically are much more common than facultative epiphyte/lithophytes. In the two other genera, we found no differences in the number of facultative epiphyte/lithophytes vs. epiphyte/terrestrials (*Asplenium*), or the total number of species with facultative habitat use was generally small (*Phlegmariurus*).

Acknowledging intraspecific variation is not restricted to the three categories of this study. Lagomarsino *et al.* (2012) have shown that at least in one *Elaphoglossum* species, *Elaphoglossum amygdalifolium*, spores consistently germinate on bark, producing epiphytic gametophytes, while sporophytes later establish root contact with the soil. This ontogenetic pattern, with an epiphytic and ground-rooted stage, characterizes so-called hemiepiphytes (Zotz *et al.*, 2021a). Categorizing a species as ‘hemiepiphyte’ faces the same problem as outlined for ‘epiphytes’ or ‘lithophytes’. It should be highly instructive to study whether the establishment in this species follows this pattern without exception and whether this ontogenetic pattern might be found, at least occasionally, in related species.

Acknowledging intraspecific variation in substrate use is also crucial for analyses of trait or life-history evolution. When studying the evolution of epiphytism, many analyses use simple dichotomies of terrestrial vs. epiphytic species (e.g. Hennequin *et al.*, 2008; Field *et al.*, 2016; Bauret *et al.*, 2018; Testo *et al.*, 2018), although more elaborate schemes have been used in a few cases. For example, Lehnert and Krug (2019) differentiate between terrestrials, lithophytes and ‘low’ and ‘high’ epiphytes.

As stated previously (Zotz and Einzmann, 2023), analyses of evolutionary transitions from, e.g. terrestrial/ lithophytic to epiphytic growth (Hennequin *et al.*, 2008) or vice versa (Chen *et al.*, 2023) would benefit from abandoning the typically adopted categorical approach. Ignoring intraspecific variation allows only step changes instead of a more realistic gradual change.

In summary, we adopt a recently introduced approach to quantify substrate preferences to four genera of ferns and lycophytes. A large majority of species show clear preferences for epiphytic, lithophytic or terrestrial growth, but strict specialization is found in only a minority of species. *Phlegmariurus* is exceptional in this regard, with almost 70 % of all species being apparently restricted to either epiphytic or terrestrial growth. Our approach should be very useful in phylogenetic and ecological studies, and we reiterate the plea by Ebihara *et al.* (2007) on the importance of field observations for evolutionary studies. Our ecological classification schemes have to embrace the complexity of the biology of these plants, but any such scheme will translate into real progress only with high-quality field data. We hope that this paper helps to motivate researchers to collect and publish such data.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Table S1: original data of habitat preferences in four genera of ferns and lycophytes from 542 sources. **Table S2:** mean substrate preference values for 1475 species in four genera of ferns and lycophytes for epiphytic (EV), lithophytic (LV) and terrestrial growth (TV).

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CONFLICTS OF INTERESTS

The authors have no conflicts of interest to declare.

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