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RESEARCH ARTICLE

Multiscale drivers of accidental epiphytism in temperate Europe

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Abstract

Accidental epiphytes — terrestrial plants that opportunistically establish in trees — occur across climatic regions, but the conditions that allow them to colonise arboreal habitats remain poorly understood. We combined field surveys along a coastal western European transect, from the Netherlands to northern Spain, with curated community-science records and used Bayesian models to test whether accidental epiphyte occurrence, abundance and richness are associated with habitat setting, host size and macroclimatic positioning within each species' climatic envelope. In the field, accidental epiphytes were more frequent, abundant and species-rich in non-forest settings than in forests and larger trees were more likely to support accidental epiphytes in both habitat types. Across species' climatic envelopes, Bayesian estimates indicated that accidental epiphytes tended to occur under cooler summer and milder winter conditions, whereas moisture and wind effects were weaker and less consistent. These results suggest that accidental epiphytism is shaped by hierarchical filtering: the availability and traits of terrestrial species determine the potential pool of accidental epiphytes, host size and associated structural complexity affect local arrival, retention and establishment probability, landscape structure determines broader opportunities for arboreal recruitment and macroclimatic context influences where terrestrial species most often appear in trees. By linking local host-level filters with species-level climatic-envelope positions, our study supports an open-landscape pathway into epiphytism, while leaving room for alternative routes in shaded, humid forests. Accidental epiphytes, therefore, provide a promising model for studying terrestrial-to-arboreal transitions across biogeographical contexts.

Highlights

- First landscape-scale assessment of accidental epiphyte encounter probabilities.
- Proposal of a hierarchical-filtering framework in which species availability and traits, dispersal and diaspore retention, host traits and structure, microhabitat availability and microclimate, landscape setting and macroclimate interact to shape accidental epiphytism.
- Open-landscape trees may provide repeated canopy colonisation opportunities and potential refugia.
- Open-adapted and closed-forest species may follow complementary routes into epiphytism.
- Accidental epiphytes can be considered a tool to study early stages of terrestrial-to-arboreal plant transitions.

Keywords

Accidental epiphytes, Atlantic European coast, citizen science, climatic envelopes, dispersal, epiphyte evolution, human-modified landscapes, moss mats, temperate epiphytism, tree-related microhabitats

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Introduction

> *"In the cold North, the bark of trees is covered only with dry lichens and mosses, while beneath the tropics the* Cymbidium *and the fragrant* Vanilla *adorn the trunks of the Anacardias and the gigantic Fig-tree. […] These and many other of the enjoyments which nature affords are denied to nations of the North".* Alexander von Humboldt (1769–1859) in Views of Nature (1850)

True epiphytes — plants that complete their life cycle non-parasitically on other plants without contact to the soil (Zotz 2016) — are essential features of most tropical vegetation (Nieder et al. 1999). Life above ground is not associated with any idiosyncratic adaptation. Rather, epiphytes exhibit exhibit striking morphological, physiological and ecological diversity and contribute to water interception and storage, nutrient retention and cycling and habitat structure (summarised in Zotz (2016)). They typically comprise only a small fraction of above-ground biomass yet often account for a disproportionately large share of local plant species richness in (sub-)tropical forests (e.g. Kelly et al. (2004)).

Contrary to Humboldt's view, a surprising number of vascular plants can be found on the trunks and lower crowns of trees even at higher latitudes (Zotz 2005). Most of these are "accidental epiphytes", i.e. epiphytic individuals of predominantly terrestrial species without obvious specialisation to epiphytic growth (Zotz 2016). Accidental epiphytes (Fig. 1A–G) were already noted in ancient Greece by Theophrastus and Pliny the Elder (as cited in Heintze (1932, 1935)), but mostly escaped scientific attention until the late nineteenth century, when they started to be reported intermittently under a variety of names, mostly in descriptive or anecdotal accounts (Zotz (2003) and references therein). Only in the current millennium has there been a rise in more standardised inventories that quantify the frequency, persistence and community structure of accidental epiphytes (e.g. Guzmán-Marín and Saldaña (2017); Hoeber et al. (2019); Brock and Burns (2021); Komada et al. (2024)).

While the species richness of true epiphytes declines steeply with latitude, tracking broad gradients in tropical forest area, precipitation and temperature (Schimper 1888; Taylor et al. 2022), accidental epiphytes are documented from (sub-)tropical (Zotz and Schultz 2008; Machado et al. 2022) through temperate (Guzmán-Marín and Saldaña 2017) to sub-arctic regions (Holmboe 1904; iNaturalist 2026a), sometimes in substantial numbers (Hoeber et al. 2019; Brock and Burns 2021; Komada et al. 2024). Despite this broad geographic spread, occurrences converge on similar ecological patterns: firstly, they follow the local species pool (Brock and Burns 2021), suggesting that, principally, any terrestrial species can exploit canopy niches provided diaspores find suitable microhabitats (Dawson 1988; Wardle 1991) or "safe sites" (*sensu* Harper et al. (1961)). Secondly, accidental epiphytes are not distributed randomly within trees, but are (mostly) restricted to a set of favourable arboreal microhabitats (Brock and Burns 2021; Hoeber and Zotz 2021; Komada et al. 2024).

These microhabitats are typically water-retentive microsites — notably moss mats (Fig. 1E, F) and knotholes, crotches or forks with accumulations of arboreal soil (Fig. 1A–D, G). They often develop on large and/or structurally complex hosts (*sensu* Moffett (2000)) with presumably benign microclimates and larger rooting volumes. Where growth on the forest floor is constrained (by, for example, competition, herbivory, litter burial or water-logging), the canopy can be comparatively — sometimes even more — favourable than the ground (Hoeber and Zotz 2021, 2022; Azuma et al. 2022). At regional scales, macroclimate might act directly on accidental epiphytes or indirectly by governing the supply of suitable microhabitats and, thus, the relative abundance or vertical position of accidental epiphytes (Brock and Burns 2021).

Compared to their ubiquity, periodic abundance and potential to deliver ecosystem functions similar to those of true epiphytes, accidental epiphytes are a vastly understudied component of forest canopies — and a system that may provide important insights into the evolutionary processes at the initial transition of terrestrial plants into arboreal niches (Zotz 2016; Hoeber and Zotz 2022; Mena-Jiménez et al. 2024). Despite growing interest, empirical studies on accidental epiphytes remain scarce, limiting broader inference about how host structure, habitat setting and climate shape their occurrence across temperate landscapes.

Here, we combine systematic per-tree surveys across 40 forest and non-forest plots spanning an ~ 11° latitudinal transect along the Atlantic coast of Europe with curated iNaturalist records to examine accidental epiphytism at complementary scales. We hypothesised that accidental epiphytism is shaped by hierarchical filtering, beginning with the available terrestrial species pool and operating from host-tree species and size through habitat setting to latitude and climate. Specifically, we expected: i) particular host-tree species and larger trees to support accidental epiphytes more frequently; ii) accidental epiphytism to be more prevalent in open than in forest settings; iii) richness and composition to vary along the latitudinal gradient and iv) epiphytic occurrences to occupy non-random climatic positions within species' expected geographical ranges. By integrating these scales, we ask when and where terrestrial plants most readily persist in canopy niches in a temperate region.

Materials and methods

Study region, site selection and plot design

The study spanned coastal temperate forests and non-forest landscapes (streetscapes and gardens) along the eastern Atlantic from the Netherlands to northern Spain (~ 52°N to ~ 43°N, Fig. 2), surveyed during a sailing expedition from April–October 2025. Candidate forest stands (≥ 1 ha, mixed composition, typical canopy heights > 10 m) were identified by screening publicly available spatial data

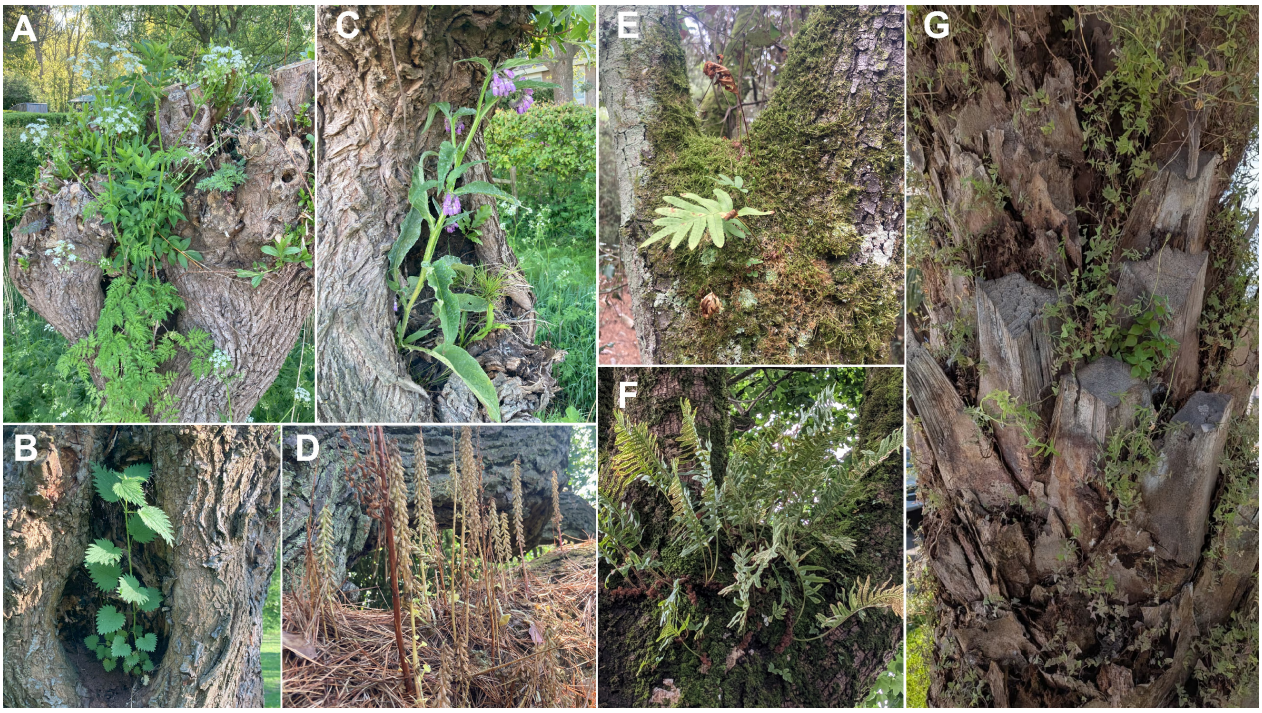

Figure 1. Examples of accidental epiphytes recorded during this study. **A–C.** Coppiced willows (*Salix* spp.) hosting cow parsley (*Anthriscus sylvestris* (L.) Hoffm.) **(A)**, stinging nettle (*Urtica dioica* L.) **(B)** and common comfrey (*Symphytum officinale* L.) on pollard heads or in knotholes **(C)**; **D.** Navelwort (*Umbilicus rupestris* (Salisb.) Dandy) growing in needle litter accumulated on a large branch; **E, F.** Polypody ferns (*Polypodium* spp.) growing in moss mats; **G** Canary Island palm (*Phoenix canariensis* H. Wildpret) with accidental epiphytes growing in cut frond bases, mainly sow-thistle (*Sonchus* spp.). All photographs were taken by the first author.

on forest age (Besnard et al. 2021), biomass (Santoro and Cartus 2025) and, where available, local forest-type layers (IGN 2006–2022; De Saeger et al. 2023; Comunidad Autónoma del País Vasco 2025) to capture a range of types and stand ages. Non-forest plots — including wild gardens, willow-lined streets or paths — were identified opportunistically on site. Accessibility was evaluated in relation to our sailing route, with on-site approach by bicycle or on foot. All observations were made from publicly accessible locations, with no entry into restricted areas. Surveys were non-invasive and limited to visual observations, photography and basic tree measurements; no biological material was collected and no collection permits were obtained.

Within each ~ 1° latitudinal band, we sampled three to four plots, resulting in 40 plots (ca. 21.7 ha) in total. Of these, 33 were located in forests with varying degrees of human influence and distance from the nearest city. Plots were mostly circular with 30 m radius where feasible, adjusted only to avoid roads or ecotones, while preserving internal homogeneity. Setting the anchor alarm on our GPS (Garmin 73, Garmin Ltd., Olathe, Kansas, USA) ensured we adhere to these borders. All living trees ≥ 10 cm DBH within each plot were grouped in DBH classes (10–< 30 cm; 30–< 60 cm; 60–< 90 cm; ≥ 90 cm). Plot-level structure and dominant taxa were documented photographically. Tree species composition was mostly mixed, with varying dominance of beech (*Fagus sylvatica* L.), oak (*Quercus* spp.), pine (*Pinus* spp.), black locust (*Robinia pseudoacacia* L.) and chestnut (*Castanea sativa* Mill.); two plots were pure pine forests. Stand ages (forest- and non-forest) ranged from 20 to 85 years (Besnard et al. 2021), with an above-ground biomass from 1,380 Mg ha^{-1} to 69,800 Mg ha^{-1} (Santoro and Cartus 2025). The expedition and field sites, as well as global accidental epiphyte observations, are presented interactively in our study's associated app (https://marie-hoensbroech-accidental-epiphytes-expedition.share.connect.posit.cloud/; Suppl. material 1: figs S1–S3), generated with the R shiny library (Chang et al. 2026).

Field surveys of accidental epiphytes

Within each plot, we conducted systematic visual scans from trunk base to outer crown using binoculars where necessary. Each accidental epiphyte was recorded with a geotagged photograph for subsequent verification, noting species names of epiphyte and host, tree DBH (using a standard measuring tape), estimated tree height, epiphyte attachment height, epiphyte size, substrate type (e.g. trunk, branch, crotch, knothole), presence of moss, counts of individuals per microhabitat and evidence of reproductive structures (flower buds, flowers, fruits or seeds or sori). When individuals were inaccessible, size was roughly estimated. The data yielded per-plot richness and abundance and per-tree occurrence for modelling encounter probabilities by DBH class. In addition to systematic field surveys, we recorded accidental epiphytes opportunistically, analogous to community-science observations.

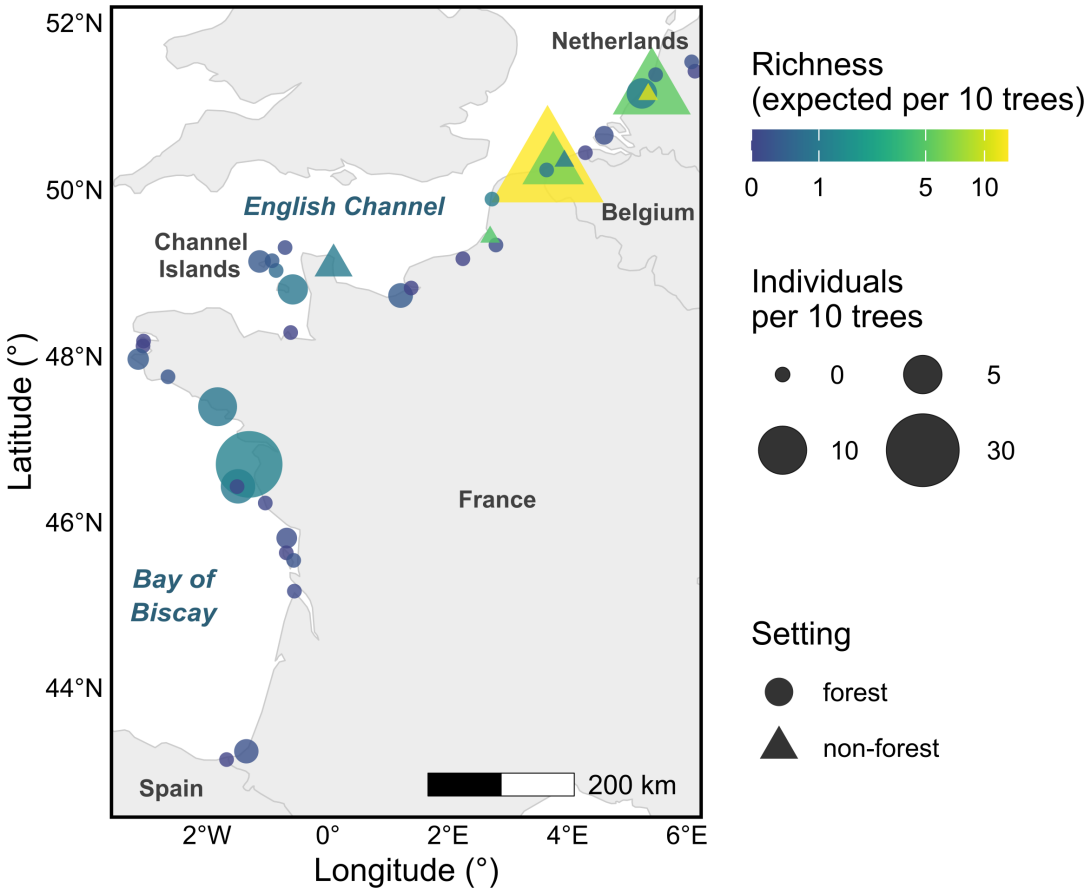

Figure 2. Standardised abundance and richness of accidental epiphytes along the eastern Atlantic temperate coast of Europe. Data are based on 40 sampling sites, represented by symbols, where points are forest settings and triangles non-forest settings. Abundance (individuals per 10 trees) is represented by symbol size and richness (expected number of species per 10 trees) is shown by log-scaled colour ramp to enhance contrast at low richness. The map is displayed using an ETRS89 / LAEA Europe (EPSG:3035) projection. Scale bar: 200 km.

iNaturalist data acquisition and filtering

To complement the field surveys, we retrieved presence-only observations of accidental epiphytes from the curated iNaturalist project using the official application programming interface (API; iNaturalist (2026a)). For species-level analyses that included community-science records, we retained only research-grade observations, i.e. observations with community-verified species identifications. Host tree identity was extracted where reported. We standardised common names to scientific names only where they could be assigned unambiguously at the genus level, based on the reported name and study location; ambiguous names, misspellings that could not be resolved confidently and entries marked with uncertainty (e.g. question marks) were assigned to an "unknown" category. All plant names follow Plants of the World Online (POWO 2026).

We also re-classified observations into forest and non-forest categories for analysis. The associated iNaturalist project distinguished records as urban or rural, but these settings were often missing or falsely reported. We therefore used a combined classification rule, based on forest age (Besnard et al. 2021) and the Global Human Settlement Layer (GHSL; Pesaresi and Politis (2023)), a spatial dataset describing the extent and intensity of built-up surfaces. Records from our systematic field surveys, for which forest and non-forest settings had already been assigned, were retained. All remaining records were classified using exact raster-cell values. Records with forest-age data and GHSL built-up values below 50 or with forest-age data and missing GHSL built-up values, were classified as forest. Records with GHSL built-up values ≥ 50 or missing forest-age data were classified as non-forest. The full workflow will be made publicly available in the study's associated file repository upon publication.

Data analyses

Local-scale setting and host tree patterns

Accidental epiphyte diversity, host tree associations and microhabitat use

All analyses were performed in RStudio with R version 4.5.2 (R Core Team 2025). We compiled accidental epiphyte–host pairs and epiphyte–growing-site pairs from field observations. For each accidental epiphyte taxon, we summarised the frequency of recorded host genera and growing-site categories and calculated the relative

contribution of each host genus or growing-site category to the total number of records for that taxon. Associations represented by more than three observations were visualised to show the dominant host and substrate contexts, associated with each accidental epiphyte taxon.

Host tree size and habitat context

From our field data, we examined how host size (DBH) and setting related to: (a) the probability that a tree served as a host; (b) accidental epiphyte abundance and (c) observed accidental epiphyte richness. Host occurrence was analysed at the tree-stratum level. For each site × setting × DBH stratum, the number of host trees was modelled as a binomial response out of the total number of surveyed trees. We fitted a Bayesian binomial GLMM with a logit link, including setting, DBH category and their interaction as fixed effects and a random intercept for site. The overall probability that an encountered tree functioned as a host was estimated from posterior predictions averaged across the observed distribution of trees amongst DBH strata within each setting.

For each site × setting × DBH category stratum (10–30, 30–60, 60–90 and 90+ cm), accidental epiphyte abundance was analysed as the total number of individual observations. Abundance was modelled using a Bayesian zero-inflated negative-binomial GLMM with a log link and an offset for the log number of trees sampled in the stratum. This placed expected abundance on a per-tree rate scale, allowing predictions to be expressed as abundance per 10 trees. Fixed effects were setting, DBH category and their interaction, with a random intercept for site to account for repeated DBH strata within plots and amongst-site heterogeneity.

As DBH-stratified incidence data were sparse, specifically for high DBH classes, we did not use iNEXT-standardised richness as the response variable for the DBH-level richness model (see next section). Instead, DBH-stratified richness was analysed as observed species richness, defined as the number of accidental epiphyte species recorded within each site × setting × DBH stratum. For the same reason, model-based estimates for these strata were sometimes highly uncertain, with wide 95% credible intervals and, in some cases, high posterior means. We therefore visualised fitted Bayesian estimates alongside the observed raw data.

Observed richness was modelled using a Bayesian zero-inflated negative-binomial GLMM with a log link. To account for unequal sampling effort amongst DBH strata, the log number of trees sampled in each stratum was included as a covariate rather than as an offset, because species richness is not expected to scale linearly with sampling effort. Fixed effects were setting, DBH category and their interaction, with a random intercept for site.

All Bayesian models used weakly informative priors and four MCMC chains. Posterior predictions were summarised on the response scale as posterior medians with 95% credible intervals (CrIs). For graphical summaries, DBH-specific predictions were shown alongside raw stratum-level observations. Overall setting-level estimates were obtained by averaging posterior predictions across DBH categories using the observed number of trees in each setting × DBH category as weights.

Broad-scale geographical and macroclimatic patterns

Latitudinal patterns

We visualised plot-level variation in accidental epiphyte richness and abundance by setting. To standardise species richness, we treated trees as sampling units, recording the presence or absence of each accidental epiphyte species on each tree. We used sample-based rarefaction with the R package iNEXT (Chao et al. 2014; Hsieh et al. 2016) to standardise richness to a fixed sampling effort of 10 trees per plot, allowing comparisons amongst plots with different numbers of surveyed trees.

Plots with no detected accidental epiphytes were retained and assigned an expected richness of zero. For plots containing only one accidental epiphyte species, we calculated the analytic rarefaction expectation directly from the hypergeometric model (Chao et al. 2014; Hsieh et al. 2016), based on the number of trees on which that species occurred, rather than estimating bootstrap confidence intervals, which are unstable for such low-information cases. Accidental epiphyte abundance was expressed as an effort-adjusted rate: individuals per 10 trees, calculated as 10× total individuals / total trees in the plot.

Based on all accidental epiphyte observations made during the sailing expedition, including both systematic field surveys and opportunistic records, we summarised latitudinal variation in taxonomic composition across forest and non-forest settings. Observations were retained when plants could be identified at least to genus level; Poaceae were treated at family level because a reliable identification from vegetative material alone was often not possible. Coordinates were binned into 1° latitude bands.

We constructed a presence–absence matrix of taxa across latitude bands and partitioned multiple-site Jaccard dissimilarity into turnover (i.e. taxon replacement amongst latitude bands) and nestedness (i.e. differences caused by taxa in less-rich bands forming subsets of those in richer bands), using the betapart package (Baselga et al. 2025). We further tested the association between taxonomic composition and latitude using permutational multivariate analysis of variance (PERMANOVA; 999 permutations) in the vegan package (Oksanen et al. 2026). We report the proportion of compositional variation explained by latitude (R^2), the *pseudo-F* statistic with model and residual degrees of freedom and the permutation-based *p*-value. For visualisation, we calculated total abundance and abundance per observation within each latitude band and setting for taxa with at least three independent occurrences. Latitudinal density was calculated separately using all taxon IDs.

Taxon-specific climatic positioning

We examined species-level environmental affinities by comparing accidental epiphyte occurrences with the environmental conditions available across each species' expected geographic range. We first identified taxa recorded during the expedition and then retrieved all research-grade records of those taxa from the curated "Accidental epiphytes" iNaturalist project (submitted by 13 September 2026; https://www.inaturalist.org/projects/accidental-epiphytes). To reduce spatial clustering and sampling bias (Boria et al. 2014), as well as the potential pseudo-replication of the same individual, we retained only one observation per taxon per CHELSA grid cell (see below) and selected taxa with more than 20 records remaining after spatial thinning. Contributing iNaturalist observers are listed in Suppl. material 2. For these focal taxa, we compiled dispersal information from literature and extracted Ellenberg-type indicator values for light, temperature, moisture, reaction, nutrients and salinity from the harmonised European dataset of Tichý et al. (2022).

For each retained species, we obtained its expected geographic range polygon from iNaturalist (iNaturalist 2026b). Within each species' expected geographic range, we generated 10,000 random background points representing the abiotic environment available to that species. We then retained one background point per CHELSA grid cell, ensuring that each sampled spatial grid cell was represented only once.

For both presence locations (accidental epiphyte occurrences) and background points, we extracted a set of macroclimatic and structural predictors commonly implicated in accidental epiphyte occurrence or in the development of suitable canopy microhabitats, including moisture, temperature and wind exposure (Hoeber et al. 2019; Hoeber and Zotz 2021, 2022; Komada et al. 2024; Zotz 2025). Specifically, we used the following CHELSA v.2.1 climatologies at 30 arc-second resolution: mean temperature of the warmest quarter (BIO10), minimum temperature of the coldest month (BIO6), mean near-surface wind speed and the aridity index (AI), which expresses the degree of dryness as the ratio of precipitation to potential evapotranspiration (PET), such that higher values indicate more humid conditions (Karger et al. 2017, 2021). For each species and predictor, we quantified the relative environmental position of every point by scaling values to a 0–1 interval using the minimum and maximum values observed amongst that species' generated background points.

To prevent the far more numerous background points from dominating the analysis, we randomly selected a species-specific subset of background points equal to ten times the number of accidental epiphyte presence records for each species.

Statistical model

We modelled relative probability of use using a Bayesian logistic regression framework with a use–availability design. For each observation *i*, the binary response variable y_i indicated whether a record corresponded to a presence (y_i = 1) or an available background point (y_i = 0). As the response was binary, it was assumed to follow a Bernoulli distribution,

$$y_i \sim \text{Bernoulli}\,(p_i)$$

where p_i is the probability that observation *i* is a presence rather than a background point. We linked this probability to environmental predictors using a logit link function,

$$\text{logit}\,(p_i) = \eta_i$$

where η_i is the linear predictor for observation *i*. The logit link is standard for binary-response models because it ensures fitted values remain between 0 and 1, while allowing predictor effects to be modelled linearly on the log-odds scale.

We fitted a fully species-specific model in which each species had its own intercept and its own slope for each environmental covariate:

$$\eta_i = \alpha_{s(i)} + \beta^{\text{AI}}_{s(i)}\text{AI}_i + \beta^{\text{maxT}}_{s(i)}\max \text{T}_i + \beta^{\text{minT}}_{s(i)}\min \text{T}_i + \beta^{\text{wind}}_{s(i)}\text{wind}_i$$

where *s*(*i*) denotes the species associated with observation *i* and $\alpha_{s(i)}$ is the intercept estimated for that species, representing its baseline log-odds of presence when all environmental predictors are fixed at their minimum scaled value (0). The coefficients $\beta^{\text{AI}}_{s(i)}$, $\beta^{\text{maxT}}_{s(i)}$, $\beta^{\text{minT}}_{s(i)}$ and $\beta^{\text{wind}}_{s(i)}$ are the species-specific slopes for aridity index, mean temperature of the warmest quarter, minimum temperature of the coldest month and mean near-surface wind speed, respectively. More generally, β^k_s denotes the coefficient for predictor *k* in species *s*, where *k* indexes the set of environmental covariates included in the model. In practical terms, this model formula is equivalent to fitting a separate logistic regression for each species within a single Bayesian modelling framework.

All regression coefficients were assigned weakly regularising Normal priors,

$$\alpha_s \sim \text{Normal}(0, 1.5), \beta^k_s \sim \text{Normal}(0, 1.5)$$

These priors are centred on zero, reflecting no strong prior expectation about the direction of species responses, while reducing the influence of implausibly large coefficients. This prior scale was chosen because all environmental predictors were expressed on a common 0–1 scale, such that a standard deviation of 1.5 allows moderate to strong changes in log-odds across the observed predictor range, while still providing regularisation against overfitting. This was particularly desirable because the dataset is updated dynamically as additional observations and species are incorporated via iNaturalist.

Models were fitted in brms (Bürkner 2017) using four Markov Chain Monte Carlo chains, each run for 4,000 iterations. To improve sampler stability and reduce divergent

transitions, we used adapt_delta = 0.95 and max_treedepth = 12. For interpretation on the probability scale, we used posterior predictions to calculate the change in occurrence probability as each focal predictor increased from the minimum value represented by the species-specific background points (0 on the scaled gradient) to the mean value amongst accidental epiphyte occurrences, while holding the remaining predictors at 0. Other R libraries incorporated in the Bayesian workflow were posterior (Vehtari et al. 2021; Bürkner et al. 2025), bayesplot (Gabry and Mahr 2025), tidybayes (Kay 2024) and emmeans (Lenth and Piaskowski 2025).

Additional R libraries used during data processing include: tidyverse (Wickham et al. 2019), janitor (Firke 2024), purrr (Wickham and Henry 2025) and data.table (Barrett et al. 2026) for general data wrangling; sf (Pebesma 2018), terra (Hijmans et al. 2026), stars (Pebesma and Bivand 2023), lwgeom (Pebesma 2025), units (Pebesma et al. 2016), rnaturalearth (Massicotte and South 2025) and ggspatial (Dunnington 2025) for spatial opeations; ggplot2 (Wickham 2016), patchwork (Pedersen 2025), ggbreak (Xu et al. 2021), viridis (Garnier et al. 2024), ggtext (Wilke and Wiernik 2022) and circlize (Gu 2014) for figure assembly and publication graphics. Figures were further edited in Inkscape v.1.3.2 (Inkscape's contributors 2023).

Results

Local-scale setting and host tree patterns

Accidental epiphyte diversity, host tree associations and microhabitat use

Across the 11° coastal transect (Fig. 2), we found a total of 767 accidental epiphyte individuals belonging to at least 64 species on 414 (~ 9.2%) of 4,479 sampled trees. Combined with opportunistic observations across the transect, we observed 2,309 individuals of at least 199 species on 1,473 hosts. Frequently recorded accidental epiphytes included polypody ferns (*Polypodium* spp.; Fig. 1E, F), common ivy (*Hedera helix* L.), elder (*Sambucus nigra* L.) and *Umbilicus rupestris* (Fig. 1D). Amongst these common taxa, reproductive structures were observed in *P. vulgare* (sori), *S. nigra* and *U. rupestris* (flower buds, flowers or fruits), as well as in less frequently recorded taxa, including garlic mustard (*Alliaria petiolata* (M.Bieb.) Cavara & Grande), cow parsley (*Anthriscus sylvestris* (L.) Hoffm.), red valerian (*Centranthus ruber* (L.) DC.), brambles (*Rubus* spp.) and dandelions (*Taraxacum* spp.). A full species list is given in Suppl. material 3: table S1 and the raw data will be made publicly available in in the study's associated file repository upon publication.

The most frequently recorded host trees were willows (mainly *Salix alba* L.; Fig. 1A–C), oak (*Quercus* spp.), *Phoenix* palms (Fig. 1G), black alder (*Alnus glutinosa* (L.) Gaertn.) and *Fagus sylvatica* (Suppl. material 3: fig. S1). There were apparent associations of some accidental epiphyte taxa with particular host taxa: *Polypodium* spp. were most frequently recorded on *Quercus*, *Alnus* and *Fagus*; maple (*Acer* spp.) on *Acer* spp.; *Umbilicus rupestris* on *Quercus* spp.; elder (*Sambucus nigra* L.) and bedstraw (*Galium aparine* L.) on *Salix*; and sow-thistle (*Sonchus* spp.) on *Phoenix* palms (Suppl. material 3: fig. S1).

Growing-site associations also differed amongst taxa (Suppl. material 3: fig. S2). *Polypodium* spp. occurred predominantly on stems and branches, mostly within moss pads, whereas most other recorded accidental epiphytes were associated with pollard heads, crotches, forks or knotholes (Suppl. material 3: fig. S2). Many records on non-mossy trunks or stem bases likely reflect the large number of observations from *Phoenix* palms, where plants frequently established in cut frond bases that lacked moss pads but contained accumulated debris.

Host tree size and habitat context

Bayesian GLMMs showed that the probability that a tree served as a host increased strongly with DBH and was consistently higher in non-forest plots (Fig. 5A). In forest settings, posterior predictions indicated that small trees had very low host probabilities (< 3%), which rose to 27% in trees > 90 cm DBH. In non-forest plots, host probabilities were substantially higher across all DBH classes: even small trees had markedly higher predicted host probabilities than small forest trees, while nearly 50% of trees ≥ 60 cm DBH and approximately 70% of trees ≥ 90 cm DBH were predicted to function as hosts. When posterior predictions were weighted by the observed distribution of tree sizes within each setting, this corresponded to an estimated 2% probability of encountering a host tree in forests, compared with 24% in non-forest settings.

Abundance also increased with DBH, particularly in the largest trees (Fig. 3B). Relative to trees of 10–30 cm DBH, estimated abundance was higher in trees of 30–60 cm DBH (rate ratio, RR = 3.4; 95% Credible Interval, CrI: 1.5–7.6), 60–90 cm DBH (RR = 3.9; 95% CrI: 1.6–9.2) and especially trees > 90 cm DBH (RR = 25.5; 95% CrI: 9.2–70.7). Abundance was also higher in non-forest than forest plots (RR = 7.1; 95% CrI: 1.3–41.8), although the CrI was wide (Fig. 5B). Richness showed a similar, but weaker DBH-related pattern (Fig. 5C). Richness was higher in non-forest than forest plots (RR = 7.0; 95% CrI: 2.6–20.3), while the clearest DBH effect was observed for trees of 30–60 cm DBH relative to 10–30 cm trees (RR = 2.2; 95% CrI: 1.1–4.5). Credible intervals for the larger DBH classes overlapped zero on the log scale, indicating weaker support for additional richness increases beyond this size class. There was no clear evidence for Setting × DBH interactions for either abundance or richness, as interaction CrIs overlapped zero. The site random intercept indicated substantial amongst-plot heterogeneity for all responses.

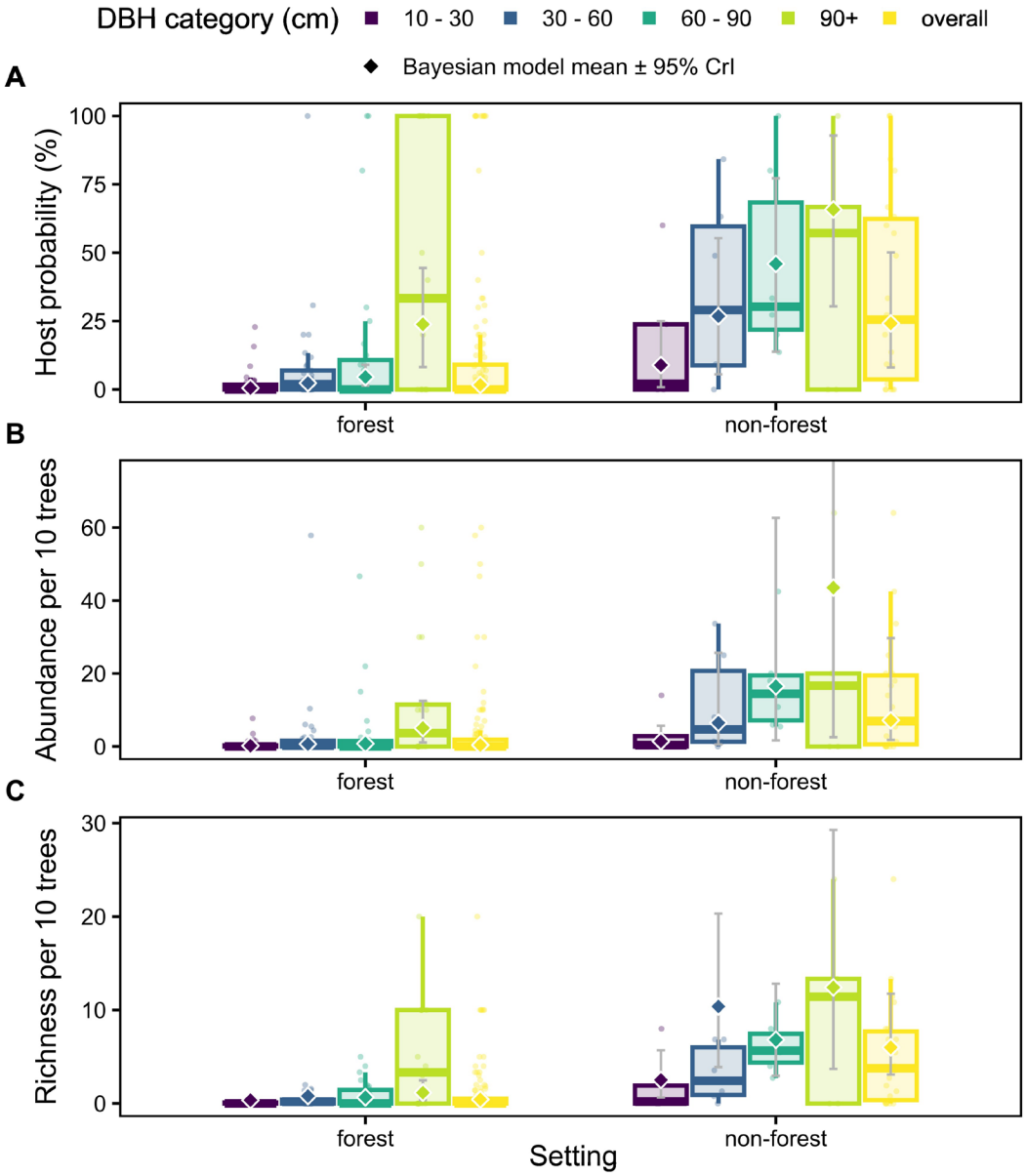

Figure 3. Host probability **(A)**, abundance **(B)** and richness **(C)** of accidental epiphytes per 10 trees by host DBH and setting. Boxplots show raw site × DBH-stratum values, with separate distributions for each DBH category and for the overall distribution across DBH classes within each setting. Transparent jittered points represent individual site × DBH strata. In each boxplot, the central line indicates the median, the box spans the interquartile range and whiskers extend to the most extreme values within 1.5× the interquartile range. Diamond symbols and vertical whiskers show Bayesian posterior predictions and 95% credible intervals (CrIs), respectively. Overall Bayesian estimates were calculated as tree-weighted posterior averages across DBH categories within each setting. Abundance and richness are expressed per 10 trees. Note that y-axis scales differ amongst panels. In panel B, the y-axis is truncated to improve readability, excluding extreme Bayesian CrIs.

Broad-scale geographical and macroclimatic patterns

Latitudinal patterns

Accidental epiphyte composition varied across the approximately 11° latitudinal transect, but richness did not follow a consistent latitudinal gradient (Figs 2, 4). Instead, the occurrence of different genera varied amongst latitude bands. Latitude explained 20% of the variation in taxonomic composition (PERMANOVA: R^2 = 0.2, *pseudo-*$F_{1,8}$ = 2.0, p < 0.01) and taxon replacement accounted for 91.1% of total Jaccard dissimilarity amongst latitude bands, compared with 8.9% attributable to nestedness. Richness and abundance were also mostly decoupled: several plots with very high accidental epiphyte numbers were species-poor, whereas abundance was low or moderate in some species-rich plots (Fig. 2). Standardised richness was generally higher in non-forest plots (e.g. willow-lined roads/paths and gardens) than in nearby forest plots. It was also generally higher in the English Channel Region north of 48°N (the Netherlands, Belgium, northern France and the British

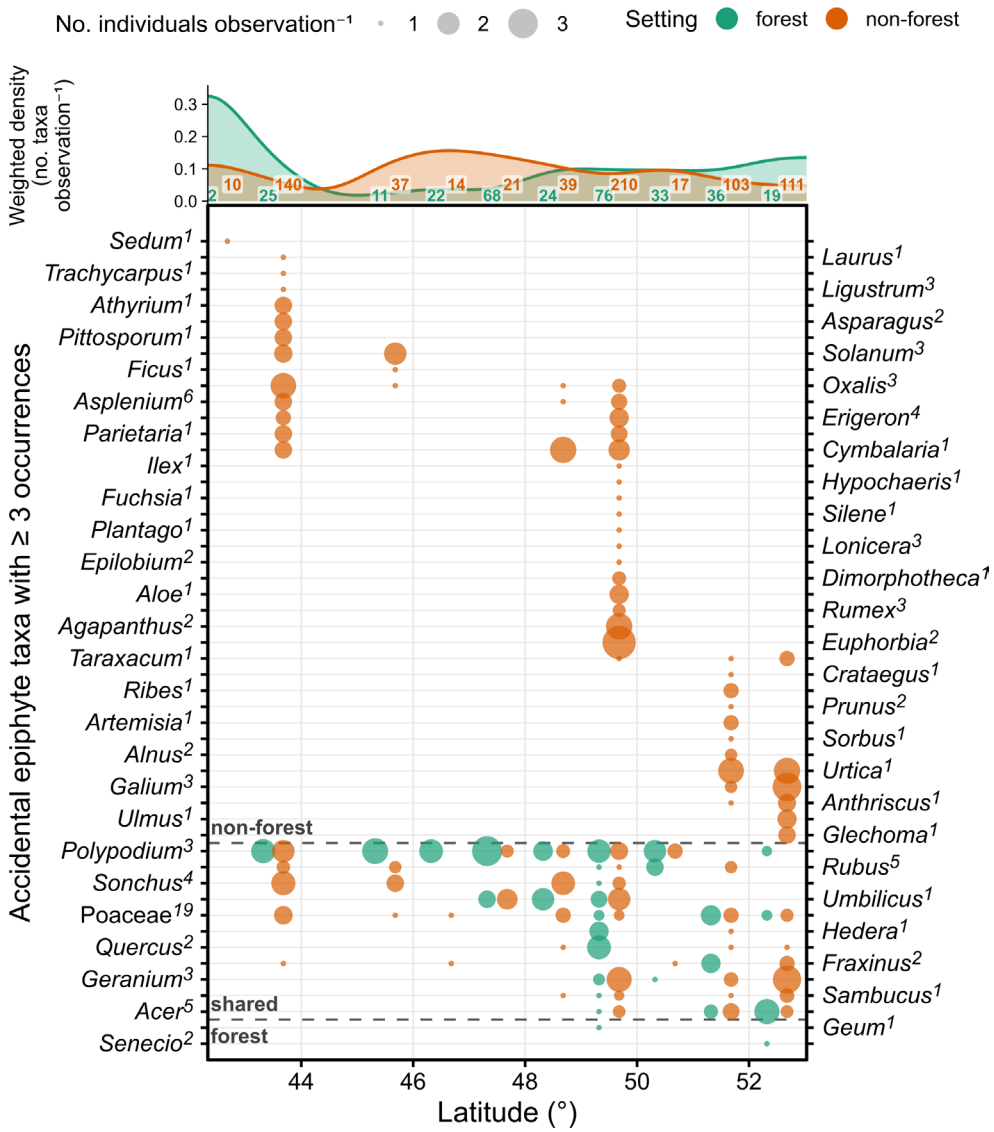

Figure 4. Latitudinal turnover in accidental epiphyte taxon pools across forest and non-forest observations. Each point indicates the occurrence of a taxon within a latitude band and habitat type; point size represents number of individuals per observation. Colours distinguish forest and non-forest habitats. Taxa are grouped by habitat association, separating taxa recorded only in forest, in both habitats or only in non-forest habitats. Superscript numbers next to taxon names denote the number of species represented within each genus; Poaceae are included at family level. The upper marginal density shows the latitudinal distribution of all observations, weighted by taxon richness per observation, with numbers indicating the number of observations per latitude band.

Channel Islands) than along the Bay of Biscay South of 48°N (southern France and northern Spain; Figs 2, 4). Along the Bay of Biscay, the assemblages were dominated by polypody ferns (*Polypodium* sp.) and ivy (*Hedera* sp.); additional genera occurred at higher latitudes and in the southernmost latitude band near the French-Spanish border (Fig. 4, Suppl. material 3: table S1).

Taxon-specific climatic positioning

In the no-pooling, species-specific Bayesian logistic models, the clearest overall pattern was associated with temperature, especially minimum temperature of the coldest month (Fig. 5, Suppl. material 3: table S2). Posterior mean effects for this predictor were positive for all 19 taxa, indicating that accidental epiphyte occurrences were generally positioned towards milder winter conditions within each taxon's expected geographic range. Credible intervals excluded zero for 18 taxa; fig (*Ficus carica* L.) was the only taxon with a CrI overlapping zero (β = +0.5, 95% CrI: −1.4 to 2.3). The largest positive effects were observed for *Umbilicus rupestris* (β = +9.8, 95% CrI: 8.3 to 11.1), common polypody (*Polypodium vulgare* L. (β = +6.9, 95% CrI: 5.5 to 8.4), wood sorrel (*Oxalis acetosella* L.: β = +6.5, 95% CrI: 5.1 to 8.1), herb-robert (*Geranium robertianum* L.: β = +5.6, 95% CrI: 4.1 to 7.1) and blueberry (*Vaccinium myrtillus* L.: β = +5.3, 95% CrI: 3.4 to 7.1).

Mean temperature of the warmest quarter showed the opposite pattern (Fig. 5). Posterior mean effects were

negative for 18 of 19 taxa, indicating that accidental epiphyte occurrences were generally positioned towards the cooler part of the warm-season temperature gradient available within each taxon's expected geographic range. The only positive effect was observed for rowan (*Sorbus aucuparia* L.), though its CrI overlapped zero (β = +0.8, 95% CrI: −0.7 to 2.2). Credible intervals excluded zero for 17 taxa, with the strongest negative warm-season temperature effects observed for *G. robertianum* (β = −5.7, 95% CrI: −7.5 to −4.0), *U. rupestris* (β = −5.0, 95% CrI: −6.2 to −3.6), smooth sow-thistle (*Sonchus oleraceus* L.: β = −4.5, 95% CrI: −6.3 to −2.8), European yew (*Taxus baccata* L.; β = −4.3, 95% CrI: −6.3 to −2.3) and *Sambucus nigra* (β = −4.2, 95% CrI: −5.6 to −2.9).

The aridity index showed a less uniform pattern across taxa (Fig. 5). Most taxa had 95% CrIs overlapping zero, but several taxa showed a clearer directional effect. *Polypodium vulgare* (β = +3.6, 95% CrI: 1.7 to 5. 9), *V. myrtillus* (β = +2.9, 95% CrI: 0.4 to 5.3) and *Oxalis acetosella* (β = +3.0, 95% CrI: < −0.1 to 4.7) showed positive effects, with occurrences shifted towards the wetter part of their expected ranges. By contrast, *Sambucus nigra* (β = −2.1, 95% CrI: −4.4 to 0.1), sycamore maple (*Acer pseudoplatanus* L.: β = −1.8, 95% CrI: −4.2 to 0.6) and *Sorbus aucuparia* (β = −1.8, 95% CrI: −4.1 to 0.4), showed negative effects, with occurrences shifted towards the drier portion of the species' climatic envelope, though their CrIs slightly overlapped zero. Compared with the temperature predictors, aridity effects were, therefore, more variable amongst taxa.

Further, most taxa occupied broadly intermediate Ellenberg profiles (Fig. 5, Suppl. material 3: figs S3, S4), with some visually distinct cases, such as high Ellenberg temperature values in *F. carica*, *U. rupestris* and southern polypody (*P. cambricum* L.). There was no clear visual pattern linking Ellenberg indicator values to the direction or magnitude of the modelled effects. For example, taxa with similar Ellenberg moisture values occurred both above and below zero.

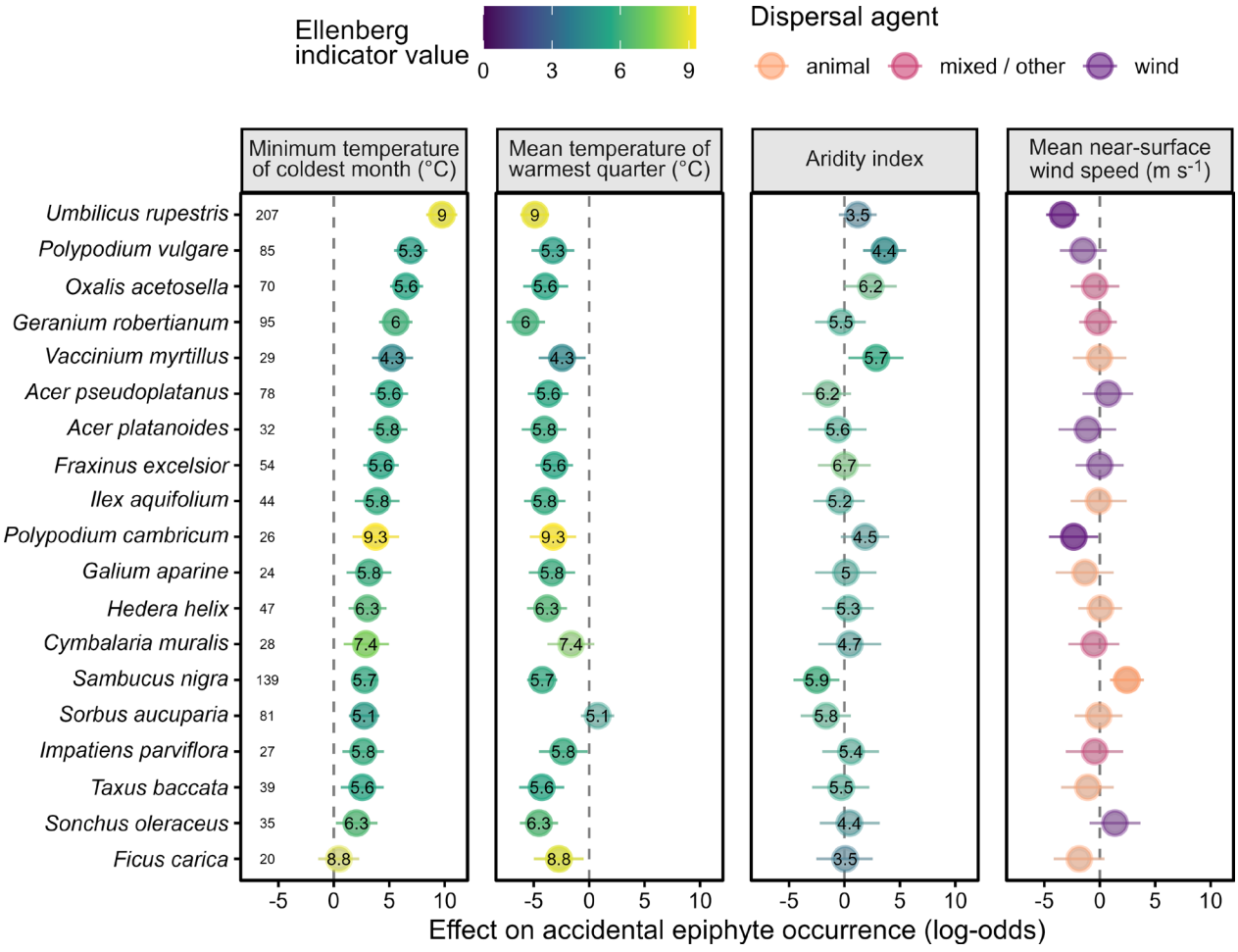

Figure 5. Species-specific accidental epiphytic occurrence in relation to environmental position within expected geographic ranges. Points indicate posterior means from Bayesian logistic models and horizontal bars show 95% credible intervals (CrIs) on the logit scale. Positive coefficients indicate that epiphytic occurrences are concentrated towards the higher end of the corresponding species-specific environmental gradient, whereas negative coefficients indicate concentration towards the lower end. Transparent points indicate species for which the 95% CrI overlaps zero. Point colour denotes Ellenberg indicator values: the two temperature panels show Ellenberg temperature values and the aridity-index panel shows Ellenberg soil-moisture values. In the wind speed panel, point colour denotes dispersal mode. Numbers next to the y-axis indicate sample size.

Near-surface wind speed also showed mixed taxon-specific patterns (Fig. 5). Most taxa had CrIs overlapping zero. Clearer negative effects were observed for *U. rupestris* (β = −3.3, 95% CrI: −4.8 to −1.9) and *P. cambricum* (β = −2.3, 95% CrI: −4.6 to −0.1), with occurrences shifted towards the less windy parts of their expected range. However, there was no simple visual separation of wind effects by dispersal category (Fig. 5): other wind-dispersed taxa, including *Sonchus oleraceus* (β = +1.4, 95% CrI: −0.9 to 3.7), had weakly positive effects, though with CrIs overlapping zero. Animal-dispersed taxa also occurred on both sides of zero. Amongst the latter, only *Sambucus nigra* showed a clear positive effect (β = +2.4, 95% CrI: 0.9 to 4.0), whereas the other taxa had intervals overlapping zero.

Discussion

As expected under our overarching hypothesis of hierarchical filtering, accidental epiphytism across the eastern Atlantic coastal transect from the Netherlands to northern Spain emerged as a structured, but uneven phenomenon, shaped by host tree identity and size, habitat setting, latitude and species-specific macroclimatic positioning. At the local scale, larger trees were more likely to host accidental epiphytes across habitat types, consistent with the general relationship between host-tree size and epiphyte richness (Flores-Palacios and García-Franco 2006). Larger trees may provide greater surface area and more diverse microhabitats, while their generally greater age may also allow more time for dispersal and establishment (Flores-Palacios and García-Franco 2006; Hoeber and Zotz 2021; Azuma et al. 2022). In human-modified landscapes, such trees may also function as refugia or habitat islands, offering substrate-rich establishment sites above ground where terrestrial conditions are unfavourable or highly disturbed (Moe and Botnen 1997; Azuma et al. 2022; Rotherham 2022). At the broader geographical scale, taxon composition across the transect varied mainly through replacement and may be influenced more strongly by macroclimate than latitude alone. Species-specific climatic models showed that accidental epiphyte records were most consistently positioned towards milder winters and cooler warm seasons within each species' expected climatic envelope, whereas moisture and wind effects were weaker and more taxon-specific. This pattern is consistent with the view that arboreal habitats can impose strong thermal and water-balance constraints on terrestrial plants establishing above ground (Bohlman et al. 1995; Hoeber and Zotz 2021; Zotz 2025). Together, our results suggest that accidental epiphytism is best understood as a repeated ecological outcome of hierarchical filtering, arising when diaspore arrival, host characteristics, habitat context and favourable climatic positioning coincide.

Accidental epiphyte probability — significantly different from 0

Accidental epiphytes were unevenly distributed across sites and host trees and were generally uncommon in forests, as expected, but they were far from isolated curiosities. Across our transects, the predicted probability of encountering an accidental epiphyte host increased with tree size, ranging from very low values in small forest trees to about 25–30% in the largest forest trees and from around 10% to about 70% in non-forest settings (Fig. 3A). Thus, although accidental epiphytes were overall rare in forest plots, posterior predictions indicate that their occurrence was consistently non-zero. In individual plots, including some forest and many non-forest sites, accidental epiphytes were sometimes surprisingly frequent (Figs 2, 3B, C). Previous surveys have identified much higher abundances in forest habitats, likely because these studies targeted epiphyte-rich hotspots rather than broader landscape transects. For instance, in Germany, a two-year census of > 1,200 trees in the Harz Mountains found that about 25% of these were hosts to 1,450 epiphytic individuals belonging to > 100 species across 39 families (Hoeber et al. 2019). In New Zealand, a latitudinal survey of 700 tree ferns across seven sites found 835 accidentally epiphytic individuals from 51 species (Brock and Burns 2021). In Japan, a standardised crown survey of eight large *Cercidiphyllum japonicum* trees yielded 1,301 accidental epiphyte individuals across 49 species (Komada et al. 2024). Their repeated occurrence and sometimes high local abundance imply that they may contribute to canopy-level ecosystem functions — for example, by retaining moisture, accumulating organic material, providing food rewards and habitat or serving as diaspore sources (Azuma et al. 2022) — yet these potential functions remain almost unexplored. Combined with our findings, these studies suggest that accidental epiphytes merit far more attention than they have historically received.

The frequent occurrence of *Polypodium* species also blurs the boundary between accidental and facultative epiphytism. Although retained here as accidental epiphytes for consistency, their repeated establishment in trees emphasises the view that epiphytism is not a binary terrestrial-versus-epiphytic condition, but includes intermediate stages along a terrestrial–arboreal continuum (e.g. Ibisch (1996); Zotz and Einzmann (2023)).

Accidental epiphytes and host specificity/bias

Across our transect, many tree genera hosted accidental epiphytes, but epiphytes occurred much more often on *Salix*, *Quercus*, *Acer*, *Fraxinus* and *Fagus* spp. than on, for example, *Pinus* or *Betula* spp. (Suppl. material 3: fig. S1), supporting our hypothesis that host-tree identity

influences accidental epiphyte occurrence. Like true epiphytes, accidental epiphytes may, therefore, show host bias rather than strict specificity, with host quality shaped by microhabitat-forming traits rather than taxonomy alone (Wagner et al. 2015; Hoeber and Zotz 2022). What makes a tree a "good" or a "bad" host appears to be jointly related to host DBH, as a proxy for host age, size and complexity (e.g. Flores-Palacios and García-Franco (2006); Su et al. (2021)), architecture, bark properties and — indirectly — to taxonomy.

Common hosts tend to develop large forks and crotches that trap litter, organic matter and moisture, especially with age or in deep shade (Drénou 2000). These microhabitats can enhance local water retention (Tatsumi et al. 2023), although their suitability may also decline where prolonged saturation or waterlogging occurs. Management can create similar features: pollarding and pruning prolong tree life and promote veteran traits such as hollows, cavities, knotted crowns and deep forks, making old pollards — especially *Salix* and *Fraxinus* — particularly favourable hosts, as reflected in our non-forest sites (Fig. 3). These host features were already repeatedly noted in the late 19th century: notably, Schimper's monograph (1888) on epiphytic vegetation stimulated a surge of interest in epiphytes on pollarded *Salix* across temperate Europe (Bolle 1891; Beyer 1895; Jaap 1895). Such trees are still regarded as biodiversity refugia in highly human-modified landscapes (Moe and Botnen 1997; Rotherham 2022), potentially allowing species to escape poor ground conditions. Further south, *Phoenix* palms offer an analogous substrate via a different architecture: persistent leaf bases and cut-frond axils retain litter and water (Brandes 2007; Cameron 2022). Conversely, even potentially suitable species can be poor hosts when structurally simple: densely planted *Quercus* or *Fagus* spp. in our plots often formed straight, branch-poor stems that rarely provide the deep forks, cavities or substrate-retaining structures required by accidental epiphytes (Hoeber and Zotz 2022). Host-associated microhabitats (or tree-related microhabitats, TREMs, but see Larrieu et al. (2018)) therefore emerge as one of the interlinked drivers of accidental epiphytism: taxonomy may influence which species are likely to develop suitable forms, but age, architecture and management determine whether individual trees actually provide the microhabitats needed for arboreal establishment.

Extending this host-trait perspective to the attachment stage further helps explain why some trees were used more often used as hosts. Larger trees may simply intercept more diaspores by presenting more surface area. However, because accidental epiphytes may lack some of the attachment traits hypothesised to facilitate persistent establishment in canopy habitats (e.g. Tay et al. (2021a, 2022); Hietz et al. (2022)), they likely depend strongly on bark crevices, branch forks, moss mats and other microhabitats that provide anchorage in accumulated organic material. Although simple bark-roughness classifications have been criticised for their vagueness (Tay et al. 2022), it is notable that effective hosts often had either coarse bark, such as *Quercus* spp. or sustained moss mats that increase the microtopographic complexity of otherwise smoother bark, such as in *Fagus* spp. By contrast, trees with smooth (and moss-free) or frequently peeling bark, such as *Pinus* or *Betula* spp., may be poorer or more transient epiphyte hosts, analogous to other systems (e.g. López-Villalobos et al. (2008)). Bark chemistry, including pH and nitrogen content, may further affect host suitability, for example, through effects on the development of water-retentive moss mats (Tatsumi et al. 2023). Together, these traits add a dispersal-retention filter to our framework: diaspores must reach a tree through dispersal and encounter surfaces that can retain them long enough for establishment to become possible.

What unites suitable hosts is, therefore, not taxonomy as such, but the contexts and architectures that repeatedly create dispersal and establishment opportunities in stable, substrate-rich canopy microhabitats (Wagner et al. 2015; Azuma et al. 2022; Hoeber and Zotz 2022; Komada et al. 2024).

Accidental epiphytes in human-modified landscapes

This apparent host bias could also help explain why accidental epiphytes were so frequent and diverse in non-forest plots (Figs 2–4). Non-forest settings often contain precisely those large, solitary and structurally complex hosts (Izuddin and Webb 2015; Van den Bossche et al. 2025) that are most likely to support accidental epiphytes. Such trees form habitat islands within highly modified landscapes and may offer safer establishment sites than the ground. These trees are also widely used by birds for roosting or nesting (Cameron 2022; Rotherham 2022; Van den Bossche et al. 2025; MH pers. obs.), potentially providing a stepping stone into the canopy for bird-dispersed species like elder (*Sambucus nigra*) or holly (*Ilex aquifolium*). Conversely, wind-dispersed species may benefit from the greater surface area of large solitary trees and locally accelerated airflow around their edges (Angelou et al. 2022). The generally strong dispersal potential of wind-dispersed diaspores may further increase the likelihood of reaching the canopy (Hoensbroech et al. 2026), especially where isolated hosts provide favourable conditions for early establishment (Einzmann and Zotz 2017).

The non-forest signal should nevertheless be interpreted with caution because community-science datasets tend to be behaviourally, spatially or temporally biased (e.g. Di Cecco et al. (2021)). However, the same non-forest signal also emerged from our structured field survey (Fig. 4), which was designed to minimise such biases, suggesting that the rural-urban distinction is unlikely to be solely an artefact of uneven observation effort. Habitat setting, therefore, acts as a filter in its own right, shaping the availability of suitable hosts, the delivery of diaspores and the conditions for early establishment. Urban and other human-modified landscapes may also shape which plant species are available to become accidental epiphytes in the first place. They often contain a larger or compositionally distinct, regional species pool, including high proportions of alien and neophyte

species, providing an explanation for the relatively high species richness at non-forest sites (Figs 3, 4). Transport corridors, trade and other anthropogenic pathways amplify propagule pressure and facilitate the spread of these taxa (Wolf et al. 2020). This may be not only a matter of species richness, but also of functional composition: urban habitats often favour ruderal and competitive strategies associated with disturbance tolerance and rapid resource acquisition (Petersen et al. 2021) and novel urban ecosystems may be disproportionately filtered for wind-dispersed species (Planchuelo et al. 2020). This could increase the number of plants capable of reaching and establishing in the canopy. However, our data do not suggest that accidental epiphytism is restricted to a narrowly defined urban, ruderal or open-habitat group of plants. The taxa recorded here were mostly ecological generalists (Fig. 5; Suppl. material 3: figs S3, S4) and included species dispersed by animals, wind and other (e.g. ballistic) mechanisms (Fig. 5). The variation in Ellenberg indicator values and dispersal modes (Fig. 5), together with reproductive structures observed across multiple taxa and in both settings (data not shown), further suggests that accidental epiphytism occurs amongst species with diverse ecological strategies and can extend beyond transient establishment (also see Hoeber and Zotz (2022)).

Moreover, the concentration of accidental epiphytes in open settings appears consistent with the classic Tietze–Pittendrigh open-habitat hypothesis, which proposes that some epiphytic lineages may originate from ancestors already pre-adapted to exposed environments (Tietze 1906; Pittendrigh 1948; Mena-Jiménez et al. 2024). However, the high abundance observed in some forest plots also lends support to the Schimperian view that shaded, humid forests provide favourable conditions for epiphyte establishment and persistence (Schimper 1888). Altogether, our results do not support the notion of a single habitat pathway into epiphytism. Instead, they suggest that accidental epiphytism arises in both open and forested contexts, depending on how the multi-scale filters identified here align. This interpretation is consistent with the view that epiphytism has evolved repeatedly in major epiphyte-rich families (e.g. Mena-Jiménez et al. (2024) and references therein).

Latitudinal turnover and macroclimatic positioning

As expected, taxonomic composition changed substantially along the latitudinal transect, mainly through the replacement of taxa amongst assemblages rather than through a simple north-south gradient in richness. A comparable pattern was reported for accidental epiphytes on tree ferns in New Zealand, where latitudinal differences in composition reflected variation in regional species pools (Brock and Burns 2021). In our study, the observed turnover may likewise reflect geographical variation in the terrestrial species pool, though this was not explicitly tested.

The species-specific climatic models identified another filter operating within these regional species pools. As expected, accidental epiphyte occurrences were non-randomly distributed across the climatic conditions available within each species' expected geographic range. The most consistent association involved temperature: occurrences were generally positioned towards thermally milder conditions (cooler summer maxima, warmer winter minima), whereas associations with moisture availability and wind were weaker and more taxon-specific. Macroclimate may, thus, represent the broadest filter in this framework, setting the regional conditions under which accidental epiphytism can arise.

Temperature showed a clear pattern: epiphytic occurrences are shifted towards milder winters and cooler summers (Fig. 5). Such clustering in more benign macroclimates is consistent with the notion that arboreal microhabitats can be comparatively exposed — experiencing stronger temperature extremes than the forest floor (Bohlman et al. 1995; Hoeber and Zotz 2021). Thus, for many species, epiphytic establishment and persistence are most likely where regional thermal stress is already reduced. In *Umbilicus rupestris*, for example, epiphytic occurrences appear largely confined to regions with little or no frost (Zotz 2025), reinforcing the interpretation that climatic extremes — especially cold events — can strongly constrain species-specific epiphytic establishment and persistence. Still, even if climatic extremes exclude individual taxa, accidental epiphytism as a phenomenon might persist through other taxa that are more tolerant of the same conditions (but see Pittendrigh (1948)).

While our results point most clearly to thermal limitation, water availability remains an important, but less consistently detected component of the macroclimatic filter. Our models showed only limited and taxon-specific associations with water availability, with relatively few species shifted towards the wetter end of their available moisture space (Fig. 5). This weaker signal does not necessarily imply that water availability is unimportant: epiphytes are largely decoupled from soil water and arboreal habitats can dry at similar or even higher rates than the forest floor (Bohlman et al. 1995; Aubrey et al. 2013). Intermittent water supply can strongly constrain performance, such that broad distributions often track precipitation regimes (Mendieta-Leiva et al. 2020; Zotz et al. 2021; Taylor et al. 2022). However, accidental epiphytes may be partly buffered against desiccation when individuals root in water-retentive arboreal substrates such as moss mats, litter accumulations or canopy soil (Hoeber et al. 2019; Hoeber and Zotz 2021, 2022; Zotz 2025). At broader scales, humid macroclimates may favour the formation and persistence of such epiphyte-supporting substrates (Mendieta-Leiva et al. 2020; Hoeber and Zotz 2022; Komada et al. 2024), potentially increasing opportunities for accidental epiphyte establishment. Overall, the limited moisture signal in our findings may indicate that macroclimatic constraints are partly mediated by host-associated microhabitats and local microclimates.

Water limitation is also closely linked to wind exposure, which can intensify desiccation while simultaneously shaping diaspore arrival and retention. Wind is often treated as

a canopy stressor because exposed epiphytes — and their diaspores (Srivastava et al., work in progress) — may face elevated risks of desiccation and dislodgement (Tay et al. 2021b; Einzmann et al. 2022). Some taxa in our data showed negative wind associations, consistent with this interpretation. Yet wind may also facilitate accidental epiphytism by increasing diaspore delivery to arboreal microhabitats, especially for wind-dispersed taxa, even if arrival from the forest floor may be rare (Hoensbroech et al. 2026). Overall, wind effects were weak and inconsistent (Fig. 5), suggesting that wind is neither broadly beneficial nor broadly stressful per se. Where positive associations occurred, they might reflect landscape contexts that enhance diaspore delivery: directly for wind-dispersed taxa (Hoensbroech et al. 2026) and indirectly for animal-dispersed taxa where exposed remnant trees concentrate deposition via perching and nesting (Galindo-Gonzáles et al. 2000).

Limitations and outlook

These macroclimatic signals should, nevertheless, be interpreted with caution. As discussed above, community-science observations are subject to spatial and behavioural biases and, in our case, many available accidental epiphyte records were collected along a sailing transect. The resulting dataset is, therefore, spatially concentrated in coastal regions and disproportionately reflects the environmental conditions of these areas. In addition, the climatic associations of accidental epiphytes are likely to vary amongst species, functional types and biomes. For example, whereas the temperate accidental epiphytes analysed here were most consistently associated with cooler warm-season temperatures, accidentally epiphytic cacti in hot, dry systems may instead benefit from avoiding extreme ground-level temperatures (Aguilar-Cruz et al. 2026). Such contrasts suggest that the factors favouring arboreal establishment are context dependent and may help explain why epiphytic strategies are highly diversified and often obligate in tropical forests, but more frequently facultative, opportunistic or accidental in many non-tropical systems.

Future work should, therefore, combine more geographically balanced sampling with finer-scale measurements designed to disentangle the main filters identified here: the composition and traits of the available terrestrial species pool, diaspore arrival and retention, host tree traits and associated microhabitat availability and microclimate, habitat setting and macroclimatic constraints. Comparative trait-based analyses across the broader terrestrial species pool could help identify which combinations of species traits increase the probability of accidental epiphytism. Diaspore traps or seed-rain surveys could quantify whether potential accidental epiphytes reach trees at all, whereas experimental diaspore addition on host trees, combined with repeated monitoring of marked diaspores or seedlings, could separate arrival from retention, germination and survival. Detailed tree-level measurements of DBH, canopy position, host identity, bark structure, cavities, forks, moss mats, litter accumulations, canopy soil and substrate moisture would help identify which host features mediate retention and establishment. These observational approaches could be complemented by reciprocal transplants across moisture or climatic gradients, paired with crown- and ground-level microclimate sensors and substrate-moisture measurements, to test whether arboreal substrates buffer, have little effect on or intensify atmospheric drought and macroclimatic stress. Finally, replication across habitat settings and climatic gradients would help separate local host-tree effects from landscape and regional climate effects. We therefore propose a multi-scale filtering framework in which accidental epiphytism is most likely where diaspore arrival and retention, suitable host-associated microhabitats, favourable habitat setting and permissive micro- and macroclimatic conditions coincide.

Conclusions

Given their ubiquity, the limited historical treatment of accidental epiphytes is striking, even amongst classical naturalists, such as Humboldt (see Introduction). Our transect provides the first quantitative landscape-level estimate of encounter probability across forest and non-forest sites and supports a hierarchical framework in which dispersal, habitat structure and climatic context jointly shape accidental epiphyte occurrence. Our proposed multi-scale filtering framework offers a basis for generating testable predictions, comparing patterns across regions and taxa and linking local host-level processes to larger-scale environmental gradients. By capturing early, facultative and often transient stages of terrestrial plant establishment in trees, accidental epiphytes may also provide a useful model for understanding how true epiphytism evolved. As such, they offer a foundation for future surveys and targeted experiments aimed at understanding why terrestrial plants repeatedly colonise the canopy and why this transition becomes obligate in some lineages and ecological contexts, but remains facultative or accidental in others.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: Microsoft Copilot
Used for: Language, style and writing, Figures, tables and charts, Data analysis
Artificial intelligence tools (Microsoft Copilot) were used during manuscript preparation for code troubleshooting and for language editing, including grammar, clarity, and style. The authors reviewed all AI-assisted outputs and remain solely responsible for the scientific content, analyses, and conclusions.

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Author contributions

Conceptualization: MH, GZ. Data curation: MH. Formal analysis: MH. Funding acquisition: ORR, MH, GZ. Investigation: MH. Methodology: MH, ORR, GZ. Project administration: GZ, MH. Supervision: GZ, ORR. Visualization: MH. Writing - original draft: MH. Writing - review and editing: ORR, MH, GZ.

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Data availability

All data generated during this study, together with the scripts used for data processing, analysis and figure generation, have been archived at https://doi.org/10.57782/VD3HEL. Data derived from publicly available sources are cited in the text and listed in the reference list.

Supplementary materials

Supplementary material 1

ShinyApp (.docx)
Link: https://doi.org/10.21425/fob.19.207331.suppl1

Supplementary material 2

iNaturalist contributor metadata used in Bayesian modelling (.xlsx)
Link: https://doi.org/10.21425/fob.19.207331.suppl2

Supplementary material 3

Additional results (.docx)
Link: https://doi.org/10.21425/fob.19.207331.suppl3