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Review

Vascular epiphytes in the Amazon: main gaps, limitations and perspectives for studies on the subject

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ABSTRACT

Vascular epiphytes stand out in tropical forests in terms of diversity. However, no comprehensive review of the group in the Amazon region has been performed so far. We carried out a literature review on the scientific knowledge of vascular epiphytes in the Amazon aiming to identify the main gaps, limitations and perspectives for studies on the subject. Searches were conducted in Google Scholar, Scopus and Web of Science using inclusion and exclusion criteria. 291 articles published in the period 1933-2022, mostly the 21st century, were included in the review. Brazil was the most studied country. However, knowledge gaps were found in regions located in the Brazilian arc of deforestation as well as in areas of Bolivia, Guyana, French Guiana and Suriname. There was a predominance of studies related to the floristics, systematics and biogeography of spermatophytes and ferns, focusing on the diversity and taxonomy of certain families (e.g. Orchidaceae). However, we found gaps for more comprehensive research, considering population dynamics, dominance (biomass), guidelines for evaluation of epiphyte and systematization of data for Amazon. We indicate the need of studies focused on ecology, floral and reproductive biology, biochemistry, phytochemistry, anatomy and physiology. Future research should also consider the impacts of current trends in deforestation and climatic changes on the diversity of vascular epiphytes in the Amazon.

Keywords: Amazon, Amazon rainforest, Brazil, diversity, epiphytism, fern, orchids, scientometric, systematic review, vascular epiphytes.

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Introduction

Vascular epiphytes, defined as plants that germinate and grow on trees in a non-parasitic relationship, are a highly diverse group in tropical forests represented by ca. 31,000 species distributed in 79 families, wich corresponds to about 10% of the vascular plant species of the world (Zotz 2016; Zotz *et al.* 2021). A total of 3,849 epiphytic species occurs in the neotropics and 518 epiphytic species occurs in the Amazon (Marcusso *et al.* 2022; Quaresma *et al*. 2022). Epiphytic species are of major ecological importance, as they act as a source of organic matter by generating litter, contribute to nutrient cycling and rainfall interception, and serve as habitats and food resources for animals, favoring the diversification of the canopy fauna (Benzing 1990; Kersten 2010; Mendieta-Leiva *et al.* 2020a; Taylor *et al.* 2021).

Despite the high taxonomic diversity, vascular epiphytes are poorly studied when compared to other components of the forest (Mendieta-Leiva & Zotz 2015; Zotz 2016). Studies about this synusia in the Amazon are also incipient when compared to those carried out in Central America and in the southeast and southern Brazil (Mendieta-Leiva *et al.* 2020a). Furthermore, the factors that influence the occurrence and diversity of epiphytes are still not completely clear (Mendieta-Leiva & Zotz 2015; Wagner *et al.* 2015; Zotz 2016; Spicer & Woods 2022).

Systematic reviews are scientific investigations based on explicit and reproducible methods that allow us to synthesize results from a comprehensive search of relevant articles on a given topic, enabling careful evaluation and interpretation to provide the current state of the art or focus of the research on the theme (Grant & Booth 2009; Mengist *et al.* 2020a). There are several literature reviews articles that help us understand the importance of epiphytes and the diversity of the group (Kersten 2010; Wagner *et al.* 2015; Ladino *et al.* 2019; Jover *et al.* 2020; Khapugin 2020; Nugraha *et al.* 2020; Spicer & Woods 2022), but no one of them has specifically focused on the vascular epiphytes of the Amazon. Moreover, large gaps in floristic-taxonomic inventories of this group in the region have been pointed out by some authors (e.g. Mendieta-Leiva *et al.* 2020a; Quaresma *et al.* 2022).

Therefore, the objective of the present study was to summarize the scientific knowledge about vascular epiphytes in the Amazon so as to identify the main limitations, gaps, and perspectives for researches on the theme.

Material and methods

The research was carried out using the SALSA (Search, Appraisal, Synthesis, and Analysis) methodology (Grant & Booth 2009) and the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) research protocol (Moher *et al.* 2009) with data obtained from the Google Scholar, Scopus and Web of Science databases. We adopted search terms (keywords) related to vascular epiphytes in the Amazon, which included the six most representative families of epiphytes in the Amazon (Orchidaceae, Araceae, Bromeliaceae, Polypodiaceae, Clusiaceae, and Dryopteridaceae; Taylor *et al.* 2021; Quaresma *et al.* 2022) and the types of Amazonian vegetation, according to surveys carried out in the region (Fig. 1) (Junk *et al.* 2011; Cardoso *et al.* 2017; Quaresma *et al.* 2022).

All articles published until 2022 were retrieved and subjected to application of inclusion and exclusion criteria in order to allow the collection and analysis of the maximum number of publications (Moher *et al.* 2009; Mengist *et al.* 2020a). Studies carried out in any of the nine countries where the Pan-Amazon occurs (Bolivia, Brazil, Colombia, Ecuador, Guyana, French Guiana, Peru, Venezuela and Suriname) (Aragón 2018) were included in the analysis as long as the predefined search terms had been found in the title, abstract or keywords. When necessary, the articles were read in full to check whether they were within the scope of the review. Articles that were unrelated to the proposed theme, articles produced outside the study area (Amazon), duplicate articles, presentations, lectures, expanded abstracts, dissertations, theses, and review articles were excluded (Mengist *et al.* 2020a).

The selected articles were classified as quantitative or descriptive to carry out a narrative analysis of the data. We extracted the following information of each article: (1) year of publication; (2) country where the study was conducted; (3) coordinates of the study site; (4) keywords; (5) category of the study [based on the thematic areas of the most recent Brazilian Botanical Congress (Congresso Nacional de Botânica 2022)]; (6) sampling methodology; (7) journal where the article was published and Impact Factor of the journals indexed in the Journal Citation Reports (JCR), considering the year 2021 as a reference (https://clarivate.com/); (8) number of citations; and (9) affiliation and country of origin of the authors.

Raw data were tabulated in Excel 2018 spreadsheets and organized into graphs and tables with the aid of the R software (R CORE TEAM 2022), using the Bibliometrix extension (biblioshyne) (Aria & Cuccurullo 2017). We also prepared a map with the study locations based on geographic coordinates (latitude and longitude), when available in the articles. When the coordinates were not available, we used less precise information, such as municipality or locality to arbitrarily assign the location where these studies were carried out using Google Maps (https://www.google .com/maps) (Magdalena *et al.* 2018).

Results

Temporal and spatial distribution of the studies

The searches resulted in a total of 3,980 articles: 3,479 from Google Scholar, 276 from the Web of Science, and 225

from Scopus. After application of the exclusion criteria, 291 articles – 155 retrieved from Google Scholar and 136 from the Web of Science and/or Scopus – about epiphytes in the Amazon were obtained. The 291 articles were published in 115 journals, from 1933 to 2022 (Fig. 2), associated with 646 authors. Regarding the language, English was the most used (195 articles), followed by Portuguese (71) and Spanish (25).

The first study of vascular epiphytes in the Amazon dates back to 1933 and it was a pioneering survey to describe the vegetation, including vascular and non-vascular plants, and environmental characteristics of Moraballi Creek, in the

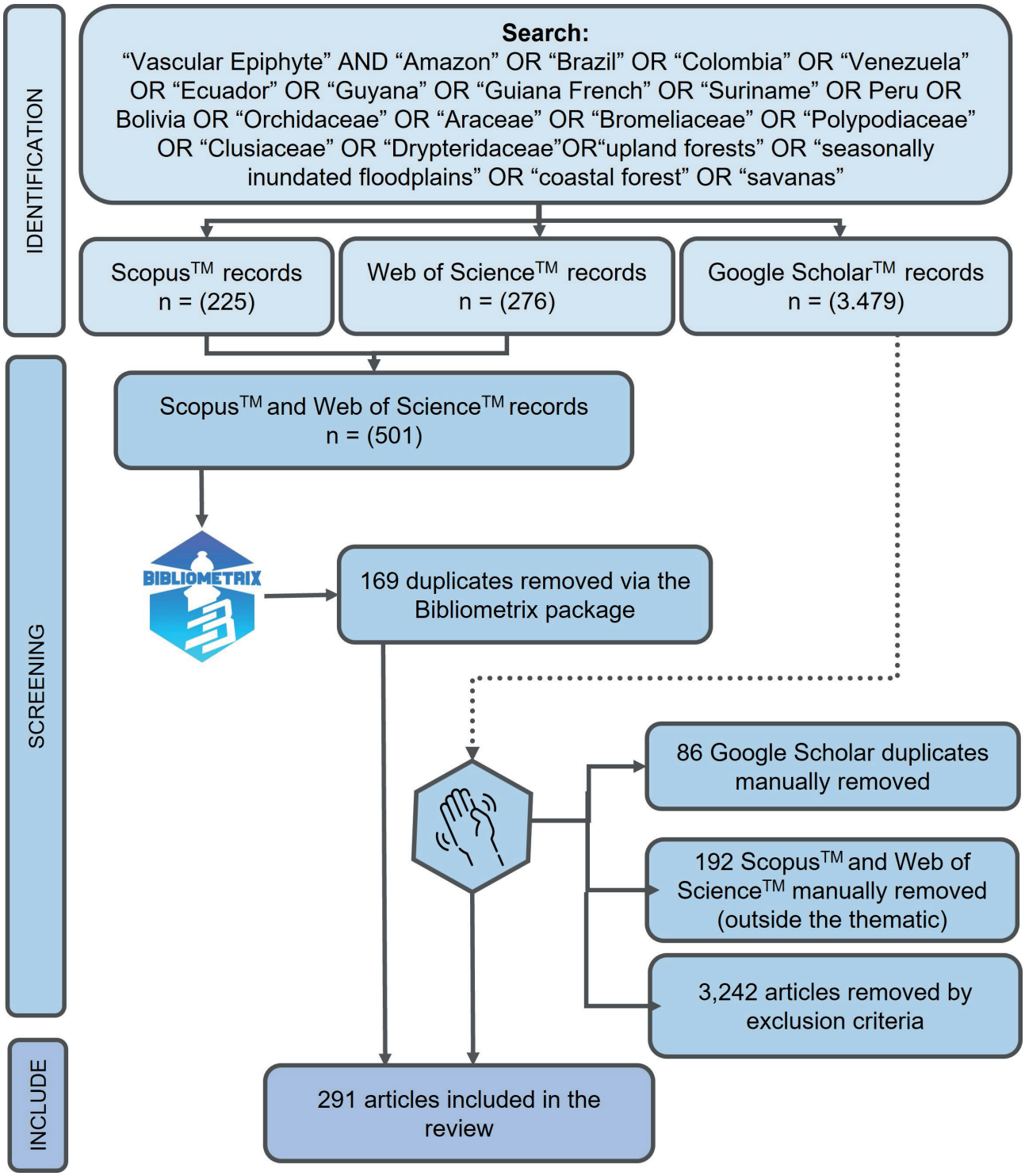

Figure 1. PRISMA flowchart of the search, inclusion and exclusion methodology for articles published about vascular epiphytes in the Amazon.

Cuyuni-Mazaruni region in Guyana (Davis & Richards 1933). After this initial milestone, the next study was published only in 1963. Until 1999, publications on epiphytes from the Amazon were few and restricted to one or two articles per year. From 2000, there was a significant increase ($p<0.001$) in the number of studies, especially in 2014, 2020 and 2022 with 25, 23 and 22 published articles, respectively, although in 2021 the publications have decreased, totalizing only 10 articles.

Most studies were conducted in Brazil (53%, 154 articles), followed by Colombia (12%, 34 articles), Ecuador (8%, 23 articles), Peru (7%, 21 articles), and Venezuela (4%, 11 articles). We highlight the low scientific production in punctual areas of the Brazilian Amazon (such as in the states of Maranhão and Tocantins and the south of the states of Amazonas and Pará), and also in Bolivia, Guyana and French Guiana, in addition to the absence of studies in Suriname (Fig. 3). Some studies were conducted in two or more Amazonian countries, such as the one presented by Cascante-Marin and Nivia-Ruiz (2013), which included floristic data from Peru and Ecuador and from six other non-Amazonian countries, and Quaresma *et al.* (2022), which included information on epiphytes from 32 localities in Brazil, Colombia, Guyana and French Guiana. We also highlight the study by Kessler (2001), who conducted an extensive assessement of the richness of ferns in 65 study sites in Bolivia and found that 56% of the surveyed species were epiphytes.

Among the 291 articles analyzed in this review, 62 were carried out in 30 conservation units of six countries (Table 1), especially in Brazil. Among the conservation units, the epiphytic floras of the Combu Island Environmental Protection Area and Caxiuanã National Forest, both in the state of Pará, and the Adolpho Ducke Forest Reserve, in the state of Amazonas, were the most studied, resulting in a total of 21 articles.

Keywords and categories of studies

A total of 2,360 keywords in English, Portuguese and Spanish (Fig. 4A) corresponding to 741 words in English were evaluated. The five most cited and with the highest number of co-occurrences were: "Amazon", "Taxonomy", "Epiphyte", "Orchidaceae", and "Diversity" (Fig. 4B). This result reflects the predominance of taxonomic studies and studies related to the diversity of epiphytes from Amazonian forests, in which Orchidaceae stands out among the families. The keywords and the approach of the studies allowed us to classify them in four categories: (1) systematics, floristics and/or biogeography of spermatophytes (195 articles); (2) systematics, floristics and/or biogeography of ferns (43

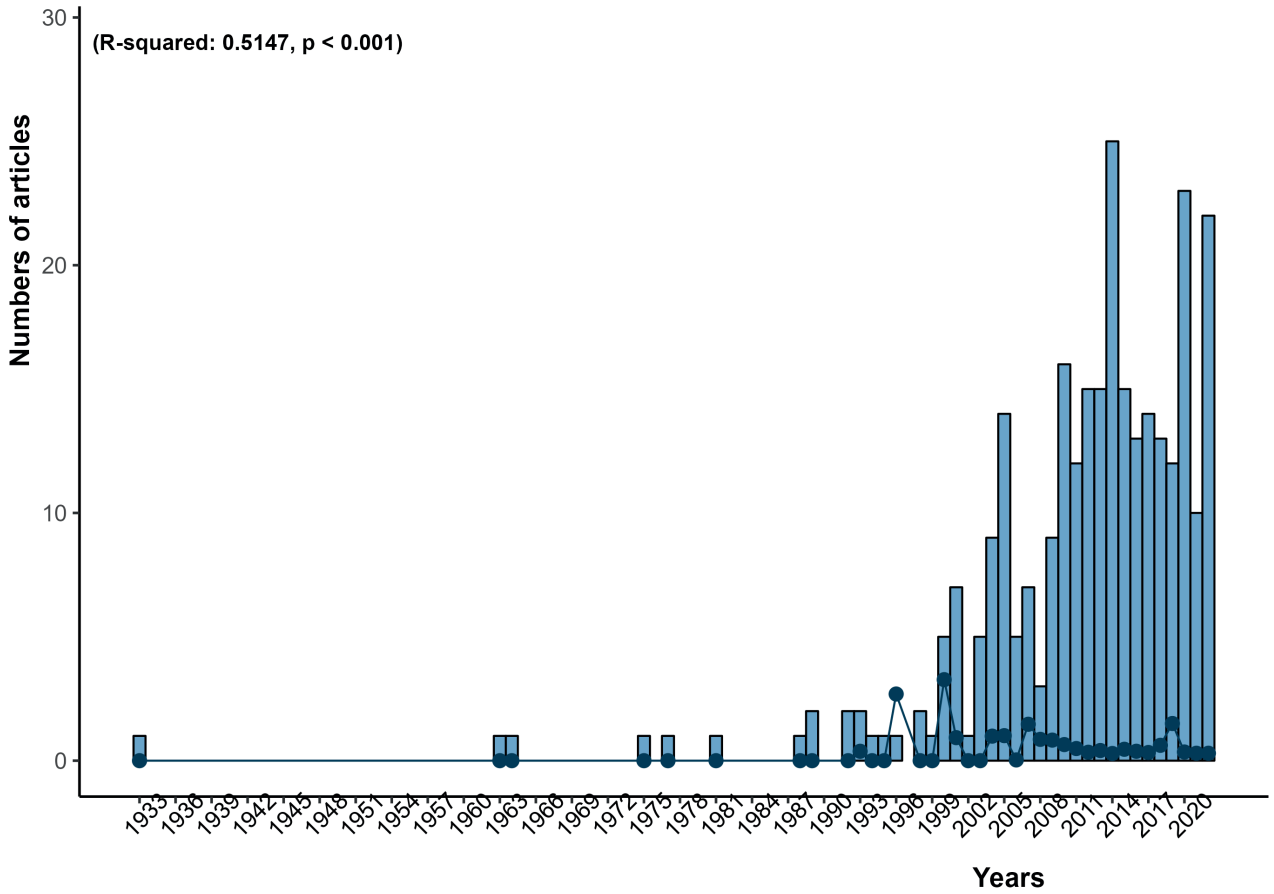

Figure 2. Number of publications about vascular epiphytes in the Amazon per year.

articles); (3) ecology, floral and/or reproductive biology (33 articles); and (4) biochemistry, phytochemistry, anatomy and/or physiology (20 articles) (Fig. 5).

A total of 67% of the articles were classified in the category one (systematics, floristics and/or biogeography of spermatophytes), which has been the main approach since the beginning of the studies. In turn, research related to other categories has declined in recent years. Among the articles classified in the category one, 101 correspond to floristic surveys and 89 are taxonomic studies. The former

Table 1. Number of articles about vascular epiphytes resulting from research in protected areas in the Amazon.

Country	Conservation units (number of publications)	Total
Bolivia	Madidi National Park	1
Brazil	Combu Island Environmental Protection Area (8), Adolpho Ducke Forest Reserve (7), Caxiuanã National Forest (6), Biological Reserve of Campina (4), Gumna Ecological Park (2), Jaú National Forest (2), Cristalino State Park (2), Uatumã Sustainable Development Reserve (2), Bacaba Municipal Natural Park (1), Algodoal-Maiandeua Environmental Protection Area (1), Cuniã Ecological Station (1), Tapajós National Forest (1), Amapá National Forest (2), Viruá National Forest (1), Belém Environmental Park (1), Gunnar Vingren Ecological Park (1), Amazon National Park (1), Chico Mendes Extractive Reserve (1), Walter Egler Forest Reserve (1), Alto Rio Guamá Indigenous Reserve (1)	45
Colombia	Amacayacu National Park (3), Chiribiquete National Park (3), Parque Nacional Natural Cueva de los Guacharos (1), Biologic Research Station Puerto Abeja (1)	8
Ecuador	Yasuní National Park (3), Podocarpus National Park (1)	4
Peru	Wayqecha Cloud Forest Research Station (1)	1
Venezuela	Alto Orinoco-Casiquiare Biosphere Reserve (1), Canaima National Park (1)	2
Total	**30**	**62**

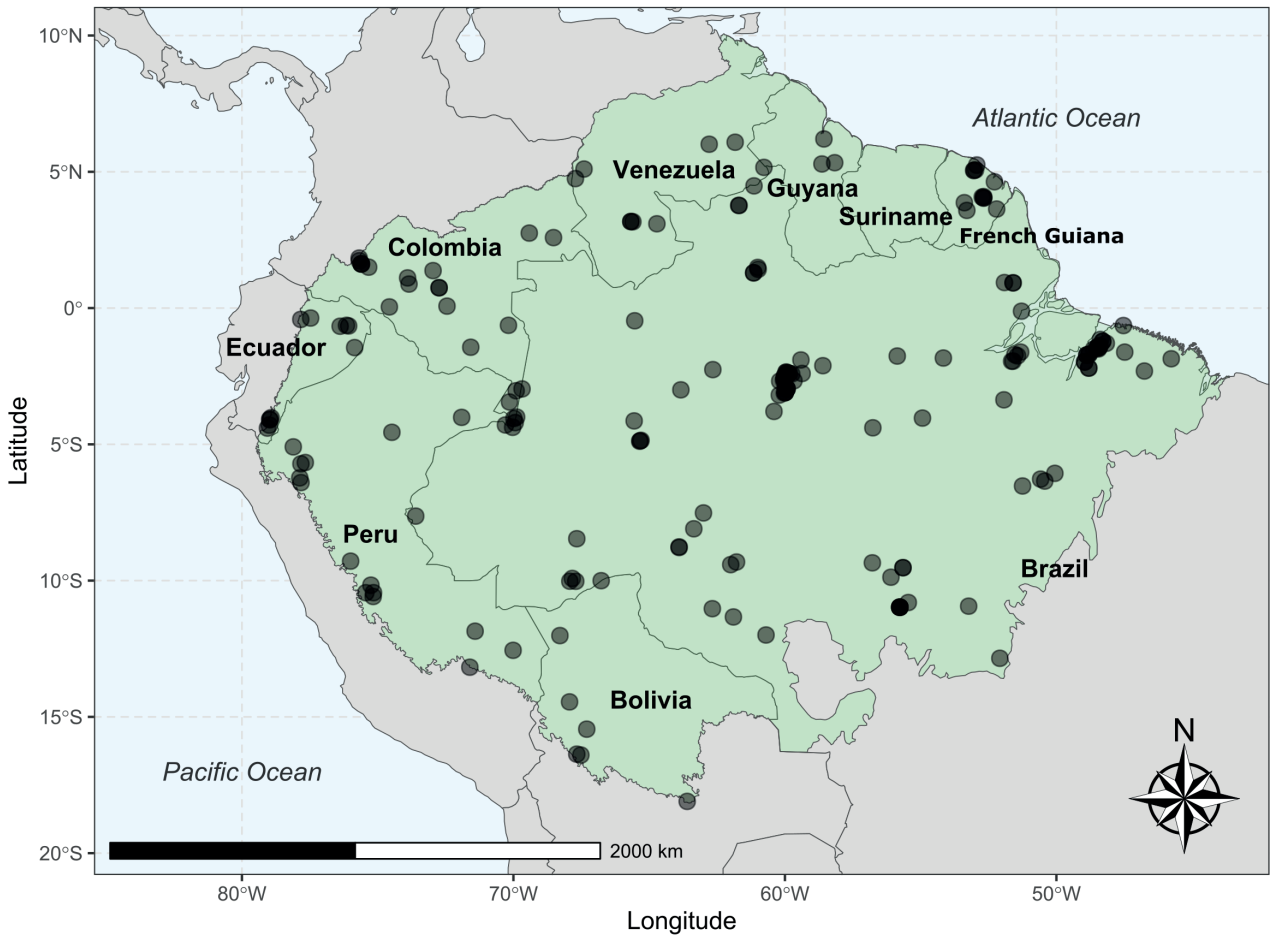

Figure 3. Location of the study sites of studies on vascular epiphytes carried out in the Amazon, based on location data provided in the articles. South America in gray and Amazon in green.

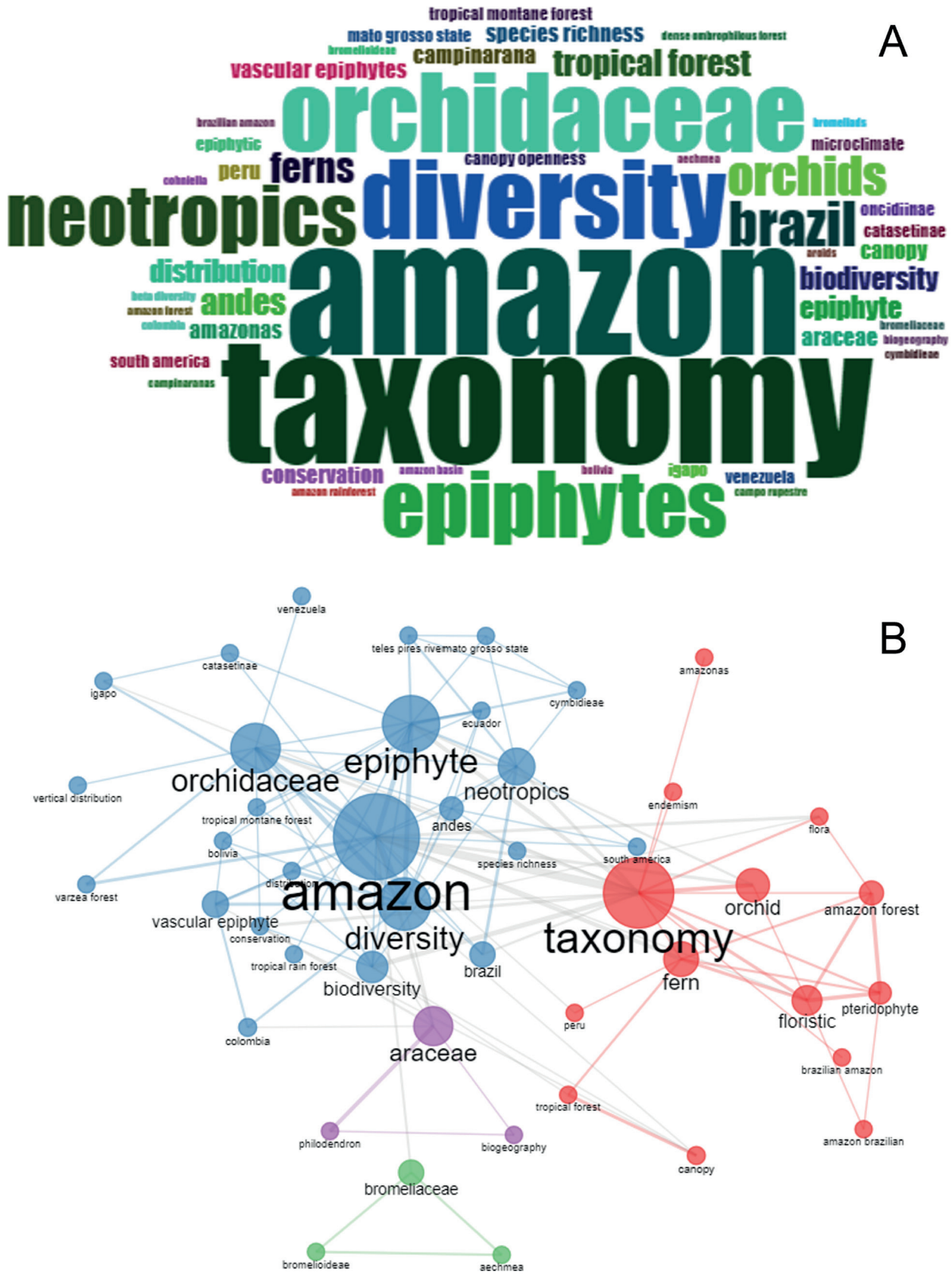

Figure 4. Word cloud (A) and co-occurrence of keywords (B) from studies about vascular epiphytes in the Amazon. The frequency of occurrence is indicated by the interlacing and the co-occurrence by the curves. Co-occurrence between words is negatively correlated with distance. Source: data extracted from Biblioshiny (Aria & Cuccurullo 2017).

consist of checklists of vascular epiphytes resulting from inventories of the whole angiosperm flora or specific taxa (e.g. Araceae, Bromeliaceae or Orchidaceae) carried out in different areas and ecosystems of the Amazon, including information about the response of the floristic composition of the group to environmental changes, such as opening of roads (McCracken & Forstner 2014) and intensive management of açaí (*Euterpe oleracea* Mart.) (Quaresma & Jardim 2013; Ferreira-Filho *et al.* 2021). Besides the list of species, some of these articles also provide information on the local richness; abundance; spatial, vertical, horizontal and geographic distribution; spatial and temporal variation; and phytosociological structure of the epiphytes.

Studies with a taxonomic focus consisted of revisions, often covering the phylogeny or geographic distribution of the species, taxonomic notes, descriptions of new species, hybrid taxa, or new records from a given region or state. Most of the new species described in the articles are of the family Orchidaceae, especially of the genera *Anathallis* Barb. Rodr. (*A. amazonica* E. Pessoa & M. Alves, *A. manausensis* Krahl, Valsko & Chiron, and *A. roseopapillosa* E. Pessoa & J.J. Valsko), *Catasetum* Rich. ex Kunth [*Catasetum* × *sheyllae* (natural hybrid), *C. sophiae* Valsko, Krahl & Benelli, *C. colidense* M.E. Engels, *C. kamatawara* Damián, Mitidieri & Bonilla, and *C. telespirense* Benelli & Soares-Lopes], *Dichaea* Lindl. (*D. bragae* Valsko, Krahl & Holanda and *D. integrilabia* Valsko, Krahl & Chiron), and *Epidendrum* L. (*E. aromoense* X. Cornejo & E. Hágsater, *E. dayseae* Krahl & Hágsater, *E. deditae* Hágsater & Krahl, and *E. olorteguii* Damián, Hágsater & Mitidieri). These studies also include descriptions, illustrations and photographic records of type species, identification keys, nomenclatural discussions, and data on habitats, phenology and conservation.

There were descriptions of new species also of the families Araceae and Bromeliaceae, of the genera *Heteropsis* Kunth from Brazil [*H. croatii* M.L. Soares and *H. robusta* (G.S. Bunting) M.L. Soares)] (Soares *et al.* 2009), *Anthurium* Schott (*A. peregrinense* O. López-Floriano, Croat & M. Correa) and *Aechmea* Ruiz & Pav. from Colombia (*A. baudoensis* Aguirre-Santoro & Betancur, *A. confertiflora* Aguirre-Santoro & Betancur, *A. longipedunculata* Betancur & Aguirre-Santoro, *A. longiramosa* Betancur & Aguirre-Santoro, *A. viridispica* Aguirre-Santoro & Betancur) (Aguirre-Santoro & Betancur 2011; López-Floriano *et al.* 2022). Among the new records of occurrence, *Scaphyglottis punctulata* (Rchb.f.) C. Schweinf., formerly restricted to highlands from Panama to Bolivia,

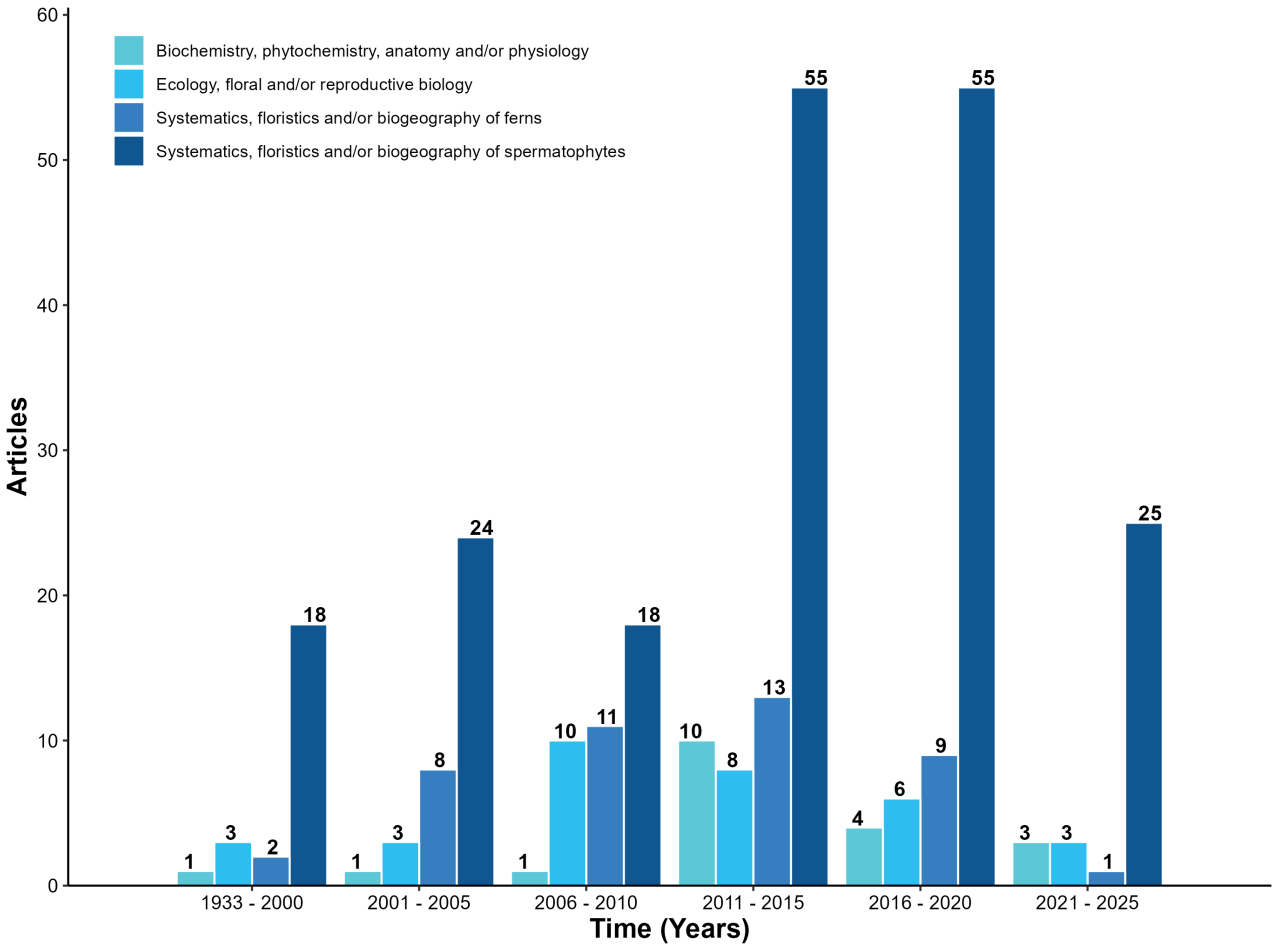

Figure 5. Number of publications about vascular epiphytes in the Amazon in the 20th century (1933-2000) and in the 21st century (2001-2022) by category.

was recorded in the Guiana Shield, in Brazil by Araújo *et al.* (2022), and some species of Araceae (*Philodendron uleanum* Engl.) and Orchidaceae [*Catasetum hopkinsonianum* G.F. Carr & V.P. Castro, *Notylia peruviana* (Schltr.) C. Schweinf., and *Platystele edmundoi* Pabst], previously reported to the states of Pará and Rondônia in Brazil and to other countries, were recorded in the state of Mato Grosso, Brazil, by Petini-Benelli *et al.* (2015).

In the category two ("systematics, floristics and/or biogeography of ferns"), descriptive studies of the fern flora of Serra dos Carajás in the state of Pará (Moura & Salino 2016) and Cuniã Ecological Station in the state of Rondônia (Sampaio *et al.* 2020), both in Brazil, stood out. Some studies also included other epiphytic organisms such as bryophytes and macrolichens, which commonly grow intermingled in tropical forests (Mandl *et al.* 2010). Mandl *et al.* (2010) demonstrated that epiphytic ferns are positively related to epiphytic liverworts and mosses in terms of diversity patterns in montane forests of Podocarpus National Park, Ecuador. The patterns of occurrence of epiphytic ferns in areas with different degrees of anthropic disturbance were the focus of the study by Oldekop et al. (2012) in Sumaco Biosphere Reserve (Ecuador), which demonstrated the dominance of common species in areas of secondary succession.

In the categories one and two, the most common methodologies used in floristic surveys included field expeditions and the establishment of plots, varying in number, shape and size. The evaluation of a predefined number of trees (phorophytes) was less frequent (only five studies). The consultation and analysis of herbarium specimens before field surveys was frequent in taxonomic studies.

The articles classified in the category three (ecology, floral and/or reproductive biology), focused predominantly on the families Araceae, Orchidaceae and Bromeliaceae. Micropropagation, *in vitro* germination and development, survival, growth, reproduction, vegetative propagation, and sustainability of extractivism and its impact on hemiepiphytes (specimens of the Araceae family) were the topics addressed. Werner and Gradstein (2008), for example, investigated the relocation and survival of epiphyte species in rescue actions, which depend on microclimatic factors (temperature and humidity), phorophyte characteristics, and degree of forest isolation. Interactions between vascular epiphytes and animals were also addressed in some studies. The association with ants was reported in six articles. For example, Gibernau *et al.* (2007) inventoried 44 ant species in 90% of the individuals of *Philodendron insigne* Schott (Araceae) evaluated. According to the authors, this association provides indirect protection to plants against herbivory and rewards ants through shelter or food resources (extrafloral nectaries of the plant).

In the articles classified in the category four (biochemistry, phytochemistry, anatomy and/or physiology), the chemical composition of oils from specimens of the genus *Philodendron* Schott [*P. fragrantissimum* (Hook.) G. Don, *P. goeldii* G.M. Barroso, *P. maximum* K. Krause, *P. solimoesense* A.C. Sm. and *P. scabrum* K. Krause] and the family Piperaceae [*Peperomia serpens* (Sw.) Loudon] were analyzed. Silva *et al.* (2016) showed that the chemical components present in extracts from these species have medicinal potential (antioxidant and antimicrobial) and possible pharmacological applications. We found only one published study in the area of phytochemistry, by Martinson *et al.* (2018), who evaluated the production rate of methane gas (CH_4) of bromeliads in mountainous tropical forests in Southern Ecuador (Reserva San Francisco).

The anatomical studies analyzed the vegetative organs (leaves, scapes, roots and velamen) of specimens of Bromeliaceae, Dryopteridaceae and Orchidaceae. We highlight the study by Silva *et al.* (2015), who performed the anatomical characterization of the roots of eight species of *Catasetum* collected in Mato Grosso, Brazil, and identified adaptations to the epiphytic habit (e.g. morphophysiological changes in the cells of the velamen, exodermis, cortex and medulla). However, this study aimed to contribute to the taxonomic identification of the genus, which reinforces the predominance of studies with taxonomic purposes.

Journals and citations

Most articles were published in journals dedicated to systematics and taxonomy (Phytotaxa and Rodriguésia), general biology (Acta Botanica Brasilica and Acta Amazonica) and nature conservation (Biodiversity and Conservation) (Table 2). Overall, 60 journals (52%) had 2021 JCR impact factors ranging from 0.110 (Genetics and Molecular Research, one article) to 9.231 (Food Chemistry, one article). The other 55 journals did not have a 2021 JCR impact factor, including five of the twenty journals with the highest number of publications.

Of the total number of articles, 212 were cited in other publications, and 106 of them had more than 10 citations. The most cited articles were Grubb *et al.* (1963), Teer Steege and Cornelissen (1989), Davis and Richards (1933), and Kreft *et al.* (2004), with 463, 393, 261 and 230 citations, respectively. Grubb *et al.* (1963) and Teer Steege and Cornelissen (1989) consist of floristic surveys carried out, respectively, in Ecuador and Guyana. The other two most cited studies were also carried out in these countries, but were more focused on the diversity and distribution of vascular epiphytes. Pinheiro *et al.* (2011) was the most cited article (78 citations) among the ones carried out in the Brazilian Amazon and the 15th among all analyzed in this review. In this study, the authors portray the medicinal potential of *Peperomia serpens* (Sw.) Loudon (Piperaceae), proving its anti-inflammatory efficacy for widespread use in folk medicine.

Table 2. List of the main journals that published articles about epiphytes in the Amazon, highlighting the impact factor (IF) and number and percentage of articles published. *According to Journal Citation Reports (JCR) 2021 (https://clarivate.com/).

Journal	IF JCR*	Number of articles	Percent of total number of articles
PHYTOTAXA	1.050	32	10.99
ACTA AMAZONICA	1.090	18	6.18
RODRIGUÉSIA	-	16	5.49
ACTA BOTANICA BRASILICA	1.395	14	4.81
BIODIVERSITY AND CONSERVATION	4.296	11	3.78
BIOTA AMAZÔNIA	-	10	3.43
BRITTONIA	0.758	8	2.74
SYSTEMATIC BOTANY	0.933	9	3.09
BOLETIM DO MUSEU PARAENSE EMÍLIO GOELDI	-	7	2.40
CALDASIA	0.487	6	2.06
JOURNAL OF TROPICAL ECOLOGY	1.800	6	2.06
BIOTROPICA	2.858	6	2.06
ECOTROPICA	0.350	4	1.37
JOURNAL OF BIOGEOGRAPHY	4.810	4	1.37
NORDIC JOURNAL OF BOTANY	0.931	4	1.37
REVISTA ÁRVORE	0.795	4	1.37
FOREST ECOLOGY AND MANAGEMENT	4.384	3	1.03
NOVON	0.530	3	1.03
REVISTA PERUANA DE BIOLOGÍA	-	3	1.03
SELBYANA	-	3	1.03
Other journals		123	41.24

Authors' affiliations and country of origin

Edlley Max Pessoa da Silva and Adriano Costa Quaresma stood out among the authors who studied vascular epyphytes in the Amazon, with 15 and 14 articles published in the period 2011-2022 (Fig. 6A), respectively. They are currently affiliated with the Federal University Mato Grosso and the National Institute for Research in the Amazon, respectively. E. Pessoa's publications are primarily related to taxonomic studies of species of Orchidaceae in Central Amazonia, Brazil, and A. Quaresma has mainly studied the floristic composition, richness, diversity and distribution of vascular epiphytes in general or specifically of Bromeliaceae, with most of the studies conducted in the state of Pará, Brazil. Mário Augusto Gonçalves Jardim and Maria Teresa Fernandez Piedade stand out among A. Quaresma's collaborators, and are among the 13 researchers with the highest number of publications (Fig. 6A).

The authors are affiliated with institutions in 20 countries (Fig. 6B). Researchers associated with Brazilian institutions were those who published the majority of the articles (171), followed by researchers from institutions based in Germany (37), United States (32), Colombia (27), Peru (15), Mexico (13), and Venezuela (9), in individual publications or parternships. Of the total of 171 articles, 137 were exclusively authored by researchers from Brazilian institutions and 34 articles involved cooperation with researchers from other countries (Germany, United States, France, Colombia, Mexico, United Kingdom, and Holland). The Emílio Goeldi Museum of Pará, the National Institute for Research in the Amazon, and the Federal University of Mato Grosso stand out among the Brazilian institutions with the greatest production of articles. The University of Goettingen in Germany and the Missouri Botanical Garden the United States were also instituitions with significant production.

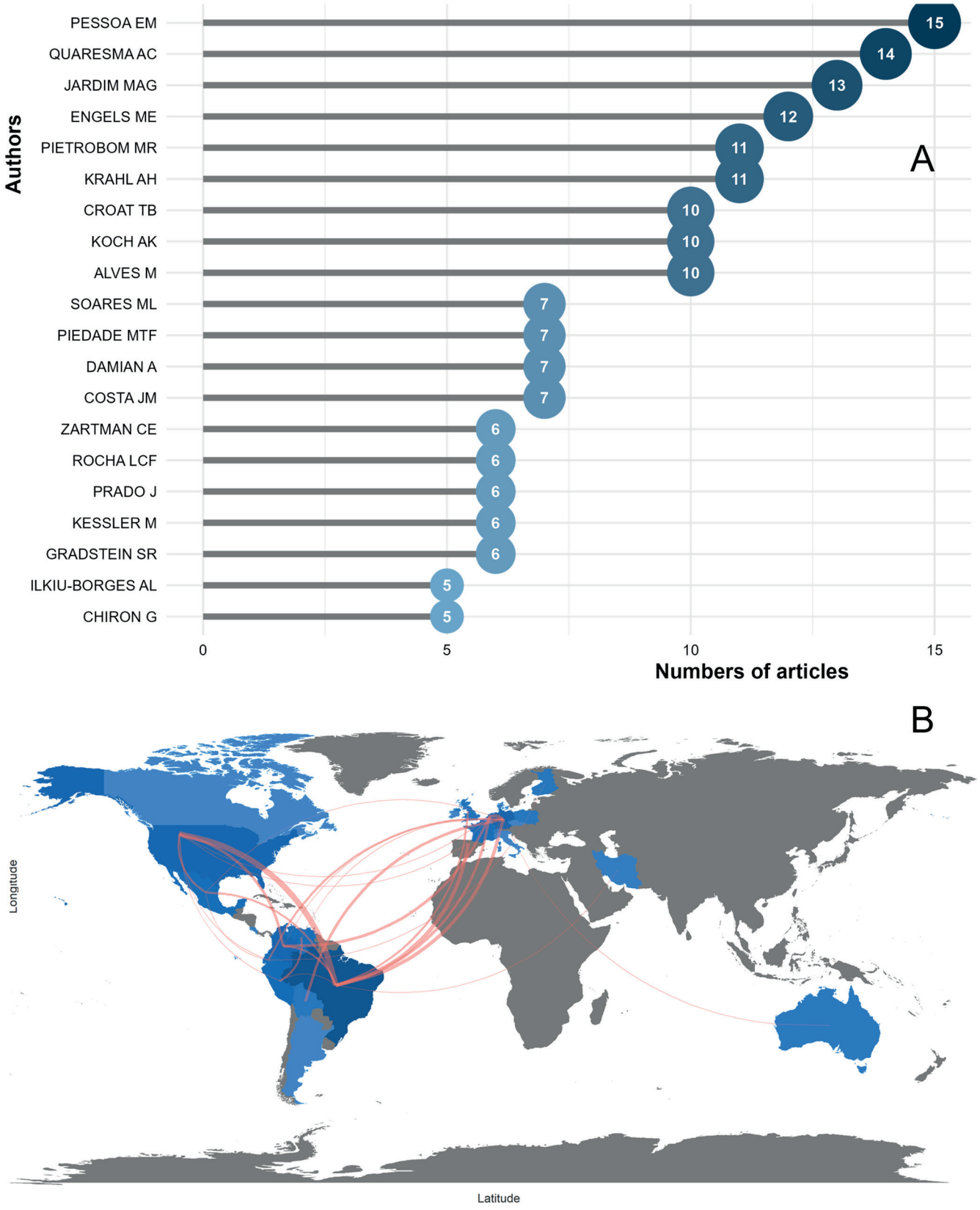

Figure 6. List of authors with the highest number of publications (A), countries of affiliation (blue color) and collaborations (orange line) (B) between authors of publications about vascular epiphytes in the Amazon, where the greater the intensity of the color (blue), the greater the number of publications per country. Source: data extracted from Biblioshiny (Aria & Cuccurullo 2017).

Discussion

Advances in studies on vascular epiphytes in the Amazon in recent decades

Of the 3,980 publications retrieved from the three databases, most were found in Google Scholar. After application of the exclusion criteria, the final number of articles was reduced to 291, or approximately 7.3% of the total number. This was mainly the result of the exclusion of documents such as books, theses, dissertations, abstracts, and technical reports that appeared in searches made in Google Scholar. The large body of literature, also observed by Jover *et al*. (2020), requires a process of manual cleaning and organization of information and this is considered a disadvantage of using this platform (Orduna-Malea *et al*. 2015). However, Google Scholar was responsible for 53% of the results obtained in this research and was, thus, essential to learn the current state of the art of research on epiphytes in the Amazon. Our review used a larger sample size than that used by the systematic study by Mengist *et al*. (2020b), who kept 5.9% (74 articles) of the total number of articles initially found (1,252) when conducting a survey of studies on ecosystem services of mountains in the northern hemisphere. In turn, our final sample was lower than that of Spicer & Woods (2022), who used 17% (233 articles) of the total number initially found (1,764) during a review of biotic interactions involving epiphytes.

Regarding the number of publications per year, the knowledge about vascular epiphytes in the Amazon, systematized in the form of scientific articles, has been built for almost 90 years, although there is a clear gap in the decades of 1940-1970. Only 24 articles were published in the period 1933-2000 and 267 articles were published in the following 22 years, indicating that the vascular epiphytes of the Amazon began to be more studied in the 21st century, which may actually be related to few investigations in the last century or late start of processing of databases consulted (Khapugin 2020). However, research gaps until the 20th century, are not exclusive to the Amazon phytogeographic domain. Gaps in the study of vascular epiphytes in the Brazilian Atlantic Forest were also identified (Kersten 2010). In turn, the decrease in the number of publications in 2021, the is possibly associated with the COVID-19 pandemic, which affected the development of researches (access to institutions or study areas) and, consequently, the scientific production worldwide (Chang *et al*. 2022). Yet, we can state that further investigations about vascular epiphytes in the Amazon are necessary and have been increasing in the last decades.

Brazil was the country where the greatest number of studies on vascular epiphytes was carried out. This can be associated to the fact that most of the Amazon (58%) is located within the Brazilian territory (Aragón 2018). However, we identified that these studies are more concentrated in the vicinity of the main research institutions (e.g. Instituto Nacional de Pesquisas da Amazônia, Museu Paraense Emílio Goeldi and Universidade Federal do Mato Grosso), and there is also a lack of inventories in Brazilian regions that coincide with the deforestation arc (Gomes *et al*. 2019; Quaresma *et al*. 2022). Furthermore, although the Amazon occupies a large territorial proportion (>50%) of Guyana, French Guiana, Suriname, Bolivia and Peru (Aragón 2018), a smaller number of publications come from these countries (Fig. 3), what highlights the need for studies in these areas. We also highlight the studies carried out in protected areas. The analysis of biodiversity in protected areas is essential to identify trends in species richness or abundance and assess the efficiency of conservation measures (Barnes *et al*. 2016). These assessments are especially important for epiphytes because the presence of this group indicates an increase in the structural complexity of forests (Richards 2020).

Main approaches, gaps and perspectives of studies on vascular epiphytes in the Amazon

We found that floristic surveys of spermatophytes and ferns prevailed over the other approaches. Floristic surveys were also predominant in the study by Bargali *et al.* (2022). This approach is common because of the need to know the flora and identify centers of biodiversity and priority areas for conservation and they help to find biological, biogeographical and ecological patterns and carry out quantitative comparisons of local diversity (Khapugin 2020; Zotz *et al.* 2021). Floristic information has confirmed the notorious diversity of plants associated with the canopy in several natural ecosystems of the Amazon (Taylor *et al.* 2021; Quaresma *et al.* 2022). However, we also noticed that few studies carried out a more comprehensive approach, considering frequency, dominance, abundance, population dynamics (growth and reproduction), information from support trees and factors that influence the occurrence of epiphytes (Kersten 2010, Mendieta-Leiva & Zotz 2015). This gap may be related to the difficulty of evaluating plants, for example, biomass studies require great field efforts, mainly in accessing the forest canopy and removing specimens for evaluation, with mostly destructive methods. In addition, there is still no clear understanding of the factors that contribute to the occurrence of epiphytes in anthropized areas, such as pastures with invasive trees and monocultures, which occupy large areas in the Amazon landscape (Projeto BioMaps Amazônia 2022).

As for the taxonomic studies, we noticed that the identification of new species and expansion of the distribution were frequent approaches throughout the period studied. However, the systematization of this information is important for the recognition of the real diversity of species that occur in the Amazon and their distribution in the Amazon Countries. In addition, the lack of comprehensive and reliable data on the richness

and distribution of vascular epiphytes in the Amazon are research gaps that hinder assessments biogeographical, of niche modeling and extinction risk (Marcusso *et al*. 2022; Quaresma *et al*. 2022).

We also identified that the sampling of floristic surveys is carried out using plots which are heterogeneous in number, shape and size, while the evaluation of the support tree (phorophytes) as a plot is still little used, although it is recommended by Wolf *et al*. (2009) and Mendieta-Leiva *et al*. (2020a). The most plausible justification for the use of plots in the evaluation of epiphytes is the possibility of comparison between sample units and the statistical methods are more applicable, although this evaluation consists of a more extensive field work. Methodologies that consider the support tree as a plot are subject to the researcher's subjectivity in choosing phorophytes with greater epiphyte richness. Therefore, discussions on methodology and guidelines for surveys still need to be debated to resolve issues related to surveying epiphytes.

In the ecological context, we did not find studies that evaluated the effects of interception of precipitation by epiphytes in the forests of Amazon, considering the high rainfall in the region and this being a subject that has been studied in other regions (Van Stan II & Pypker 2015; Mendieta-Leiva *et al*. 2020b). Plant-animal interaction studies are more related to myrmecory, making it necessary to investigate possible associations with other organisms, such as bacterias and endemic Amazonian animals (Spicer & Woods 2022). We can also highlight the need to establish protocols and the need to assess the translocation of epiphytes in pre-exploitation forest concession activities or reduced impact management in Amazonian areas (see Benavides *et al*. 2023).

Some angiosperm families, notably Araceae, Bromeliaceae and Orchidaceae, have received much attention, while studies focusing on other botanical families (e.g. Piperaceae and Clusiaceae) have been less studied. The focus on these families can be explained by their high representativeness in number of species in the Amazon (769 species of Orchidaceae, 456 species of Araceae, and 105 species of Bromeliaceae, according to Cardoso *et al*. 2017) and economic importance for ornamental use, with emphasis on the commercialization of flowers (Anacleto *et al*. 2017; Anacleto & Negrelle 2019).

Most studies were published in taxonomic and floristic journals. The approach of most of the studies was within the scope of these journals, confirming that research in these lines has attracted more attention of researchers. Even the anatomical studies were carried out with the objective of contributing to the taxonomic differentiation of species and clarification of the dynamics of geographic distribution of the taxa. More recently, taxonomic and phylogenetic studies began to include more robust analyses to confirm the expansion of the geographic distribution of taxa and evolution of adaptive strategies (Martins *et al*. 2018; Smidt *et al*. 2021).

As stressed by the researchers cited below, the main limitations recognized in the investigations of epiphytes are: (1) the lack of studies on certain families, preventing the comparison of results obtained in floristic surveys in the Amazon (Quaresma and Jardim 2012); (2) difficulties to visually locate and collect epiphytes in areas with high (≥20 m) and closed forest canopy (Ivanauskas *et al*. 2004); and (3) lack of determination of the threat level of species due to the lack of categorization by national and international agencies (Rodrigues *et al*. 2020). In our diagnosis, we also showed that the most productive researchers – precisely 13 researchers who are authors of seven or more articles each – are in Brazil and non-Amazonian countries. This low number authors who continuously publish on the subject suggests that they have unified work teams and access to research funding, especially thos with international collaborations in more developed countries, such as the United States and Germany. In this sense, the need for inclusion and improvement of access is evident, with incentives for grants and financing of research projects with vascular epiphytes aimed at researchers in the Amazonian region, aiming at expanding interdisciplinary and international networks.

We recommend that future studies on the epiphytic synusia include topics neglected in recent years, such as ecological studies (e.g. interactions with animals and mycorrhizal fungi), floral and reproductive biology, biochemistry, phytochemistry, anatomy, and physiology. The importance of biotic interactions and the medicinal use of vascular epiphytes have already been well documented in other continental-scale reviews (Nugraha *et al*. 2020; Spicer & Woods 2022), demonstrating the need for these assessments in the Amazon. We also reinforce that future research should consider the impacts of climate change on the diversity of vascular epiphytes (Gomes *et al*. 2019; Chang *et al*. 2022), mainly in the Amazon, taking into account current trends in deforestation, environmental changes, and expansion of the deforestation arc (Gomes *et al*. 2019). Long-term studies and studies of the population dynamics of epiphytes in the face of climate and land use changes are also essential for understanding the interactions and potential vulnerability of these plants (Richards 2020).

Conclusion

We found that vascular epiphytes in the Amazon have attracted the interest of researchers in the last two decades. In the scientific literature, there is a clear predominance of studies on the richness, spatial, vertical, horizontal and geographic distribution, and taxonomy of vascular epiphytes and researchers associated with Brazilian institutions actively participate in research carried out in the Amazon. However, there are still poorly studied regions and knowledge gaps.

Our study presented a comprehensive and cross-sectional approach on studies of vascular epiphytes carried out in the Amazon. However, we found some limitations. The exhaustive search for articles that characterize the state of the art of research on epiphytes in the Amazon resulted in publications with a low frequency of citations. Still, these studies are important and indicate that research is being conducted. As the main lessons resulting from this systematic review, we can state that there is a need to expand the network of researchers through continuous and long-term studies, strengthening institutional collaborations and interactions in the scientific community to produce knowledge on this theme.

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