REPORT

EpIG-DB: A database of vascular epiphyte assemblages in the Neotropics

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Abstract

Vascular epiphytes are a diverse and conspicuous component of biodiversity in tropical and subtropical forests. Yet, the patterns and drivers of epiphyte assemblages are poorly studied in comparison with soil-rooted plants. Current knowledge about diversity patterns of epiphytes mainly stems from local studies or floristic inventories, but this information has not yet been integrated to allow a better understanding of large-scale distribution patterns. EpIG-DB, the first database on epiphyte assemblages at the continental scale, resulted from an exhaustive compilation of published and unpublished inventory data from the Neotropics. The current version of EpIG-DB consists of 463,196 individual epiphytes from 3,005 species, which were collected from a total of 18,148 relevés (host trees and 'understory' plots). EpIG-DB reports the occurrence of ‘true’ epiphytes, hemiepiphytes and nomadic vines, including information on their cover, abundance, frequency and biomass. Most records (97%) correspond to sampled host trees, 76% of them aggregated in forest plots. The data is stored in a TURBOVEG database using the most up-to-date checklist of vascular epiphytes. A total of 18 additional fields were created for the standardization of associated data commonly used in epiphyte ecology (e.g. by considering different sampling methods). EpIG-DB currently covers six major biomes across the whole latitudinal range of epiphytes in the Neotropics but welcomes data globally. This novel database provides, for the first time, unique biodiversity data on epiphytes for the Neotropics and unified guidelines for future collection of epiphyte data. EpIG-DB will allow exploration of new ways to study the community ecology and biogeography of vascular epiphytes.

Keywords
biodiversity, community ecology, database, forest plot, hemiepiphytes, Neotropics, nomadic vines, taxonomic diversity, vascular epiphytes, vegetation relevé
Epiphytes are plants that germinate and grow non-parasitically on other plants, mainly trees. They can be divided into non-vascular (mosses, liverworts, lichens, algae and cyanobacteria) and vascular epiphytes (e.g. orchids, bromeliads, aroids and ferns; Mendieta-Leiva, Bader, & Porada, 2020). In the case of the latter, ‘true’ epiphytes never establish contact with the soil, but this is different in other structurally dependent plants. Hemiepiphytes start epiphytically and later tap soil resources via aerial roots. The true nature of nomadic vines, which germinate on the ground and may (or may not) lose their initial contact with the soil, thus becoming epiphytic, to then restore (or not) contact via aerial roots is questioned and is currently under investigation (Zotz, 2013a).

Epiphytes (unless noted otherwise specifically refers to true epiphytes) fulfill important ecosystem functions related to water and nutrient cycles and biodiversity. As epiphytes have no direct contact with the soil, they often capture water and nutrients from the atmosphere (Feild & Dawson, 1998). Many epiphytes have a high capacity for water interception, storage and/or transpiration (Mendieta-Leiva et al., 2020), and they often recycle nutrients from the litter of their host tree and other epiphytes (Nadkarni & Sumera, 2004). Other functions can include maintaining and/or increasing air humidity locally (Benzing, 1998) and decreasing solar irradiation by increasing canopy cover (Cruz-Angón & Greenberg, 2005), which might positively affect the diversity of arboreal arthropod fauna (Stuntz, Simon, & Zotz, 2002). In addition, epiphytes offer food and habitat resources for many animals such as arthropods, birds or mammals (Cestari, 2009; Cruz-Angón & Greenberg, 2005; Fontoura et al., 2010).

The assembly of vascular epiphytes strongly depends on the growth of their host trees and the spatiotemporal variation of related ecological niches on each host tree (Parra, Acuña, Corcuera, & Saldaña, 2009; Taylor & Burns, 2015; Zotz & Vollrath, 2003). During host tree ontogeny, the total bark area as well as the environmental heterogeneity increases as a function of tree architecture, growth rate and crown dynamics (Einzmann, Beyerlacht, Hofhansl, Wanek, & Zotz, 2014; Flores-Palacios & García-Franco, 2006; Sarmento Cabral et al., 2015; Wagner, Mendieta-Leiva, & Zotz, 2015; Wagner & Zotz, 2020; Zotz & Vollrath, 2003). The characteristics of host individuals in combination with the vertical stratification of the forest stand may allow for an impressive number of epiphyte species to coexist in a single tree (Hietz, Winkler, Scheffknecht, & Hulber, 2012; Petter et al., 2016; Ruiz-Cordova, Toledo-Hernández, & Flores-Palacios, 2014), the record being over 200 species found on a single tree in a cloud forest in Peru (Catchpole & Kirkpatrick, 2011). Nevertheless, the lack of comparative studies makes it difficult to assess whether major drivers of local species richness are consistent across regions.

Globally, vascular epiphytes are primarily found in the tropics and subtropics, and exhibit a pronounced latitudinal diversity gradient, with their diversity peaking in the Neotropics (Gentry & Dodson, 1987; Zotz, 2016). Epiphytes contribute substantially to global species richness, accounting for ca. 9% of all vascular plant species (Zotz, 2013b) and in some cases up to 50% of local plant species richness (Kelly, Tanner, Lughadha, & Kapos, 1994). Compared with other life forms, such as trees and lianas, vascular epiphytes show higher degrees of endemism (Casas-Marin & Nivia-Ruiz, 2013; Freitas et al., 2016; Van der Werff & Consiglio, 2004). Nonetheless, biodiversity patterns of this hyper-diverse group are poorly known, because most efforts to understand epiphyte diversity in the Neotropics are at the level of local, idiosyncratic studies or floristic inventories.

At large spatial scales (e.g. elevational transects), the literature on biogeographic diversity patterns of epiphytes is scarce (e.g. Krömer, Acebey, Kluge, & Kessler, 2013; Krömer, Kessler, Gradstein, & Acebey, 2005; Zuleta, Benavides, López-Rios, & Duque, 2016). For example, the general notion that broad-scale gradients in epiphyte species richness are very strongly linked to moisture availability is based on just a few studies (Gentry & Dodson, 1987; Kreft, Köster, Küper, Nieder, & Barthlott, 2004; Küper, Kreft, Nieder, Köster, & Barthlott, 2004; Wester et al., 2011). Indeed, current hypotheses about macroecological patterns of epiphyte diversity are mostly based on regional or national species lists without a proper compilation of spatially explicit data, despite the wealth of local studies, for which underlying data are typically not available (Mendieta-Leiva & Zotz, 2015). In addition, the available data on vascular epiphytes are taxonomically and geographically biased, with studies mostly focused on orchids and bromeliads, and concentrated in certain regions (Zotz, 2016). A necessary step for a better understanding of the community ecology and biogeography of vascular epiphytes is to broaden our knowledge base by mobilizing and integrating existing data (on community composition, species abundance and richness) and make it available to the scientific community.

As a contribution towards this goal, we present a database infrastructure for collecting and integrating diversity data on vascular epiphyte assemblages. This will allow epiphyte ecology to move beyond local studies. We expect this effort to be both an important step in the development of epiphyte ecology but also in community ecology and biodiversity research, promoting the expansion of ecological research in the tropics by including this important biodiversity component. Moreover, in combination with detailed knowledge on the ecology and physiology of species, EpILG-DB has the potential to help us to understand the distribution of organisms and the extent of their ecological roles (e.g. contribution to the water and nutrient cycling, buffering potential, etc.), all of which will help us to better understand community and biome dynamics under current and future changes in climate and habitats.

1.1 | International consortium on epiphytic plant assemblages

The Epiphyte Inventory Group (EpIG) was formed in 2018 as a working group for collecting and analysing vascular epiphyte assemblage data. The group was established during a workshop at the University of Marburg (Germany), with the participation of 25 experts in the fields
of epiphyte ecology, database management and macroecology. The participants of the workshop represented most of the research groups working on vascular epiphytes in the Neotropics. The aims of the database consortium were (a) to create a database following international standards for integration of plant community data; (b) to establish the specific properties of a database for managing and integrating data on vascular epiphyte assemblages; (c) to discuss taxonomic issues related to data generally collected on vascular epiphytes; (d) to develop a roadmap for updating and analysing this database. These objectives were achieved by a combination of plenary discussions and parallel sessions with topic specialists, defining a set of agreement protocols that were synthesized in a document that served as a basis for this paper.

1.2 | Description of epiphyte assemblage records

We used TURBOVEG for Windows (Hennekens & Schaminee, 2001) as the reference software for digitizing data, implementing a species checklist (‘epiphytes’) based on a new Global Checklist of Vascular Epiphytes (Zotz, unpub., an updated version of Zotz, 2013b). In the database, the minimum sampling unit of reference is a host individual (generally a tree, thus hereafter referred to as such), which is also marked and sampled (e.g. ID, tree species, tree height, tree diameter at breast height or DBH, Appendix S1). Many times, host individuals were sampled nested within forest plots (Figure 1). Typical information for a sampled host includes the presence, surface cover, abundance, frequency or biomass of resident epiphytes. Frequently, datasets also report the absence of epiphytes from a potential host. In very few cases, the minimum sampling unit is a plot, i.e. an area in which epiphytes have been sampled without distinction of host individuals, referred to as ‘understory’ plots (Krömer, Kessler, & Gradstein, 2007). In ‘understory’ plots, epiphytes may be sampled until a determined height or throughout the whole canopy (sensu Moffett, 2000). In the former case, this is because epiphyte flora on shrubs and small trees in the forest understory is usually different from that on the large canopy trees (Krömer et al., 2007). Each species list sampled on a single host individual or in an ‘understory’ plot corresponds to a species assemblage, called a ‘relevé’ in TURBOVEG. When species were sampled on host individuals nested within forest plots (Figure 1), the records were kept to the minimum sampling unit (host individual), thus allowing the user to summarize the data at larger scales when needed.

We accepted records of vascular epiphytes in the broad sense (‘true’ epiphytes, hemiepiphytes and nomadic vines sensu Zotz (2013a)). It is permitted to include morphospecies but vines, lianas and accidental epiphytes are excluded (Zotz, 2013a). Morphospecies are considered under the assumption that the data contributors made a conscientious effort to differentiate these as potentially different species. We are aware that in the majority of cases these morphospecies will remain unresolved but, in some cases, species names may be assigned later. Nonetheless, we consider this data necessary and important to answer several questions, for example those related to alpha diversity. Morphospecies need to include the data contributors’ collection number (e.g. ‘Polypodium SB1001’) or an unambiguous name assigned by the contributor. Species that are identified as ‘cf.’ can be kept if the record is a distinct morphospecies (removing the cf. and indicating the epithet as the species it is compared with, e.g. Polypodium cf. vulgare becomes Polypodium vulgare). Species that are identified as ‘aff.’ can be considered as a morphospecies. For example, ‘vel. aff.’ means: this species or related, while ‘aff.’ means not this species, but related, all as part of the epiphyte flora we documented. In addition, some species have not been yet determined to the species level (e.g. Polypodium aff. vulgare). Varieties and subspecies are all considered at the species level. Juveniles that could not be determined or differentiated into morphospecies are excluded. Morphospecies are manually added to the species checklist but they can be omitted in specific data analyses.

1.3 | Data collection, harmonization and integration

We contacted the largest number of researchers working on epiphytes that we could reach and provided a protocol for importing
The current version of EpIG-DB (version 1.0; December 2019) comprises 18,148 relevés of which 17,762 represent trees and 386 represent 'understorey' plots, in which epiphytes were sampled without distinction of hosts, the unambiguous distinction between 'understorey' plot or tree is given in the field 'plot/tree'. Alternatively, when the minimum sampling unit is an 'understory' plot, i.e. an area where the epiphytes were sampled without distinction of hosts, the unambiguous distinction between 'understorey' plot or tree is given in the field 'plot/tree'.

Sampling of vascular epiphytes was carried out differently depending on forest type and the research aims of each field team. Thus the specification of the sampling method (Appendix S1) is provided for all relevés. The most common sampling method included a combination of tree climbing and ground observation with binoculars (56%). Ground observation with binoculars or climbing alone is used in second and third place (31% and 11%, respectively), and only a very small number of relevés were sampled using ground observation without optical devices (<1%). The assessment of the abundance is also heterogeneous in epiphyte sampling. In addition to presence/absence, which is straightforward, abundance may be quantified as the number of individuals or stands (Sanford, 1968), biomass or frequency (Appendix S1). The latter refers to the number of Johansson zones (Johansson, 1974) in which an epiphyte species was found within a single host. In EpIG-DB the majority of relevés had some measure of abundance (74%, mostly number of individuals), while presence/absence data was only recorded for 20% of trees and for all those plots where sampling was not on a tree base ('understory' plots). To a smaller extent data represent frequency and biomass (ca. 6%).

Information on the taxonomic groups and the life forms (sensu Zotz, 2013a) sampled were included. In almost 60% of relevés all vascular plants were sampled, while in ca. 30% only angiosperms and in a 13% of relevés only selected taxa were sampled (mostly ferns, orchids and bromeliads). The majority of the relevés include all three life forms (45%, epiphytes, hemiepiphytes and nomadic vines) or a combination of epiphytes and either hemiepiphytes (20%) or nomadic vines (11%). Only a small number of relevés include a single life form (e.g. epiphytes only 16% and hemiepiphytes only 8%).

The characteristics of host individuals are well documented in EpIG-DB. For example, 92% of all trees have DBH data while 63% have height data and 85% have been identified at least to the genus level. The data on host size revealed that the DBH of the majority of the sampled trees fall between 5 cm and 30 cm with
very few large trees >100 cm DBH comprising about 2% (390 trees, Appendix S4).

Naturalness of sampling sites was provided for all relevés in all datasets and indicates that relevés are mainly distributed in natural ecosystems (66%) and to a lesser degree in anthropogenic (19%) and semi-natural (15%) ecosystems.

1.5 Spatial and sample coverage

The first version of the database covers most of the potential latitudinal distribution of vascular epiphytes in Tropical and Subtropical America (Figure 2). We plotted all records sampled understorey plots and hosts across a map of terrestrial world biomes for the American tropics and subtropics. We used the classification of the WWF (Olson et al., 2001), which comprises 14 terrestrial world biomes based on existing global maps of floristic or zoogeographic provinces, the world’s biotic province maps and global maps of broad vegetation types, and defines 867 Ecoregions based on regional classification systems and expert opinion. Our datasets are distributed across nine countries, eight biomes and 45 WWF ecoregions out of the 234 recorded in the Neotropics (Olson et al., 2001).

To assess the climatic representativity of our data, we obtained two bioclimatic variables (mean annual temperature and annual precipitation) for all records using geographic coordinates from CHELSA (Karger et al., 2017). For matching our data with major gradients of mean annual temperature and annual precipitation we applied Whittaker’s biome model (Whittaker, Levin, & Root, 1975), using the plotbiomes (Ricklefs, 2008, https://github.com/valentinitap/plotbiomes) and ggplot2 (Wickham, 2016) packages. The climate range of datasets covers tropical and subtropical biomes of the Neotropics where epiphytes are generally found (Figure 3). Some datasets were located outside of designated biome areas, such as in cold and very rainy ecoregions from the tropics (e.g. the Peruvian Yungas, Eastern Cordillera real montane forests and northern Andean páramo; Figure 3).

Finally, for assessing relative sample completeness (the relationship between sample coverage and species diversity, Chao et al., 2014) across WWF Ecoregions (Olson et al., 2001), we used sampled-based rarefaction curves based on interpolation and extrapolation of species richness with the iNext package (Hsieh, Ma, & Chao, 2016). Species diversity refers to species richness (Hill numbers, q = 0, Hsieh et al., 2016). Sample coverage was calculated using frequency data and only for ecoregions with at least 100 trees sampled. Sampling completeness reveals the large variability in sampling coverage across ecoregions and points to those where more sampling effort is needed (Figure 4, Appendix S5).

In ecoregions of South America, very few of the confidence intervals overlap except at very small coverage values, implying significant differences in epiphyte diversity among ecoregions at comparable coverage; this was not the case for most ecoregions in Central America (Figure 4), where diversity seems to be comparable among most ecoregions. In certain ecoregions, undersampling was very high (e.g. Bolivian Yungas and Cauca Valley montane forests), whereas in some other regions (e.g. Chaco, Bahia interior forests and Campos Rupestre Montane savanna) sampling seems to have reached a high degree of completeness (Figure 4).

1.6 Further perspectives

EpIG-DB consists of fine-grained data sampled at the local scale and integrated at a wide geographical spread, including many datasets with unpublished information on epiphyte abundance, which have been made available to the scientific community. Analyses of the database will be instrumental not only in answering questions related to large-scale patterns of epiphyte assemblages, but will also contribute to the understanding of plant diversity in general with a broad biogeographic and macroecological focus. EpIG-DB also aims to collate vascular epiphyte inventory data across the world. The current database comprises a substantial and important amount of data and sites - from nine countries, eight biomes and 45 ecoregions in the Neotropics, and it also reveals how many ecoregions and ecosystem types are not yet accounted for (Appendix S5). This effort needs to be extended geographically and, most importantly, it needs to include data already collected which may or may not be described in grey literature and is at risk of being lost.

Future efforts in data sampling or data collection will need to consider current biases towards Central America and southeast/southern Brazil, near the Atlantic coast and towards natural habitats. The lack of data from the Caribbean and Amazonia reflects undersampling in these regions, where current data are distributed across a few locations. The inclusion of epiphyte inventory data from Africa, Asia and Oceania is planned and will need to start with the most available data, but it is unlikely that these will cover the latitudinal and climatic gradients as well as the current dataset does in the Neotropics. Therefore, datasets from tropical and subtropical regions outside of the Neotropics are highly welcome.

Vascular epiphytes as structurally dependent organisms, which grow on dynamic island-like substrates, fundamentally differ from terrestrial plants in their population and community dynamics. Further, their considerable contribution to diversity and biomass in tropical ecosystems makes them an important Neotropical diversity component. Compared with, for example trees, epiphytes are particularly vulnerable to the effects of landscape modification and climate change, particularly in montane cloud forests, because of their tight coupling with the atmosphere and structural dependency (Laube & Zotz, 2006; Zotz, Bogusch, Hietz, & Ketteler, 2010; Zotz & Hietz, 2001). Therefore, the presence of certain species may reflect a conserved state of the forest (Benzing, 1990). Predictions of the effect of climate change for mountain forests imply a decrease in atmospheric water availability (e.g. dew and mist; Feeley et al., 2011; Urrutia & Vuille, 2009), which would negatively affect epiphyte biomass and have a cascading effect in the ecosystem. Efforts in conservation will be more informed and ultimately more successful with a clear theoretical understanding of the diversity and dynamics of epiphyte assemblages.
We strongly encourage epiphyte ecologists to contribute to this database initiative. To this end, we recommend future epiphyte inventories and database managers collect in the standardized format proposed here, including at least the following data: (a) epiphyte abundance per host individual, (b) epiphyte species, (c) host individual species, (d) host tree DBH and height, (e) host

1.7 | Database consortium and data use agreements

FIGURE 2  Spatial distribution of 40 datasets integrated in EpIG-DB 1.0 across the Neotropic WWF biomes

FIGURE 3  Climate envelope of EpIG-DB 1.0 data (black dots) across Whittaker biomes. The Whittaker plot shows the distribution of vegetation types as a function of mean annual temperature and precipitation
coordinates, and (f) whenever sampling within forest plots to also include empty (potential) host individuals. The EpIG-DB consortium is open to any researcher willing to contribute data, especially from poorly sampled regions within the Neotropics and across the world.

For the completion of first data analyses, only database contributors can access and use the data during the first two years (until March 2022). After the embargo period, all data will be made available to any researcher upon request through a digital repository (e.g. Zenodo) that provides the option of conditional access. As the database contains georeferenced records and information of abundance, there is a danger of misuse for the illegal collection of endangered species. We, therefore, will not allow completely open access, but researchers with a legitimate interest will be given full access by the database curators under conditions ensuring that the data will not be shared outside of academia. Regarding authorship agreements, by default, we will apply the principles stated in the sPlot rules (Bruelheide et al., 2019) to which this database is also contributing. Any request should be done by contacting the Custodian (Glenda Mendieta-Leiva) or the Deputy Custodian (Borja Jiménez-Alfaro).

**FIGURE 4** Coverage-based rarefaction (interpolation) and extrapolation plots for vascular epiphyte diversity per ecoregion and subcontinent. The curves indicate the observed (interpolated) and extrapolated species richness with respect to sample coverage (number of trees) for 28 out of the 45 ecoregions for which at least 100 entire trees were sampled. For (a) Central America there are nine ecoregions and for (b) South America 19 ecoregions. The colour gradient follows species diversity according to ecoregion and the shaded polygons represent 95% confidence intervals. Calculations are based on incidence data.
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AUTHOR CONTRIBUTIONS
GML had the original idea and led the consortium from the start, while GZ provided support throughout the conception of the idea, funding application and conceptualization of the workshop. GML coordinated the workshop and together with FNR, GZ, MAT, SPB, AMB, ERN, HJRE, VGJ, PH, MVI, DAJL, MK, HK, TK, NMM, ACQ, EASM, AT, JHDW, CZ and DZ contributed to the foundation of the manuscript under the guidance of BJA. GML compiled the datasets to be included in EpIG with the help of JPCE. GML and BJA led the writing together with FNR and input from GZ, and comments and suggestions by MAT, SPB, AMB, MJG, HJRE, ALG, PH, MVI, DAJL, MK, HK, TK, NMM, SRM, LP, AT, KW, FAW, JHDW and DZ. All authors (except for AT and BJA) contributed data. All authors agreed with the final manuscript.

DATA AVAILABILITY STATEMENT
The data contained in EpIG will be available on request, after the embargo period, through contacting the custodian and deputy custodian for submitting a paper proposal. The EpIG consortium follows the Governance and Data Property Rules of the sPlot Working Group, which are available on the sPlot website (https://www.idiv.de/en/splot.html). The respective data will be provided after acceptance.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** New header data specific for vascular epiphyte assemblage records in EpIG-DB 1.0 added to TurboVeg.

**Appendix S2.** List of databases detailing authors, project, funding source and references.

**Appendix S3.** Number of plots distributed across area size classes.

**Appendix S4.** Number of trees per diameter at breast height (DBH) and height class.

**Appendix S5.** Density of EpIG-DB datasets across the tropics and sub-tropics.

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