FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of aquatic macrophytes in freshwater

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Abstract Aquatic macrophytes are aquatic photo-synthetic organisms, large enough to see with the naked eye, that actively grow permanently or periodically submerged below, floating on, or growing up through the water surface. Aquatic macrophytes are represented in seven plant divisions: Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta, Bryophyta, Pteridophyta and Spermatophyta. Species composition and distribution of aquatic macrophytes in the more primitive divisions are less well known than for the vascular macrophytes (Pteridophyta and Spermatophyta), which are represented by 33 orders and 88 families with about 2,614 species in c. 412 genera. These c. 2,614 aquatic species of Pteridophyta and Spermatophyta evolved from land plants and represent only a small fraction ($\sim 1\%$) of the total number of vascular plants. Our analysis of the numbers and distribution of vascular macrophytes showed that whilst many species have broad ranges, species diversity is highest in the Neotropics, intermediate in the Oriental, Nearctic and Afrotropics, lower in the Palearctic and Australasia, lower again in the Pacific Oceanic Islands, and lowest in the Antarctic region. About 39% of the c. 412 genera containing aquatic vascular macrophytes are endemic to a single biogeographic region, with 61–64% of all aquatic vascular plant species found in the Afrotropics and Neotropics being endemic to those regions. Aquatic macrophytes play an important role in the structure and function of aquatic ecosystems and certain macrophyte species (e.g., rice) are cultivated for human consumption, yet several of the worst invasive weeds in the world are aquatic plants. Many of the threats to fresh waters (e.g., climate change, eutrophication) will result in reduced macrophyte diversity and will, in turn, threaten the faunal diversity of aquatic ecosystems and favour the establishment of exotic species, at the expense of native species.

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Introduction

The term 'aquatic macrophytes' refers to a diverse group of aquatic photosynthetic organisms, all large enough to see with the naked eye. It includes macroalgae of the divisions Chlorophyta (green algae), Xanthophyta (yellow-green algae) and Rhodophyta (red algae) and the "blue-green algae" (more correctly known as Cyanobacteria), Bryophyta (mosses and liverworts), Pteridophyta (ferns) and Spermatophyta (seed-bearing plants), the vegetative parts of which actively grow either permanently or periodically (for at least several weeks each year) submerged below, floating on, or growing up through the water surface (Denny, 1985; Pieterse, 1990) (Table 1). Aquatic macrophytes range in size from *Victoria amazonica* with a leaf diameter up to 2.5 m, to the smallest angiosperms, tiny *Wolffia* spp. with a frond diameter less than 0.5 mm. Aquatic macrophytes include emergent macrophytes (plants that are rooted in submersed soils or soils that are periodically inundated, with foliage extending into the air), floating-leaved macrophytes (plants rooted to the lake or stream bottom with leaves that float on the surface of the water), submersed macrophytes (plants that grow completely submerged under the water, with roots or root-analogues in, attached to, or closely associated with the substrate) and free-floating macrophytes (plants that typically float on or under the water surface). Plant species which occur in ephemeral waterbodies (seasonally filled and refilled waters,

such as floodplains and temporary ponds) challenge this definition. Our decision has been to include such species as "aquatic macrophytes", only if their environmental survival is clearly dependent upon regular refilling of their aquatic habitat with a source of fresh to brackish water.

The freshwater macroalgae are primarily represented by the green algae, especially the Charales, commonly known as the stoneworts or brittleworts (e.g., *Chara* and *Nitella* spp.). The Charales are often mistaken for higher plants because they have erect central stalks that are divided into short nodes and long internodes of elongated multinucleate cells, with a whorl of "branchlets" at each node (Fig. 1). Individual plants can vary greatly in size, from 5 cm to 1 m in length. This conspicuous stage is the haploid generation. Sexual reproduction commences with production by the haploid plant of complex oogonia and antheridia (often orange in colour and nested in the bases of the branchlets). Flagellated sperm produced in antheridia fertilize egg (oospheres) retained in oogonia, with the result being a diploid oospore. Germination commences with meiosis of the diploid oospore; a haploid protonemal stage develops from one product of meiosis and develops into the haploid plant. Only six genera and a few hundred species of Charales are extant, although a rich fossil record reveals far greater species diversity extending back to the Silurian (Tappan, 1980). The Charales are found in fresh and brackish waters on all continents except Antarctica, generally

Table 1 Freshwater macrophyte divisions and representative genera

Kingdom	Freshwater Macrophyte Divisions	Descriptive Term	Representative Freshwater Macrophyte Genera
Monera	Cyanobacteria	Blue-green algae	*Oscillatoria, Lyngbya*
Protista	Chlorophyta	Green algae	*Chara, Nitella, Cladophora, Enteromorpha*
	Rhodophyta	Red algae	*Lemanea, Batrachospermum*
	Xanthophyta	Yellow-green algae	*Vaucheria*
Plantae	Bryophyta	Mosses and liverworts	*Fontinalis, Riella, Ricciocarpus*
	Pteridophyta	Ferns and allies	*Azolla, Salvinia, Isoetes*
	Spermatophyta	Seed-bearing plants	*Sagittaria, Alisma, Butomus, Brasenia, Cabomba, Callitriche, Ceratophyllum, Scirpus, Carex, Myriophyllum, Elodea, Vallisneria, Juncus, Lemna, Utricularia, Nelumbo, Nymphaea, Nuphar, Spartina, Eichhornia, Potamogeton, Ranunculus, Sparganium, Typha*

in slow-flowing water or in lakes, where they can colonize down to great depths (100 m) in very clear water. In addition to the Charales, freshwater macroalgae include certain other genera of green algae (Chlorophyta: e.g., *Cladophora* and *Enteromorpha*

Fig. 1 Examples of aquatic macrophytes: (**a**) macroalgae *Chara* sp. (Order Charales), (**b**) *Salvinia molesta* (Division Pteridophyta), (**c**) *Lemna minor* (angiosperm), (**d**) *Potamogeton richardsonii* (angiosperm), (**e**) *Eichhornia crassipes* (angiosperm) and (f) *Hydrilla verticillata* (angiosperm). Line drawings are from the University of Florida, IFAS Center for Aquatic and Invasive Plants

spp.), yellow-green algae (Xanthophyta: e.g., *Vaucheria*) and red algae (Rhodophyta: e.g., *Lemanea* and *Batrachospermum* spp.). Multicellular filamentous "blue-green algae" (Cyanobacteria: e.g., *Oscillatoria* spp.) are also sometimes included in the "macroalgae", particularly species which form large tangled floating mats which can cause a nuisance in freshwater systems (Pieterse & Murphy, 1993). The brown algae (Phaeophyta), so characteristic of marine rocky shore systems, include seven periphytic species that occur in freshwaters but their inclusion in the "macroalgae" is debatable as filamentous forms are typically <10-mm long (Wehr, 2003).

The mosses, ferns and seed plants are all embryophytes, in that they have a common life cycle involving alternation of sporophyte and gametophyte generations, with the embryo sporophyte retained within the gametophyte at least initially. The bryophytes (mosses and liverworts) differ, however, from ferns and seed plants in that the haploid gametophyte generation, rather than the diploid sporophyte generation, is the most conspicuous. Thus the green moss, with its erect shoot bearing tiny leaf-like structures arranged in spirals, or the thin leathery liverwort are haploid gametophytes. The diploid generation arises after egg and sperm from male and female gametophytes fuse to produce a diploid zygote. The latter grows into a sporophyte, a stalked structure bearing a capsule that produces haploid spores (the future gametophyte generation). The sporophyte is never independent of the gametophyte, remaining attached for provision of water and nutrients. Also unlike ferns and seed plants, bryophytes lack true roots and vascular tissues for uptake and transport of water and organic and inorganic nutrients. About 0.5% of the 20,000 to 25,000 species of bryophytes are truly aquatic macrophytes, in that they require submergence in water to complete their life cycle (Cook, 1999). Other non-aquatic bryophyte species still require water for transfer of spermatozoids, but this can be accomplished simply by raindrops splashing sperm from male to female organs. Aquatic mosses and liverworts are often seen growing attached to rocks in mountain streams, but some (e.g., *Fontinalis antipyretica*) also grow in the shallow to moderately deep water of lakes and in slow-flowing lowland streams and canals. Bryophytes often dominate the macrophyte community found in polar lakes.
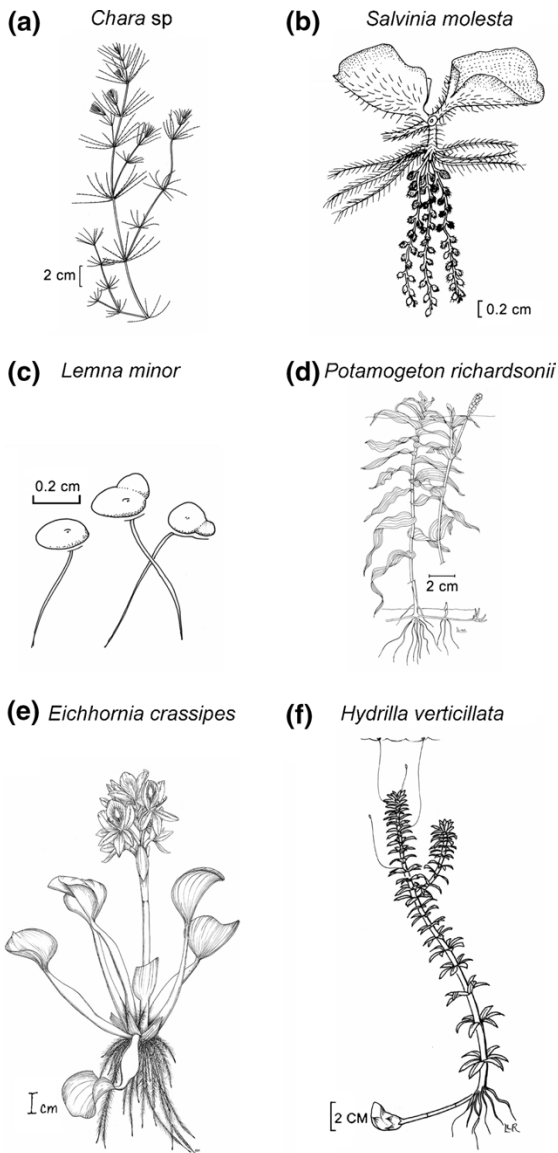
The Pteridophyta (ferns and allies) differ from the more primitive bryophytes in that the sporophyte is the dominant and more conspicuous generation, typified by the leafy frond of terrestrial ferns. However, unlike the more advanced seed plants, Pteridophyta lack seeds. Sporophyte plants develop sporangia that contain spores and for most ferns, the spores are identical (i.e., homosporous) and develop into a gametophyte with both antheridia and archegonia. However, some aquatic ferns (e.g., *Isoetes*) are heterosporous, producing separate male spores (microspores) that develop into male gametophytes with antheridia and female spores (megaspores) that develop into female gametophytes with archegonia. Unlike seed plants, the fern gametophyte is a free-living organism typically consisting of a small (<10-mm broad and long) green one-cell thick structure (the prothallus) with single greatly elongated cells (rhizoids) for absorption of water and minerals. The prothallus produces gametes (sperm and egg) that then fuse to form a zygote that grows by mitosis into the sporophyte. Of the 10,500–12,500 species of ferns and fern allies, there are about 171 species (1–2% of all species) that are truly aquatic macrophytes. Aquatic ferns and fern allies include horsetail or scouring rush (*Equisetum* spp.), quillwort (*Isoetes* spp.) and giant salvinia (*Salvinia molesta*), the latter being one of the world's worst aquatic pests (Fig. 1).

The Spermatophyta or seed-bearing plants, consist of two major groups: angiosperms, which have seeds enclosed in an ovary (which matures to become a fruit), and gymnosperms, in which the seeds are not so enclosed. Only the angiosperms, however, have aquatic species. Sporophytes are the dominant generation, and produce haploid microspores and megaspores that divide to form gametophytes. Haploid microspores develop by mitosis into haploid male gametophytes that contain a tube cell and two nonmotile sperm cells. Male gametophytes (pollen grains) are distributed by wind, rain, insects or other organisms. Haploid megaspores develop by mitosis into a haploid female gametophyte, which is composed of seven cells including a large central cell with two polar nuclei and an egg cell with one nucleus. The female gametophyte is retained in the megasporangium in the ovule. During a process that is unique to angiosperms and known as double fertilization, the nucleus of one sperm cell fuses with the nucleus of the haploid egg cell to produce a diploid zygote, and the nucleus of the other sperm cell fuses with the two polar nuclei of the large central cell to produce a triploid endosperm cell. Both the zygote and the endosperm cell divide by mitosis, producing a diploid embryo (the new immature sporophyte) and triploid endosperm (a food reserve for the embryo). Once this embryonic stage is reached, growth is temporarily halted. This stage is known as a seed and consists of the diploid embryo, triploid endosperm and diploid seed coat (from the female gametophyte). Of the 250,000–400,000 angiosperm species, there are only about 2,443 species (<1% of all species) that are aquatic. Aquatic angiosperms include the small free-floating duckweeds (e.g., *Lemna* and *Wolffia* spp.), the cosmopolitan submerged pondweeds (*Potamogeton* spp.) and invasive weeds such as water hyacinth (*Eichhornia crassipes*) and hydrilla (*Hydrilla verticillata*) (Fig. 1).

Species and generic diversity

Aquatic macrophytes are represented in seven plant divisions: Cyanobacteria, Chlorophyta, Rhodophyta, Xanthophyta, Bryophyta, Pteridophyta and Spermatophyta, consisting of at least 41 orders and 103 families. Including the filamentous green algae, the Chlorophyta contribute some 20 genera of aquatic macrophytes, comprising a few hundred species (mostly in the Orders Cladophorales and Charales). There are a few additional freshwater macrophyte species in the Rhodophyta and Xanthophyta, and probably fewer than 20 genera (though the taxonomy is confused) of Cyanobacteria which could be considered as macrophytes. The Bryophyta contribute 22 genera of aquatic macrophytes with about 110 freshwater species (Cook, 1999). Species composition and distribution of aquatic macrophytes in these more primitive divisions are less well known than for the vascular macrophytes (Pteridophyta and Spermatophyta); the remainder of this article focuses on the latter two plant divisions only.

Vascular aquatic macrophytes are represented by 33 orders and 88 families, with about 2,614 species (Table 2) in c. 412 genera (Table 3). Exact numbers are not possible to determine because it is not known whether many so-called 'wetland' species are truly

Table 2 Number of vascular aquatic macrophyte species currently known in the major biogeographic areas

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Pteridophyta									
Azollaceae	2	3	2	4	1	1			7
Blechnaceae	1		2		2	3	4		7
Equisetaceae	3	2	1		1		1		3
Isoetaceae	8	27	1	12	18	8			70
Marsileaceae	11	4	24	12	12	11	2		66
Polypodiaceae					1	1			1
Pteridaceae	1	3	2	3	3	2	2		5
Salviniaceae	1	2	2	8	2				10
Thelypteridaceae			2	1	2	2	2		2
Spermatophyta (Angiosperms)									
Acanthaceae	3	3	2	3	10	4	2		18
Acoraceae	1	1			2				2
Alismataceae	19	32	14	39	18	7	1		96
Amaranthaceae	1		1	5	2				7
Amaryllidaceae		1	1	2	1				4
Apiaceae	17	30	3	11	2	1			55
Apocynaceae	1				1				1
Aponogetonaceae			31		10	14			54
Araceae	15	22	19	31	90	19	7		139
Araliaceae		3	2	4		2			5
Asteraceae	1	12	16	29	18	3	1		56
Balsaminaceae	1				1				1
Boraginaceae	2		5	2	6	1			6
Brassicaceae	6	3	2	3	2				12
Burmanniaceae					3	1			3
Butomaceae	1				1		1		1
Cabombaceae	1	3	1	6	1	1			6
Campanulaceae	2	22	8	6	4	7			41
Cannaceae		1		1					1
Ceratophyllales	4	3	3	3	3	2	2		4
Commelinaceae	4	1	5	1	13	3	2		13
Convolvulaceae	2	1		2	1				3
Crassulaceae	2	1	2	3		1			8
Cyperaceae	73	123	78	149	87	67	35	3	276
Droseraceae	1		1		1	1			1
Elatinaceae	10	11	2	6	3	1			25
Eriocaulaceae	6	12	7	45	17	1	1		71
Euphorbiaceae		1		4					4
Fabaceae		6	1	13	2				17
Haloragaceae	10	15	4	11	7	41			65
Hanguanaceae					3	1	1		3

Table 2 continued

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Hydatellaceae					1	8			9
Hydrocharitaceae	20	12	43	15	40	23	5		108
Hydroleaceae	1	2		2	1	1			4
Hydrostachyaceae			29						29
Hypericaceae	1								1
Hypoxidaceae			1						1
Iridaceae	1	8	1	1					10
Juncaceae	7	9	4	3	4	2	2	1	14
Juncaginaceae	1	1	1	1		3			5
Lamiaceae	7	8	6	1	9	2	1		23
Lentibulariaceae	11	21	17	26	12	13			70
Limnocharitaceae		2	1	7	1	1			8
Linderniaceae	2	2	1	5	2	1			7
Lythraceae	13	8	13	33	26	6			78
Marantaceae		1	2	1	1	1	1		3
Mayacaceae		1	1	4					5
Melastomataceae				6					6
Menyanthaceae	8	5	16	8	15	36			73
Myrsinaceae	1	3	2						5
Nelumbonaceae	1	1		1	1	1			2
Nymphaeaceae	12	15	15	22	13	14			68
Onagraceae	2	7	4	11	5	4	1		17
Orobanchaceae			1						1
Oxalidaceae			2						2
Pedaliaceae	1								1
Philydraceae	1				1	1	1		1
Phrymaceae		1	1			7			8
Phyllanthaceae			1	1					2
Plantaginaceae	20	28	31	41	16	11	2	2	91
Poaceae	65	78	54	84	64	51	21	1	190
Podostemaceae	7	3	84	188	47	3			330
Polemoniaceae		3		1					4
Polygonaceae	7	9	3	9	3	2			20
Pontederiaceae	2	9	4	23	4	4			33
Portulacaeae	1	2	1	2	1	2		1	3
Potamogetonaceae	46	28	23	31	28	29	9	2	117
Primulaceae	1	1							2
Ranunculaceae	19	13		19	1	1		2	39
Rapateaceae				1					1
Rubiaceae			1	5					6
Saururaceae	1	1			2				3
Sparganiaceae	20	9		1	6	2			22
Sphenocleaceae			2		1				2
Tetrachonraceae				1		1			2

Table 2 continued

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Theophrastaceae		2	1	3					3
Thurniaceae			1	2					3
Typhaceae	8	3	3	3	7	2	1		9
Xyridaceae				3	1	1			4
Total	497	644	614	984	664	439	108	12	2614

PA: Palaearctic; NA: Nearctic; AT: Afrotropical ; NT: Neotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic. Notes: Introduced species not considered. Species were identified as "aquatic" on the basis of published records (in particular Cook, 1996a, 1996b, 2004; Preston & Croft, 1997; Crow & Hellquist, 2000; Ritter, 2000) and the knowledge of the authors. Taxonomy (division, order, family, genera) was updated to APG 2003. Geographic distributions were obtained primarily from the Royal Botanical Gardens, Kew, England checklists for monocots and other selected families (Govaerts et al., 2007a, b) and for grass flora (Clayton et al., 2006), US Department of Agriculture's Germplasm Resources Information Network (GRIN, 2007), the Missouri Botanical Garden's VAST (VAScular Tropicos) nomenclatural database (Missouri Botanical Garden, 2007) and the International Plant Names Index (2004)

aquatic (i.e., their vegetative parts actively grow either permanently or periodically submerged below, floating on, or growing up through the water surface). We have been conservative in our identification of aquatic macrophytes, including only those species that have been determined by the authors or other experts to meet the above definition of 'aquatic'. In addition, previously unknown species continue to be discovered, particularly in tropical areas, thus confounding our estimates of species numbers and geographic distribution. Finally, recent advances in molecular phylogenetics have resulted and will continue to result in revisions of classification at nearly all levels. We based our classification at the ordinal, family and generic levels on the schema of the Angiosperm Phylogeny Group (APG, 2003).

Overall, vascular macrophyte species diversity is highest in the Neotropics (984 spp), intermediate in the Orient, Nearctic and Afrotropics (664, 644 and 614, respectively), lower in the Palearctic and Australasia (497 and 439, respectively), and lower again in the Pacific region and Oceanic islands (108 spp), whilst only very few vascular macrophyte species have been found in the Antarctica bioregion, all confined to sub-Antarctic freshwater habitats (Fig. 2). The higher number of species in the Neotropics is in great part due to the large contribution from the Podostemaceae (188 species) compared to other regions. In terms of both number of genera and species, the Podostemaceae is the largest exclusively aquatic family of angiosperms. Plants in this family are confined to fast-flowing waters, mainly in the tropics, and many species have narrow distributions, such as a single watershed. For all regions (except Antarctica), two of the three most species-rich families were Cyperaceae and Poaceae. The other species-rich family varied amongst regions: Alismataceae for the Nearctic, Araceae for the Orient, Haloragaceae for Australasia, Podostemaceae for the Afrotropics and Neotropics, and Potamogetonaceae for the Pacific and Palaearctic.

Generic diversity of vascular aquatic macrophytes is much less variable compared to species diversity (Table 3). The total number of genera ranged between 152 and 196 for 6 of the 8 bioregions and was highest (192–196) for the Afrotropical, Neotropical and Oriental regions (Fig. 2). As with species diversity, lower generic diversity occurred in the Pacific and Antarctic regions. Within the families, approximately 47% (41 families) have only one genus that includes aquatic plants, although there are often other genera of terrestrial and wetland plants, not meeting the criteria for true aquatic habit, in each of these families. The occurrence of isolated genera that are completely or partially aquatic suggests that the aquatic species in these genera are relatively recent returns to water compared to orders or families that are entirely aquatic and therefore likely returned to water early in the divergence of their lineages.

Twelve genera encompass about 28% of the total vascular macrophyte species richness worldwide (Table 4). With the exception of the genus *Apinagia* that is found only in South America, the other genera have a wide range extension, being present in at least three bioregions. Two of the genera are ferns; the remaining 10 are angiosperms. The 12 species-rich

Table 3 Number of vascular aquatic macrophyte genera currently known in the major biogeographic areas

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Pteridophyta									
Azollaceae	1	1	1	1	1	1			1
Blechnaceae	1		1		2	2	3		3
Equisetaceae	1	1	1		1		1		1
Isoetaceae	1	1	1	1	1	1			1
Marsileaceae	2	2	1	3	1	2	1		3
Polypodiaceae					1	1			1
Pteridaceae	1	1	1	1	1	1	1		1
Salviniaceae	1	1	1	1	1				1
Thelypteridaceae			2	1	2	2	2		2
Spermatophyta (Angiosperms)									
Acanthaceae	1	2	1	2	1	1	1		3
Acoraceae	1	1			1				1
Alismataceae	7	4	8	2	7	5	1		12
Amaranthaceae	1		1	1	2				2
Amaryllidaceae		1	1	1	1				1
Apiaceae	6	11	2	3	3	2			14
Apocynaceae	1				1				1
Aponogetonaceae			1		1	1			1
Araceae	8	9	9	12	11	8	6		24
Araliaceae		1	1	1		1			1
Asteraceae	1	9	11	10	9	3	2		24
Balsaminaceae	1				1				1
Boraginaceae	1		2	2	2	1			2
Brassicaceae	3	3	2	2	2				5
Burmanniaceae					1	1			1
Butomaceae	1				1		1		1
Cabombaceae	1	2	1	2	1	1			2
Campanulaceae	1	5	4	3	1	4			9
Cannaceae		1		1					1
Ceratophyllales	1	1	1	1	1	1	1		1
Commelinaceae	3	1	2	1	4	3	2		4
Convolvulaceae	1	1		1	1				1
Crassulaceae	1	1	1	1		1			1
Cyperaceae	14	18	25	24	22	20	14	3	33
Droseraceae	1		1		1	1			1
Elatinaceae	2	2	2	2	2	1			2
Eriocaulaceae	1	2	3	5	1	1	1		6
Euphorbiaceae		1		1					1
Fabaceae		1	1	2	2				2
Haloragaceae	2	2	2	2	4	3			5
Hanguanaceae					1	1	1		1

Table 3 continued

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Hydatellaceae					1	2			2
Hydrocharitaceae	7	4	8	6	7	7	4		14
Hydroleaceae	1	1		1	1	1			1
Hydrostachyaceae			1						1
Hypericaceae	1								1
Hypoxidaceae			1						1
Iridaceae	1	1	1	1					2
Juncaceae	1	1	1	1	1	1	1	1	1
Juncaginaceae	1	1	1	1		1			2
Lamiaceae	4	3	3	1	4	2	1		6
Lentibulariaceae	1	2	2	2	1	1			2
Limnocharitaceae		1	1	2	1	1			3
Lindemaceae	1	1	2	1	1	1			2
Lythraceae	4	4	5	4	4	3	1		9
Marantaceae		1	2	1	1	1	1		3
Mayacaceae		1	1	1					1
Melastomataceae				2					2
Menyanthaceae	3	3	2	1	3	3			5
Myrsinaceae	1	1	1						2
Nelumbonaceae	1	1		1	1	1			1
Nymphaeaceae	3	3	1	1	3	3			6
Onagraceae	1	2	1	1	1	1	1		2
Orobanchaceae			1		1				1
Oxalidaceae			1						1
Pedaliaceae	1								1
Philydraceae	1				1	1	1		1
Phrymaceae		1	1			2			3
Phyllanthaceae			1	1					1
Plantaginaceae	7	8	6	6	6	7	1	2	15
Poaceae	31	28	30	25	32	27	10	1	59
Podostemaceae	1	1	16	21	13	2			49
Polemoniaceae		1		1					1
Polygonaceae	2	2	1	1	1	2			2
Pontederiaceae	1	3	3	4	1	1			6
Portulacaeae	1	1	1	1	1	2			2
Potamogetonaceae	4	3	4	3	3	4	2	1	5
Primulaceae	1	1							1
Ranunculaceae	2	2	1	1	1	1		1	2
Rapateaceae				1					1
Rubiaceae			1	2					2
Saururaceae	1	1			2				2
Sparganiaceae	1	1		1	1	1			1
Sphenocleaceae			1		1				1
Tetrachonraceae				1					2

Table 3 continued

Taxon	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Theophrastaceae		1	1	1					1
Thurniaceae			1	1		1			2
Typhaceae	1	1	1	1	1	1	1		1
Xyridaceae				2	1	1			2
Total	154	172	196	192	192	152	62	9	412

PA: Palaearctic; NA: Nearctic; AT: Afrotropical; NT: Neotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic. Notes are the same as for Table 2

Phylogeny and Historical processes

In the early Paleozoic, ancestral marine plants colonized land, giving rise to evolution of vascular plants. Land plant fossils (small, dispersed spores dating from the Ordovician; Wellman et al., 2003) as well as molecular analysis (Sanderson, 2003) place the origin of land plants at 450–475 Mya. Most major land plant lineages (i.e., bryophytes, lycophytes, ferns, gymnosperms) date to the Paleozoic, however the first unequivocal angiosperm fossils appeared ∼135 Mya and thereafter radiated into most of the major angiosperm lineages over a period of ∼10–15 million years (see review of Feild & Arens, 2007 and references therein). Biologists have long acknowledged a link between green algae and terrestrial plants (Lemieux et al., 2000; Chapman & Waters, 2002; Pombert et al., 2005; Turmel et al., 2006) with some suggesting specifically that the green algae known as stoneworts (Order Charales) are the extant sister group to all land plants (reviewed by McCourt et al., 2004).

Of the many species of terrestrial vascular plants (Pteridophyta and Spermatophyta), only a small fraction of these land plants returned to life in aquatic and marine environments. Since aquatic vascular plants evolved at different times, the return to water was not a single, or even an infrequent, event. Cook (1999), in a survey of the number of plants which

Fig. 2 Diversity of vascular aquatic macrophytes: number of species/number of genera per biogeographic region. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, Au: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic
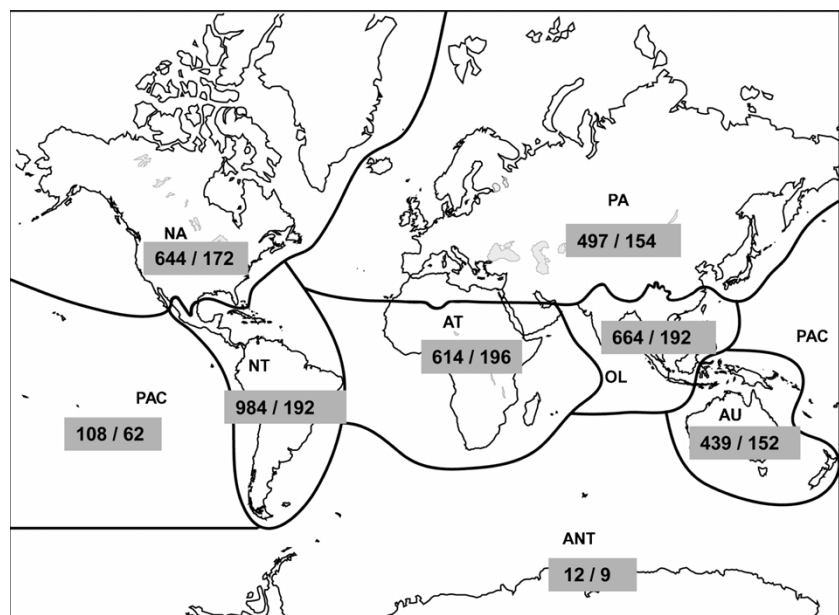
Table 4 Primary distribution and habitat of vascular plant genera with more than 50 aquatic species

Genus	Family	Number of Aquatic Species in Genus	Total Number of Species in Genus	Distribution	Habitat of aquatic species
Potamogeton	Potamogetonaceae	99	99	All regions	Leaves submerged or floating
Isoetes	Isoetaceae	70	∼150	All regions except Pacific and Antarctic	Permanently or periodically submerged
Eleocharis	Cyperaceae	70	∼200	All regions except Antarctic	Emergent
Marsilea	Marsileaceae	60	60	All regions except Antarctic	Leaves floating on surface or emergent
Apinagia	Podostemaceae	57	57	South America only	Permanently or periodically submerged
Cryptocoryne	Araceae	56	56	Paleoarctic, Orient, Australasia only	Leaves submerged or emergent
Aponogeton	Aponogetonaceae	54	54	Afrotropics, Orient, Australasia only	Leaves submerged or floating
Myriophyllum	Haloragaceae	54	54	All regions except Afrotropics, Pacific and Antarctic	Leaves submerged or emergent
Nymphaea	Nymphaeaceae	53	53	All regions except Pacific and Antarctic	Leaves floating on surface
Cyperus	Cyperaceae	53	∼900	All regions except Antarctic	Emergent
Nymphoides	Menyanthaceae	53	53	All regions except Pacific and Antarctic	Leaves floating on surface
Utricularia	Lentibulariaceae	52	216	All regions except Pacific and Antarctic	Leaves submerged or floating

have become secondarily aquatic, estimated that 11 of ∼315 genera (or 3%) of ferns and fern allies (i.e., Pteridophyta) and 407 of ∼13,200 genera (or 3%) of angiosperms include aquatic species. The evolutionary step of becoming secondarily aquatic probably took place at least 211 times but more likely 252 times (possibly more), with reversion to aquatic life having taken place at least seven times in the Pteridophyta and 204–245 times in the angiosperms (Cook, 1999). In cases where entire orders or families are aquatic, the return to water likely occurred early in the divergence of the lineage. In a review of early angiosperms, Feild & Arens (2007) observed that most molecular analyses place the New Caledonian shrub *Amborella trichopoda* as diverging closest to the root of the angiosperm phylogenetic tree, with the second basal lineage being the entirely aquatic families of Cabombaceae, Nymphaeaceae and Hydatellaceae, the third basal lineage being the Austrobaileyales (lianes occurring in Australia), and the fourth basal lineage being the entirely aquatic

family Ceratophyllaceae along with the terrestrial Chloranthaceae. Fossils of water lilies (Nymphaeaceae) have been recorded back to the Early Cretaceous (125–115 Mya) (Friis et al., 2001). The remaining angiosperms form three, well-supported monophyletic lineages (the magnoliids, dicots and monocots), although relations amongst these lineages are still in flux.

As a result of this return to water from the terrestrial environment, aquatic angiosperms have evolved numerous physiological and morphological adaptations to cope with limited carbon dioxide (including the problem of scarcity of CO_2 in solution in many waters, compared to HCO_3^-) and oxygen availability, and reduced light. Aquatic plants operate under dramatically increased diffusion resistance for CO_2 and oxygen as a result of high aqueous resistance to gas diffusion and formation of boundary layers, especially in lentic habitats. To enhance carbon acquisition, submerged leaves are often highly dissected so as to increase surface area (e.g., the

thread-like filiform leaves of *Cabomba* and *Cerato-phyllum*) and show concentration of the chloroplasts near the leaf surface. Macrophytes in relatively shallow water overcome aqueous inorganic carbon limitations to photosynthesis by drawing on atmospheric CO_2 via aerial or floating leaves. Higher concentrations of CO_2 in bottom sediments (as a result of microbial activity) are also exploited by some macrophytes (e.g., *Isoetes*) whereby CO_2 in the interstitial sediment water diffuses into the roots and then through gas-filled lacunae to the leaves (Raven et al., 1988). In addition to morphological changes, physiological strategies such as utilization of bicarbonate (in addition to CO_2) as an inorganic carbon source and additional biochemical carboxylation pathways (including crassulacean acid metabolism, found, for example, in *Isoetes, Crassula, Littorella, Sagittaria* and *Vallisneria*, and C4—like metabolism found in *Hydrilla verticillata* and *Egeria densa*) have evolved to cope with reduced availability of CO_2 and the prevalence of HCO_3^- as the dominant form of inorganic carbon in higher-pH waters (Maberly & Madsen, 2002). The limited availability of oxygen in aquatic systems has also resulted in development of aerenchyma—tissue containing enlarged gas spaces—for transport of oxygen from shoot to roots and venting of gases (carbon dioxide, ethylene, methane) from the root and soil (Sculthorpe, 1967). Roots are often buried in anoxic sediments and translocated oxygen serves to sustain their aerobic metabolism, at the same time contributing to increased uptake of mineral nutrients as a result of oxygenation of the rhizosphere. To cope with light limitation and changes in spectral quality underwater, many species of submerged plants also evolved strategies such as rapid elongation and physiology, typical of shade plants (Kirk, 1996). In addition, many species considered as nuisance weeds, such as the elodeids *E. densa* and *H. verticillata*, increase their competitive attributes by concentrating their photosynthethic tissues close to the water surface ("canopy forming" strategy). In contrast to adaptations specifically developed by macrophytes for life underwater, many morphological characteristics that evolved to cope with the terrestrial environment have been reduced or eliminated, notably the stomata and cuticles of the leaves, the vascular tissue such as xylem, and structural tissue such as lignin (Sculthorpe, 1967).

Present distribution and main areas of endemicity

Vascular aquatic macrophytes have a world-wide distribution, being found in all biogeographic regions of the world. The broad distributional ranges of vascular macrophytes were noted as early as the mid-1800s by investigators such as de Candolle (1855) and Darwin (1859), and our analyses confirm that many vascular macrophytes are cosmopolitan: 11% of all species occurred in at least three bioregions and 41% of all families spanned ≥6 bioregions (Tables 2 and 3). Species with broad ranges, found in at least seven of the eight bioregions, are *Arundo donax, Brachiaria mutica, Brachiaria subquadripara, Carex echinata, Ceratophyllum demersum, Ceratophyllum muricatum, Ceratopteris thalictroides, Cladium mariscus, Cyperus digitatus, C. odoratus, Echinochloa colona, Echinochloa crus-galli, Echinochloa crus-pavonis, Fimbristylis dichotoma, Fimbristylis littoralis, Ischaemum rugosum, Juncus bufonius, Landoltia punctata, Lemna aequinoctialis, Leptochloa fusca, Montia fontana, Najas marina, Oryza sativa, Panicum repens, Paspalum distichum, Paspalum notatum, Paspalum vaginatum, Pistia stratiotes, Potamogeton nodosus, Ruppia maritima, Schoenoplectus tabernaemontani, Spirodela polyrrhiza* and *Typha domingensis*. Many aquatic vascular plant families can be classed into one of three floristic groups on the basis of species richness: cosmopolitan (e.g., Cyperaceae, Juncaceae, Poaceae), north-temperate (e.g., Potamogetonaceae, Sparganiaceae, Haloragaceae, Elatinaceae and Hippuridaceae) or pan-tropical (e.g., Podostemaceae, Hydrocharitaceae, Limnocharitaceae, Mayacaceae, Pontederiaceae, and Aponogetonaceae) (Crow, 1993). It should be noted that whilst families classed as pan-tropical or north-temperate show much higher species richness in these climatic regions, they may still include species that occur outside their climatic region: a good example being the Haloragaceae, with its numerous Australasian representatives.

The wide distributional ranges of aquatic plants have traditionally been explained by long-distance dispersal by migratory birds (Darwin, 1859; Arber, 1920; Sculthorpe, 1967; Hutchinson, 1975) and human activity (Cook, 1985). However, observations such as the disjunct distributions of aquatic families at the base of the angiosperm phylogenetic tree (i.e., Cabombaceae, Nymphaeaceae and Hydatellaceae)

contributed to acceptance of continental drift as a major explanatory factor for modern angiosperm distributions (Raven & Axelrod, 1974). Recently, Les et al. (2003) examined the role of dispersal versus displacement in the distribution of aquatic macrophytes. Using molecular estimates of divergence time involving 71 aquatic angiosperm species from phylogenetically related aquatic taxa that exhibit discontinuous intercontinental distributions, Les et al. (2003) found that for 79 of 87 comparisons, divergence times were far too recent (<30 Mya) to implicate continental drift as a major determinant of these discontinuous distributions. Even *Ceratophyllum demersum*, which is found in all continents except Antarctica, had divergence times of <2.5 Mya for comparisons of specimens from North America, Asia and Australia, indicating recent dispersal rather than a paleodistribution amongst these continents. In an analysis of aquatic macrophyte species and subspecies endemic to Europe and portions of North Africa bordering the Mediterranean, Cook (1983) considered that c. 75% of 61 endemic taxa evolved after the ice age whereas only c. 25% were relicts left by extinction. Long-distance dispersal by birds as well as human activity (both active, through introduction of useful crop plants, and inadvertent) remain viable explanations for widely disjunct aquatic plant distributions although, as Les et al. (2003) note, continental drift may have influenced dispersal

patterns by facilitating successful transoceanic dispersal between continents that were previously physically closer in proximity. The successful long-distance dispersal of aquatic plants has been facilitated by the broad ecological tolerances and plastic responses of many aquatic plants, their enhanced survivorship because of clonal growth (very common in macrophytes) and the abundance of easily dislodged propagules (Santamaria, 2002; Les et al., 2003).

Our results showed that vascular macrophyte generic diversity is highest in the tropics (Afrotropics, Neotropics and Orient) and lower in the Nearctic, Palaeoarctic and Australasia (Fig. 2). Species diversity is highest in the Neotropics followed by the Orient, with the Nearctic showing the third highest species diversity (Fig. 2). Previous assessments of macrophyte diversity between temperate and tropical regions indicated that richness (S) was similar, or even richer, in temperate regions (Crow, 1993; Jacobsen & Terneus, 2001). Whilst we have not specifically tallied species numbers in tropical versus temperate latitudes, our comparisons amongst bioregions indicate that vascular macrophyte generic diversity for the tropics is greater than for temperate regions. Species diversity may also be greater for certain tropical compared to temperate regions. Considering the relative lack of data from the tropics compared with temperate regions, this difference may

Fig. 3 Vascular aquatic macrophyte endemism, by species (Sp) and genera (Gn) presented as percentage (and number) of endemics per biogeographic region. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, Au: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic
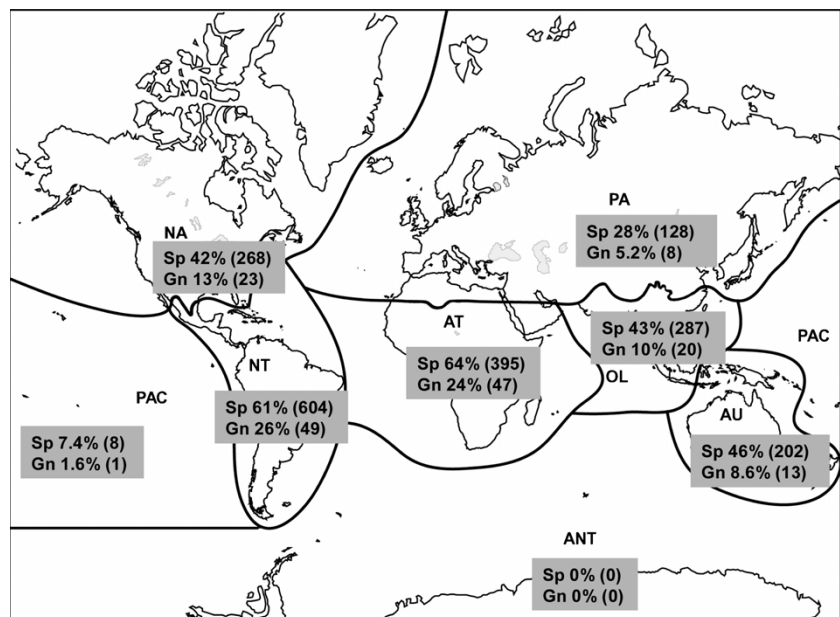
increase with time as more investigations are undertaken in the tropics, leading to discoveries of new species or genera. However, even given the high probability of new macrophyte species being found in tropical regions, differences in richness between tropical and temperate regions will likely remain less for aquatic than for terrestrial plants because conditions favouring greater richness in tropical regions (e.g., higher and more uniform temperature) may be offset by increased precipitation in tropical regions (resulting in water level fluctuation and lower underwater light) and greater inorganic carbon availability in temperate regions (Payne, 1986).

Similar to the latitudinal differences in macrophyte distribution, aquatic macrophytes also show decreases in species numbers with altitudinal gain (Jones et al., 2003; Lacoul & Freedman, 2006a). Whereas certain species such as *Callitriche palustris* cover a wide altitudinal range, from sea-level up to 2,500 m in Europe, 3,000 m in Californian mountains and >4,000 m in mountains in the Andes and Himalayas (Beger, 1932; Schotsman, 1954; McLaughlin, 1974; Lacoul, 2004), others such as *Isoetes bolanderi*, *Myriophyllum exalbescens*, *Nuphar lutea* and *Potamogeton alpinus* have restricted distributions in cold high-altitude waters (usually softwater lakes: Murphy, 2002) similar to the restricted distributions observed in the arcto-boreal environment. Some of the highest published altitude records for the aquatic angiosperms include *Zannichellia* sp. at 5,350–5,400 m in Cerro Cóndor, Argentina (Kühn & Rohmeder, 1943; Halloy, 1981, 1983); *Potamogeton* sp., *Myriophyllum* sp., *Isoetes* sp., and *Nitella* at 4,880 m in Peru (Halloy et al., 2005; Seimon et al., 2007); *Myriophyllum* cf. *elatinoides*, *Potamogeton* cf. *pectinatus* and *Isoetes* sp. at 4,400–5,244 m in Peru (Seimon et al., 2007); *Chara* sp. (algae) at 5,030 m in Tibet (Mitamura et al., 2003) and *Ranunculus trichophyllus* at 4,680–4,750 m in Nepal (Lacoul & Freedman, 2006b). Moreover, it is not only the number of macrophyte species that are less at higher altitudes but also the number of endemic species, an example being the fewer endemic species in the northern mountainous regions of Northern India, Nepal and Bhutan compared to peninsular south India and Sri Lanka.

There is strong evidence that within-system diversity (alpha-diversity) of aquatic macrophytes is related not only to geographical factors (e.g., latitude, altitude, as discussed above), and size of waterbody (e.g., Rørslett, 1991), but also to within-system heterogeneity of environmental factors affecting macrophyte growth (e.g., Murphy et al., 2003; Feldmann & Nõges, 2007), and to the intensity of environmental and human-related stress and disturbance pressures acting upon the system. In relation to the last point, data from Swiss lake macrophyte communities (Lachavanne, 1985), for example, show strong evidence that environmental stress associated with nutrient availability (trophic status) of individual lakes is related to macrophyte alpha-diversity, following a classic "hump-back" distribution. Ultra-oligotrophic and oligotrophic lakes at one end of the scale support few species. Mesotrophic lakes, in the middle, tend to support the richest macrophyte diversity, whilst macrophyte richness declines again in eutrophic and hypertrophic lakes.

In contrast to the widely distributed genera (Table 3), it is worth noting that 39% of the genera containing aquatic vascular macrophytes (ignoring any terrestrial species in such genera) are endemic to a single realm. Many of these are genera with single or few aquatic species, but others are multi-species genera, especially in the Podostemaceae. Endemism is rich in two tropical regions (Afrotropical—64% of total species present; Neotropical—61%); intermediate in Australasia (46%), the Oriental region (43%) and the Nearctic (42%); low in the Palaearctic (28%); and negligible or absent in the Pacific (7.4%) and Antarctic (no endemic macrophyte species) (Fig. 3). On a smaller geographic scale, endemism is still rich in some tropical and subtropical regions but also in some temperate systems: 119 endemic species were recorded by Cook (2004) in South Africa; 100 endemic species were recorded in a region including South Brazil, Uruguay and Paraguay and North Argentina (Irgang & Gastal Jr., 2003); 61 endemic species and subspecies were reported for Europe and the portions of North African countries that border the Mediterranean (Cook 1983); 38 endemic aquatic plant species were recorded for New Zealand (Coffey & Clayton, 1988). Surprisingly, ancient large lakes such as Baikal and Biwa are poor in endemic aquatic macrophytes: no endemic aquatic macrophyte has been reported in Lake Baikal, Russia (Kozhova & Izmestéva, 1998) and Lake Biwa, Japan has only two endemics (*Vallisneria biwaensis* and *Potamogeton biwaensis*; Nakajima, 1994).

Human related issues

Aquatic macrophytes play an important role in the structure and function of aquatic ecosystems by altering water movement regimes (flow and wave impact conditions), providing shelter and refuge, serving as a food source, and altering water and sediment quality (e.g., Chambers & Prepas, 1994; Sand-Jensen, 1998; Chambers et al., 1999). They provide a structurally complex environment over spatial scales ranging from millimetres (e.g., foliage structure of macrophytes: Dibble et al., 2006) to hundreds of metres (e.g., distance between weed beds in a lake; Dibble et al., 1996; Rennie & Jackson, 2005). This environmental heterogeneity can increase numbers and types of niches, and can uncouple interacting predators and prey (Harrel & Dibble, 2001). As a result, aquatic macrophyte habitats often represent the most diversified, productive and heterogeneous portions of water bodies. In addition to their important role in maintaining aquatic biodiversity, diverse macrophyte communities also contribute to the maintenance of aquatic ecosystem functioning, for example by sustaining filamentous algal growth (that potentially supports a greater abundance of fish and wildlife) and reducing phosphorus concentrations in the water (Engelhardt & Ritchie, 2001). Eutrophication is one of the greatest environmental problems worldwide and aquatic macrophytes may prove to be "biological engineers" to aid in restoring water quality (Byers et al., 2006).

Perhaps because many vascular macrophyte species exhibit high productivity, broad ecological tolerances and easily dispersed propagules, several of the worst invasive weeds in the world are aquatic macrophytes (Pieterse & Murphy, 1993). Originating in South America, the aquatic fern *Salvinia molesta* and the water hyacinth *Eichhornia crassipes* have become serious aquatic weed problems in the southern USA, Australia, South-East Asia, the Pacific and south, central and eastern Africa. Considered two of the world's worst aquatic pests, these plants are aggressive, competitive species that can cover the surface of lakes and slow-moving rivers, thereby impacting aquatic environments, local economies and human health. Under favourable conditions, plants can double their dry mass in 3–7 days with mats, in some cases, being up to 3-m thick. Another serious aquatic weed is hydrilla (*Hydrilla verticillata*),

arguably the most problematic invasive aquatic plant in North America. Native to central and south Asia, it was introduced to Florida in the 1950s or 1960s via the aquarium trade and is now well established in the southern United States and in the west coast states of California and Washington. Hydrilla forms dense submerged mats of vegetation (which may reach to the surface) that interfere with recreation and destroy fish and wildlife habitat. Each year, US agencies spend millions of dollars for hydrilla control involving aquatic herbicides, biological agents, mechanical removal and physical habitat manipulation. Many aquatic weed species are tropical to sub-tropical in origin and global warming will certainly extend the potential range and frequency of occurrence of such species in temperate regions.

In contrast to the threat posed by invasive aquatic macrophytes, a number of macrophyte species are cultivated for human use. Rice (*Oryza* spp.) is the world's most important staple food crop. In 2005, rice production exceeded 6×10^8 Mt (FAO, 2006) with China, India and Indonesia being the top three producers. More than 2.7 billion people rely on rice as their major source of food with this number expected to grow to 3.9 billion by the year 2025. There is increasing concern about current rice production practices being unable to meet future demands as a result of constant or declining yields in many Asian countries, limited possibilities for arable area expansion, and fewer water resources for expanding rice planted areas, as well as concerns related to environmental degradation, genetic erosion and nutritional quality of rice. Whilst rice is probably the most widely used macrophyte by humankind, many other species receive local or widespread use, for example in pulp production (e.g., *Phragmites*), as thatch for houses, mats, etc (e.g., *Cyperus*), in medicine (e.g., *Alternanthera philoxeroides* and *Sagittaria rhombifolia*) and for aesthetic value (e.g., *Nymphaea* spp., *Hydrocleys* spp. and *Victoria amazonica*). The use of several species in phytoremediation has increased recently as an alternative technique for treatment of domestic as well as industrial effluents.

Large gaps still exist in our knowledge of aquatic macrophyte abundance and distribution. Several aquatic vascular macrophytes are recognized as critically endangered (*Isoetes sinensis, I. taiwanensis, Ledermanniella keayi* and *Saxicolella marginalis*), endangered (*Ledermanniella letouzeyi, L. onanae* and

Macropodiella pellucida) or vulnerable (*Ledermanniella thalloidea*), primarily as a result of habitat loss (caused by forestry and agricultural expansion) and water pollution (IUCN, 2004). Many of the threats to fresh waters (e.g., climate change, eutrophication, acidification, alien species introductions) will lead to reduced macrophyte diversity and will, as a result, threaten the faunal diversity of aquatic ecosystems, favour the establishment and expansion of exotic species at the expense of native species, and challenge our abilities to sustain productions of aquatic macrophytes that are needed to meet human consumptive demands.

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