

Wetlands: Ecology, Conservation and Management 10

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# World Atlas of Freshwater Macrophytes

Dicotyledonous species I (Acanthaceae –  
Menyanthaceae) - Volume 1

 Springer

# Wetlands: Ecology, Conservation and Management

Volume 10

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The recognition that wetlands provide many values for people and are important foci for conservation worldwide has led to an increasing amount of research and management activity. This has resulted in an increased demand for high quality publications that outline both the value of wetlands and the many management steps necessary to ensure that they are maintained and restored. Recent research and management activities in support of conservation and sustainable development provide a strong basis for the book series. The series presents current analyses of the many problems afflicting wetlands as well as assessments of their conservation status. Current research is described by leading academics and scientists from the biological and social sciences. Leading practitioners and managers provide analyses based on their vast experience.


The series provides an avenue for describing and explaining the functioning and processes that support the many wonderful and valuable wetland habitats, such as swamps, lagoons and marshes, and their species, such as waterbirds, plants and fish, as well as the most recent research directions. Proposals cover current research, conservation and management issues from around the world and provide the reader with new and relevant perspectives on wetland issues.

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# Preface

This book is the first volume of a series of five forming a World Atlas of Freshwater Macrophytes. The need for such an Atlas became apparent from the work of an informal international research network dedicated to advancing macroecological knowledge of freshwater macrophytes, set up by Kevin Murphy in 2017. This has to date produced a number of well-cited publications, collectively authored by network collaborators, which together form the primary underlying material for this Atlas (e.g., [7, 79–81, 104, 105]). During this work, it became clear that the knowledge base of macrophyte distribution and associated ecological information, at world scale, was extremely scattered in the literature and often difficult to access, hence the decision to produce an Atlas that seeks to bring together such knowledge in an easily accessible location.

We define vascular macrophytes as being vascular plants large enough to see with the naked eye, which actively grow permanently or periodically submerged below, floating on, or up through the water surface of inland freshwater or brackish waterbodies [104]. This is a group of plants of very varied age, taxonomic origin, and functional characteristics, though all have, by definition, at least some populations with an obligate requirement for inland open water conditions to complete their life cycle. A good example is the rare Neotropical endemic *Isoetes jamaicensis* Hickey with a range restricted to ephemeral pools in open xerophytic scrublands of Jamaica. The dormant corms of this species only sprout in years when enough seasonal rainfall has occurred to fill the pools [53]. Our definition excludes terrestrial plant species that occur in wetland systems, such as Brazilian várzea floodplain grasslands (e.g., [25, 76, 92]). These species are adapted to tolerate periodic flooding but usually do not have a physiological requirement for inundation as an essential part of their population survival strategy (e.g., [114]).

The majority of the 92 vascular plant families that contain macrophyte species also have other species that are non-aquatic, and most of the c. 3544 accepted macrophyte species also have populations that occur outside of inland fresh or brackish water bodies (though often closely associated with water, for example, as riparian populations). Even in those families which entirely comprise obligate macrophytes (notably Podostemaceae, Nymphaeaceae and Hydrostachyaceae), it is possible to find examples

of species which have such populations. A good example is provided by the species of Podostemaceae (e.g., *Inversodicraea bosii* (C. Cusset) Rutish. & Thiv, *I. cristata* Engl.), which live in riparian spray-zone habitats, as well as in the water itself in the cascades and waterfalls of fast-flowing tropical rivers.

Macrophytes are generally a rather young group of plants in evolutionary terms, and it appears that the speed with which they have successfully managed to move into an aquatic lifestyle at least in part reflects this. Although the oldest species for which a reliable speciation age estimate has been made is *Lycopodiella inundata* (L.) Holub, at 110 million years ago, Ma, most macrophyte species evolved much more recently. Of the approximately 560 macrophyte species for which speciation age data are available [80], 73% evolved in the Pleistocene, Pliocene, or late Miocene, and a few species are even younger. The evidence suggests that at least two species (*Nymphaea loriana* Wiersema, Hellq. & Borsch and *Ranunculus schmalhausenii* Luferov, both high-latitude northern hemisphere plants) arose in the post-glacial Holocene, via rapid hybridization events, and have probable speciation ages <0.01 Ma [13, 15].

There is evidence that the survival strategies (sensu [50]) of most macrophyte species encompass a strong element of stress tolerance (e.g., [9, 101]). However, it is likely that the very varied environmental conditions experienced by different macrophyte species have resulted in the evolution of a wide range of survival strategies across the macrophytes as a group, given that they may experience pressures on their survival ranging from extreme disturbance (e.g., in fast-flowing rocky rivers, occupied by Hydrostachyaceae and Podostemaceae) to highly competitive conditions in shallow eutrophic lakes occupied by mixed stands of submerged and floating species [104].

Overall, it is clear that the vascular macrophytes are a very diverse group of plants, united by a common life requirement for aquatic conditions, which also provide vital support for other aquatic biota (e.g., [85, 109]) in inland waterbodies. In this Atlas, we have tried to bring together available information for aquatic macrophytes, which is otherwise widely scattered through the literature, highlighting aspects of their ecology, including range size, endemism, world rarity, ecozone/macroegeographical occurrence, ploidy state, species age, nuisance state, uses, and endangered status, as a resource to inform and assist the management and conservation of these remarkable plants. Although similar books exist for local regions (e.g., [62, 73, 117, 139]), none provides detailed information for macrophytes at global scale, so this atlas provides a novel resource on the distribution and ecology of macrophytes around the world.

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# Introduction to the Atlas Series

In this Anthropocene era, life on Earth is going through unprecedented changes driven by human activities. As the human population has grown faster than ever over the past century, so has the demand for resources. Cities cover an estimated 1% of the Earth's surface and are home to about 56% of the human population, while 38% of the land is used for agriculture [49, 126, 165]. As a result of land use changes such as providing shelter for humans, food production, infrastructure, and industrial activities, distributions of species have been significantly altered. For example, crops and livestock have been intentionally and widely distributed outside their original ranges, while agricultural practices have unintentionally provided habitat for less desirable species [23]. Surface and subsurface hydrology have been significantly altered to secure water supplies for consumption and food production, moving water from places where it is stored naturally to places where humans need it, drying out natural bodies of water, while increasing water levels of others, changing natural fluctuations in water levels, and creating new bodies of water as well as new pathways for migration. Global change through altered land use changes is driving climate change. Species distributions are changing rapidly, and extinctions of species occur at a very high rate [27, 38].

These changes on a global scale pose unprecedented challenges to environmental management. As we come to understand how human health and welfare are intrinsically linked with environmental quality and provision of ecosystem services, we also realize that we lack the information needed to determine environmental management needs and approaches properly. Not only do we lack knowledge about the numbers of species on earth, but also about their distributions. In addition, what we know is biased toward species and places that are easily accessible [40, 56]. For example, it is much easier to study plants on land than underwater, which is one of the reasons why terrestrial plants have been studied in more detail than aquatic plants [89, 144]. Terrestrial plants can be observed by walking the surface of the earth. Specialists, as well as hobbyists and citizen scientists (e.g., [140]), have contributed to our knowledge of terrestrial, and to a lesser extent aquatic plants. It is generally easy anywhere in the world to find a regional flora with images for identification of terrestrial plants, and in recent decades, electronic databases of



terrestrial plants for use on mobile devices have been developed. But when it comes to aquatic plants, the story is different. To study aquatic plants, one must get into the water and under the water's surface. Some species float at least partially at the surface and can be easily observed, but others are entirely submerged, often not just obscured from view by turbidity or reflections on the surface of the water but also by floating and emergent plants. Not to mention the fact that safety is a concern in deeper water and special equipment is needed to venture under the surface. Of course, this does not mean that extensive data on aquatic plants do not exist. The data are there, but less accessible than for terrestrial plants.

This World Atlas of Freshwater Macrophytes for the first time brings together available data on global distributions of those vascular aquatic plants which occur in inland freshwater and brackish waterbodies. It is based particularly on five recent publications on the world distributions of >3500 species of aquatic macrophytes in 453 genera from 92 families ([79–81, 104, 105]). Aquatic macrophytes here are defined as “aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or up through the water surface” of inland freshwater or brackish waterbodies [28, 104]. That definition would include macrophytic algae (such as green filamentous algae and charophytes, as well as liverworts and mosses that have aquatic populations), but we do not include these non-vascular plants here, in part because their distributions at world scale are very incompletely known, though the situation is improving [26]. Our definition emphasizes the importance of the presence of water as an essential part of the population survival strategy (*sensu* [50, 51]) of freshwater macrophytes. This, in turn, means that many “obligate” wetland plants (following the US definition of wetland plants for assessment of wetlands for legal purposes, [152]) are included in this group, but “facultative” wetland plants are not. Facultative wetland plants are tolerant of temporary waterlogging and submersion but do not require that to complete their life cycles [114]. All aquatic macrophytes are wetland plants, but the reverse is not so. This restrictive definition of “aquatic macrophyte” is a pragmatic approach, allowing us to deal exclusively, in this Atlas, with those plants which are most closely associated with inland brackish and fresh waterbodies. The most widely accepted definition of wetlands follows the Ramsar Convention, which reads: “wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres” [120]. Plants that occur in those wetlands then are “wetland plants.” If this project had included all species of plants associated with wetlands according to the Ramsar definition, it would have included many more species, for example, from floodplains along rivers and coastal marine environments down to six metres: a very ambitious undertaking. However, upon completion, we hope that this Atlas will provide a starting point for a broader-scale effort to catalogue and map the world distributions of all wetland plants, both marine and freshwater.

## Purpose of the Atlas

This Atlas provides invaluable information to anybody interested in freshwater macrophytes, from citizen scientists to professional scholars and environmental managers. It also provides a framework for further study, particularly near the boundaries of distributions. The grid size used for this Atlas is 10 degrees of latitude by 10 degrees of longitude, which means that, for example, one grid cell contains several of the smaller countries of Europe. Two grid cells cover Madagascar. It shows, therefore, accurate information about global distributions of aquatic macrophytes and a rough indication of the outer boundaries of their distributions. Still, it lacks information suitable for assessment of detailed changes in plant distributions, for example, driven by a changing climate [122]. For such studies, details of distributions at a much finer scale are needed, but across large swathes of the planet such fine-scale data are simply not available, and this Atlas serves to identify areas that need further investigation. Of particular interest are the boundaries of global distributions where significant changes in plant distributions in response to changes in land use and climate are likely to occur, but also inside distributions, such as regions prone to desertification. The North American Plains, for example, may see more frequent and prolonged droughts in the west [63] but are understudied. One example is the state of North Dakota, where large areas of the western half have not been surveyed. The only flora of North Dakota to date was compiled during the 1950s by O.A. Stevens, who spent his life surveying the counties of eastern North Dakota on foot or by bicycle because he did not own a car [148]. Similar examples exist from around the world, particularly where human population densities are low, and access is difficult, such as the vast taigas and tundras of North America and Eurasia, remote islands in the world's oceans, the Sahara Desert, and the rain forests of South America, Africa, and Asia [70, 84].

## Structure of the Atlas

The Atlas consists of five volumes, with one or more chapters providing an overview of topics relevant to plant distribution, followed by detailed descriptions of the distributions of each species within families. Each book will include an introduction followed by a chapter or more on select topics related to the subject matter of plant distributions, such as endemism, rarity, and invasiveness, then by descriptions of species within plant families and species in alphabetical order. The first two volumes contain data on plants that were until relatively recently considered to belong to the "Dicots," Dicotyledonae. However, that is not a monophyletic group and is now divided into the monophyletic Eudicots ("true" dicots), while several families, including the Nymphaeales, are now outside that group [65, 141]. For the purpose of this book, which is not about systematics but about distributions, we have separated the Monocots from all other vascular families, which we will refer to by the

older term “Dicots.” Volumes three and four will focus only on Monocots, and the final volume will encompass a final round of Monocot species as well as the Lycopodiophyta, Pteridophytes, and Gymnosperms. The latter is based on an initial dataset from Murphy et al. [104], [79–81, 105]. Finally, we include information from the Pacific Ocean islands of Oceania, and the sub-Antarctic islands and Antarctic peninsula (which collectively contain only extremely small areas of inland waterbodies suitable for macrophyte colonization) in a separate chapter of the final volume.

## **Volumes Included in This Atlas**

### Vol. 1: Dicotyledonous species I

- Aquatic macrophytes and wetlands
- Global distribution of macrophytes
- Species descriptions by families in alphabetical order

### Vol. 2: Dicotyledonous species II

- Macrophyte endemism and rarity
- Species descriptions by families in alphabetical order

### Vol. 3: Monocotyledonous species I

- Genetic diversity and global ploidy distribution of macrophytes
- Species descriptions by families in alphabetical order

### Vol. 4: Monocotyledonous species II

- Vectors of long-distance movements and distribution of invasive macrophyte
- Species descriptions by families in alphabetical order

### Vol. 5: Monocotyledonous species III, Lycopodiophyte, Pteridophyte, and Gymnosperm species

- Macrophyte distributions on Pacific Ocean islands of Oceania, and the sub-Antarctic islands and Antarctic peninsula
- Species descriptions by families in alphabetical order
- Summary of all families

# Introduction to Volume 1

This first Volume of the World Atlas of Freshwater Macrophytes includes two chapters describing where in general freshwater macrophytes occur. Chapter 1 discusses how all freshwater macrophytes are wetland plants, but not all wetland plants are freshwater macrophytes. Why is that? What are the similarities and differences between the two groups of plants? Chapter 2 addresses the question of which overarching factors determine global distributions of freshwater macrophytes. For example, there are differences in animal and tree species diversity between Eurasia and North America at the same latitudes, but is that also true for freshwater macrophytes? This is followed by Chapter 3, which describes the global distributions of >700 individual species of aquatic macrophytes, based on geographical gridcell areas of 10° latitude by 10° longitude. These species are listed alphabetically within 33 dicotyledonous families (from 18 orders of the class Magnoliopsida), which are also listed alphabetically. The families (with order in brackets, and number of macrophyte species given per family) included in this volume are as follows:

Acanthaceae (Lamiales):	15 species
Amaranthaceae (Caryophyllales):	6 species
Apiaceae (Apiales):	66 species
Apocynaceae (Gentianales):	1 species
Araliaceae (Asterales):	8 species
Asteraceae (Apiales):	60 species
Balsaminaceae (Ericales):	1 species
Boraginaceae (Boraginales):	12 species
Brassicaceae (Brassicaceae):	29 species
Burmanniaceae (Dioscoreales):	5 species
Cabombaceae (Nymphaeales):	6 species
Campanulaceae (Asterales):	44 species
Caryophyllaceae (Caryophyllales):	2 species
Ceratophyllaceae (Ceratophyllales):	4 species
Convolvulaceae (Solanales):	4 species
Crassulaceae (Saxifragales):	9 species

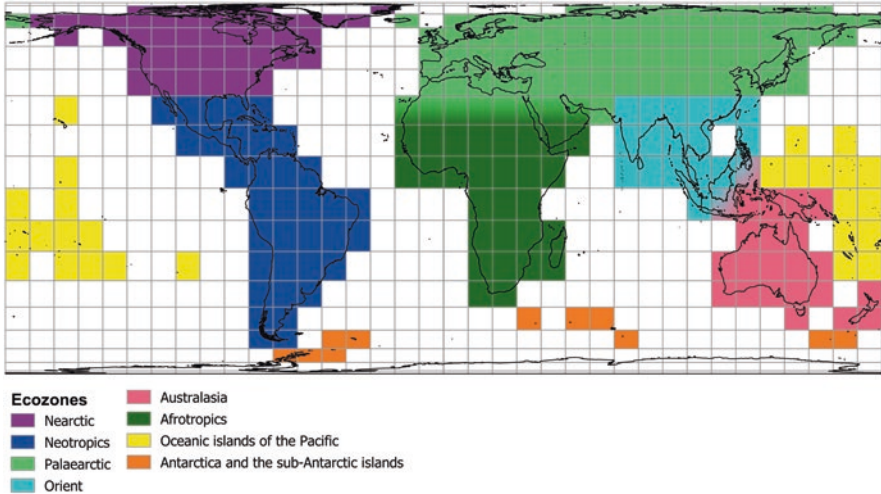
Droseraceae (Caryophyllales):	1 species
Elatinaceae (Malpighiales):	29 species
Euphorbiaceae (Malpighiales):	3 species
Fabaceae (Fabales):	24 species
Haloragaceae (Saxifragales):	69 species
Hydatellaceae (Nymphaeales):	13 species
Hydroleaceae (Solanales):	4 species
Hydrostachyaceae (Cornales):	22 species
Hypericaceae (Malpighiales):	2 species
Lamiaceae (Lamiales):	23 species
Lentibulariaceae (Lamiales):	103 species
Limnanthaceae (Brassicales):	4 species
Linderniaceae (Lamiales):	10 species
Lythraceae (Myrtales):	103 species
Malvaceae (Malvales):	3 species
Melastomataceae (Myrtales):	6 species
Menyanthaceae (Asterales):	69 species

# Key to Atlas Species Entries

**Macrophytes definition:** “vascular aquatic photosynthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or up through the water surface” of inland freshwater or brackish waterbodies [28, 104]. The definition emphasizes the importance of the presence of water as an essential part of the population survival strategy (sensu [50]) of freshwater macrophytes. Here we included plants in brackish inland waterbodies as well as freshwater ones. This Atlas encompasses world distributions of more than 3500 species of aquatic macrophytes.

**Synonyms:** Homotypic synonyms are usually provided, mainly following those allocated to the species by Plants of the World Online [118]. Synonyms labelled “nom. illeg”, “nom. superfl.”, or “not validly publ.” are not given here, while infra-specific synonyms are generally avoided. An exhaustive list of synonyms is not given in most cases. Hybrids and infraspecific taxa are not included in the Atlas.

**World ecozones:** The Atlas primarily covers macrophyte species present in the six terrestrial world ecozones, which primarily provide areas of inland freshwater and brackish waterbodies, potentially open to occupancy by macrophytes. These are the Palearctic (PAL), Nearctic (NEA), Neotropics (NEO), Orient (OR), Australasia (AUS), and Afrotropics (AFR) (Fig. 1). Records from the Pacific islands of Oceania (OCE), and mainland Antarctica together with the sub-Antarctic islands of the Southern Ocean, such as Kerguelen (collectively ANT), are noted where relevant to world distribution in individual species entries but are excluded from range estimates because of the extremely small areas of inland freshwater or brackish waterbodies present in these ecozones. To provide some examples, figures available for inland water area (comprising rivers, lakes, floodplains, reservoirs, wetlands, and inland brackish systems) (<http://data.un.org/Data.aspx?d=FAO&f=itemCode%3a6680>) suggest a value of just 1 km<sup>2</sup> for Samoa, 3 km<sup>2</sup> for Tonga, 30 km<sup>2</sup> for New Caledonia, and 91 km<sup>2</sup> for the Solomon Islands. A listing of macrophyte species present in each of the five main island groups of Pacific Oceania, as well as Antarctica, and the sub-Antarctic islands, is provided in Volume 5. For a comprehensive listing of 10 × 10° (latitude × longitude) gridcells covering each of the six main ecozones, see Appendix A7 [104].



**Fig. 1** Map of the world ecozones divided into 10 × 10° gridcells

**Ecozone macroregions** (for full details, codes, locations and gridcell coverage of each, see [104, 105]):

*Palaeartic (PaW Western Palaeartic; PaC Central Palaeartic; PaE Eastern Palaeartic)*

<b>ARC</b>	Arctic	PaC S – V; PaE DD – KK
<b>CH</b>	China, Mongolia	PaC L, PaC P; PaE R – T; PaE X – Z
<b>W EUR</b>	Western Europe (incl. Azores)	PaW G, PaW H, PaW I (western half: 10–15°E); PaW M, PaW N (northern half: 45–50°N), PaW O (northern half: 45–50°N)
<b>E EUR</b>	Eastern Europe	PaW I (eastern half: 15–20°E); PaW J – L; PaW P – R; PaW X
<b>N EUR</b>	Northern Europe	PaW A – F
<b>MED</b>	Mediterranean	PaW S – U; PaW N (southern half: 40–45°N); PaW O (southern half: 40–45°N); PaW V, W
<b>NAA</b>	North Africa/ Arabia/Canaries)	PaW Y, Z; PaW AA – EE (all 20–30°N)
<b>UR/ W SIB</b>	Urals/ Western Siberia	PaC A – G; PaC H (western half: 80–85°E)
<b>E SIB</b>	Eastern Siberia	PaC H (eastern half: 85–90°E); PaE A – M
<b>FER/J</b>	Far Eastern Russia/Japan	PaE N – Q; PaE U – W; PaE AA – CC
<b>C ASIA</b>	Khazakhstan/ Iran/ Hindu Kush	PaC I – K; PaC M, N; PaC O (northern half: 35–40°N); PaC Q (20–30°N); PaC R (20–30°N, incl. eastern Oman)

***Nearctic (NeaN Northern North America; NeaS Southern North America)***

<b>ARC CAN</b>	Arctic-Canadian Shield	NeaN A – K; NeaN P – Z; NeaN AA – EE
<b>W NAM</b>	Western North America	NeaN L – O; NeaS A – C; NeaS I
<b>E NAM</b>	Eastern North America	NeaS D – H; NeaS L – N
<b>SW NAM</b>	Southwestern North America	NeaS J, K

***Neotropics (NeoC Central America; NeoN Northern South America; NeoS Southern South America)***

<b>MG MX</b>	Mega Mexico I	NeoC A, B; NeoC C (northern half: Florida, 25–30°N); NeoC K
<b>MES AM</b>	Meso America	NeoC C (southern half: Cuba, Yucatan, 20–25°N); NeoC D – J
<b>NWSA</b>	North Western South America	NeoN C, NeoN D (northern half: 5–10°N); NeoN F (western half: 75–80°W)
<b>AMZ</b>	Amazon	NeoN D (southern half: 0–5°N); NeoN E, NeoN F (eastern half: 70–75°W); NeoN G, H; NeoN L (northern half: 10–15°S); NeoN M
<b>CHA</b>	Chacoan	NeoN I, J; NeoN N; NeoS B (eastern half: 60–65°W), NeoS F, G
<b>PAR</b>	Paranaense	NeoN O; NeoS C, D
<b>AND</b>	Andean	NeoN K; NeoN L (southern half: 15–20°S); NeoS A, NeoS B (western half: 65–70°W); NeoS E; NeoS H – K

Dividing line with Neotropic region, actually runs through gridcells NeoC A and NeoC B in N. Mexico, through gridcell NeaS L (excluding SW corner of gridcell, which comprises northwestern Texas), then following 30° N line of latitude along south edge of eastern gridcell NeaS L, then NeaS M and NeaS N through northern Florida, and N of Bahamas (see [43]). For the purposes of this exercise, the dividing line was taken as corresponding with 30°N line of latitude.

***Orient (Or)***

<b>IND</b>	Indian Subcontinent	Or A – C; Or G, H; Or L, M
<b>ICH</b>	Indochina	Or D – F; Or I, J
<b>SUP</b>	Sunda Shelf and Philippines	Or K; Or N – S



***Australasia (Aus)***

<b>NG</b>	New Guinea and associated islands to Sulawesi and Lesser Sunda Is.	Aus E – H
<b>NA</b>	Tropical to subtropical Northern Australia (Northern Territory, The Kimberley, Queensland)	Aus I – K; Aus N, O (northern half of both: 20–25°S)
<b>WA</b>	Western Australia	Aus L, M; Aus Q, R
<b>ESA</b>	Eastern and Southern Australia, including Tasmania	Aus N, O (southern half of both: 25–30°S); Aus P; Aus S – U; Aus W
<b>NZ</b>	New Zealand	Aus V; Aus X, Y

***Afrotropics (AfrN northern Afrotropics; AfrS southern Afrotropics)***

<b>SAH/AR</b>	Sahara/ Sahel/S. Arabian Peninsula/ Horn of Africa	AfrN I – P; AfrN W
<b>FOR</b>	African Forest Zone	Afr N Q – U; Afr S A, B
<b>EA</b>	East African Savannah and Highlands	Afr N V; Afr S C
<b>ZAM</b>	Zambesian Region	Afr S D – F; AfrS J
<b>SDES</b>	African Southern Deserts	AfrS H, I
<b>CAPE</b>	Cape Region	AfrS L, M
<b>MAD</b>	Madagascar	AfrS G, K

In addition to the six ecozones above, within which macrophyte records were mapped on a gridcell basis, macroregions are broadly defined for the two remaining ecozones where gridcells were not used, owing to the extremely small areas of freshwater present on the Pacific oceanic islands, sub-Antarctic islands, and Antarctic Peninsula, making up the parts of these ecozones where freshwater macrophytes can exist. However, macrophyte records from within these broad macroregions were collated at macroregion scale, so they are described below.

***Oceanic islands of the Pacific (Oce)***

<b>SW Oce</b>	South Western Oceania (Melanesia, including New Caledonia and Norfolk Is.)	approx. lat. 0–30°S; long. 160–175°E
<b>SC Oce</b>	South Central Oceania (incl. Tuvalu, Fiji, Tonga, Samoa and adjacent islands)	approx. lat. 5–30°S; long. 175°E – 170°W
<b>SE Oce</b>	South Eastern Oceania (Cook Is., Line Is., Polynesia, Pitcairn Is., Easter Is.)	approx. lat. 0–30°S; long. 105–170°W
<b>Mic Oce</b>	Micronesia (incl. Palau, Mariana Is., Marshall Is., Kiribati)	approx. lat. 0–20°N; long. 130–180°E
<b>Haw Oce</b>	Hawaii	approx. lat. 20–30°N; long. 150–160°W

*Antarctica and the sub-Antarctic islands (Ant)*

<b>SG Ant</b>	South Georgia/ South Orkney/ South Sandwich/ South Shetland Is.	approx. lat. 55–65°S; long. 30–60°W
<b>PE Ant</b>	Prince Edward Is.	approx. lat. 45–50°S; long. 35–40°E
<b>CKH Ant</b>	Crozet/ Kerguelen/ Heard Is.	approx. lat. 45–55°S; long. 50–75°E
<b>MCA Ant</b>	Macquarie/ Campbell/ Auckland Is.	approx. lat. 50–55°S; long. 155–170°E
<b>Ant P</b>	Antarctic Peninsula	approx. lat. 65–70°S; long. 60–70°W

**Range area** (grAH km<sup>2</sup>): Area of inland freshwater and brackish water potentially open to occupancy by macrophytes, as sum of gridcell aquatic habitat area (grAH: derived from satellite imagery data) values for each species, for whole world, or for individual ecozones. Due to seasonal and year-on-year variations in within-gridcell areas of inland water, these values are only approximations and for that reason are rounded to the nearest hundred km<sup>2</sup> here. Because of this rounding, ecozone totals may not sum exactly to the given world total grAH for each species. See [104, 105] for full details.

**Ecozone origin-status:** E: ecozone-endemic, i.e., natural occurrence in only a single world ecozone; N: native in >1 world ecozones; I: introduced, naturalised, or invasive in one or more ecozones outside the native range of the species; E(I) endemic in a single ecozone but also present in one or more additional ecozones via human interference vectors (anthropochory). See [80] for details.

**World rarity status:** VR: very rare: occupancy range <1% total world grAH; R: rare, occupancy range 1–5% total world grAH; C: common, occupancy range >5% total world grAH. See [81] for details.

**Species world distribution maps:** For each species entry, the world distribution maps show species occurrence per gridcell within the six primary target world ecozones, on an azimuthal equal-area projection, within 5 range bands of grAH (km<sup>2</sup>) occurrence. The Equator (zero° latitude) and Greenwich Meridian of zero° longitude are shown in thicker line size.

**Life form(s):** In vascular macrophytes, life form relates to the position of plant foliage relative to the water surface [140], usually classified into four main groups (Fig. 2):

- I. **Emergent plants (EM):** Plants normally erect and standing above the water surface, but some species tolerate submergence; all produce aerial reproductive structures.
- II. **Floating-leaved rooted plants (FR):** Plants produce surface-floating leaves that differ in morphology from any submerged leaves present; produce floating or aerial reproductive structures and are rooted, attached to, or closely associated with submerged substrate.



**Fig. 2** Life forms of macrophytes. Image copyright: JJ Herrera-Gallegos, with permission

- III. **Submerged plants (SU):** Plants with most or all foliage permanently submerged (some may also produce emergent or floating leaves), and rooted, attached to, or closely associated with submerged substrate, produce floating, aerial, or submerged reproductive structures.
- IV. **Free-floating plants (FF):** Plants not rooted in, attached to, or closely associated with the submerged substrate, floating on or below the surface, produce floating, aerial, or rarely submerged reproductive structures.

Note: In *Genlisea* (Lentibulariaceae), usually with EM or SU life-form or both, the “roots” are actually heavily modified underground leaves which act as traps for subterranean microorganisms, mainly protozoa, which the plant digests. In *Salvinia* (Salviniaceae: FF life form), modified hair-like submerged leaves dangle into the water from the surface-floating fronds and act as roots, taking up nutrients from the water column.

Many macrophyte species may possess more than one life form in some of their populations, or at different points in their life cycle. A question mark against the life form means that possession of this life form is rarely observed or uncertain for the species.

Where relevant, additional information is given about the plant’s life form: primarily whether it shows tree, shrub, or subshrub habit (a subshrub is a plant that bears hibernating buds on persistent shoots, sometimes woody, near the ground; a hydrosbush usually has these structures underwater); climbing habit; rheophytic habit (direct attachment to rock substrates); epiphytic habit (growing on other

plants); or some combination of these (information mainly sourced from Plants of the World Online; POWO [118]. Where such information is not given, the species is an annual/ perennial herbaceous plant.

**Ploidy state:** H: haploid; D: diploid; P: polyploid; DP: species with haploid or diploid and polyploid races. See [79] for details.

**Speciation age (Ma):** age of speciation, Ma, millions of years ago, providing an indication of species old enough (speciation age older than end of the Miocene, 5.3 Ma) to have had their world distribution potentially influenced by ancient vicariance factors associated with changes in sea level and tectonic land movement. See [80] for details.

**Populations also occur in terrestrial, wetland and/ or riparian habitats:** many macrophyte species occurring in inland freshwater or brackish waterbodies also have populations that occur in other habitats, usually but not always associated with watercourses or other inland waters.

**Long-distance movement vectors:** natural and human-related potential vectors of long-distance propagule movement: BIRD (ectozoochorous or endozoochorous transport, primarily between ecozones, by migratory and wandering bird species); HYDROCHORY (potential long-distance hydrochorous movement of propagules, only noted for transboundary waterways crossing between ecozones, and indicating sending and receiving ecozone); ANTHROPOCHORY (human-interference effects facilitating long-distance movement of propagules within or between ecozones); ?AV (potential ancient vicariance influences on global distribution because the speciation age of the species is old enough (before the end of the Miocene,  $\geq 5.3$  Ma) for it to have been potentially affected by tectonic land movement or sea level change). A question mark against a vector means that full details are not established, but there is some evidence, or potential, for the species utilizing the vector concerned. See [80] for details.

**Nuisance status and uses:** notes on aquatic weed or other nuisance (e.g., toxicity) status of the species; and uses made of it by humans, e.g., medicinal, horticultural, aquarium trade, phytoremediation, ornamental, food, forage).

**Endangered status (IUCN):** global conservation status of species as given by IUCN Red List of Threatened Species [60]: LC: Least Concern; DD: Data Deficient; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered. Occasionally other sources are also cited if IUCN designation has not been made.

**NA:** no data available.

# Methodology Used for Compilation of Atlas Data

Full details of the methods used in collecting, collating, and analyzing the data used to compile the Atlas species entries are provided by [104, 105] and [79–81]. Here, we summarize the main approaches used in compiling the datasets. For a detailed explanation of the criteria for including or excluding species in the world list of macrophytes, see Appendices A1 and 5 of [104].

Post-1950 world geospatial records were collated for all known vascular aquatic macrophyte species. Native, introduced, naturalized, and invasive records were all included, but not records known to be for plants growing in cultivated locales such as crops and ornamental parks or gardens. Records were primarily extracted from the Global Biodiversity Information Facility world species distribution database [47]. The data were supplemented by information from primary datasets held by the authors, and records from other online geospatial plant species distribution information resources covering large areas of the planet (notably Flora of China, Flora of North America, e-Monocot, CJB African Plant Database, IUCN Red List, [www.plantarium.ru](http://www.plantarium.ru), Moscow Digital Herbarium, Checklist of the Flora of the Caucasus, Flora do Brazil, Flora Zambesiaca, and *Cátalogo de Angiospermas Acuáticas de México*), as well as numerous sources providing more local distributional coverage (for the full list of sources, see Appendix A4 of [104]). The primary dataset was updated regularly from its first publication in 2019 (Appendix A2 of [104]), with the version used to compile Vol. I of the Atlas revised up to April 2023. Records were included from inland freshwater and brackish waterbodies, but not coastal or marine low-salinity aquatic habitats such as coastal salt-marsh channels, and the Upper Baltic Sea, nor highly-saline or highly-alkaline (“soda lake”) inland waterbodies such as the Great Salt Lake (Utah, USA), and Lake Bogoria (Kenya). Records were collated from sites located in 238  $10 \times 10^\circ$  (latitude  $\times$  longitude) grid-cells, located between 80°N and 60°S, covering the six major global land ecozones which primarily provide macrophyte habitat, PAL, NEA, NEO, OR, AUS, and AFR (see Appendix A3 of [104] for full details of gridcell locations in each ecozone). Detailed records from the two ecozones which only provide very limited areas of freshwater habitat: Antarctica and the Pacific islands of Oceania were excluded, but a summary of the macrophyte floras of these global regions is provided in Vol. 5 of

the Atlas. Some species were excluded from the database for other reasons, which are outlined in detail in Appendix A5 of Murphy et al. [104]. In brief these grounds for exclusion included the following:

- (i) Inaccurate or impossible records were ignored if other evidence, such as original site location information on voucher specimen sheets, could not be found to correct the error.
- (ii) Fossil records and records derived from cultivated locales such as Botanic Gardens.
- (iii) Some species were omitted from the study because they lack post-1950 geo-spatial records (and any corroborative information on more-recent occurrences, from the IUCN Red List or other reliable sources), or because available information about their location(s) was too vague to allow them to be correctly spatially positioned in one or more world gridcells.
- (iv) A few macrophyte species were identified with ranges entirely restricted to areas outside the target ecozones. These are species endemic to parts of Oceania (e.g., the Hawaiian Islands) or the sub-Antarctic islands (see Appendix A6 of [104]). These are included in this Atlas in Volume 5.

A single species record, in a single year during the study period, within a gridcell unit was considered the minimum needed for a positive result for a given species in that unit of the planet surface. For the Atlas, in providing an estimate of the range of each species, within gridcells and ecozones, and across the world, the “extent of occurrence” (broadly following the concept used in the IUCN Red List) was calculated as the total area of inland water bodies present in the gridcell(s) in which a given species is present. The gridcell aquatic habitat area (grAH, km<sup>2</sup>) occupied by inland waterbodies such as lakes, reservoirs, rivers, and canals (see details in [104]) for gridcells supporting individual species was then summed to provide an overall estimate of range for the species at ecozone and global scales. Due to seasonal and year-on-year variations within gridcell areas of inland water, these range values are only approximations and for that reason are rounded to the nearest hundred km<sup>2</sup> in Atlas species entries. The limitations and advantages of this approach to assessing macrophyte range size are further discussed in [104, 105], and [79–81], but an important point to note here is that the range estimates represent only potential areas of inland water that macrophytes might occupy. In actuality, the area occupied by macrophytes within the grAH of an individual gridcell will almost always be smaller than the value given here, because depth, exposure, and other physico-chemical limitations will usually restrict the area open to macrophyte colonization. The lowest extremes of this approach to measuring macrophyte range size are seen in some desert gridcells, especially in the Sahara, with tiny grAH values, representing lakes and pools present in isolated oases, but probably offering most of these usually shallow areas of open water as potential habitat for aquatic macrophyte growth. At the other extreme, the gridcells containing the Nearctic Great Lakes have extremely high grAH values, but most of this water is unsuitable as macrophyte habitat primarily due to depth of the lakes, and also high wave disturbance impacts on open

stretches of lake shore with very large wind and wave fetch, preventing macrophyte growth.

The cartography of the grAH values for each species was produced with QGIS (version 3.16). First, a preliminary map was designed, adding the required layers (continents, gridcells with a sample of grAH data, equator and Greenwich meridian) and assigning them a North Pole Lambert azimuthal equal area projection. The Arctic and Antarctic  $10 \times 10^\circ$  gridcells without data at this level of representation were removed to improve map's visualization. The authors then agreed on a final map design, including a blue palette legend with four classes.

Subsequently, grAH data was cleaned and sorted into different spreadsheets, one per subsection in Chapter 3. The "Join" function in QGIS was used to incorporate the grAH data into the gridcells shapefile attribute table, thus preserving the entire species name regardless the number of characters. Then, a sequence of three Python scripts was created with the invaluable help of Nikolai Shurupov (see acknowledgements) to read the data spreadsheets, create a list of species' names, find those in the gridcells shapefile attribute table, and plot a map per species with the selected design. The scripts were run within the Python console included in QGIS for each data spreadsheet, and a quality control was then carried out to ensure that the script was reading the right data column when producing the maps, plotting some of them manually. For each species in each ecozone, information was collated on its "origin status," as endemic to a single ecozone, E; native to  $\geq$  one ecozone, N; introduced/invasive (i.e., present in the ecozone via anthropochorous "human interference" transfer vectors acting into the ecozone, I; or endemic to one ecozone but transferred to  $\geq$  one additional ecozone by anthropochorous vectors, E(I) origin-status [80]. For I and E(I) species only, a note was also made of the home ecozone(s) in which the plant is native. We also made a note of the ecozone macroregions (defined in Appendix A2 of Lobato-de Magalhães et al. [80]) and also summarized in the Key to Species Entries in the Atlas) within which each I or E(I) species occurred. Primary sources for assigning origin status included Plants of the World Online [118], and major national floras such as those mentioned above, as well as other publications providing more geographically limited information on macrophyte species ranges and origins (listed in Appendix A1 of [80]). Full details are also given in that Appendix of the approaches used to assess:

- (i) Co-occurrence and potential ecozones of origin for N and I species
- (ii) Inter-ecozone hydrochory vector status for macrophyte species per gridcell
- (iii) Speciation age and Late Quaternary glaciation effects potentially influencing macrophyte world distribution
- (iv) Bird vector status for long-distance movement of macrophyte species

We include in the Atlas information on the ploidy state of macrophyte species, where available. Chromosome number change (e.g., polyploidy or whole-genome duplication; dysploidy or change in single chromosome numbers) is a class of common genetic mutations in plant species with complex effects on plant ecological responses and several evolutionary implications [153]. Ploidy state ("cytotype") has been determined, initially by chromosome counts and more recently by techniques

such as flow cytometry [124], though variation in DNA content among cytotypes is still unknown for many aquatic plant species, especially in tropical regions [121]. Collation of ploidy information was undertaken from a total of 532 sources (see Appendix A of [79]), commencing with the database underpinning [125], who included >800 angiosperm macrophyte species in their world dataset, and complemented by information derived from Floras, scientific papers, and unpublished compiled databases that review in detail data for chromosome number and ploidy level of each species. Our study covers non-angiosperm vascular species of aquatic clubmosses, horsetails, ferns, and fern-allies (but not non-vascular macrophytes, the macroalgae and bryophytes) as well as angiosperm macrophyte species. A substantial part of the relevant ploidy information was found in local journals, dissertations, books, as well as non-English language publications.

Ploidy state was characterized in three classes, following [162] and [41]:

- (i) Haploid/Diploid (H, D), species having solely haploid or diploid (or both) populations
- (ii) Polyploid (P), species exhibiting various levels and forms of polyploidy
- (iii) Mixed ploidy (DP), species showing “other” ploidy, i.e., with both haploid/diploid, and polyploid populations (or variants showing, for example, agmatoploidy or dysploidy) occurring in different parts of their range

For uses of macrophyte species, we utilized the species name and keywords such as “plant use,” “ethnobotany,” “medicine,” “folk medicine,” “bioactive,” “phytoremediation,” “ornamental” to search into databases such as PubMed, Web of Science, and Google Scholar to include scientific publication (e.g., [14, 18, 61, 68, 72, 87, 96, 160]) as well as common uses mentioned in the web (e.g., aquarium, ornamental, folk medicine). We included each chapter’s website links and publication Digital Object Identifier (DOI) links. To build a database of photographs, we collected pictures from research colleagues with permission and on the iNaturalist website [58], considering only materials with CC0 and CC-BY licenses. All photos were confirmed by at least one specialist in aquatic macrophytes.



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