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EDITED BY

Yi Zhang,
Chinese Academy of Sciences (CAS),
China

REVIEWED BY

Hao Wu,
Xinyang Normal University, China
Doru Stelian Banaduc,
Lucian Blaga University of Sibiu, Romania
Lingwei Kong,
Westlake University, China

*CORRESPONDENCE

Letícia da Silva Brito,
✉ let.brito@ua.pt

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Global distribution of *Pontederia crassipes*: a systematic and bibliometric review of biomass variations and environmental correlations

Letícia da Silva Brito*, Ana I. Lillebø and Heliana Teixeira

CESAM—Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, Aveiro, Portugal

Introduction: *Pontederia crassipes* is widely recognized as one of the world's most problematic invasive species. Although its spread and the impact it has on aquatic ecosystems have been the subject of numerous studies, there are still many unanswered questions regarding its invasive behavior outside its native range. This review addresses two key questions: (1) What is the current, science-based understanding of the invasiveness of *P. crassipes* as documented in peer-reviewed literature? (2) Which functional traits best explain its success as an invasive species beyond its native environment?

Methods: We conducted a systematic review and bibliometric analysis of 3,845 peer-reviewed publications up to December 2024.

Results: Studies in the native range primarily focus on ecological characteristics, while those in invaded areas emphasize phytoremediation, with biotechnology emerging as an expanding area of interest. This is the first study to combine bibliometric and environmental field data to explore the functional traits of *P. crassipes* on a global scale. Despite its acknowledged invasiveness, only 3.2% of publications addressed the functional traits and environmental variables found to be relevant during this review, in comparable manner. This has limited our understanding of the ecological niche of water hyacinth across its range.

Discussion: Our findings highlight persistent knowledge gaps and the urgent need for standardized reporting of Essential Biodiversity Variables across the species' global distribution. By combining systematic and bibliometric review, this study provides a comprehensive overview of research trends, identifies critical gaps, and guides hypothesis development for future studies. Standardized data collection and global cooperation are essential to develop evidence-based strategies, improve nature-based solutions, and promote sustainable management of *P. crassipes* worldwide.

KEYWORDS

essential biodiversity variables, freshwater habitats, invaded range, invasive alien species, water hyacinth

1 Introduction

Water hyacinth, the common name for *Eichhornia crassipes* (Mart.) Solms is now known as *Pontederia crassipes* (Mart.), the acknowledged synonym (Pellegrini et al., 2018). It has long been listed among the World's 100 Worst Invasive Alien Species (IAS) (Téllez et al., 2008), being recognized by the latest Global Assessment Report on IAS and their Control

(Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2023) as the most widespread macrophyte in freshwater habitats, such as lakes, ponds, rivers, and wetlands. It has been reported in more than 80 countries covering all continents except Antarctica (Jafari, 2010). *P. crassipes* is a freshwater free-floating aquatic plant with circular to oval-shaped leaves with swollen and spongy petioles, allowing buoyancy and oxygen flow up the petiole, with each inflorescence carrying up to 6–10 purple to blue color flowers (Dymond, 2002; Barret, 1980). Free-floating capacity is possible due to the presence of air-filled sacs in the petioles of leaves and stems (Mujere, 2015; Penfound and Earle, 1948). The average plant height is about 40–60 cm but it can grow up to 1 m (Mujere, 2015; Penfound and Earle, 1948). The long roots system beneath the water surface enables the uptake of nutrients from the water column and provides anchoring capacity (Huang et al., 2025; Penfound and Earle, 1948). *P. crassipes* reproduce both sexually, through the production of seeds, and asexually via clonal growth (stolons or rhizomes). The combination of both types of reproduction enhances its potential for rapid reproduction and expansion on the surface of aquatic habitats (Barret, 1980). In sexual reproduction, each capsule can contain 300 seeds (Poomsawat et al., 2019; Barret, 1980), and they can germinate in a few days or remain dormant for 30 years (Sullivan and Wood, 2012). In vegetative reproduction, stolons are dispersed in water, allowing this plant to reproduce easily (Pott and Pott, 2000; Gopal, 1987). This type of reproduction occurs through the development of stolons from the central rhizomes originating daughter plants (Thomaz, 2025). To develop roots and become a new plant by cloning, the rosette, a whorl of leaves that emerges from the base of the plant, can split through vegetative ramets. If these new plants find nutritious water and suitable habitat. Conditions, the size of the mat can double in 5 days (Nguyen et al., 2015; Malik, 2007).

The native biogeography of this species has been long discussed by the scientific community (e.g., Barrett and Forno, 1982), and although the Amazon River Basin is currently widely accepted as its native range, as expressed across global databases on invasive alien species (such as GISD and GRIIS), some authors argue that its origin covers South America more widely (e.g., Luque et al., 2014; Penfound and Earle, 1948). Data on its introduction history outside its native range reveals that it was introduced in Europe around 1879 (Téllez et al., 2008), in Africa, between 1879 and 1892 (Edwards and Musil, 1975), and in the United States in 1884 (Penfound and Earle, 1948). In Australia and Southeast Asia, its introduction dates to the early 1900s (Gopal, 1987). The introduction of this macrophyte to new geographical areas has typically coincided with significant human transportation across continents (Simberloff, 2020) and its use as an ornamental plant (European and Mediterranean Plant Protection Organization, 2008; Téllez et al., 2008).

Biomass and growth rate of *P. crassipes* have been estimated both in native and invaded ranges. Relevant examples of biomass for native range in Brazil are 57.19–70.14 t dw year⁻¹ in Pantanal Lake systems (Nunes and Silva, 2021) and 20.6 t dw year⁻¹ in a reservoir in Minas Gerais (Greco and de Freitas, 2002), while the reported growth rate is 259.34 g dw m⁻² day⁻¹ and 22.17 g dw m⁻² day⁻¹, respectively. For invaded ranges, relevant examples of biomass are 23–25 t dw year⁻¹, reported in a eutrophic lake (Center and Spencer, 1981), and of 50–60 t dw year⁻¹ in a wastewater reservoir (Reddy,

1984), both in Florida in the United States. Many studies have reported specific environmental conditions influencing growth of *P. crassipes*. Biomass fluctuations were observed between the dry and flood seasons in the Pantanal (Nunes and Silva, 2021), with the peak of growth being in summer when higher temperatures are observed. Temporal variations in biomass also reveal the importance of the “flood pulse.” The ability of water hyacinth to double biomass in just a few days has been attributed to the efficiency of light interception through the horizontal growth of stolons and the arrangement of new branches in less shaded places (Méthy et al., 1990; Thomaz, 2025). Since the 1920s, these features have made *P. crassipes* a perfect candidate for phytoremediation to remove excess nutrients as well as toxic elements from the water column (Pereira and Castro, 2023; Shahabaldin et al., 2021; Penfound and Earle, 1948). However, this macrophyte has become a significant problem worldwide due to its accelerated growth, lack of biological control agents, and the difficulty in controlling most infested areas (Hill et al., 2020; Nentwig et al., 2018). However, classic biological control methods, such as the release of *Megamelu scutellaris* (Berg) in South Africa over several seasons, have demonstrated effective control of the weed, particularly in cool temperate and eutrophic locations (e.g., Miller et al., 2023; Smith et al., 2024).

Among the negative impacts of the proliferation of this macrophyte is the low availability of oxygen in aquatic habitats, as the plant covers the water surface and blocks sunlight from penetrating the water column. This results in lower photosynthetic rates by the native primary producers, potential death of fish, and changes in the trophic structure of aquatic communities (Dereje et al., 2017; Villamagna and Murphy, 2010). These consequences can also have a significant impact on the biodiversity of the invaded aquatic habitat (Su et al., 2018; Villamagna and Murphy, 2010) as well as on human-related activities, like fishing (e.g., Adan, 2014). Dense mats at the water surface also cause the clogging of waterways, obstruct water transportation and interfere with bathing, navigation, and other recreational activities (e.g., Maulidyna et al., 2021; Segbefia et al., 2019; Su et al., 2018; Villamagna and Murphy, 2010). Concerns regarding negative impacts on water availability for irrigation have also been raised (Mailu, 2001; Penfound and Earle, 1948), due to the high evapotranspiration rates of expansive *P. crassipes* mats compared to open water surfaces. This impact is likely to be aggravated under altered flow regimes caused by highly modified freshwater systems (e.g., impounded waterways) and current climate change conditions (Oberdorff, 2022; Rivaes et al., 2022; Cordeiro et al., 2020), with devastating consequences in latitudes where drought events are already preventing the achievement or maintenance of ecological flows (Alvarez-Garretton et al., 2023). In Africa, water hyacinth infestations have been associated with water quality degradation, and direct impacts on human health where the plant provides an ideal habitat for the proliferation of malaria-transmitting mosquito larvae (Gezie et al., 2018). According to these authors, plant control would be a possible solution to reduce the risk of malaria epidemics in the region. The proliferation of this aquatic plant in hydroelectric dams also has a negative impact, as it can cause damage to generators, thus threatening the supply of electricity, and negatively impacting activities that depend directly on electricity (Lu et al., 2007).

Despite the significant challenges, researchers are exploring ways to turn the water hyacinth problem into an opportunity. To

reduce this macrophyte's negative impacts, current research is looking for ways to control its abundance through the valorization of water hyacinth biomass, focusing on diverse aspects that include the production of animal feed (Su et al., 2018) including fish feed (Mahmood et al., 2018); its potential for bioremediation and bioaccumulation of pollutants and metals (Singh and Balomajumder, 2021); for energy production, like vermicomposting and bioenergy (Balasubramanian et al., 2013); and also through medicinal use (Ayanda et al., 2020). Constructed wetlands have been used to treat domestic sewage (Kumwimba et al., 2017), for aquaculture (Betanzo-Torres et al., 2025; Sipaúba-Tavares et al., 2017) and to purify microplastics (Gao et al., 2024). While finding economically viable uses for *P. crassipes* could be beneficial, this would not necessarily mitigate the species' ecological impacts, as its invasive behavior and environmental effects would likely persist even after such uses are implemented (Drenovsky et al., 2012).

To understand the invasion process of *P. crassipes* from South America to the world, it is useful to consider hypotheses that aim to explain the phenomenon of biological invasions (Enders et al., 2020), as well as the potential empirical relationships among those hypotheses. For example, hypotheses related to resource availability associate invasion success with invader access to resources, which is affected by both abiotic and biotic conditions and their interactions. Along these lines, the knowledge gained from studying more than twenty invasive alien aquatic plants (Hussner et al., 2021) enabled a focus on attributes that better describe organismal invasive behavior, such as growth form, dispersal and spread, seasonality and evergreen life cycle, phenotypic plasticity, allelopathy and herbivore defences, frost tolerance, drought tolerance and avoidance strategies, and carbon-concentrating mechanisms. Likewise, there is a growing body of research on *P. crassipes* that includes aspects related to its introduction beyond its native range, including the species functional traits (e.g., reproduction) as well as the environmental factors that may explain its successful establishment, such as nutrient availability, temperature conditions (European and Mediterranean Plant Protection Organization, 2008; Barret, 1980). The limiting factors for the survival of *P. crassipes* are based on deviations from optimal pH (between 5 and 8), temperature (between 28 °C and 30 °C), and salinity (<2,900 ppm), as well as water nutrient concentrations, namely, phosphorus and nitrogen (Télez et al., 2008; Owens and Madsen, 1995; Reddy et al., 1990; De Casabianca and Laugier, 1995). This information makes it possible to create scenarios about the conditions that explain the species' successful establishment in new environments worldwide and is crucial to refining ecological niche models.

Despite the wealth of knowledge about its invasive capacity, spread and impacts, there are still several unanswered questions about the combination of factors and exact triggers of the invasive behavior of *Pontederia crassipes* outside its native environment (Lolis et al., 2020). Through a systematic review, this study addresses two key questions: (1) what is the science-based knowledge on *P. crassipes* invasiveness in peer-reviewed publications? (2) what functional traits have been most consistently associated with the invasive potential of *Pontederia crassipes* across different regions of introduction? This review provides an overview of the existing scientific knowledge concerning the biological characteristics and environmental

factors influencing the behavior of *Pontederia crassipes* in its native and invaded habitats. We hypothesize that differences in these traits and conditions may explain why the species exhibits contrasting behavior in different regions. Additionally, we highlight key knowledge gaps and limitations that constrain our understanding of the species' ecological dynamics. Importantly, this study is the first to integrate bibliometric analysis with field-based environmental data to investigate the functional traits and ecological niche of *P. crassipes* across its global distribution. Improving our understanding in this way can support the development of more effective management strategies by promoting the integration of relevant information about the species and its environmental interactions.

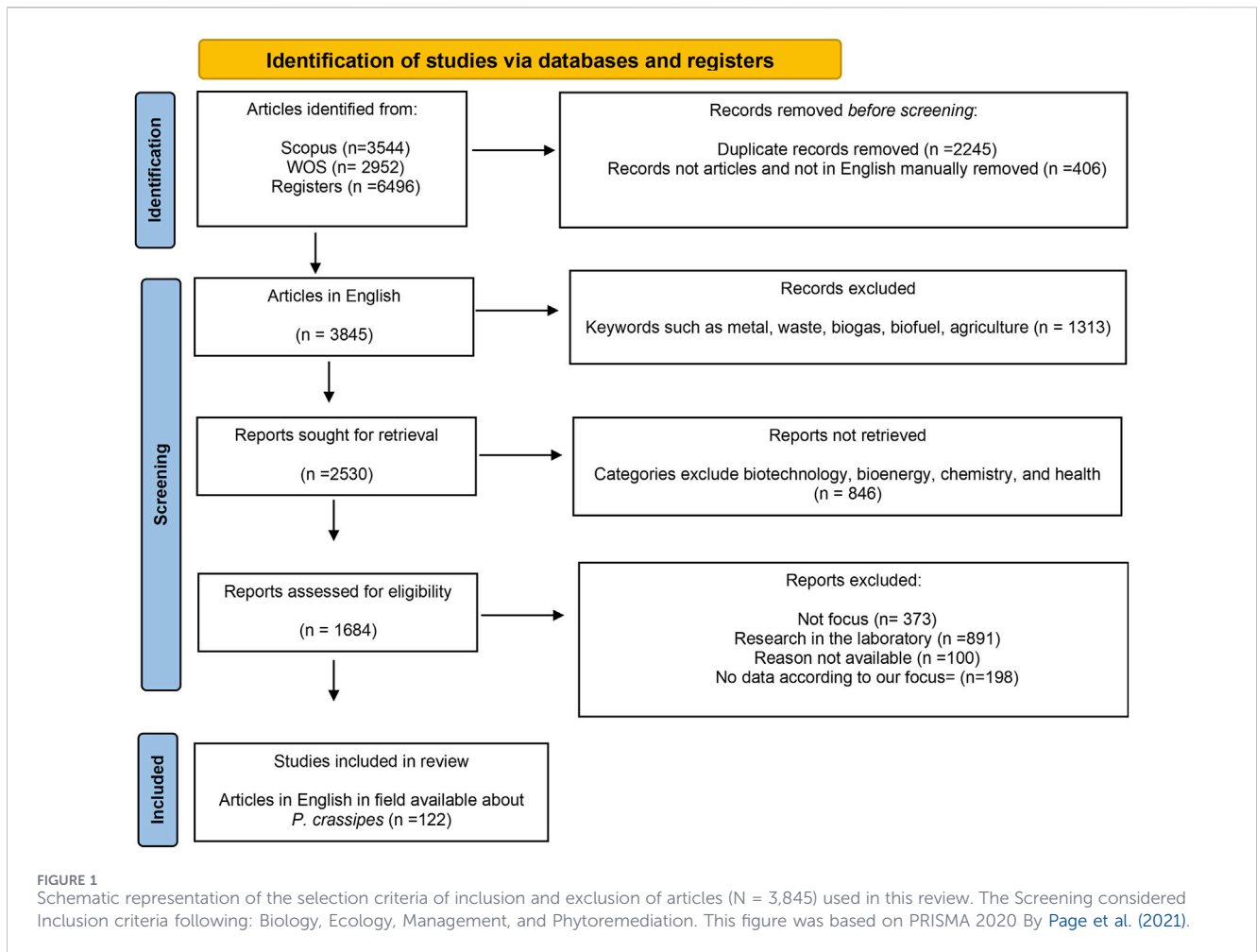
2 Materials and methods

2.1 Structured systematic literature search

A systematic literature review was conducted up to December 2024, targeting article titles, abstracts and keywords, using the Web of Science (WoS) and Scopus databases. The search was based on the following terms: TI = (*crassipes*) OR TS = (*Eichhornia* AND *crassipes*). Additionally, we replicated the search using the species updated taxonomic name, as defined by Pellegrini et al. (2018). For this, we used: TI = (*crassipes*) OR TS = (*Pontederia* AND *crassipes*), applied in both the WoS and Scopus databases using the same fields (article title, abstract and keywords).

In total, 6,496 articles were retrieved, covering a period from 1927 to December 2024, which were subject to a *posteriori* selection process following criteria fit to attain this study's objectives (Figure 1). This list of International Scientific Indexing (ISI) articles contains relevant metadata associated with it, organized into the following 12 fields: Title, Doi, Year of publication, Research area, Category Web of Science (WoS), Source of publication, Keywords Plus, Keywords by authors, Range of Distribution, Study Country, Authorship, and Abstract. Most of the metadata was extracted directly from the WoS search and Scopus. At the same time, the fields "Study Country," and "Range of Distribution" were added *a posteriori*, based on the information contained in the articles. The country (ies) was the place(s) where the research was carried out. The range of distribution was included to identify the geographic scope of the study according to three categories: (1) Native range (the study was carried out within the geographic range where the species is native), (2) Invaded range (the study was carried out in an area invaded by the species), (3) Both ranges (the study was carried out in more than one geography, including both the native and invaded distribution areas given for the species). The full articles list and respective metadata are available in a structured dataset (Supplementary Material 1, [Doi: 10.5281/zenodo.16989142]).

The following systematic review was carried out using the PRISMA process (Figure 1) and did not include (a) any type of publication other than peer-reviewed scientific articles, (b) articles written in languages other than English, (c) articles where *Pontederia crassipes* was not the focus and articles where *P. crassipes* was only mentioned in the References, (d) studies carried out under laboratory conditions, and finally (e)



publications for which the full article was not found in any online search (searched for full text on Web of Science, Scopus, Google Scholar and other search portals) or the corresponding author (contacted by e-mail) did not share the full text. The overall systematic review process is presented in Figure 1.

2.2 Data analysis to address each of the two research questions

To address the first question “What is the science-based knowledge on *P. crassipes* invasiveness in peer-reviewed publications?” a bibliometric analysis was performed to provide an overview of the research landscape on this species. The bibliometric analysis focused on the full list of the 3,845 peer-reviewed WoS and Scopus articles, considering the fields “authors,” “countries of publication,” “sources of publications” and “keywords by authors.” This analysis makes it possible to verify the structure of knowledge of the species studied based on groups formed based on keywords. The high frequency of keywords in different countries indicates the possibility of comparative studies of this species in various environmental conditions, providing relevant information about this plant’s ecological niche.

Word cloud analyses and thematic maps were carried out on all the articles with keywords (N = 3,111). The cloud of the most

frequent keywords used by the authors made it possible to identify the evolution of the themes and the lack of studies in this area. For this analysis, the data was further structured according to two periods: “before” (First article with keyword-2010) and “after” (2011–2024) the establishment of the Convention on Biological Diversity Aichi Targets in 2010. Aichi Target 9 specifically acknowledged the problem of biological invasions and focused on the control and eradication of invasive species as well as on the management of their pathways of introduction. In the analysis, we have removed the name of the studied species as well as its variations (e.g., “*Eichhornia crassipes*,” “water hyacinth”), as their high frequency could reduce the effectiveness of this technique to adequately represent the study categories of interest.

Before analysis, we applied the stop word technique, which involves removing words that frequently appear in the data but do not contribute meaning to the sentence, e.g., prepositions and conjunctions. This technique reduces noise in unstructured texts, thus increasing the statistical significance of terms that may be important for a specific task. A total of 23 keywords were removed (Supplementary Material 2-[Doi: 10.5281/zenodo.16989142]). In addition, the data were cleaned to standardize variations of the same word, such as plural and singular forms, acronym use and capitalization (e.g., “metal” and “metals”). To build a word cloud, we used the articles’ keywords (N = 9,432) but only the 50 most frequent

terms were used to produce the figures in this article. To enhance reproducibility and align the procedures with bibliometric standards, the keyword co-occurrence clustering and thematic map construction were performed using the default algorithms implemented in Bibliometrix. Keyword clustering was based on a co-occurrence network normalised using the association method, with a minimum edge-frequency threshold of five co-occurrences applied to retain statistically meaningful relationships among terms. Clusters were extracted using the Louvain community detection algorithm, which identifies groups of keywords that are cohesive within the global network.

Thematic maps were generated using the thematicMap() function in Bibliometrix, which computes a strategic diagram based on two quantitative parameters: centrality and density. Centrality was calculated as the sum of the strengths of external links between each cluster and all others, representing thematic relevance in the broader research domain. Density represented internal cohesion and was calculated as the average strength of links between keywords within each cluster. In the strategic diagram, clusters with centrality values above the 50th percentile were classified as basic or motor themes (depending on their density), whereas those below the 50th percentile were classified as emerging/declining or highly specialised/niche themes. All bibliometric and word-cloud analyses were carried out using Bibliometrix (Massimo and Cuccurullo, 2017), Wordcloud2 (Lang and Chien, 2018) and Tidyverse (Wickham et al., 2019) in R, version 4.3.2.

To address the second question “What functional traits have been most consistently associated with the invasive potential of *Pontederia crassipes* across different introduced ranges?” 122 peer-reviewed publications selected through the inclusion criteria were considered. It is important to note that 100 of the articles initially identified were unavailable, despite prior attempts to contact some of their authors. These studies are listed as “not available” in Supplementary Material 1. Excluding these articles may have introduced publication bias, as studies with negative or less significant findings may not have been included. The restricted set of publications was categorized according to their core research focus: Biology, Ecology, Management, and Phytoremediation. The biology category focuses on the traits, distribution and population dynamics of *P. crassipes*, while the ecology category focuses on understanding how the plant interacts with the biotic and abiotic factors present in its ecosystem. Publications in the Management category focus on applying techniques to control the biomass of *P. crassipes* effectively in the ecosystem. Finally, the phytoremediation category focuses on using macrophytes to absorb, reduce or stabilize toxicity caused by compounds from different sources.

The reduced list of 122 articles was assessed to extract the variables used in the studies that allow the characterization of the ecological niche of the *P. crassipes* species in invaded and native ranges. The extracted variables were divided into “Response,” for those plant-related variables, including all categories referring to the species *P. crassipes*, and “Explanatory,” for environment-related variables. *P. crassipes*-related variables were organized following the concept of Essential Biodiversity Variables (EBVs) (Pereira et al., 2013), as it has been used to aggregate biodiversity observations collected through different methods such as *in situ* monitoring (Latombe et al., 2017). The variables related to the aquatic environment were organized considering the most relevant elements of the European Union’s

Water Framework Directive (2000/60/EC) (European Union, 2000) for assessing water quality, which include: supporting physical and chemical quality elements; chemical quality elements; and hydro-morphological conditions. The choice of this framework was based on its wide acceptance and international recognition, its comprehensiveness and detail, and its solid scientific and technical basis. The extracted “Response” and “Explanatory” variables (Tables 1 and 2) represent all the variables found in the 122 articles, which allow us to infer the ecological dynamics of the plant.

Although we identified several response and explanatory variables, these were not sufficient to establish a relationship with plant characteristics due to the limited number of articles with both sets of information, i.e., the response and explanatory variables, in the invaded and native range. For example, only five articles presented similar data to evaluate biomass response to environmental conditions (e.g., Biomass and Temperature). To fill this gap, we decided to check the amplitude of the most frequently mentioned variables in the native and invaded ranges (Table 3), analyzing the mean, standard deviation and confidence interval. As detailed in the dataset description, all biomass estimates were standardised to dry weight per unit area (g DW m^{-2}). Of the 122 studies, many reported biomasses in fresh weight (FW) without specifying the moisture content. In these cases, the biomass was converted using the classical assumption that *P. crassipes* contains approximately 95% water [based on the work of Penfound and Earle (1948)], resulting in the conversion $\text{DW} = 0.05 \times \text{FW}$. This conversion was applied only when the original study did not provide dry weight data or an FW–DW conversion factor. We checked whether the authors of each study had reported specific moisture values, species-specific DW/FW ratios, or simultaneous FW and DW measurements. When these original ratios were available, they were used instead of the 95% assumption. As our dataset includes sites across tropical and temperate regions, we modified only 19.8% of the data, which covers diverse locations (China, the United States, Indonesia and India) across tropical and temperate zones. Most studies in literature, including those from these regions, also use a water content of 95% (Penfound and Earle, 1948; Gopal, 1987; Gao et al., 2014).

Analyzing the range and dispersion of the variables enabled us to identify potential differences or overlaps in the environmental conditions between the native and invaded areas. By investigating tolerance patterns, it enabled us to infer whether the plant exhibited greater tolerance in invaded areas, which could indicate ecological plasticity or adaptation. Furthermore, an analysis of variance (ANOVA) was performed in R (R Core Team, 2023) using the aov() function. Distribution maps of category frequencies were generated using the scatterpie package (Yu, 2018). All analyses were conducted using R version 4.3.2.

3 Results

3.1 Evolution and current science-based knowledge on *Pontederia crassipes*

The current science-based knowledge on *Pontederia crassipes* in the peer-reviewed literature was supported by an analysis of 3,845 scientific publications. India had the highest number of

TABLE 1 Response variables found in the review of 122 articles about *Pontederia crassipes*, grouped according to the essential biodiversity variables framework.

Response variables		
EBV class	EBV category	EBV name
Species traits	Morphology	Leaf area index
Species traits	Morphology	Leaves per plant
Species traits	Morphology	Plant part measurements
Species traits	Morphology	Petiole length
Species traits	Physiology	Carbon in parts of the plant
Species traits	Physiology	Carbon: nitrogen ratio
Species traits	Physiology	Carbon: phosphorus ratio
Species traits	Physiology	Chlorophyll (α)
Species traits	Physiology	Evaporation
Species traits	Physiology	Fiber
Species traits	Physiology	Hemicellulose
Species traits	Physiology	Light extinction coefficient
Species traits	Physiology	Lignin
Species traits	Physiology	Lignin: nitrogen ratio
Species traits	Physiology	Lignin: phosphorus ratio
Species traits	Physiology	Lipids
Species traits	Physiology	Magnesium in parts of the plant
Species traits	Physiology	Nitrogen in parts of the plant
Species traits	Physiology	Phosphorus in parts of the plant
Species traits	Physiology	Potassium in parts of the plant
Species traits	Physiology	Relative growth phosphorus
Species traits	Physiology	Sodium in parts of the plant
Species traits	Physiology	Decomposition rate
Species traits	Phenology	Doubling time of growth rate
Species traits	Phenology	Number of inflorescences
Species populations	Species abundances	Cover
Species populations	Species abundances	Biomass
Species populations	Species abundances	Density
Species populations	Species abundances	Dominance

publications, accounting for 21% of all research on water hyacinth, followed by China (Figure 2). Together, these two countries were responsible for one-third (32%) of all publications.

In India, the largest number of articles fall within the phytoremediation research area. BioSource Technology was the journal with the highest number of publications on this species: 98 articles out of 3,845 were reviewed, corresponding to a 2.5% share of publications across the 1,422 journals that were registered in this review. Prominent authors Martin Hill and Julie Coetzee contributed significantly to scientific literature,

accounting for 2.8% of total publications with a total of 108 articles. Of these, 41 were attributed to Coetzee, 33 of which were co-authored with Hill. Both are associated with Rhodes University, a biological control research centre in South Africa. Hill and Coetzee first published on this topic in 1999 and 2003, respectively. Their publications from 1999 to 2024 demonstrate that their research has centered on the biological control of water hyacinth, with a focus on exploring the use of insect species, particularly *Neochetina eichhorniae* Warner, *Neochetina bruchi* Hustache (Coleoptera:

TABLE 2 Explanatory variables grouped according to the Water Framework Directive found in 122 articles about *Pontederia crassipes*.

Explanatory variables (Water Framework Directive)	
Community	% Females of predator
Community	% Reproduction of predator
Community	Adult of weevil, larvae
Community	Alga species
Community	Bacteria species
Community	Eggs of predator
Community	Evenness (J')
Community	Fish
Community	Fungi
Community	Mollusc
Community	Plankton species
Community	Predation
Community	Shannon (H')
Community	Simpson (S)
Community	Sociologic dates
Community	Survival of predator
Hydromorphology	Area
Hydromorphology	Evapotranspiration
Hydromorphology	Flow
Hydromorphology	Hardness
Hydromorphology	Irrigation
Hydromorphology	Shade
Hydromorphology	Volume
Hydromorphology	Waterflow
Hydromorphology	Width of lagoon
Physical and chemical	<i>Climatic</i>
Physical and chemical	Air temperature
Physical and chemical	Precipitation
Physical and chemical	Relative humidity
Physical and chemical	Water evaporation
Physical and chemical	Water temperature
Physical and chemical	Wind Pressure
Physical and chemical	<i>Nutrients</i>
Physical and chemical	Aluminium
Physical and chemical	Boron
Physical and chemical	Calcium
Physical and chemical	Carbon measured in different forms
Physical and chemical	Chlorine
Physical and chemical	Cobalt

(Continued)

TABLE 2 Continued

Explanatory variables (Water Framework Directive)	
Physical and chemical	Copper
Physical and chemical	Dissolved inorganic nitrogen
Physical and chemical	Magnesium
Physical and chemical	Manganese
Physical and chemical	Molybdenum
Physical and chemical	Nitrogen measured in different forms
Physical and chemical	Phosphorus measured in different forms
Physical and chemical	Potassium
Physical and chemical	Rubidium
Physical and chemical	Sodium
Physical and chemical	Soluble Reactive Silica
Physical and chemical	Strontium
Physical and chemical	Sulfur
Physical and chemical	Sulphate
Physical and chemical	Uranium
Physical and chemical	Zinc
Physical and chemical	Oxygen related
Physical and chemical	Biologic Oxygen Demand
Physical and chemical	Dissolved Oxygen
Physical and chemical	Oxidation-reduction potential
Physical and chemical	Water Transparency
Physical and chemical	Secchi Depth
Physical and chemical	Turbidity
Physical and chemical	<i>Biological parameters</i>
Physical and chemical	Organic Matter
Physical and chemical	Sediment redox
Physical and chemical	Relative Thermal Resistance
Physical and chemical	<i>Physical parameters</i>
Physical and chemical	Conductivity
Physical and chemical	Light intensity
Physical and chemical	pH
Physical and chemical	Salinity
Physical and chemical	Total dissolved solids
Physical and chemical	<i>Inorganic parameters</i>
Physical and chemical	Carbon dioxide
Physical and chemical	Silicon dioxide
Specific pollutants	2,4-D amine
Specific pollutants	Diquat
Specific pollutants	Mercury
Specific pollutants	Polyvinylpyrrolidone

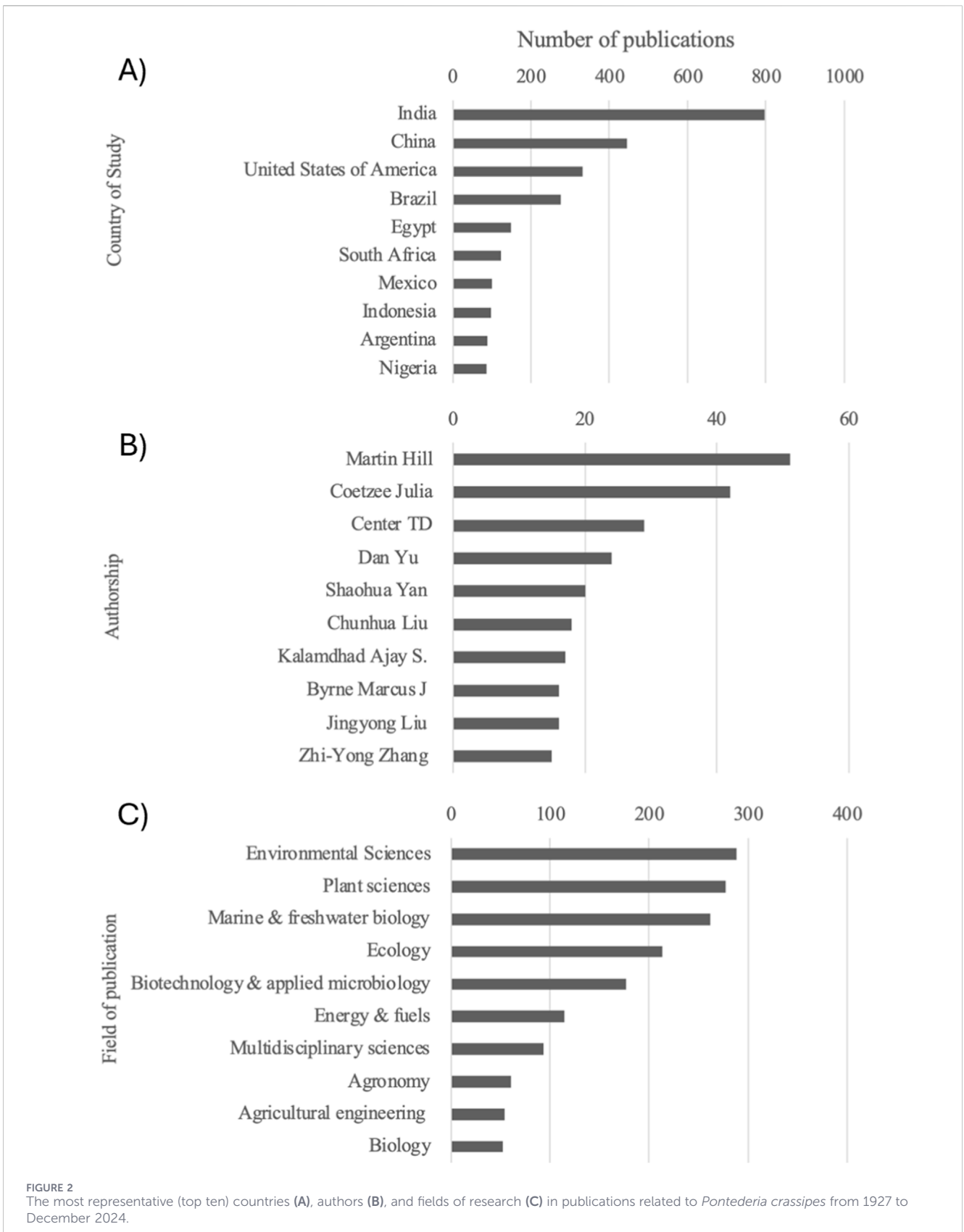
TABLE 3 *Pontederia crassipes* variables comparison in invaded and native range (after consultation of N = 122 articles).

Distributional range	Variables	n	Mean	Deviation	Error	t critical	95% CI lower bound	95% CI upper bound
Invaded range								
Response variable	Biomass in plant (g.dw.m ⁻²)	86	354.35	458.40	49.43	1.99	256.07	452.63
Explanatory variables	Alkalinity (mg/L)	15	189.89	43.26	11.17	2.14	165.93	213.84
	Ammonia (mg/L)	45	1.77	4.77	0.71	2.02	0.33	3.20
	Conductivity (µm/cm)	25	449.74	455.41	91.08	2.06	261.75	637.72
	Depth (m)	30	0.94	0.64	0.12	2.05	0.70	1.18
	Dissolved oxygen (mg/L)	57	4.55	2.51	0.33	2.00	3.88	5.21
	Nitrate (mg/L)	49	1.27	2.44	0.35	2.01	0.57	1.97
	Nitrite (mg/L)	18	0.41	0.34	0.08	2.11	0.24	0.57
	Orthophosphate	17	0.27	0.15	0.04	2.12	0.19	0.35
	Salinity (ppt)	29	6.77	9.40	1.75	2.05	3.20	10.35
	pH	42	7.58	0.42	0.06	2.02	7.45	7.71
	Secchi (m)	7	1.03	0.88	0.33	2.45	0.22	1.85
	Total nitrogen (mg/L)	35	12.98	27.31	4.62	2.03	3.60	22.36
	Total phosphorus (mg/L)	50	0.90	1.33	0.19	2.01	0.52	1.27
	Temperature (°C)	94	22.02	8.45	0.87	1.99	20.29	23.75
Water temperature (°C)	36	22.68	10.40	1.73	2.03	19.16	26.20	
Native range								
Response variable	Biomass in plant (g.dw.m ⁻²)	17	577.48	718.97	174.38	2.12	207.82	947.14
Explanatory variables	Alkalinity (mg/L)	11	45.08	74.69	22.52	2.23	-5.10	95.26
	Ammonia (mg/L)	37	0.08	0.12	0.02	2.03	0.04	0.12
	Conductivity (µm/cm)	43	184.35	70.38	10.73	2.02	162.69	206.01
	Depth (m)	26	4.51	7.39	1.45	2.06	1.52	7.49
	Dissolved oxygen (mg/L)	62	3.19	2.14	0.27	2.00	2.65	3.73
	Nitrate (mg/L)	19	0.11	0.13	0.03	2.10	0.05	0.17
	Nitrite (mg/L)	9	0.79	1.56	0.52	2.31	-0.40	1.99
	Orthophosphate	30	0.06	0.03	0.01	2.05	0.04	0.07
	Salinity (ppt)	4	1.01	0.64	0.32	3.18	0.00	2.02
	pH	30	7.42	0.79	0.14	2.05	7.13	7.71
	Secchi (m)	41	0.84	0.61	0.10	2.02	0.65	1.04
	Total nitrogen (mg/L)	31	5.40	7.05	1.27	2.04	2.82	7.99
	Total phosphorus (mg/L)	32	0.22	0.32	0.06	2.04	0.10	0.33
	Temperature (°C)	67	22.18	3.85	0.47	2.00	21.24	23.12
Water temperature (°C)	35	23.30	2.94	0.50	2.03	22.29	24.31	

Brachyceridae) and *Megamelus scutellaris* Berg (Hemiptera: Delphacidae), to control the plant in South Africa.

Five of the top 10 authors were from China, followed by South Africa, the United States, and India. Notably, both developed (the

United States) and developing countries (Argentina, Brazil, China, Egypt, India, Indonesia, Mexico, Nigeria and South Africa) are researching this plant species. The four continents were well represented in literature: Asia, America, Oceania and



Africa. Europe is not represented at this table at all, demonstrating that fewer works on this subject have been published there than on the other continents. The first paper on *P. crassipes* was published

in the Journal of Experimental Zoology in 1927, dealing with the interaction between plants and animals in continuous bioelectric currents. It was not until 1933 that the American Journal of

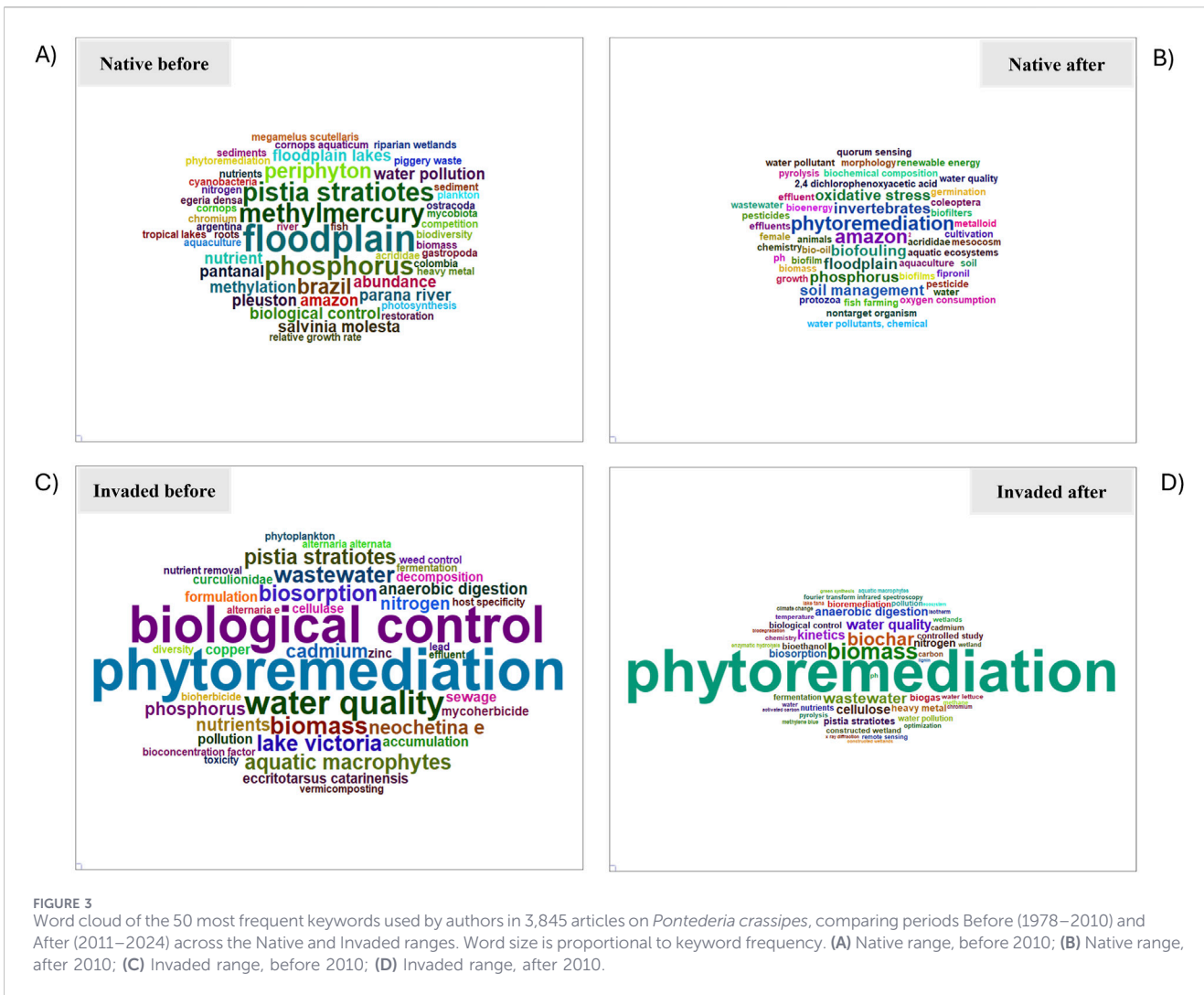


FIGURE 3 Word cloud of the 50 most frequent keywords used by authors in 3,845 articles on *Pontederia crassipes*, comparing periods Before (1978–2010) and After (2011–2024) across the Native and Invaded ranges. Word size is proportional to keyword frequency. (A) Native range, before 2010; (B) Native range, after 2010; (C) Invaded range, before 2010; (D) Invaded range, after 2010.

Botany published a paper focusing on a new genus of this plant. This suggests that the initial focus was on characterizing the species.

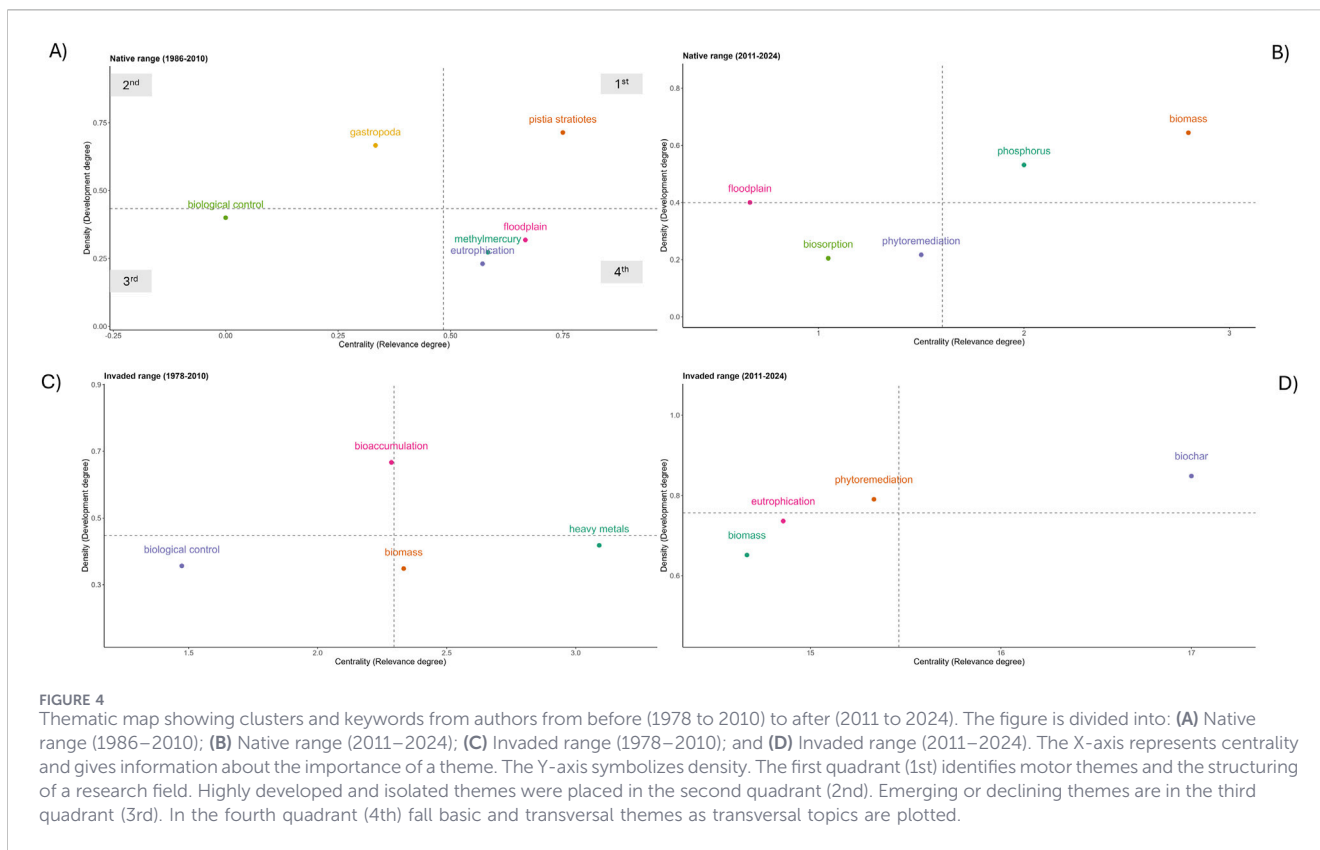
Further insight into research trends was gained through bibliometric keyword analysis (Figure 3).

Across both the native and invaded ranges in both periods, before and after the establishment of the CBD (Convention on Biological Diversity, 2010) Aichi Target 9 in 2010, the term “phytoremediation” emerged as the most frequent, reflecting the broad scientific interest in using *P. crassipes* to mitigate aquatic pollution. In the native range, prior to the implementation of the CBD, common keywords included “*Pistia stratiotes*,” “floodplain” and “methylmercury,” suggesting a focus on the species’ ecological role in eutrophication and nutrient cycling. These themes emphasized the plant’s role in natural ecosystem dynamics and its importance in conservation and management studies.

During the period of invasion (1978–2010), the keyword “phytoremediation” was cited the most frequently (N = 33, see Figure 3), indicating sustained scientific interest in the potential environmental benefits offered by *Pontederia crassipes*. Biological control followed closely behind (N = 29), reflecting national efforts

to manage invasive populations through nature-based interventions. These trends suggest a strategic alignment between scientific enquiry and policy priorities aimed at sustainable management and biodiversity conservation. These insights were reinforced by the thematic map generated from author keywords (see Figure 4), which revealed well-defined clusters of knowledge across geographic ranges and time periods.

Notably, biological control emerged as a recurring theme in both native and invaded contexts, highlighting the need for further research into its effectiveness and adaptability. Meanwhile, phytoremediation appeared consistently across both periods and regions, reaffirming its status as a key application of the species for ecosystem restoration. In the native range, its presence in the “emerging” quadrant indicated the need for further research to realize its full remediation potential within its original ecological context. Thus, the evolution of the scientific literature on *P. crassipes* reflected the dynamic interplay between ecological challenges and technological opportunities. The current research landscape was shaped by well-established themes, such as phytoremediation, and emerging areas, such as biological control. This illustrated the multifaceted role of this species in global environmental science.



3.2 Mapping the literature: study distribution and reported environmental traits

To further understand the distribution of *P. crassipes* and its relationship with environmental variables the extracted “Response” (Table 1) and “Explanatory” (Table 2) variables found in the 122 articles were analyzed to infer the ecological dynamics of the plant in response to its environment.

The explanatory variables, grouped according to the Water Framework Directive, included biotic factors (diversity and abundance of aquatic organisms, predation, and predator reproduction), hydro-morphological factors (area, volume, flow, shading, and irrigation), physicochemical factors (pH, salinity, nutrients, metals, and water quality), and specific pollutants (herbicides and heavy metals). These data provide insights into how environmental, chemical, and biotic factors influence the distribution, population dynamics, and invasive potential of the species across different ecosystems.

These studies, that included both lentic and lotic ecosystems, were conducted in 30 countries and their main research focus was on ecology (N = 62), management implications (N = 36), and the plant’s biological traits and features (N = 15). A few also considered *in situ* applications for phytoremediation purposes (N = 9) (Figure 5).

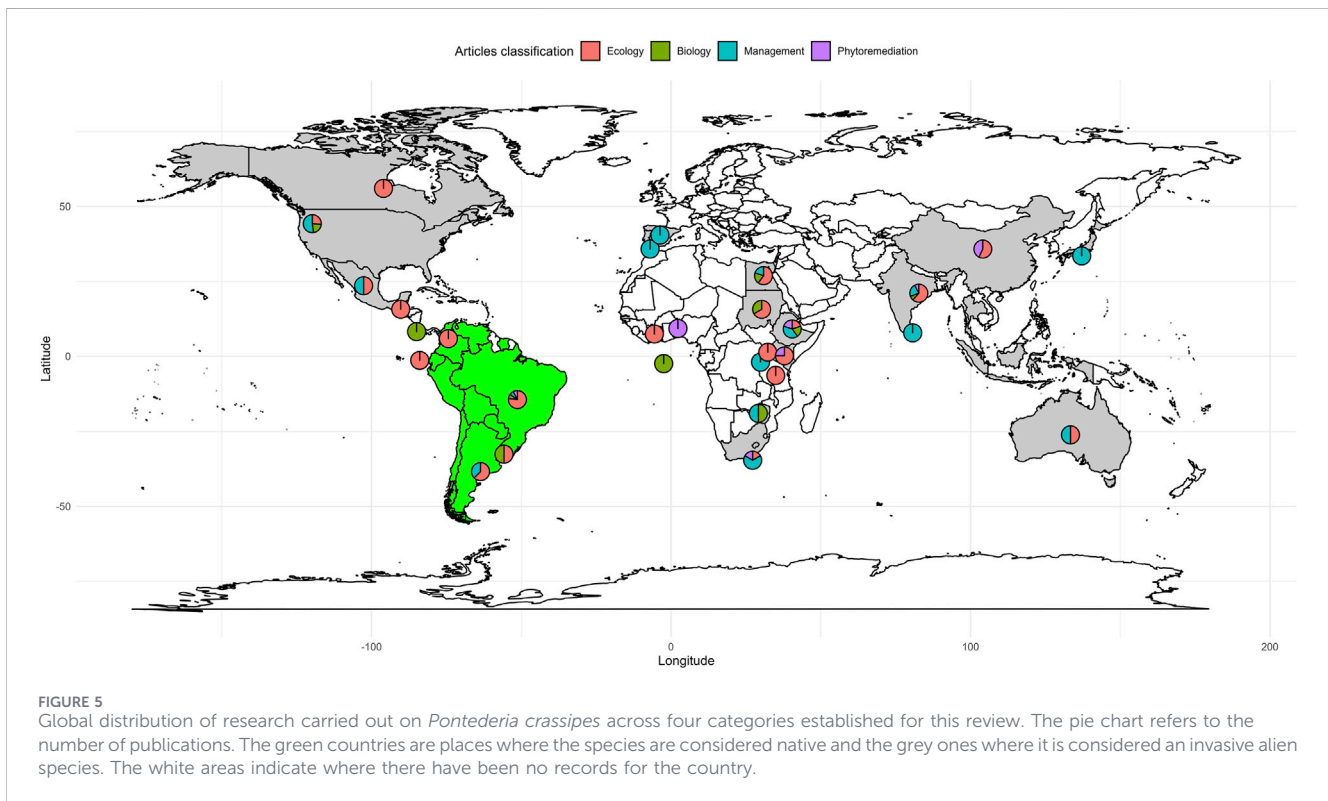
Most of these publications were regarding studies conducted in the United States (N = 22), followed by studies in Brazil (N = 15), Argentina (N = 14), and China (N = 8). The countries that presented the greatest diversity of themes in their publications were China, the United States, Brazil and Argentina. In African countries, studies

focused on management, while in the countries where the species is native, the focus of the studies was on ecology. In the native distribution range, most studies were carried out on the Paraná River, which is shared by Brazil, Argentina, and Uruguay. In the invaded area, most of the articles focused on the Delta River in the United States. In Africa, a common ecosystem reported was Lake Victoria, the third largest lake in the world and shared by Kenya, Tanzania, and Uganda. In China, work was carried out in different freshwater ecosystems.

Of the reduced list of 122 articles, 90 were conducted in the invaded range and 32 in the native range. The number of variables available for both distribution ranges, i.e., native and invaded, was only 16, with only one *P. crassipes*-related variable and 15 environment-related variables covering information on the water and biotic compartments (Table 3).

The selected variables analyzed to further explain the invasive behavior of *P. crassipes* included one response variable *P. crassipes* biomass (N = 103) and the following environmental explanatory variables: the associated biological community (N_{flora} = 145, N_{macrofauna} = 102, N_{plankton} = 30) and, physical and chemical variables such as air temperature (N = 161), ammonia (N = 82), conductivity (N = 68), depth (N = 54), dissolved oxygen (N = 119), nitrites (N = 27), nitrates (N = 68), pH (N = 72), orthophosphate (N = 47), secchi depth (N = 48), total nitrogen (N = 66), total phosphorus (N = 82), and water temperature (N = 71) (See in Table 4).

Despite the wide range of available environmental data, only a few peer-reviewed scientific publications (N = from 5 to 8) have measured and analyzed environmental variables to explain



variations in biomass both in invaded and native areas. While five studies employed various classification methods, they all identified high summer temperatures as the main factor influencing peak biomass. Most of the research was conducted in tropical countries under eutrophic conditions. The capacity of plants to uptake nutrients is closely linked to, and reinforces, their ability to clear water. Conversely, species density may impact water quality. However, certain limiting water parameters may not influence plant density or vegetative propagation.

Data gathered from 122 articles in this review revealed that the mean biomass in invaded areas was 354.35 g dw m², with high variation (±458.40 g dw m², N = 86), indicating substantial heterogeneity among the 19 sampled sites. This variability reflects the differences in the methodological approaches adopted in all the categories considered in this review, including biology, ecology, management and phytoremediation. The locations sampled span both the Northern and Southern Hemispheres, including sites in Benin, China, India, Guatemala, Egypt, the United States, Indonesia, South Africa and Sri Lanka. This represents a wide range of ecological settings.

In the native range, the mean biomass was 577.48 g dw m², with very high variation (±718.97 g dw m², N = 17) based on samples from seven sites. Despite the higher average biomass observed in the native range, substantial variability among the samples was evident, as reflected by the large standard deviation and wide 95% confidence interval (207.82–947.14 g dw m⁻²). These data are relatively homogeneous in terms of geographic origin and represent regionally concentrated natural ecological conditions (see Figure 6).

Analysis of water hyacinth (*P. crassipes*) presence revealed no significant differences in plant biomass ($F = 2.73$; $p = 0.101$) across geographic ranges despite strong variation in several physicochemical and environmental parameters. Notably,

alkalinity ($F = 38.95$; $p < 0.001$), conductivity ($F = 14.17$; $p < 0.001$), depth ($F = 6.94$; $p = 0.011$), dissolved oxygen ($F = 10.14$; $p = 0.002$), and nutrients such as ammonia ($F = 4.58$; $p = 0.035$), nitrate ($F = 4.24$; $p = 0.043$), orthophosphate ($F = 53.01$; $p < 0.001$), and total phosphorus ($F = 8.02$; $p = 0.006$) showed significant variation (Table 4). In contrast, no significant differences were observed in water temperature ($F = 0.11$; $p = 0.736$), pH ($F = 1.22$; $p = 0.274$), salinity ($F = 1.46$; $p = 0.236$), secchi depth ($F = 0.50$; $p = 0.485$), or temperature ($F = 0.02$; $p = 0.886$) conditions between ranges, nor in some nutrients in water, such as total nitrogen ($F = 2.25$; $p = 0.138$) and nitrite ($F = 1.06$; $p = 0.313$). Overall, these findings suggest that *P. crassipes* invasion success is closely linked to tolerance to high alkalinity, and conductivity conditions (Figure 6), variable depths and dissolved oxygen levels, as well as nutrient enrichment conditions especially high concentrations particularly of ammonia, orthophosphate and nitrate. Such tolerances highlight the plant’s potential to establish under a wide range of conditions, and its potential to significantly affect aquatic ecosystems, their water quality, habitat conditions and ecological functions.

4 Discussion

4.1 What scientific knowledge about the invasiveness of *Pontederia crassipes* is available in peer-reviewed publications?

The bibliometric analysis conducted in this study reveals the dual nature of the scientific literature on *Pontederia crassipes*. While the plant is widely recognized as an invasive alien species with

TABLE 4 Analysis of variance (ANOVA) for each variable, showing Df (degrees of freedom), F-value, and p-value; significant differences between native and invaded ranges are indicated at $p < 0.05$.

Variable		Df	F value	p value
Response variable	Biomass in plant (g.dw.m ⁻²)	1	2.731	0.101
Explanatory variable	Alkalinity (mg/L)	1	38.954	0.000
	Ammonia (mg/L)	1	4.585	0.035
	Conductivity (µm/cm)	1	14.171	0.000
	Depth (m)	1	6.941	0.011
	Dissolved oxygen (mg/L)	1	10.136	0.002
	Nitrate (mg/L)	1	4.244	0.043
	Nitrite (mg/L)	1	1.059	0.313
	Orthophosphate (mg/L)	1	53.014	0.000
	pH	1	1.218	0.274
	Salinity (ppt)	1	1.462	0.236
	Secchi (m)	1	0.496	0.485
	Temperature (°C)	1	0.021	0.886
	Total nitrogen (mg/L)	1	2.251	0.138
	Total phosphorus (mg/L)	1	8.018	0.006
	Water temperature (°C)	1	0.114	0.736

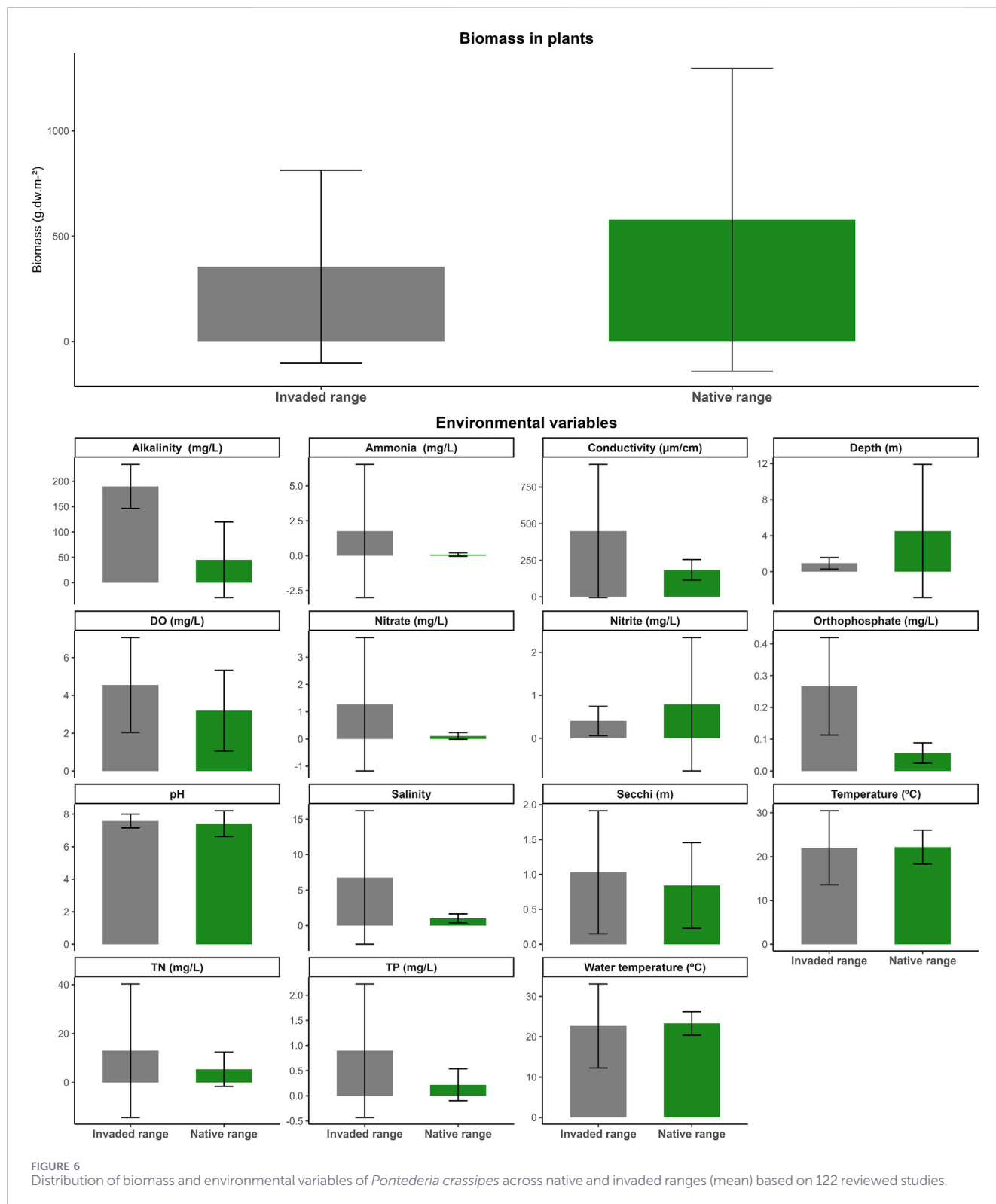
Values in bold indicate statistically significant differences between the native and invaded ranges at the $p < 0.05$ level, as determined by the ANOVA test.

negative ecological and economic impacts, it has also been increasingly valued as a natural resource with potential for sustainable environmental applications, particularly in phytoremediation and energy production. The 3,845 publications analyzed demonstrate the geographical breadth of scientific production and the thematic evolution that has occurred in recent decades. The largest number of significant contributions comes from China and India, which are the most populous countries with the highest levels of aquatic ecosystem contamination (Pink, 2016). This reflects the strategic importance of the species in the context of accelerated urbanization and the degradation of water resources in these countries (Saha et al., 2016; Gao et al., 2014). Although not well documented, it is believed that the initial invasion of Asia by *P. crassipes* was associated with colonization activities, such as the construction of canals and the deliberate introduction of ornamental aquatic plants (Simberloff, 2020). In China, farmers began cultivating *P. crassipes* as animal feed in the mid-20th century. However, once industrialized feed became available, the plant spread from domestic ponds into rivers and lakes, resulting in significant agricultural and ecological consequences (Lu et al., 2007). The earliest study of this species in India focused on its vascular anatomy in 1962 (Singh, 1962), while its ecological impacts were first documented in 1979 (Rai and Munshi, 1979). *P. crassipes* only began to be widely used in phytoremediation research and applications in the 1980s (Vaidyanathan et al., 1983). It was only in the 1980s that water hyacinth became used for phytoremediation. Nowadays the

prevalence of phytoremediation in these contexts is in line with the objectives of the 2030 Agenda, demonstrating the interest in using *P. crassipes* as a nature-based solution (NBS) to environmental problems of water pollution and its societal consequences.

In native regions, such as Brazil and Argentina, there has been a gradual shift in focus from studies centered on the ecology of the plant and its biotic interactions, to research into its potential to provide ecosystem services. This transition was already consolidated around 2010, showing an in-depth understanding of the plant's ability to mitigate anthropogenic impacts by absorbing pollutants such as nitrates and ammonium (Alonso et al., 2017; Bernardino et al., 2016). In contrast, in invaded regions, research focuses on biological control, which remains the most recurrent management strategy, given its biological and economic effectiveness, as demonstrated by Franceschini et al. (2023). As shown by the bibliometric maps, the thematic reorganization reveals a real paradigm shift after 2010 with greater attention being given to phytoremediation compared to biological control. This is not simply a case of replacing one approach with another, since each one addresses different challenges and objectives. While biological control regards *P. crassipes* as an invasive species with significant ecological impacts, phytoremediation considers it a potential solution to other environmental issues. This dual perspective reflects diversification in research agendas rather than a complete shift. One example is a model based on NBS, which considers the potential value of the plant as a raw material (Harun et al., 2021; Guna et al., 2017). This model involves using the plant after the phytoremediation process to collect and utilize its biomass for use in agriculture as biocompost (Sharma et al., 2025). The plant's stem, which is rich in fiber, can also be used in handicraft production (Rakotoarisoa et al., 2016). It is important to emphasize that these activities should be integrated into the stages of controlling the plant, rather than promoting its cultivation for commercial purposes. Nevertheless, this broader conceptual framework remains consistent with international agendas such as Aichi Target 9 of the Convention on Biological Diversity, the Sustainable Development Goals (SDGs), the UN Decade of Restoration and the European Green Deal (Oliveira et al., 2024).

Emerging themes such as biotechnology, anaerobic digestion and the use of biomass in the circular economy are fragmented but represent significant scientific and technological opportunities. Studies indicate that biogas production and effluent treatment from water hyacinth biomass are promising avenues for further research (Wembe et al., 2023; De Stefani et al., 2011). These studies indicate that using *P. crassipes* biomass could contribute to generating clean energy and reusing waste, which are key issues on the agendas of the energy transition and the bioeconomy. Aligning this tendency with open science policies, such as the Open Science movement (Peršič and Straza, 2023), could accelerate the development of solutions and promote the sustainable management of this invasive plant. Nevertheless, it is important to recognize the significant gaps in literature, including the scarcity of integrated studies combining thematic areas such as ecology, control, biotechnology and economic use, and the under-representation of regions such as Europe and tropical island countries.



The global spread of *P. crassipes* across 101 countries on five continents, according to the 3,845 scientific publications in this review, highlights the urgent need for international cooperation in both research and management. Comparative studies between temperate and tropical regions, for example, can generate crucial insights into the ecological and socio-

environmental factors that shape the invasive dynamics of this species. Progress toward effective management, therefore, requires interdisciplinary and multi-scalar approaches capable of integrating ecological, social, and economic dimensions and adapting strategies to the specific conditions of each region.

4.2 Which functional traits have been consistently associated with the invasive potential of *Pontederia crassipes* in different distributional ranges?

This systematic review, based on an analysis of 122 field studies conducted in 30 countries, revealed consistent patterns in the invasive behavior of *Pontederia crassipes*, particularly outside its native range. The plant's ability to thrive in diverse biotic and abiotic conditions highlights its high ecological plasticity, which is an important trait for invasive species (Zarkami et al., 2021; Wang et al., 2017). This flexibility aligns with the expanded concept of the ecological niche, whereby the capacity to adapt to various environments enables the plant to establish itself in diverse ecosystems far beyond its region of origin (Chaloner et al., 2020). A comparison of limnological data from native and invaded areas shows that variables often cited in the literature as limiting the growth of *P. crassipes*, such as pH, water temperature, and air temperature, were similar in both contexts (approximately 23 °C and 22 °C; pH 7.4–7.6, see Figure 6). Notably, even within the native range, areas with high plant biomass exhibited lower concentrations of dissolved oxygen and nitrogen. These observations are consistent with a global meta-analysis (Jha and Li, 2025), which found that the presence of *P. crassipes* significantly decreases the levels of both dissolved oxygen and nitrogen while also affecting other abiotic parameters. Together, these findings emphasize the significant ecological impact of this species on freshwater ecosystems, including in its region of origin.

Establishing and thriving within relatively narrow ranges of these variables suggests that *P. crassipes* is restricted in its distribution by ecological thresholds. Therefore, despite its success under such conditions, the species apparent adaptability is likely linked to other factors rather than tolerance to broader ranges of these specific parameters. Conversely, variables related to water quality and nutrient availability, such as conductivity, salinity and total nitrogen, were higher in invaded areas. This finding corroborates the observation that the plant flourishes in eutrophic and disturbed environments, which are frequently associated with human activity (Harun et al., 2021; Villamagna and Murphy, 2010). The average biomass in native areas was slightly higher than in invaded areas, confirming that these favorable conditions drive its vigorous growth (Lakane et al., 2024; Fridley, 2002; Gopal, 1987). This predominance in nutrient-rich systems also reinforces continued interest in using *P. crassipes* for phytoremediation applications, a central theme identified in the bibliometric analysis. However, a significant limitation is the scarcity of comprehensive and methodological studies correlating plant biomass with environmental variables in different geographical contexts.

Reports on traits such as reproductive rate, nutrient uptake efficiency and phenotypic plasticity are inconsistent, making quantitative correlation analyses unfeasible. To gain a better understanding of the invasive potential of *P. crassipes*, it is helpful to compare its functional traits with those of other typical invasive aquatic plants. *Alternanthera philoxeroides*, *Pistia stratiotes* and *Pontederia crassipes* are all native to South America (Martins et al., 2009). *P. stratiotes* and *P. crassipes* are free-floating species, whereas *A. philoxeroides*

is an emergent macrophyte. All three species reproduce both sexually and vegetatively and have become invasive in several regions worldwide (Brundu et al., 2012; Téllez et al., 2008; Geng et al., 2007). These species are widely recognized for their phytoremediation potential and are used for water purification, even within their native range (Martins et al., 2009). They are characterized by rapid growth, high expansion rates and substantial phenotypic plasticity, traits that contribute to their invasive success. *P. crassipes* exhibits additional competitive advantages, such as its strong association with eutrophic conditions and its ability to form dense, extensive floating mats in the water's surface area and limit the availability of resources for native vegetation (Téllez et al., 2008; Morris, 1974). These functional traits, combined with favorable environmental conditions, enable *P. crassipes* to colonize a wide range of regions, earning a place on the list of the world's 100 most significant invasive species (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, 2023).

A substantial body of literature has documented the ecological mechanism underlying the invasive success of *P. crassipes* (e.g., Penfound and Earle, 1948). However, these studies are often based on isolated case studies and employ heterogeneous methodologies, hindering the establishment of robust, comparable causal relationships. Differences in experimental design, measured traits, spatial scale, and environmental context limit our ability to quantitatively synthesize results and compare mechanisms operating in native versus invaded ranges. Additionally, the limited availability and variability of published data restrict the exploration of functional traits that could explain species invasiveness (Kaushik et al., 2022) and could have affected the comparability of our analyses. In this context, Essential Biodiversity Variables (EBVs) are a valuable framework because they define a standardized minimum set of metrics for monitoring the presence, condition, and impacts of invasive species (Jetz et al., 2019; Latombe et al., 2017). Of the six EBV classes and 21 EBV types, those relating to species traits are particularly valuable. These encompass not only general traits (such as growth form and physiology), phenology, and reproductive details, but also variation within species along the axis of taxonomic diversity such genetic and lineage-level differences among populations. Considering intra-specific trait variation including differences in growth rate, biomass allocation, nutrient uptake efficiency, morphological traits, and tolerance to environmental stressors at the population or genotype level, enables a more nuanced understanding of the ecological performance and adaptive capacity of species across native and invaded ranges. Adopting EBVs describing species traits would facilitate data alignment, promote international collaboration, and support evidence-based management decisions, thereby aligning with the objective of SDG 17: Partnerships and Means of Implementation.

It is important to recognize that EBVs derived from low-resolution spatial data on species occurrence or abundance are not sensitive to fine-scale ecological variation. This limitation makes it difficult to detect small, sparse, or irregularly distributed populations occupying microhabitats, which can lead to an underestimation of variation in plant abundance.

Nevertheless, they provide a robust, internationally harmonized basis for monitoring biological invasions. This was highlighted in An Essential Biodiversity Variable Approach to Monitoring Biological Invasions (McGeoch and Squires, 2015). The effectiveness of EBVs hinges on the viability, quality, and continuity of data flows from national and international monitoring platforms supported by multiple stakeholders, including government agencies, research institutions, and citizen science initiatives (McGeoch and Squires, 2015).

Additionally, it is important to acknowledge that relevant ecological data may be locked in both unavailable scientific literature and scientific literature published in non-English languages, which were not considered in this study (see Supplementary Material 1). This common gap can lead to the underutilization of relevant data and possibly introduce bias when collecting evidence in support of conservation actions (Hannah et al., 2025). This may be particularly relevant in this study given the native range of *P. crassipes* (South America) and the large number of disregarded studies in native languages (Portuguese and Spanish), which reached 29% in this review (see Supplementary Material 1). This is close to the 36% of literature disregarded due to a language barrier frequently found in many other ecological studies (Hannah et al., 2025). In our dataset, Portuguese-language articles mainly focus on ecology, plant management and phytoremediation. Ecological studies address the structure and composition of communities associated with the plant's roots, as well as its temporal and spatial dynamics expressed through limnological variables and evaporation rates. Management studies evaluate the effects of herbicides on plant control and the applicability of *P. crassipes* in biofilters, while phytoremediation studies demonstrate its tolerance to toxic elements such as arsenic and cadmium and its capacity to remove metals from the water. Consequently, excluding this body of non-English literature likely under-represents native-range ecology and local-scale management experience in our synthesis, and may bias our conclusions towards patterns reported in English language studies conducted mostly outside the native range.

Taken together, the results of this systematic review do not identify a single ecological threshold or trait-based breakpoint at which *Pontederia crassipes* shifts from native to invasive behavior across its geographical range. Rather, a synthesis of biomass, limnological, and environmental data suggests that invasion success is linked to a consistent set of functional characteristics that enable the species to maintain comparable biomass in different ecological contexts. Specifically, the literature converges on three features: (1) high tolerance to nutrient-enriched conditions, particularly elevated phosphorus and inorganic nitrogen, (2) persistence under low dissolved oxygen and variable depth regimes, (3) capacity to establish across a broad range of conductivity and alkalinity conditions. Although these traits do not permit the identification of a precise transition point between native and invasive behavior, they clearly define the types of ecosystems in which *P. crassipes* is most likely to proliferate eutrophic, polluted, and hydro-morphologically disturbed freshwater systems. Biomass data from native and invaded areas indicates that the invasive potential of a species species is not demonstrated by

consistently larger biomass outside of its native distribution area. Rather, it is demonstrated by the species' ability to maintain biomass growth in conditions that restrict many native macrophytes. This functional flexibility gives *P. crassipes* a competitive advantage, which explains its global spread across tropical and subtropical regions. Therefore, this review's main contribution lies in consolidating the empirical evidence that the invasiveness of *P. crassipes* is driven by functional characteristics based on tolerance and not just exceptional growth performance. This distinction has direct implications for management. Rather than relying strictly on biomass removal, mitigation strategies should prioritize reducing nutrient input and hydromorphological disturbance.

5 Conclusion

Pontederia crassipes is widely recognized as one of the most visually striking and attractive ornamental aquatic plants. However, it is also listed as one of the world's worst invasive species. Since the first record of it outside its native range, the number and thematic diversity of studies on this species have increased substantially. Our analysis shows that research within the native range mainly addresses ecological characteristics, whereas studies from invaded regions predominantly focus on phytoremediation and to some extent, on impacts and management options. Biotechnological application of *P. crassipes* in biogas, paper, pharmaceuticals, have emerged as an increasingly popular research topic, mainly outside the native range.

Although the invasiveness of the species is widely established, this review is valuable in that it identifies knowledge gaps and synthesizes available data to support the development of hypotheses and guide future research. In this context, we highlight the urgent need for the scientific community to adopt a standardized set of essential biodiversity variables (EBVs) for *P. crassipes*. These EBVs should be internationally recognized and include biological and environmental indicators throughout its global range. Key variables should include growth rate, reproductive capacity, nutrient uptake efficiency, water surface coverage, tolerance to abiotic and biotic stressors, susceptibility to natural enemies, and the potential production of allelopathic compounds, as well as other ecological interactions.

Crucially, this study is the first to integrate bibliometric analysis and systematic review in field-based environmental data to explore the functional traits and ecological niche of *P. crassipes* across its global range. By combining these two complementary approaches, our review provides a novel framework for understanding invasion dynamics more holistically. Our synthesis of the literature reveals a consistent set of functional characteristics associated with invasion success. These characteristics include tolerance to wide ranges of nutrient concentrations, persistence under low dissolved oxygen and variable hydro-morphological conditions and pronounced phenotypic plasticity across environmental gradients. To more accurately quantify this plasticity, we recommend combining physiological indicators, such as photosynthetic rate, with environmental data rather than relying solely on statistical comparisons of biomass and water

quality. Additionally, analyzing changes in functional traits across different stages of invasion using time-series data can elucidate the strategic adjustments the species makes during the invasion process, providing a more complete mechanistic understanding.

Furthermore, we demonstrate that the absence of harmonized monitoring data impedes international comparisons and cooperation and undermines the effective management of biological invasions on a large scale. To develop truly evidence-based strategies for the sustainable management of *P. crassipes* and other invasive macrophytes worldwide, it is essential to strengthen global collaboration, improve data accessibility, and standardize methodologies.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: [Supplementary Material 1](#) and [Supplementary Material 2](#) for this study can be found in the [Zenodo] [<https://doi.org/10.5281/zenodo.16989142>].

Author contributions

LB: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review and editing. AL: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – review and editing. HT: Conceptualization, Investigation, Methodology, Supervision, Validation, Writing – review and editing.

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Conflict of interest

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