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Differential "Tree Attraction"—Epiphytic Growth of *Umbilicus rupestris* and Other Lithophytic Crassulaceae

Gerhard Zotz *

Functional Ecology Group, Institute of Biology and Environmental Sciences, Carl von Ossietzky Universität Oldenburg, Box 2503, D-26111 Oldenburg, Germany

* Corresponding author. E-mail: gerhard.zotz@uol.de (G.Z.)

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ABSTRACT: Epiphytic species grow (almost) exclusively on a living substrate, typically a tree, but epiphytic growth is not restricted to them. Individuals of normally lithophytic or terrestrial species may occasionally be found on a tree as so-called accidental epiphytes. Species of the focal group of this study, Crassulaceae, are typically found on rocks and in rock fissures. While there is a small proportion of true epiphytes globally, the propensity of the other family members to occur as accidental epiphytes is largely unexplored. Here, I investigated this question for 29 European members of the family with the use of the participatory science data platform iNaturalist. *Umbilicus rupestris* stands out in regard to epiphytic occurrences, although the incidence of epiphytic growth is still rather low with c. 1% of c. 14,000 observations. For all other species, epiphytic growth has not been reported or was exceptional. As expected, epiphytic individuals of *U. rupestris* were limited to regions without frost, while a predicted limitation to the wettest parts of the species' geographic range was not supported by the data. Arguably, *Umbilicus rupestris* could be a promising model to study the early steps of epiphyte evolution by comparing epiphytic and terrestrial individuals in regard to differential germination success, ease of establishment, differences in morphological and physiological traits and general population dynamics. The results of such studies should be highly instructive for our understanding of the challenges that terrestrial species face when conquering tree crowns.

Keywords: Accidental epiphytes; Crassulaceae; Crassulacean acid metabolism; Dispersal; Lithophyte

1. Introduction

About 30,000 species of vascular plants grow exclusively or at least mostly epiphytically, *i.e.*, they spend their entire lives on a living host without contact to the soil and, in contrast to mistletoes, do not parasitize their host, EpiList 1.0, [1]. While a few families, in particular Orchidaceae, Bromeliaceae, Araceae and Polypodiaceae, account globally for the large majority of species with this life style, epiphytic growth is also found in about 80 other families of vascular plants (e.g., Asteraceae, Crassulaceae, Rubiaceae). There is not a single unique trait that sets those species that primarily grow epiphytically apart from the majority of vascular plants, which grow rooted in soil or on rock. However, considering the intermittent water supply in the epiphytic habitat, which is frequently named as a major abiotic challenge for epiphytic growth [2,3], some kind of external (phytotelms) or internal water storage (succulent leaves, shoots or roots) or physiological traits associated with efficient water use such as crassulacean acid metabolism (CAM) are rather common [4].

Members of the Crassulaceae are typically found on rocks or rocky soils, are characterized by leaf and stem succulence of varying degree and a considerable proportion of the species use CAM [5,6]. Since there is some overlap in the general growth conditions of an epiphyte and a lithophyte one could expect a considerable proportion of species in this family to be growing on trees. However, only 27 out of 1482 accepted species (=2%) are listed as typical epiphytes by Zotz et al. 2021 [1]. However, it becomes increasingly clear that the long-standing practice of defining "species" as epiphytes, or not, conceals substantial intraspecific and interspecific variation in the propensity to grow epiphytically. Two recent studies with several genera of vascular plants [7,8] have clearly shown that it may be a potentially misleading oversimplification to assign species to the distinct categories epiphyte, lithophyte or terrestrial.

Rather, species differ in their preference for either habit in a gradual manner. Thus, instead of categorizing a plant species as epiphyte or terrestrial ("0 *or* 100%") one should quantify its *tendency* to grow as an epiphyte, which arguably can take on any value between 0–100%.

A well-documented biogeographical pattern in the global distribution of epiphytism is a strong latitudinal gradient in the occurrence of epiphytic growth [9]. Vascular epiphytes are a typical feature of most tropical forests. In the extreme case, epiphytic species may account for the majority of taxa in a local tropical florula [10], while in temperate forests epiphytic growth is mostly restricted to non-vascular mosses and lichens, a few noteworthy exceptions are discussed in [9]. The majority of vascular plants that can be found growing on trees in temperate Europe are actually "accidental epiphytes", *i.e.*, individuals of clearly terrestrial species that have established in special tree microhabitats with rather benign conditions like detritus-filled crotches or knotholes [11]. Some fern species are exceptional in that regard in Europe: *Davallia canariense*, *Polypodium macaronesicum* or *Polypodium vulgare* may be found at least occasionally in other microhabitats, on bare bark or in low moss turves [12–14].

As in the family in general, the European species of Crassulaceae are primarily found on rocks or skeletal soil [15]. Remarkably, the Flora Europaea explicitly mentions occasional epiphytic growth for one species: *Umbilicus rupestris*. This highly variable species has a large distributional range from Turkey and Cyprus to Scotland in the North and the Azores in the West. It is mostly found on natural rock outcrops or skeletal soil, but also on human-made structures like stone walls or roofs. While the national floras of Spain and Great Britain do not mention epiphytic growth of this species, e.g., [16,17], there are also contrasting reports from both countries that document epiphytic occurrence in particular localities in Spain [13] and Ireland [18]. Further epiphytic occurrences are documented for Portugal [19] and for Croatia [20]. However, there are also scattered reports of rare epiphytic occurrences of other Crassulaceae, e.g., of *Sedum hirsutum* in Portugal [21], and of *Umbilicus horizontalis* in Croatia [20].

The current study quantifies epiphytic occurrences of 29 species of Crassulaceae by reviewing more than 30,000 observations that had been uploaded on the participatory science data platform iNaturalist, 2024 [22]. The use of this platform as a research tool has been discussed in detail in several recent publications [23–25]. All of them conclude that this platform can be a very useful tool for biological research. Since observations are typically georeferenced it is possible to visualize the geographic distribution of these observations and to approximate the climatic conditions of each observation with climate models. This allowed me to address the following questions for the species with the largest percentage of epiphytic occurrences: (1) How frequent is epiphytic growth in *Umbilicus rupestris* over its entire distributional range? (2) Does the geographical distribution of epiphytic occurrences differ from that of the species at large? (3) Given that the occurrence of frost is sometimes suggested as a limitation for epiphytic growth [9]: do epiphytic individuals of *Umbilicus rupestris* only occur in frost-free regions within the total range of the species? (4) Given that intermittent water supply is often given as a major limitation to epiphytic growth: do epiphytic individuals only occur in regions with relatively high precipitation with low seasonality?

2. Materials and Methods

I reviewed iNaturalist data of 29 species of the family Crassulaceae that occur in continental Europe for epiphytic growth. In all cases with more than 1000 observations (17 species) I reviewed the first 1000 of them, in all cases with fewer observations I reviewed all (12 species, 89–870). The species with the largest proportion of epiphytic occurrences, *Umbilicus rupestris*, warranted further scrutiny. Here, I reviewed each of the 14,308 observations of this perennial herb (as of 22 September 2024). First, since *U. rupestris* overlaps in its southern range with *U. horizontalis*, I checked the species identification in iNaturalist when plants were fertile. This was not possible when plants were vegetative, which introduces the possibility of misidentifications, albeit only in the regions of overlap—*Umbilicus* leaves cannot be confused with any other taxon. For epiphytic individuals, I noted the specific location on a tree, distinguishing plants growing at the "stem base", "stem", "crotch", "branch", or "knothole". The reproductive status (vegetative, flowering, fruiting) was noted as was an association with moss. In a few cases, it was not possible to ascertain on a picture that a moss-covered surface belonged to a rock or a tree trunk. When a request to the original observer for clarification was not answered, I did not include such a doubtful observation.

Very few observations were not georeferenced and were thus not included in the analyses described in the following. The georeferenced observations allowed me to visualize the geographic distribution of *Umbilicus rupestris* and to compare climatic conditions of epiphytic *vs.* non-epiphytic plants. Guided by the questions outlined above I estimated the following climatic variables for each observation: annual mean temperature (MAT, °C), temperature seasonality

(T_S, °C), mean daily minimum air temperature of the coldest month (°C), the mean annual precipitation (MAP) and precipitation seasonality (P_S, °C), using the CHELSA V.1.2 climate dataset. For details see [26,27].

Statistical Analysis

The climatic variables derived for each observation of *Umbilicus rupestris* were compared for the group of epiphytic *vs.* the group of non-epiphytic plants. The data structure did not allow parametric tests. Thus, I used a Wilcoxon sign-rank test to assess the significance of differences for each of the five climatic variables [28]. For all tests, models, and the map I used R version 4.2.3. [29].

3. Results

3.1. Epiphytic Occurrences of Crassulaceae

In the majority of cases (23 species = 79% of all studied species) I did not find a single epiphytic occurrence documented in iNaturalist in a sample of 1000 observations per species. In 3 *Sedum* and 1 *Aichryson* species there was at least 1 observation each, and in *Umbilicus horizontalis* 3 observations that documented epiphytic growth. Congeneric *Umbilicus rupestris* seems to be exceptional among European members of Crassulaceae concerning epiphytic growth with 12 observations, which is equivalent to about 1% of all individuals (Table 1).

Table 1. Epiphytic occurrences of 29 species of Crassulaceae from continental Europe. Given are species names, the number of reviewed observations in iNaturalist, and the number (#) and the percentage (%) of observations with epiphytic growth. n/a = too few observations for a reasonable estimate. For details see Materials and Methods. Note that the percentage estimate of epiphytic *U. rupestris* in the sample of 1000 observations slightly deviates from that of the whole set of more than 14,000 observations.

Species	# Epiphytes	# Sample	% Epiphytic
Aeonium arboreum	0	277	n/a
Aichryson laxum	1	126	n/a
Cotyledon orbiculata	0	102	n/a
Crassula tillaea	0	1000	0
Hylotelephium maximum	0	1000	0
Petrosedum rupestre	0	1000	0
Phedimus spurius	0	1000	0
Rhodiola rosea	0	1000	0
Sedum acre	0	1000	0
Sedum album	0	1000	0
Sedum alpestre	0	684	0
Sedum annuum	0	519	0
Sedum atratum	0	870	0
Sedum cepaea	0	561	0
Sedum dasyphyllum	0	1000	0
Sedum forsterianum	0	1000	0
Sedum hirsutum	1	1000	0.1
Sedum hispanicum	0	1000	0
Sedum palmeri	1	840	0.1
Sedum praealtum	1	609	0.2
Sedum rubens	0	568	0
Petrosedum sediforme	0	1000	0
Sedum sexangulare	0	1000	0
Sedum villosum	0	1000	0
Sempervivum arachnoideum	0	1000	0
Sempervivum globiferum	0	1000	0
Sempervivum tectorum	0	392	n/a
Umbilicus horizontalis	3	641	0.5
Umbilicus rupestris	12	1000	1.2

3.2. Epiphytic Occurrences of Umbilicus rupestris

The 14,308 observations of *Umbilicus rupestris* in iNaturalist covered almost its entire known range from Turkey in the East to the Azores in the west, and from Southern Spain to Scotland in the North (Figure 1).

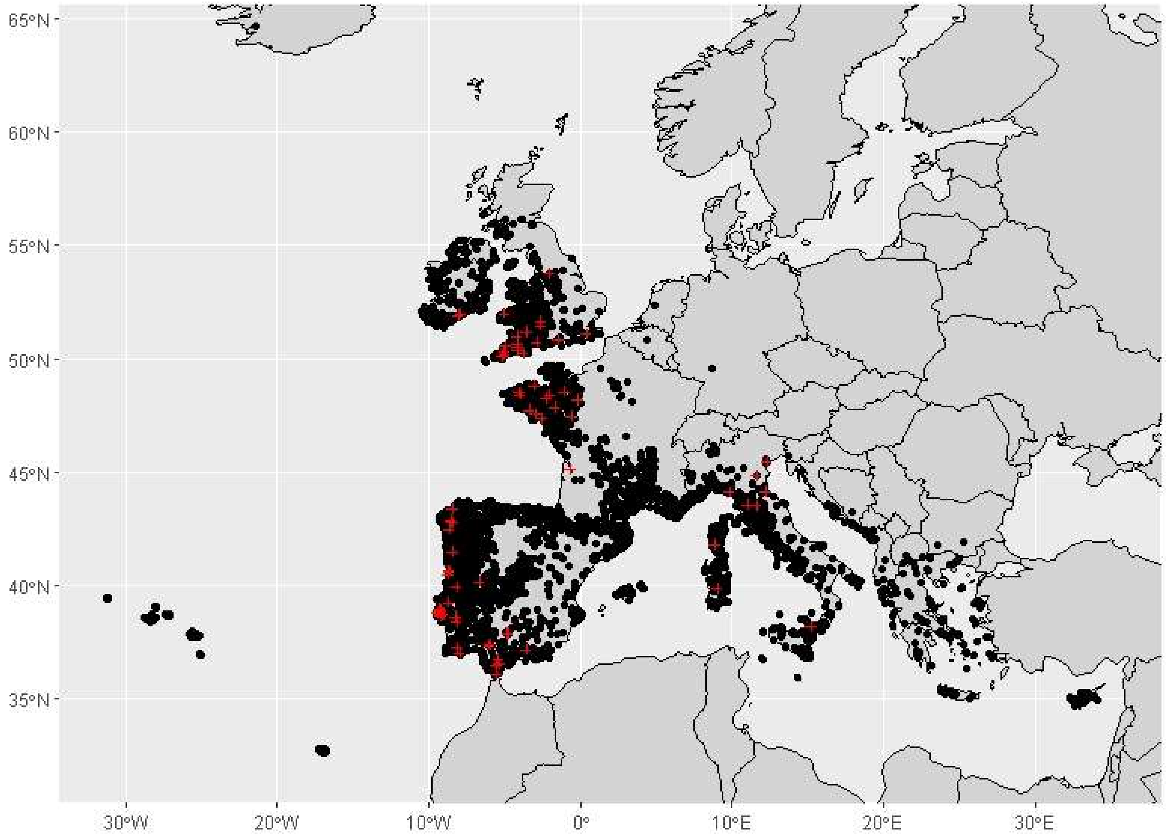

Figure 1. Geographical distribution of iNaturalist observations of *Umbilicus rupestris*. Each black dot represents one observation of terrestrial growth, each red cross one with epiphytic growth. Note that in many cases dots may totally or partially overlap if conspecifics were so close that a distinction is impossible given the scale of this map.

Of the total, only 97 (=0.7%) observations documented plants growing on a tree (Figures 1 and 2). The majority of these epiphytic individuals were growing on trunks or branches with no association with moss (Table 2). A large proportion of them (57%) were either flowering or fruiting.

Table 2. Substrate type on which the 97 epiphytic individuals of *Umbilicus rupestris* were found on. Given are both the respective absolute and relative number of individuals per substrate type.

Substrate	Individuals	% Total
branch	7	7.2
crotch	15	15.5
dead wood	1	1.0
knot–burr–gnarl–knothole	5	5.1
stem base	14	14.4
trunk	55	56.7

Epiphytic occurrences of *Umbilicus rupestris* were clearly not evenly scattered over the entire distributional area, but clustered in regions near the sea, e.g., in Southwest England, Brittany, or along the Atlantic coast of the Iberian Peninsula (Figure 1). A comparison of the climatic conditions of the sites of epiphytic occurrences *vs.* terrestrial ones revealed that all three climatic variables related to temperature were significantly different, while the two variables related to precipitation were not (Table 3). Particularly noteworthy was the (near) absence of frost at the 97 localities with epiphytic *Umbilicus rupestris*. There, the average daily minimum was above 0 °C in all cases, while a substantial number of terrestrial counterparts clearly experiences subzero temperature.

Figure 2. Flowering *Umbilicus rupestris* growing on a *Castanea sativa* trunk, near Locmariaquer, France. Date July 2013, © Gerhard Zotz.

Table 3. Comparison of climatic variables of growing sites of epiphytic *vs.* non-epiphytic individuals. Shown are medians and *p*-values of Wilcoxon sign-rank tests. Variables are annual mean temperature (MAT, °C), temperature seasonality (T_S, °C), mean daily minimum air temperature of the coldest month (°C), mean annual precipitation (MAP) and precipitation seasonality (P_S, °C).

Variable	Epiphytes	Non-Epiphytes	*p* (Wilcoxon)
MAT	14.6	12.7	0.01
T_S	4096	4483	0.01
T_{min}	5.4	4	0.001
MAP	827	873	0.12
P_S	40	33	0.06

4. Discussion

Dawson, 1988 [30] and Wardle, 1991 [31] both claimed that, in principle, any terrestrial species can grow epiphytically in nature given (1) successful dispersal and the availability of a (2) suitable microhabitat on a tree. The results of this study suggest that in the case of most European species of Crassulaceae such a situation is extremely rare. This finding comes somewhat as a surprise since the challenges of lithophytic and epiphytic growth are often described as comparable [32,33]: both habitats share a largely impenetrable substrate that inevitably leads to problems of anchorage and procurement of water and nutrients. Both types of challenges may explain why accidental epiphytism of terrestrial species in Europe is typically limited to particular microsites on a tree, e.g., detritus-filled crotches [34]. This should not affect Crassulaceae, however, because lack of humus or establishment on a vertical substrate are usual challenges in their typical growing sites such as rocks or rocky soils. Moreover, many of the species included in this study occur occasionally on human-made structures like roofs or establish on vertical stone walls with little organic material, e.g., [35], which is testimony to successful dispersal to "unusual" growing sites.

The only species that seems to stand out in regard to growth on trees among the studied set of Crassulaceae is *Umbilicus rupestris*. My findings suggest that about 1% of its members grow as epiphytes. Unlike most other accidental epiphytes in Europe, which are typically restricted to special, relatively benign microhabitats on their host tree like crotches with accumulated humus or knotholes [34], a majority of epiphytic *Umbilicus* plants were found growing directly on bark, in the lower and mid portions of the trunk or even higher up on branches (Table 2). This may reflect the legacy of its typical growth as a lithophyte, which grows on more or less impenetrable substrate. Moreover, the ability of growth at desiccation-prone microsites may also be related to its photosynthetic pathway—the species is one of relatively few species within the European flora that uses crassulacean acid metabolism (CAM), at least facultatively [36]: plants that use CAM can achieve much higher water use efficiencies than C3 plants [37]. However, CAM is also found in many other species in the family like *Sedum acre* or *Sedum album* [38], for which I found no observations of epiphytic growth (Table 1).

Since it is well-established that variation in water availability is typically much more pronounced in the epiphytic habitat compared to the ground [39], one would expect that epiphytic occurrences of *Umbilicus rupestris* are mostly found at the wetter end of the species' geographical distribution, particularly when growing directly on bark. This is clearly not the case: the modelled estimates of MAP of the growing sites of terrestrial and epiphytic individuals are statistically indistinguishable (Table 3); the median of the latter was even substantially lower. However, clear differences were found in regard to temperature. On average, epiphytic individuals grew at relatively warm sites close to the sea, with little or no frost. This is in line with a proposed explanation for a global limitation of epiphytic growth by sub-zero temperatures [2], although there are also many observations that are not in agreement with this notion [40,41]. Hence, the general role of frost as key factor for the distribution of vascular epiphytes remains contentious [9].

Hoeber, Zotz, 2022 [11] emphasized that the study of accidental epiphytes may reveal much about epiphytism in general. Specifically, Lüttge, 2008 [3] conceptualized epiphytism as the opportunistic use of space, and in evolutionary terms this conquest of tree crowns by vascular plants has happened numerous times independently in different families [42]. Thus, identifying what sets *Umbilicus rupestris* apart from other Crassulaceae may allow us to understand the circumstances associated with the first step in the evolution of a species that may eventually grow primarily or even exclusively epiphytically such as *Sedum tortuosum* or *Echeveria racemosa* [1,43,44]. Such an evolutionary trajectory is only possible, however, if a species does not only establish itself in an arboreal habitat, but is also capable of in situ reproduction. This is clearly the case in *Umbilicus rupestris* as more than 50% of all observations show plants with inflorescences or infructescences. Moreover, this number most likely underestimates the real proportion of reproductive individuals as photographs uploaded to iNaturalist were taken throughout the year, *i.e.*, also show plants in an early phenological phase that may have later developed reproductive organs. However, the major value of a descriptive study like the current one is to set the scene for experimental approaches like comparisons of the germination and establishment success in epiphytic and lithophytic situation or demographic studies of epiphytic and lithophytic populations.

Admittedly, the frequencies of epiphytic occurrences documented for *Umbilicus rupestris* and other Crassulaceae (Table 1) can only be taken as rough estimates since observations were not made systematically. Thus, it is unclear whether iNaturalist contributors were somehow biased when uploading observations. For example, it is conceivable that epiphytic occurrences seemed to be more worthy of reporting than yet another occurrence in the "typical" habitat, but, alternatively, the author knows from own experience that epiphytic occurrences may often be missed. Globally, very few studies have directly quantified the numbers of individuals of a species that grew either epiphytically, lithophytically or terrestrially in a particular study area, e.g., [45,46], or that documented changes in the proportion of epiphytic *vs.* terrestrial occurrences along an environmental gradient [47].

In the large majority of plant species, available information on habit is only qualitative. Such information can still be used to come up with a rough estimate of habit preference by translating verbal descriptions like "terrestrial, rarely epiphytic" or "both epiphytic and terrestrial" in reasonable percentages, e.g., 95%/5% for the former and 50%/50% for the latter, but even with averages from multiple sources for each species such an approach obviously can only be semi-quantitative [7,8]. To date, this numerical translation is inevitably arbitrary—a *calibration* with actual data such as the ones reported here is needed to evaluate the realism of the quantitative results of these studies.

Irrespective of the question whether the tendency of a given species to grow epiphytically is quantified entirely correctly or not, these recent papers and the present report call attention to the fact that the traditional form of assigning species to the categories "epiphytic", "lithophytic" or "terrestrial" does not adequately represent the gradual nature of substrate preferences. Although a scheme of distinguishing "accidental (<5% epiphytic individuals)", "facultative" (5–95% epiphytic individuals), and "true epiphytes" (>95% epiphytic individuals), has been in use for decades [48], there are hardly any data that would allow us to investigate, e.g., how many of the so-called "epiphytic species" collated in Epilist 1.0 [1] are actually only facultatively using trees as substrate. The two studies by [7,8] suggest that these may amount to a substantial number.

In summary, this paper quantifies the proportion of epiphytic occurrences among 29 lithophytic species and presents an in-depth analysis for one species over its entire range. It shows that, among European Crassulaceae, the perennial *Umbilicus rupestris* is the species with the highest incidence of epiphytic occurrences, although overall epiphytic growth is still rather rare. Epiphytic individuals seem to be limited to regions without frost, while the expectation of a similar limitation to the wettest parts of its geographic distribution was not supported by the data. Species like *Umbilicus rupestris* could be models for the early steps of epiphyte evolution: I suggest to directly study possible physiological and morphological differences of epiphytic *vs.* terrestrial individuals as well as to study germination success, establishment and general population dynamics of epiphytic *vs.* terrestrial individuals. The results should be highly instructive and lead to a better understanding of the challenges that terrestrial species face when conquering tree crowns.

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Not applicable.

Informed Consent Statement

Not applicable.

Data Availability Statement

Data are publically available on iNaturalist or upon request from the author.

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