Received: 12 February 2024 | Accepted: 11 June 2024

DOI: 10.1111/1365-2745.14372

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

BIOLOGICAL FLORA

International Biological Flora: *Trapa natans*[†]

No. 5

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Abstract

1. This account presents information on all aspects of the biology of *Trapa natans* L. (water caltrop and water chestnut) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *International Biological Flora*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history, conservation and global heterogeneity.
2. The water caltrop is an annual herbaceous hydrophyte rooted in the sediment of water bodies, forming flexuous underwater stems that create a buoyant, light-capturing leaf rosette at the water surface. The submerged stem nodes additionally bear linear leaves. These are replaced by photosynthetically active, pinnately branched structures and unbranched adventitious roots early on, which complement previously established roots on the hypocotyl, altogether facilitating anchorage, nutrient and water absorption, aeration and capture of subsurface irradiance. Solitary flowers pollinated primarily through autogamy and incidentally through entomophily give rise to a fully developed edible single-seeded drupe with two to four barbed horns. Fruits are dispersed with the help of hydrochory, epizoochory and anthropochory.
3. Throughout its lowland, global temperate, subtropical and tropical distribution in Eurasia and Africa, the thermophilic macrophyte is found in shallow, sun-exposed, nutrient-rich freshwater bodies with low-velocity flows and steady water levels. These offer slightly acidic to mildly basic conditions. The accompanying soft substrate is usually characterized by a high organic matter content. Regularly co-occurring with other macrophytes, some of which are also of conservation concern, such as those in rare stands of the association Trapetum natantis in Europe, the water caltrop has at times been outcompeted, though it may form monodominant stands, due to several competitive features.

[†]Nomenclature of vascular plants follows Kew Plants of the World Online https://powo.science.kew.org.

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4. Formerly widespread in Europe, *T. natans* is today recognized as a rare, strictly protected macrophyte. It has been introduced to Australia and North America; on the latter continent, its naturalization, spread and aggressive overgrowth have led to extensive control efforts. Having been used as a crop since Neolithic times, it is still exploited in Asia for means of food production, phytoremediation, ornamental purposes, medication and alternative uses.

KEYWORDS
biotic interactions, communities, conservation and control, geographical and altitudinal distribution, habitat, taxonomy, utilization, vegetative and reproductive characters

Water caltrop, or water chestnut. Lythraceae, Myrtales. *Trapa natans* L. is an annual herbaceous sediment-rooted hydrophyte that develops a buoyant leaf rosette at the water surface.

Stem submerged, slender (diameter, 1–6 mm), thread-like, reaching from the bottom of the water body to its surface, length 50–200 (500) cm, stem unbranched or branched with 2–14 branches, each terminating in a buoyant leaf rosette (diameter, 15–50 cm) at the water surface. Leaves dimorphic. Submerged leaves opposite, sessile, linear, entire, caducous (20–30 mm in length, 2–2.5 mm in width; Nedukha & Kitten, 2012), replaced by unbranched adventitious roots and paired or whorled, pinnately branched, adventitious structures emerging at leaf scars (diversely referred to as leaves or roots in anatomical studies). Buoyant leaves alternate in terminal rosettes, leathery, with blades rhombic to deltoid (c. long as wide: 4–5 (6.5) cm long; 3.5–6 (8) cm wide), bases broadly cuneate or nearly truncate, entire, margins ± irregularly toothed distally, glossy dark green and glabrous adaxially, light green and glabrous or pubescent abaxially. Rosette leaf petiole up to 21 cm in length, c. 1–4 times as long as blade (leaf including petiole 7–29 cm long), pubescent, often inflated halfway into an ellipsoidal swelling.

Flowers bisexual, actinomorphic (radially symmetric), solitary in rosette leaf axils, flowering at the water surface, peduncles pubescent. Sepals 4, valvate, lanceolate to slim triangular, stiff, externally keeled and usually felted hairy, persistent as 2, 3 or 4 hardened, thorn-like horns in fruit. Petals 4, white to lilac or pink, obovate, 7–10 mm long, caducous. Stamens 4, antesepalous, anthers introrse, versatile. Ovary semi-inferior, 2-locular; ovules anatropous, pendulous, with axile placentation, one per locule, only one developed after anthesis. Pistil 1. Style, subulate. Stigma capitate, caducous. Fruit a single-seeded drupe, turbinate to short-rhombic, (0-)2-4-spined, spines broadly conic, recurved, flat triangular or horizontal, ascending, spine apex with sharp, retrorse barbs, fruit apex with dome-shaped or rounded to tetragonal crown, seldom crownless, crown apex a tuft of hairs or conic beak, exocarp ephemeral, succulent, endocarp blackish-brown, stony (Caspar & Krausch, 1981; Chen et al., 2007; Cook, 1990; Muenscher, 1944; Tutin et al., 1968).

Trapa natans was first described by Linné (1753). The generic name '*Trapa*' originates from *calcitrapa*, the Latin term for caltrop, an iron instrument equipped with spikes that was used in warfare as an area denial weapon, which resembles the distinctively horned water caltrop fruits. The specific name '*natans*' is based on the Latin word for floating, which depicts the buoyant life form of the water caltrop (Borojevic, 2009; Brown, 1880). Since its scientific description, extensive efforts have been made to adequately integrate the water caltrop into the taxonomic system (see Section 10.1). After a long-standing debate, *Trapa* is now a member of the Lythraceae family, classified in the order Myrtales (Graham et al., 1998, 2005; Sun et al., 2020; The Angiosperm Phylogeny Group, 1998). Despite ongoing confusion regarding species delimitation (see Section 10.1), the World Checklist of Vascular Plants (WCVP, 2023) currently accepts *Trapa* as a genus that encompasses eight species, namely *T. assamica* Wójcicki, *T. hankensis* Pshenn, *T. hyrcana* Woronow, *T. incisa* Siebold & Zucc., *T. kashmirensis* Wójcicki, *T. kozhevnikoviorum* Pshenn, *T. natans* L. and *T. nedoluzhkoi* Pshenn (synonyms in Table S1). Among these species, *T. natans* is the only species recognized as polymorphic, consisting of eight varieties, namely *T. natans* var. *natans*, *T. natans* var. *bispinosa* (Roxb.) Makino, *T. natans* var. *pseudincisa* (Nakai) ined., *T. natans* var. *quadricaudata* (Glück) B. Y. Ding & X. F. Jin, *T. natans* var. *magnicorona* (Z. T. Xiong) B. Y. Ding & X. F. Jin, *T. natans* var. *africana* Brenan, *T. natans* var. *japonica* Nakai and *T. natans* var. *quadrispinosa* (Roxb.) Makino. Several homo- and heterotypic synonyms have been classified into the currently accepted scientific variety names (Table S2; WFO, 2024). The accepted species and varieties vary in their vegetative features, such as leaf shape and size, as well as reproductive structures, such as flower colour, fruit shape and size, beak shape and height, crown shape and size, and horn number, position, size and shape (Chen et al., 2007; Ding & Jin, 2020; Wójcicki, 2001). While commonly referred to as (European) water chestnut or water caltrop, *Trapa* is known by various English names such as bat nut, devil nut or bull's head. Additionally, diverse country-dependent vernacular names have been documented (Borojevic, 2009; Graham, 2013; Lim, 2013).

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Trapa is native to Europe, Africa and Asia, occurring in tropical, subtropical and temperate climates, in a disjunct manner (Figure 1; Caspar & Krausch, 1981; Dementeva & Petushkova, 2010;

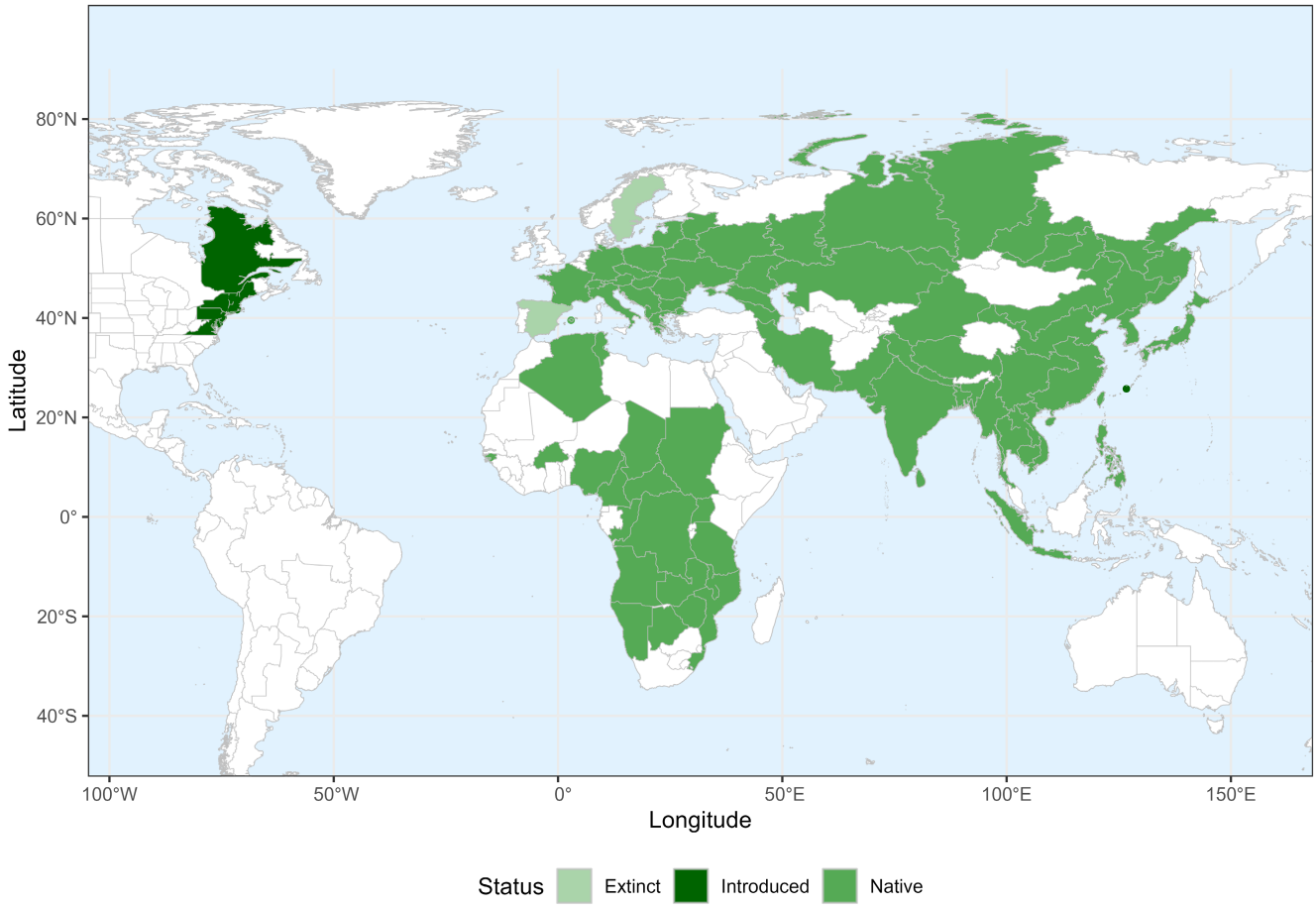


FIGURE 1 Global distribution of *Trapa* including its status as extinct (in light green), native (in green) or introduced (in dark green). Occurrence data were sourced from the World Checklist of Vascular Plants (WCVP) database (Govaerts et al., 2021), excluding doubtful records (Palm et al., 2024). Due to ambiguous taxonomy, the map was not created at the species- or infraspecific level. Geographic classification follows the International Working Group on Taxonomic Databases (TDWG) botanical country standard (Brummitt, 2001).

POWO, 2023; Samuelsson, 1934; Zhu, 2016). *T. assamica* is found in the wet tropical biome, from northeast India to Bangladesh. *T. incisa* grows primarily in the subtropical biome, occurring from northeast India to Far East Russia and temperate eastern Asia. *T. nedoluzhkoi*, *T. hankensis*, *T. kozhevnikoviorum*, *T. hyrcana* and *T. kashmirensis* grow primarily in the temperate biome. The former three are native to southern Far East Russia, *T. hyrcana* occurs in southwestern Russia, and *T. kashmirensis* is found in the western Himalayas. The native range of *T. natans* is in Eurasia and northwest Africa, whereas five out of the eight accepted infraspecifics of *T. natans* grow primarily in the temperate biome. The variety *T. natans* var. *natans* is widely found in Eurasia and northwest Africa. The native range of the variety *T. natans* var. *magnicorona* spans Far East Russia to China and Japan. Similarly, *T. natans* var. *pseudincisa* is distributed in the southern Far East of Russia, extending to China and Japan. *T. natans* var. *quadrispinosa* occurs from the Himalayas to Japan. *T. natans* var. *japonica* is native to Korea and Japan. *T. natans* var. *quadricaudata* is the only infraspecific recognized to grow in the subtropical biome, native to Cameroon, South Africa and southern Far East Russia to Indochina and Japan. Both *T. natans* var. *bispinosa* and *T. natans* var. *africana* grow primarily in the seasonally dry tropical biome. The former is native to tropical and southern Africa, as well as southern Russia continuing Far East to tropical Asia but has been introduced to the Ryukyu Islands. The latter occurs in eastern tropical Africa, specifically at Lake Victoria in Tanzania and Uganda. Throughout its native distribution area, the relationship between *Trapa* and humans varies. Within its native range, *T. natans* was once widespread, but is now a rare species of conservation priority in part of it, especially in Europe (see Sections 10.2 and 11.1). At the same time, it has a history of utilization in Asia and Europe reaching far back to Neolithic times and is still utilized as a multipurpose crop, for instance in India and China (see Section 10.4).

Outside its native range, the water caltrop has been recorded as a weed of the natural environment in Australia (Hummel & Kiviat, 2004; Mikulyuk & Nault, 2023; Randall, 2007) but is not currently known to be present there (Government of South Australia, 2021). The macrophyte has additionally been introduced to the northeastern United States (Figure 1). More specifically, *T. natans* var. *natans* was introduced, but it is now apparent that there was also a cryptic introduction, resembling *T. bispinosa* Roxb. var *iinumai* Nakano (accepted synonym unknown in Table S2; Chorak et al., 2019; Fan et al., 2024). Due to its aggressive growth habits

that cause negative ecological, social and economic consequences, the macrophyte is recognized as a noxious aquatic plant species and is managed with the help of various control methods in the United States (see Sections 10.3 and 11.2).

The water caltrop is commonly found in the lowlands (Hegi, 1926). Caspar and Krausch (1981) associate it with the planar-colline altitudinal zone in Central Europe, extending up to 600 m above sea level (m a.s.l.) in the southeastern Alps. It occasionally grows up to 700 m a.s.l.; for instance, it regularly occurred at the Großer Ursee in the Allgäu in Germany (Rösch et al., 2021). In south-western China, it occurs at even higher elevations of up to 2700 m a.s.l. (Chen et al., 2007) and in northern India, up to 3200 m a.s.l. (Zutschi et al., 1980).

2 | HABITAT

2.1 | Climatic and topographical limitations

The water caltrop commonly occupies shallow water bodies that rapidly warm up, indicating that it is a thermophilic macrophyte (meaning that it favours warm habitats with relatively high water temperature), having an Ellenberg indicator value (EIV) for temperature of 7 (Ahlqvist, 2007; Ellenberg et al., 1992). The thermal northern range of *Trapa* has been depicted to coincide with a limit where a daily maximum temperature of 22°C is exceeded for at least 63 summer days per year (Enquist, 1924 as cited in Apinis, 1967). Seed germination in spring requires a critical water temperature of 10–15°C and only when the water warms above 20°C for several months can the development of floral structures and fruits take place (Apinis, 1940 as cited in Apinis, 1967; Caspar & Krausch, 1981; Gams, 1927 as cited in Samuelsson, 1934; Karg, 2006; Kunii, 1988a; Kunii & Maeda, 1982). In addition to high spring and summer temperatures, the thermally favoured areas in which *Trapa* prevails also have a long vegetation period, characterized by a daily average air temperature of 10°C and above for at least 160 days per year (Caspar & Krausch, 1981). Climatic fluctuations, especially in temperature, have thus been detected to be a driving force of the water caltrop's occurrence dynamics (see Sections 10.2 and 11.1; Apinis, 1967; Karg, 2006). Increased precipitation events may have negatively impacted the distribution, as *Trapa* has been found to preferably occur in areas where rainfall is lowest, although this has only been reported in Lithuania (Vuorela & Aalto, 1982).

While the climatic preference of *T. natans* can greatly influence its distribution and abundance, the macrophyte has been observed to be rare in rather warm and dry conditions, but common in cooler, wetter climates (Rösch et al., 2021). This occurrence is contrary to the expected climatic pattern and appears to be caused by non-climatic drivers. In this context, alterations in habitat availability and local water body conditions (which may be indirectly affected by climatic conditions) have been discussed to have influenced *T. natans* occurrence dynamics (see Sections 2.2 and 5.2; Apinis, 1967; Korhola & Tikkanen, 1997; Rösch et al., 2021; Samuelsson, 1934; Vuorela & Aalto, 1982).

2.2 | Substratum

Naturally (when referring to EIV for moisture of 11), the major factor governing the distribution of *T. natans* is the availability of suitable water bodies. The confinement of the water caltrop in freshwater basins may be attributed to its sensitivity to salinity since it is not present in water bodies in which the sodium chloride concentration surpasses 0.1%, as reflected in the EIV for salt of 0 (Apinis, 1967; Ellenberg et al., 1992; Hoque, 2005; Hoque et al., 2009; Hoque & Arima, 2000; Lewandowska et al., 2019; Nishihiro et al., 2014; Vuorela & Aalto, 1982). The water caltrop predominates in shallow water bodies, typically ranging from 0.2 to 3 m depth (Apinis, 1967; Caspar & Krausch, 1981; Countryman, 1978; Dementeva & Petushkova, 2010; Hegi, 1926; Hummel & Kiviat, 2004; Karg, 2006; Korte et al., 2010; Marinova et al., 2013; Marković et al., 2015; Mikulyuk & Nault, 2009; Papastergiadou & Babalonas, 1993; Samuelsson, 1934; Yuan et al., 2021; Zervas et al., 2020). It is commonly found in protected and sheltered, still or slowly flowing water bodies (such as lakes, ponds, river reaches and estuaries) with low-velocity flows and steady water levels (i.e. those with reduced hydrodynamic energy level), whereas strong winds and harsh seasonal water level fluctuations (e.g. due to flood events) have been discussed as reasons for its rarity (Ahlqvist, 2007; Apinis, 1967; Bolender & Kaplan, 1979; Brown, 1880; Countryman, 1970; Gaillard & Birks, 2007; Hummel & Kiviat, 2004; Kiviat & Beecher, 1991; Lansdown, 2019; Marinova et al., 2013; Mikhaylova, Artyukhin, Panfilova, et al., 2021; Rösch et al., 2021; Tolar et al., 2011; Villa et al., 2018). *Trapa*'s floating strategy in combination with loose rooting in the sediment may be disadvantageous during heavy storms or wind, strong water currents and wave action since the vegetation layer covering the water surface can be disrupted or destroyed and stands are vulnerable to being washed out (Kunii, 1988b; Nohara, 1991, 1993). However, at times, *Trapa* may tolerate stronger fluctuations in water level, higher flow rates, wave action and wind exposure (Caspar & Krausch, 1981; Dementeva & Petushkova, 2010; Džigurski et al., 2013; Schneider-Binder, 2021). Interestingly, *T. natans* stands may reduce current velocity and wave amplitude, which may calm waters in adjoining, otherwise unsuitable areas, as stand density increases, sufficiently modifying hydrodynamics to enable the population to slowly expand further across the embayment (Kiviat, 1993; Powles, 2006).

The bottoms of inhabited water bodies can be mineral-based, consisting of a saturated clay-silt, sand or mud, meaning a soft substrate, for instance, containing an average of 44% sand, 43% silt and 14% clay (Ahlqvist, 2007; Hummel & Kiviat, 2004; Klosowski & Tomaszewicz, 1996; Strayer et al., 2003). However, *Trapa* has often been found in humus-rich *gyttja* deposits (Apinis, 1967; Kowalski et al., 2018), and substrates usually have a high organic matter content

(Apinis, 1967; Vuorela & Aalto, 1982). The vegetative material from the water caltrop that is abscised throughout the growing season and at senescence accumulates over time, enriching the total organic matter pool (Findlay et al., 1990; Naylor, 2003). This decomposing water caltrop detritus rapidly releases high amounts of dissolved organic and inorganic nutrients (e.g. c. 42% of nitrogen and 70% of phosphorus within 2 weeks) into the water column, allowing efficient mobilized nutrient recycling, which promotes the ongoing expansion of the water caltrop plants during the rest of the vegetation period and in subsequent ones (Dementeva & Petushkova, 2010; Findlay et al., 1990; James et al., 2002; Li, 2004 as cited in Li et al., 2010; Park & Cho, 2003; Powles, 2006; Singhal & Saraf, 2000). Despite the adverse effects of turbidity on *Trapa* productivity, the waters in which the water caltrop flourishes may have diverse sediment loads, reaching from clear, poorly loaded to richly loaded, turbid waters on muddy ground (Korhola & Tikkanen, 1997; Schneider-Binder, 2021). Compared with submerged plants, the floating-leaved nature of *T. natans* mitigates the adverse effects of turbidity on its phytomass (Kiviat & Beecher, 1991). Nevertheless, the macrophyte is restricted to lower water levels in turbid and sediment-rich waters (e.g. in lakes with high humus content and brown colour) due to reduced light penetration, whereas, in clear, sediment-poor waters, greater light availability allows colonization of greater water depths (Vuorela & Aalto, 1982).

Generally, *Trapa* appears to occur along a wide spectrum of nutrient availability (Vuorela & Aalto, 1982), with total phosphorus concentration ranging from 0.03 to 0.3 mg/L, and total nitrogen concentration ranging from 0.4 to 4.0 mg/L (Takamura et al., 2003). Several authors, however, note that *Trapa* with an EIV for nutrient availability of 8 occurs more frequently in nutrient-rich and very nutrient-rich, meaning eutrophic and hypereutrophic, habitats than in those of moderate, that is, mesotrophic, fertility and is only rarely found under both oligotrophic and hyper-oligotrophic nutrient-poor circumstances (Ellenberg et al., 1992; Kurihara & Ikusima, 1991; Papastergiadou & Babalonas, 1993; Samuelsson, 1934; Vuorela & Aalto, 1982). The higher temperatures in the commonly inhabited shallow sheltered water bodies (see Section 2.1) may contribute to the favoured high nutrient environment, due to increased microorganism activity (Vuorela & Aalto, 1982). The EIV for soil reaction for *T. natans* in Central Europe is 6, suggesting a preference for weakly acidic to weakly basic conditions (Ellenberg et al., 1992). Accordingly, a pH amplitude of 6.7–8.7 has been suggested (Erkamo et al., 1960; Mikhaylova, Artyukhin, Panfilova, et al., 2021; Walter, 1954 and Walter & Straka, 1970 as cited in Vuorela & Aalto, 1982). The macrophyte also appears to be disturbance tolerant (Mikulyuk & Nault, 2009). Though the water caltrop primarily grows in unpolluted surroundings, it does not appear to suffer from heavy metal pollution, raised pH or increased nutrient levels (Baruah et al., 2021; Kurihara & Ikusima, 1991; Lansdown, 2019). Consequently, it may occur in moderately contaminated water bodies and some studies suggest that it can even thrive in environments with domestic sewage input (Chandra et al., 2013; Countryman, 1970). Relatedly, the establishment of waste treatment facilities in watersheds appears to have led to improved water quality, leading to a considerable decline in the number of *Trapa* plants in recent years (Chandra et al., 2013; Countryman, 1970). However, it does disappear with overly strong pollution (Caspar & Krausch, 1981). In summary, findings suggest that in addition to favourable climatic conditions (see Section 2.1), the success of *T. natans* relies on the fulfilment of requirements related to local water body conditions, such as microclimate, hydrodynamics, edaphic factors and water quality (Apinis, 1967; Schofield & Bunting, 2005; Vuorela & Aalto, 1982).

3 | COMMUNITIES

According to European phytosociology, *T. natans* is typically part of aquatic plant communities associated with the Potametea Klika in Klika et Novak 1941 class (vegetation of bottom-rooted aquatic plants), Potametalia W. Koch 1926 order and Nymphaeion (albae) Oberdorfer 1957 alliance (vegetation of bottom-rooted aquatic plants with buoyant leaves on the water surface). Although it can also be found in thermophilic manifestations of Myriophyllo-Nupharetum and Nymphoidetum peltatae (Caspar & Krausch, 1981), the macrophyte is the diagnostic, constant, and dominant taxon and main indicator species of the Trapetum natantis Müller et Görs 1960 association (Lukash et al., 2021; Zervas et al., 2020). Within the phytocoenoses, additional floating-leaved species such as *Potamogeton natans*, *Nuphar lutea*, *Nymphaea alba*, *Salvinia natans*, *Marsilea quadrifolia* and duckweeds such as *Lemna minor* and *Spirodela polyrhiza* occur. Additionally, *L. trisulca* has been observed among fairly dense *Trapa* rosettes in the Danube Delta (Erik Kiviat, personal communication). Submerged hydrophytes such as *Ceratophyllum demersum* and *Myriophyllum spicatum* are also among the major companions of *T. natans* (Džigurski et al., 2013; Galanti et al., 1990; Klosowski & Tomaszewicz, 1996; Magnus, 2015; Nagl, 1966; Philippi, 1980; Vuorela & Aalto, 1982; Zervas et al., 2020). The respective macrophyte composition, as well as the number and distribution of the species within the association, can depend on prevalent parameters of water chemistry (e.g. nutrients, pH and alkalinity) and hydromorphological waterbody characteristics such as depth, width, flow rate and mode of water supply (Džigurski et al., 2013; Schneider-Binder, 2021). In phytocoenoses, *T. natans* achieves a projected cover of 30%–100% (Lukash et al., 2021), whereas seasonal changes in surface cover occur, leading to alterations in dominance (Kunii & Maeda, 1982). Generally, as compared to the other six nymphaeid associations, the Trapetum natantis Müller et Gors 1969 association is characterized by distinct habitat conditions and specific habitat requirements (Kočić et al., 2008; Kowalski et al., 2018; Szańkowski & Kłosowski, 1999). It thrives in relatively fertile, warm, closed water bodies with a favourable water level of 50–70 cm and a low flow rate, characterized by sandy or silty sediments often enriched with detritus with a slightly acidic, neutral or slightly alkaline reaction (Klosowski, 1995; Klosowski & Tomaszewicz, 1996; Lukash et al., 2021).

Similarly, in China and India, *Trapa* occurs among emergent and floating-leaved species such as *Nelumbo nucifera*, *Nymphoides peltata* and *Salvinia natans*, submerged hydrophytes such as *Najas minor*, *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Vallisneria natans*, *V. spiralis*, *Hydrilla verticillata*, *Stuckenia pectinata*, as well as several *Potamogeton* species such as *P. acutifolius*, *P. natans*, *P. maackianus*, *P. lucens* and *P. crispus* and the amphibious plant *Persicaria amphibia* (Dong et al., 2013; Unni, 1976; Yuan et al., 2021; Zutschi, 1975; Zutschi et al., 1980). In its non-native range, duckweeds (*Lemna minor*, *Spirodela polyrhiza* and *Wolfia* spp.) and filamentous algae grow among the *Trapa* rosettes that provide shelter from wind and currents (Kiviat, 1993; Kiviat & Beecher, 1991).

4 | RESPONSES TO BIOTIC FACTORS

Throughout its lifecycle, a set of competitive characteristics elicits the great competitiveness of the water caltrop (Kunii, 1988b; Les & Mehrhoff, 1999). Once *Trapa* has occupied a site with suitable prevailing environmental conditions, it can rapidly monopolize plant communities due to its high relative growth rate, rapid shoot elongation, greatly productive 'clonal' growth, and canopy formation (see Section 6), which allow it to cover large areas quickly. The optimally timed substantial investment in reproductive structures, that is large seed production, further allows for the maintenance of a high density population (see Sections 5.1 and 6.3; Groth et al., 1996; Kunii, 1988b; Les & Mehrhoff, 1999). The resulting large seedbanks contribute to stand stability and maintenance in combination with the well-protected successful seeds with high germination rates that favour establishment (see Sections 8.3 and 8.4; Groth et al., 1996; Kunii, 1988b; Kurihara & Ikusima, 1991; Monacelli & Wilcox, 2021; Nohara, 1993; Phartyal et al., 2018). *Trapa* seedling establishment further benefits from the production of large seeds with abundant food reserves, enabling them to reach the water surface under limited light availability at the bottom of the water body (Ahmad & Singh, 1998; Kunii, 1988b). Nevertheless, compared with other rooted macrophytes with rhizomes, *Trapa* seeds accumulate fewer reserve substances, possibly suggesting a reliance on high levels of inorganic nutrients to sustain the observed high growth rates, thus preferring eutrophic waters with organic-rich sediments (Bolpagni et al., 2006; Kunii, 1988b). An additional nutrient source for *Trapa* is provided by the decomposition of its own detritus and the consequent leaching of previously captured mineral nutrients (see Section 2.2). In this respect, *T. natans* has been identified to be an efficient nutrient sink (Bolpagni et al., 2006). The macrophyte obtains mineral nutrients from both the sediment and water column through its main absorbing organs (i.e. dimorphic leaves together with adventitious anchoring roots and photosynthetic pinnately dissected structures; see Section 6.1), thus effectively meeting its nutritional needs (Arima et al., 1988, 1990; Barko & Smart, 1981; Li et al., 2010).

Upon quickly reaching the water surface, the water caltrop's floating life form maximizes light interception, whereas its submerged photosynthetically active plant organs (linear leaves and pinnately dissected structures) capture the remaining subsurface irradiance (see Section 6.5.1; Figures 2 and 3a,g; Bornette & Puijalon, 2011). This highlights *Trapa*'s efficiency in utilizing light. At the same time, the macrophyte can act as an ecosystem engineer thanks to its growth form (Pierobon et al., 2010). In spring, when *Trapa* has not reached the water surface yet, atmospheric oxygen exchange is high and photosynthesis and respiration, both occurring in the water column, are close to balanced, resulting in unproblematic, relatively high O_2 concentrations (Goodwin et al., 2008). In summer however, under favourable conditions, the viable rosette leaf layers, together with senescent detached rosette leaves, and flowers and fruits at the terminal stem portion, make up 68% of total *Trapa* biomass and result in a dense, approximately 15 cm thick floating mat of 1575 g/m^2 dry mass covering 85%–100% of the water surface (Galanti et al., 1990; Hummel & Kiviat, 2004; Poudel et al., 2023). This mat serves as a physical barrier, reducing atmospheric gas exchange and water column mixing (for instance through wind action), which minimizes the quantity of atmospheric oxygen diffusing into the water column (Fleming & Dibble, 2015; Hummel & Findlay, 2006; Pierobon et al., 2010). Additionally, *T. natans* releases much of its oxygen produced in photosynthesis into the atmosphere, while its shaded submerged tissues have low photosynthetic rates but large respiratory demand, ultimately resulting in a highly negative difference between photosynthesis and respiration within the water column and thus high rates of oxygen depletion (Goodwin et al., 2008). The water caltrop also has a restricted capacity to transport gases to submerged tissues compared with other species such as *Nelumbo nucifera*, *Nuphar luteum*, *Nymphaea alba* and *Nymphoides peltata*, and radial oxygen loss is comparatively negligible (Caraco & Cole, 2002; Pierobon et al., 2010). Thus, oxygen transfer is insufficient to compensate for oxygen consumption (Pierobon et al., 2010). The evoked low oxygen conditions are aggravated under high plant densities, as soon as abundant detritus is produced when plants senesce and decompose in autumn (Findlay et al., 1990; Naylor, 2003). In addition, the mats may intercept 95% of incoming sunlight, depriving other competing photosynthetically active organisms located below of light, reducing primary production rate, impeding their development, outcompeting them by shading and hindering aeration (Cattaneo et al., 1998; Džigurski et al., 2013; Feldman, 2001; Groth et al., 1996; Hummel & Kiviat, 2004; Juget & Rostan, 1973; Pemberton, 2002; Pinardi et al., 2011; Strayer et al., 2003; Tall et al., 2011; Zhonghua et al., 2007). Ultimately, fibrous, slow-decaying plants are substituted by soft, rapid-decaying *Trapa* material (Kiviat, 1993). Because of these several direct and indirect effects of the water caltrop on oxygen metabolism, the water column and adjacent sediments in which it occurs are often exhausted of oxygen (Bolpagni et al., 2007; Cattaneo et al., 1998; Kunii & Maeda, 1982; Pinardi et al., 2011; Strayer et al., 2003). Hypoxia was thus more frequent in *T. natans* beds as compared with nearby beds of *Vallisneria americana*, and these may even become anoxic (Caraco & Cole, 2002). Together with concomitant alterations in water quality and sediment chemistry such as changes in redox-sensitive nutrient and metal cycling, the low dissolved oxygen concentrations may lead to increased CH_4 emissions, acidification (i.e. lower pH) or eutrophication (Bolpagni

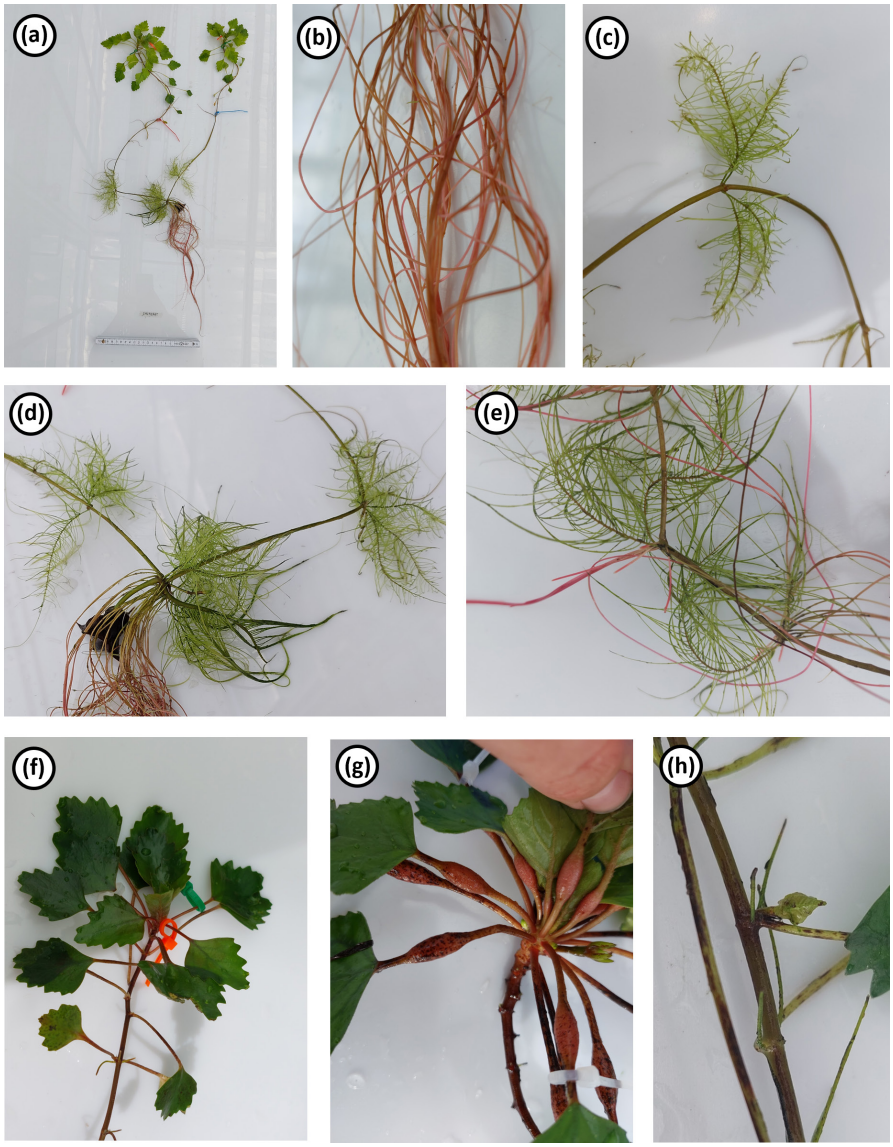


FIGURE 2 *Trapa natans* morphology. (a) Overview of the whole plant. (b–h) Close-ups of various features including: (b) Hypocotyl 'underground' roots. (c) Stem photosynthetic pinnately dissected structures. (d) Fruit with attached macrocotyledon petiole, hypocotyl with 'underground' and 'water' roots and base section of two primary stems with photosynthetic pinnately dissected structures. (e) Stem 'underground' roots and photosynthetic pinnately dissected structures. (f–g) Buoyant terminal leaf rosette with alternate leaves and swollen petioles. (h) Secondary stem emergence. Photographs by Anna Heisig and Natalie Palm.

et al., 2007; Caraco & Cole, 2002; Goodwin et al., 2008; Harrison et al., 2005; Kemp et al., 1990; Pierobon et al., 2010; Tall et al., 2011; Yuan et al., 2021).

Generally, the aquatic plant species can be found co-occurring with other hydrophilic plants in the typical communities (see Section 3). At times, more competitive hydrophytes may cause *Trapa* displacement due to their wide tolerance to multiple environmental conditions, rapid development as well as strong growth (Lewandowska et al., 2019; Villa et al., 2018; Yuan et al., 2021). For instance, some emergent- and floating-rooted aquatic plant species such as *Typha*, *Nuphar luteum*, *Nymphaea odorata* and *Nymphoides peltata* exert greater competitive pressure on the water caltrop than vice versa (Kiviat, 1993; Monacelli & Wilcox, 2021; Zhonghua et al., 2007). Additionally, algal blooms adversely impact *Trapa*'s development (Tsuchiya & Iwaki, 1979). At the same time, the water caltrop may be highly competitive. It has been observed to be the second most dominant macrophyte in a hierarchy of nine assessed floating-leaved and submerged plants (Kunii & Maeda, 1982). Under favourable conditions, submerged macrophytes such as *Potamogeton perfoliatus*, *Vallisneria americana* and *Myriophyllum spicatum* have been shaded out and substituted by water caltrop in many parts of the northeastern United States (Hummel & Kiviat, 2004; Kiviat, 1993). In their native range, vigorously growing *T. natans* stands have also contributed to the displacement of the weakly competitive *Marsilea quadrifolia*, which is threatened with extinction in Europe (Magnus, 2015; Nagl, 1966). Moreover, the water caltrop frequently forms monospecific stands (Lewandowska et al., 2019; Marković et al., 2015; Philippi, 1980; Pinardi et al., 2018; Schneider-Binder, 2021; Vuorela & Aalto, 1982). Usually, *T. natans* does not dominate an aquatic community during its initial growing season after colonization, but once its population is established, it can become strongly competitive (Monacelli & Wilcox, 2021). For instance, in Lake Champlain (Vermont/New York, USA; Quebec, Canada), a 10-fold enlargement in the total biomass of *T. natans* has been observed from 1 year to another (Bogucki et al., 1980). The transition of a varied aquatic flora to a virtual *Trapa* monoculture may take place relatively quickly within a period of 5 years (Groth et al., 1988 as cited in Groth et al., 1996). As a consequence, *Trapa*

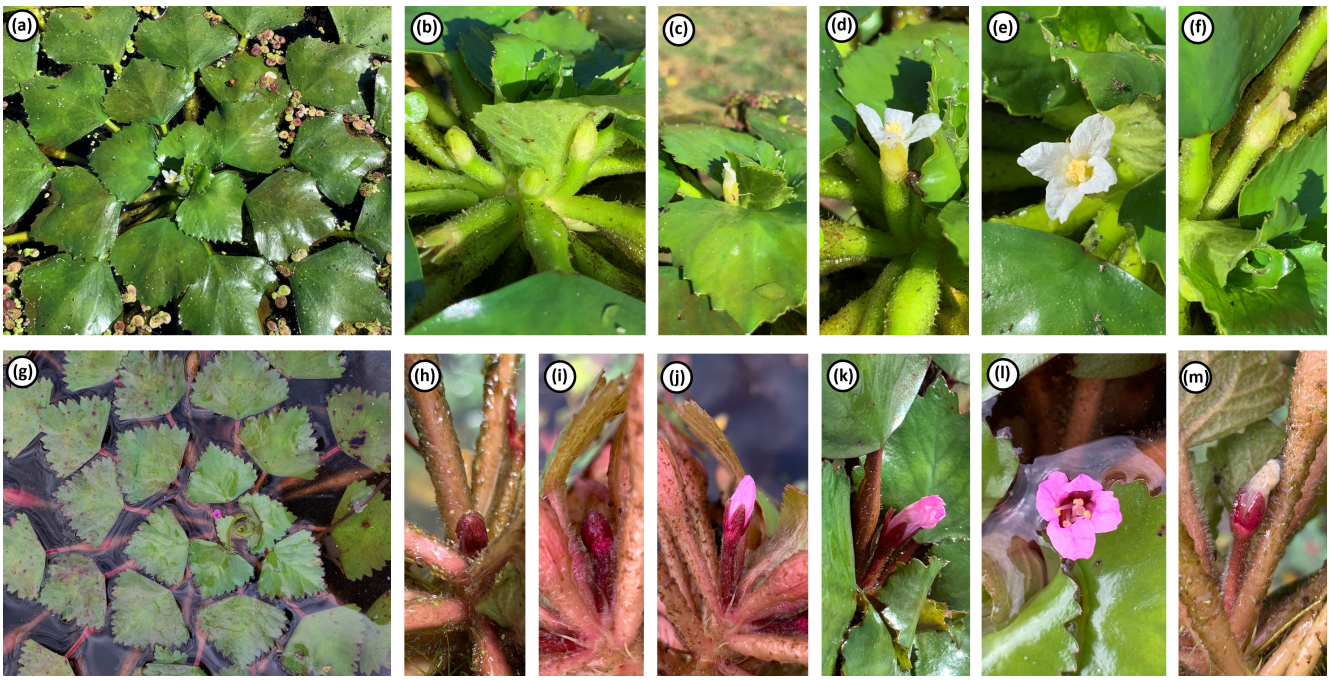


FIGURE 3 Flower development in *Trapa* for (a–f) German population of *T. natans* and (g–m) the *T. bispinosa* var. *iinumai* morphotype (accepted synonym unknown in Table S2) present in North America. (a, g) Flower in leaf rosette centre flowering above the water surface during anthesis. (b, h) Emerging flower buds visible. (b, i) Flower stalk extension. (c, j) Closed corolla visible. (d, e, k, l) Flower during anthesis. (f, m) Wilted flower. Photographs by Natalie Palm.

has not only been controlled in its non-native (see Section 11.2) but also in its native range, for instance, by means of occasional harvesting and cutting efforts (Pinardi et al., 2018; Yuan et al., 2021).

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

The water caltrop occurs in patches that may be small and isolated, or as large as 575 ha (Cattaneo et al., 1998; Countryman, 1978; Hummel & Findlay, 2006; Kiviat & Beecher, 1991; Marion & Paillisson, 2003; Nieder et al., 2004; Pinardi et al., 2021; Strayer et al., 2003). It is usually highly gregarious, with a tendency to build dense monospecific stands (see Sections 4 and 5.1; Countryman, 1978; Hegi, 1926; Schmeil & Fitschen, 2016; Villa et al., 2018). However, a study conducted at contrasting locations within Lower Lake (South Hadley, Massachusetts, USA) demonstrated that population density affects growth module demography. Specifically, water caltrop plants in initially low-density sites (5–15 ramets/m^2) produced 10 times as many clonal offshoots, that is ramets or rosettes, as those at sites with 104 ramets/m^2 initially (Groth et al., 1996). Kurihara and Ikusima (1991) additionally demonstrated that, compared with the highest, the lowest initial plant density treatment led to a 66-fold increase in branches per main stem. Accordingly, Galanti and Esposito (1996) discovered an inverse relationship between water caltrop density and single plant biomass, whereas a four times lower plant density led to a two to fourfold increase in plant rosette number, rather than an enlargement of rosette size or enhanced fruit production. Additionally, harvesting of *T. bispinosa* (syn. *T. natans* var. *bispinosa*, Table S2) to a remaining cover of 25%, has been seen to increase rosette number, suspend its decay phase and prolong its life cycle (Xu et al., 2014). Density-dependent rosette growth is also suggested by a negative correlation of rosette number per m^2 and total leaf dry mass per rosette towards the growing season end, suggesting upper limits and temporal declines in rosette density due to overcrowding (Kunii, 1988b). Altogether, these observations on intraspecific competition suggest a supremely proliferous clonal growth response under circumstances of low density. Together with the greater allocation of biomass to reproductive plant parts observed by Groth et al. (1988) as cited in Groth et al. (1996), propagule production is greatly enhanced at low initial density sites (Groth et al., 1996). Thus, *Trapa* may not only pre-empt the water surface early each year and cover large areas quickly but can also subsequently sustain a population at extremely high density, often occurring in very dense stands with 100–1575 g/m^2 dry mass (Findlay et al., 1990; Galanti & Romo, 1997; Groth et al., 1996; Hummel & Kiviat, 2004; Kiviat & Beecher, 1991; Strayer et al., 2003). This further explains the enormous capacity of *T. natans* to populate and monopolize an aquatic habitat, together with the factors explained in Section 4.

5.2 | Performance in various habitats

Phartyal et al. (2018) found that *T. natans* from Croatia has a wide germination niche, adequately coping with varying temperatures, oxygen

levels and light availability. Additionally, a study by Mikhaylova, Artyukhin, Panfilova, et al. (2021) in Russia, revealed a wide range of growth conditions related to water quality and regime such as water depth, salinity and pH, whereas *Trapa* showed resistance to sulphate salinization but sensitivity to low water temperatures and chlorides. These findings are supported by palaeobotanical investigations on *T. natans* in Finland as well as recent general *Trapa* distribution patterns, conveying a wide pH amplitude as well as a broad range of nutrient requirements (Alhonen, 1964; Erkamo et al., 1960 as cited in Vuorela & Aalto, 1982). A remote sensing study in Italy also demonstrated that *T. natans* can adapt to heterogeneous environmental circumstances and trophic levels within various subsystems of a water system, showing spatially the highest phenological intra-site variation concerning growing season onset and offset and seasonal growth peak, becoming dominant in most lakes, and constituting half of the total macrophyte area (Villa et al., 2018). Research in the Danube Delta further showed the broad ecological conditions in which *T. natans* may occur. There, it occurs in standing to slowly flowing, clear to turbid waters, showing especially large biomass and a high cover degree in inflow areas of water streams into lakes that carry sediment-rich water (Schneider-Binder, 2021). Concurrently, lake surveys show that its spread is mainly constrained by water level and current, bottom sediment composition as well as wind exposure (Dementeva & Petushkova, 2010). Despite habitat preferences (see Section 2), there is therefore an indication of a wide habitat amplitude of *T. natans*. Nevertheless, this still requires further deliberate comprehensive investigation, especially when taking into account potential variation in ecological requirements of different *Trapa* taxa (Gams, 1958 as cited in Vuorela & Aalto, 1982).

5.3 | Effect of frost, drought, fire etc.

While *Trapa* plants can endure short freezing intervals in the seed stage depending on exposure duration (see Section 8.4), young germinants with emerged hypocotyls exhibited high sensitivity to freezing, as they were unable to endure even a relatively low freezing temperature of −4°C (Phartyal et al., 2018). The diminishment of freezing tolerance from seed germination to hypocotyl emergence may reflect an ecological adaptation in terms of preserving the survivability of non-dormant, non-germinated seeds in cold or freezing water and optimizing young germinant viability by postponing germination until temperatures are sufficiently warm for establishment of seedlings (Phartyal et al., 2018). Mature plants are adversely affected by frost and plants can only continue to produce flowers and fruits until the first heavy frost kill (Hook, 1977; Madsen, 1990).

Due to their high desiccation sensitivity, *Trapa* seeds typically cannot survive in drying water bodies (see Section 8.4). Insufficient water depth caused by infilling (terrestrialization, silting) due to vegetation succession or increased evaporation and desiccation of water bodies as outcomes of climate change or hydrotechnical interventions (for instance, dyking, drainage and conversion of wetlands into agricultural domains and polders) can cause the decline of *Trapa* populations (Ahlqvist, 2007; Apinis, 1967; Jusik et al., 2023; Rösch et al., 2021; Schneider-Binder, 2021). This could be a reason for the scarce standing of this species in part of its native range (e.g. Russia and Europe), together with the fact that lakes and (fish) ponds therein are commonly drawn down and dried in the context of management (Phartyal et al., 2018). Nevertheless, *Trapa* seeds may persist if completely overlaid by a moist mud or silt layer, which may be the reason why they have been occasionally observed to overcome not only short-term but also long-term drainage for up to 20 years (Bolender & Kaplan, 1979; Hummel & Kiviat, 2004; Kunii, 1988a; Menegus et al., 1992; Muenscher, 1936; Phartyal et al., 2018; Zetter & Ferguson, 2001).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

6.1.1 | Stem

The water caltrop typically generates three main (or primary) stems that all emerge from the cotyledonary node (see Section 8.5; Figures 2a,d and 6; Arima et al., 1990; Groth et al., 1996). They are classified as the first, second and third main stem according to the order of emergence, having a fixed position of emergence (Arima et al., 1990). Whereas the first stem develops from the propagule apex, the second emerges on the side opposing the hypocotyl, and the third arises between the hypocotyl and the first stem (Groth et al., 1996). The primary stems may produce secondary stems (Figure 2h), which may, in turn, develop third-order stems capable of producing higher-order stems (Groth et al., 1996). A maximum branching order of five has been observed, though the higher-order stems may fall off during the growth process (Arima et al., 1990). The lower-order stems show the same growth pattern as the mother stem, normally emerging in the early flowering stage (Arima et al., 1990). Earlier-produced stems generally grow more vigorously and reach the water surface sooner than later-established ones (Arima et al., 1990). The great branching ability may mediate resilience to recurrent disturbances such as harvesting, as observed in *T. bispinosa* (syn. *T. natans* var. *bispinosa*, Table S2; Xu et al., 2014).

Nodes are formed at the stem apex in regular intervals throughout the growing period, although the node forming rate has been observed to be faster in higher (i.e. 1.5 nodes day^{-1}) compared with lower (i.e. 1.0 node day^{-1}) temperature periods (Arima et al., 1990). This may mediate adaptation to continuously varying environments, for instance to weather or water depth (Arima et al., 1990). The stems grow through internode elongation, with the length of the bottom internodes exceeding 30 cm and sometimes reaching 40 cm, and the elongation process is regulated by plant hormones such as gibberellin and ethylene (Arima et al., 1990; Kunii, 1988b). *Trapa* stem elongation rates are rapid, with a rate two to three times faster compared with a selection of submerged plants (Kunii, 1988b). The elongation rate is influenced by habitat conditions (Arima et al., 1990). For instance,

the extent and rate of shoot extension among different *Trapa* genotypes vary based on water level and its fluctuation (Nohara, 1991). A stem elongation rate of 2.6 cm day^{-1} has been observed for *T. natans* at Takahamari Bay by Nohara (1991), while it was 10 cm day^{-1} in Ojagaike Pond for *T. japonica* (syn. *T. natans* var. *bispinosa*, Table S2; Kunii, 1988b). The taxonomic descriptions mentioned above report a stem length of 0.5–2 m, with a maximum of 5 m, while other studies have reported it to exceed 6 m (Arima et al., 1990; Borojevic, 2009; Chowdhury et al., 2003; Kunii, 1988b; Nohara, 1993). Plant height positively correlated with water depth in different varieties, indicating the water caltrop's adaptability to increasing water levels and the ability to grow in water bodies where there is a chance of increasing water depth (Chowdhury et al., 2003). The stems may even extend beyond water column depth, enabling lateral spread of *Trapa* and mediating some range of motion in the event of water level fluctuations (e.g. in the context of flooding) and thus resilience to it (Nohara, 1991, 1993). Despite vulnerability to flooding, it thus has an intermediate flooding tolerance, lower than *Nymphoides peltata* but higher than that of *Nelumbo nucifera* (Nohara, 1991). The stem shows different growth patterns and fulfils distinct functions before and after the onset of flowering. During the vegetative stage, the water caltrop stems show elongation growth and successive branching, resulting in an increased number of rosettes rapidly reaching the water surface, consequently enlarging fruit number. During the reproductive stage, the stem thickens, offering greater support to the floating rosette with its larger leaves and accommodating fruit growth (Arima et al., 1990). The shoot apex may become four to five times as thick after the onset of flower production, while the stem was thin and weak before (Arima et al., 1990). Stem diameter usually ranges from 2.5 to 6 mm (Chen et al., 2007).

6.1.2 | Leaves

The water caltrop is characterized by heterophylly. Submerged, linear, sessile or stipulate leaves emerge from the nodes of the main stems and their branches during the initial phase of development (Nedukha & Kitten, 2012). These submerged leaves abscise at an early stage (Nedukha & Kordyum, 2016). Subsequently, structures emerge in oppositely borne pairs at the leaf scars along the stem, which are at first unbranched but soon become green-coloured, pinnately dissected structures (mean ± standard error: 53 ± 4.9 cm in long axis, 2.7 ± 0.3 cm in short axis, Figure 2c–e). The needle-like branches within these structures are up to 25 mm long (Nedukha & Kordyum, 2016). These structures are photosynthetically active, as they contain photosynthetic pigments such as chlorophyll, and assist in nutrient absorption and gas (e.g. oxygen) transport as they contain air space (Countryman, 1978; Groth et al., 1996; Hegi, 1926; Hoque et al., 2009; Tsuchiya & Iwaki, 1984). Nevertheless, the long-standing debate is still ongoing on whether these structures are submerged, feather-like leaves, which are typical for aquatic plant species (Bercu, 2004; Caraco & Cole, 2002; Countryman, 1978; Muenscher, 1944; Nedukha & Kitten, 2012; Nedukha & Kordyum, 2016; Wu & Wu, 2007) or adventitious roots that perform photosynthesis (Agrawal & Ram, 1995; Crow & Hellquist, 2006; Kuluev et al., 2018; Mikhaylova, Artyukhin, Musin, et al., 2021; Seago et al., 2016; Tsuchiya & Iwaki, 1984).

On the water surface, alternate floating leaves with rhomboid blades and coarsely toothed (serrate or dentate) margins form terminal buoyant rosettes (Figures 2f,g and 3a,g) sustained by inflated petioles, which entail aerenchyma (see Section 6.5.2; Brown, 1880; Crow & Hellquist, 2006; Jäggi, 1883). The diameter of the expansion, that is the 'swelling', of the cylindrical petiole in the middle, is 1.5–1.9 times greater than the diameter of the petiole on the base (Nedukha & Kitten, 2012; Figure 2g). Newly developed leaves emerge in the centre of the rosette and lean over previously produced floating leaves (Tsuchiya, 1991). Hence, several rosette leaf layers have been distinguished (Tsuchiya & Iwaki, 1984). Rosette diameter ranges from 10 to 40 cm (Suriyagoda et al., 2007). Rosette diameter increase throughout the growing season strongly correlates with air degree-days, water degree-days and calendar days, whereas calendar days had the strongest predictive power (Poudel et al., 2023). Each rosette contains approximately 15–40 leaves with seven leaves emerging weekly, that is new leaves appear continuously at a rate of about one per day, with a life span below a month, suggesting rapid leaf turnover (Kunii, 1988b; Suriyagoda et al., 2007). However, plants may have slightly differing leaf emergence rates according to the growth period, ranging from 1.1. to 1.5 and 0.8 leaves/day (Arima et al., 1990). Mean rosette area increases over time by 2.4% day^{-1}, starting at 40 cm^2 and reaching 441.9 cm^2 at season growth peak (Kunii, 1988b). An observed increase in leaf width-to-length ratio suggests that the form of floating leaves changes as they grow, more specifically, floating leaves are initially longer than wide and gradually become wider than long (Arima et al., 1990). In Europe, compared with *Nelumbo nucifera*, a species known to dominate *T. natans* (Kunii & Maeda, 1982), and another non-native, emergent-perennial species named *Ludwigia hexapetala*, the native floating-leaved *T. natans* has been found to have a lower leaf area index (LAI) (Pinardi et al., 2018; Villa et al., 2018). LAI also varied seasonally in *T. natans* in several European freshwater bodies according to local ecological and hydrological conditions (Villa et al., 2018), while another study showed LAI to be unaffected by hydro-meteorological variables (Pinardi et al., 2018).

As for other macrophytes with a floating-leaved nature, stomata are only present in the upper epidermis of floating leaves (i.e. adaxial surface) and none on the abaxial surface (Nedukha & Kitten, 2012). The submerged leaves and photosynthetic pinnately dissected structures are characterized by an absence of stomata (Bercu, 2004; Nedukha & Kitten, 2012; Nedukha & Kordyum, 2016). The stomatal width was reported to be 8.05 µm, while the highest stomatal length was 17.43 µm. The stomatal pore length was 13.52 µm, whereas the maximum stomatal pore width was 5.16 µm (Gond et al., 2019). Stomata number ranges from 180 to 260 mm^{-2}, depending on leaf age (Arima et al., 1990).

6.1.3 | Roots

The water caltrop does not have a primary root system (Groth et al., 1996; Seago et al., 2016). When the spirally elongated hypocotyl is approximately 10 cm, around 150 roots emerge on its side, forming vertical rows elongating in all directions due to the twist of the hypocotyl. The roots demonstrate heterorhizy (i.e. root dimorphism), developing into two different root types (Figure 2d). First, naturally brown, dark purple or uncoloured 'underground' roots emerging from the basal part of the hypocotyl show positive geotropism, pierce the substrate when reaching the bottom, have a length of 40–50 cm, and sparsely give rise to secondary roots (Figure 2b). Secondly, green hairy 'water' roots containing chlorophyll emerge between the basal part and the end of the hypocotyl, show negative geotropism and are suspended in the water (Arima et al., 1990; Mikhaylova, Artyukhin, Musin, et al., 2021; Figure 2d). Their length depends on water depth (Arima et al., 1990).

Roots additionally emerge from the stem(s). The stem nodes may bear slender, long, unbranched white or violet roots with a length of 7.5–31 cm (Nedukha & Kordyum, 2016; Figure 2e). Although it has often been neglected in taxonomic descriptions (Caspar & Krausch, 1981; Chen et al., 2007; Cook, 1990), this root type has been termed 'anchoring' or 'underground' root in other morphological *Trapa* studies and exhibits a similar morphology and growth pattern compared with the hypocotyl 'underground' root (Arima et al., 1990). It mainly serves to absorb water and nutrients and provide anchorage, as observed in instances where it anchors decumbent stems at one or more spots in the sediment when the stems extend so much that the lower parts come into contact with the sediment (Agrawal & Ram, 1995; Arima et al., 1990; Groth et al., 1996; Kuluev et al., 2018; Muenscher, 1944). Besides this root type, as already mentioned above, submerged pinnately dissected, photosynthetically active structures that emerge from the stems (Figure 2c–e; resembling the hypocotyl 'water' root type described by Arima et al., 1990 and Mikhaylova, Artyukhin, Musin, et al., 2021) are discussed as a second type of root (Borojevic, 2009).

6.2 | Mycorrhiza

None reported.

6.3 | Perennation: Reproduction

Therophyte. In the latter part of the growing season, the water caltrop reproduces sexually, as flower development and fruit maturation take place (see Section 7; Huss et al., 2023). Upon maturity, the fruits are released from the rotting peduncle and sink to the sediment. The detached fruits of *T. natans* typically remain in the sediment over the winter season (Jäggi, 1883), meaning that *T. natans* overwinters by seed (Borojevic, 2009; Groth et al., 1996; Huss et al., 2023). The growth observed in each new season is entirely derived from the seeds of the annual macrophyte (Hook, 1977).

In the earlier part of the growing season, vegetative growth in terms of main stem emergence and development as well as further branching takes place (see Section 7; Groth et al., 1996). Following a definition of clonal growth for annual species, Groth et al. (1996) have acknowledged *Trapa* to be capable of extensive clonal propagation, since ramet succession increases the chances of a genetic individual (genet) for sexual reproduction as each newly cloned rosette may develop fruits and thus enhances the fertility of the genetic individual (Groth et al., 1996). However, between the end of the growth period and the first frost, the vegetative parts of the genet senesce and start to decompose (Arima et al., 1990; Countryman, 1978; Hummel & Kiviat, 2004). Some researchers have thus negated vegetative propagation in *Trapa*, as it does not enlarge the amount of genets within a population (Cook, 1987 as cited in Agrawal & Ram, 1995; Hoque et al., 2009; Les & Mehrhoff, 1999). Regardless, the processes of vegetative growth (ramet succession with rosettes) and sexual reproduction (biomass allocation to reproductive structures) are optimized as the level of direct competition between them is reduced through temporal segregation within an individual vegetation period (Groth et al., 1996).

6.4 | Chromosomes

In Europe, different chromosome numbers have been reported for *Trapa*. Specimens collected in Italy had two different chromosome numbers, $2n=36$ (original count made by Palmgren, 1943 but discounted as erroneous counting by Oginuma et al., 1996) and $2n=48$, with small chromosomes of c. 1 µm length (Tornadore et al., 2000). Populations in Southern Poland of *T. conocarpa*, *T. media*, *T. natans* and *T. muzzanensis* (all syn. for *T. natans* var. *natans*, Table S2) similarly had chromosome numbers of $2n=48$ but also $2n=40$ (Hoque et al., 2009; Oginuma et al., 1996). As $2n=40$ was found in only two out of eight studied localities, Oginuma et al. (1996) suggested it to be a cytotype. Also, *T. conocarpa*, *T. media*, *T. natans* and *T. muzzanensis* (all syn. for *T. natans* var. *natans*, Table S2) were attributed $2n=2x=48$ as chromosome number by Trela-Sawicka (1965) as cited in Hoque et al. (2009). After hybridization, polyploidy appears to be a relevant speciation process in water caltrop infraspecifics (Kim et al., 2010). Allozyme data have suggested the '*T. japonica*' group to comprise allopolyploid taxa ($2n=96$), originating from hybridization between members of the '*T. natans*' group (including *T. bispinosa*, syn. *T. natans* var. *bispinosa*, Table S2; $2n=48$) and *T. incisa* ($2n=48$; Takano & Kadono, 2005).

6.5 | Physiological data

6.5.1 | Solar irradiation and temperature

The water caltrop is adapted to moderately to full-sun-exposed sites, only exceptionally occurring at a relative illuminance lower than 40%

(i.e. EIV for light availability of 8; Ellenberg et al., 1992). *Trapa* may persist at the edges of patches covered by the emergent *Nelumbo nucifera*, however, shaded *Trapa* plants under *N. nucifera* cover have been observed to be smaller in size than unshaded plants (Kunii & Maeda, 1982). In Japan, with decreasing light availability, plant dry mass and total stem length gradually declined and at 99%–100% shading all plants showed chlorosis, although under 99.5% shading the pioneer stem was still initiated (Powles, 2006). Additionally, shading decelerated leaf canopy formation and first flowering time, thereby decreasing productive rosette number, total fruit weight and number as well as yield (Arima et al., 1992). Low irradiance may thus adversely affect the water caltrop's productivity.

Photosynthesis is conducted in different plant organs of *T. natans*. Several floating leaf layers (see Section 6.1.2) absorb incident sunlight, with the upper layer receiving full sunlight and the lower layers receiving sunlight passing through the upper layer(s) (Tsuchiya & Iwaki, 1984). The light-capturing rosette may not only expand horizontally (Figure 3a,g) but can also rise above the water surface and spread vertically, especially at the growing season peak in response to high density or crowded conditions, thereby forming emersed leaves (Arima et al., 1990; Kunii, 1988b). Below the water surface, the residual subsurface irradiance (solar radiation uncaptured by the rosette) may still be captured by *Trapa* based on the submerged linear leaves, and after their drop, by the photosynthetic pinnately dissected structures (Tsuchiya & Iwaki, 1984).

There is an indication that different photosynthetic systems exist within different organs of *Trapa* infraspecifics (Ishimaru et al., 1996). In Japan, the photosynthetic rate of buoyant leaves of *T. bispinosa* (syn. *T. natans* var. *bispinosa*, Table S2) increased as the water temperature rose to 40°C and the dark respiration rate rose to 40°C. Despite the relatively high optimal photosynthesis temperature compared with that of approximately 30°C normally observed in C_3 plants, the authors depict the buoyant rosette to exhibit leaf photosynthesis C_3-type attributes (Ishimaru et al., 1996). Different patterns were observed for the submerged photosynthetic pinnately dissected structures, whereas the authors emphasize that temperature differences of 3°C between the surface and the underwater may have influenced the photosynthetic characteristics. Their photosynthetic rate reached a maximum at 35°C and then slightly decreased at 40°C, while the maximum rate in dark respiration was observed at 30°C. Furthermore, increased activity in PEPCase and malate accumulation was detected at night, suggesting a type of photosynthesis that resembles that of CAM plants but for aquatic plants, named submerged photosynthesis (SUM). The authors conclude that C_3-type photosynthesis may occur in buoyant rosette leaves in the atmosphere while photosynthesis in submerged structures is characteristically that of the SUM type (Ishimaru et al., 1996). They imply that the plural photosynthetic systems may mediate the enhancement of biomass production efficiency in the water caltrop (Ishimaru et al., 1996). Nevertheless, compared with the buoyant rosette leaves, whose photosynthetic rate and thus relative importance increases throughout the growing season, the contribution of lower leaf layers in the rosette to total gross production is very small (1%–9% at the most), due to shading and submergence (Ishimaru et al., 1996; Tsuchiya & Iwaki, 1984). Also, the submerged photosynthetic pinnately dissected structures appear to have a negligibly small contribution to gross production, due to comparatively very low rates of gross photosynthesis that decrease throughout the growing season, with these rates never exceeding those of leaf respiration, even at light saturation, together with the very low light flux received below the water surface (Ishimaru et al., 1996; Tsuchiya & Iwaki, 1984). Collectively, photosynthesis primarily occurs at the water–atmosphere interface for floating-leaved plants such as *T. natans* which assimilate CO_2 mainly from the atmosphere, alongside inorganic carbon uptake from the water column (Goodwin et al., 2008; Nekrasova et al., 2003; Pierobon et al., 2010; Pinardi et al., 2011).

Seasonal variation in abiotic factors influences the photosynthetic pigment content of the buoyant foliage (Maksimović et al., 2020). Minimum chlorophyll content values were lowest at the end of the season in the ageing phase in October (0.252 mg/g FW) and in July (0.350 mg/g FW), while being largest in May throughout the active growth and development phase (0.604 mg/g FW) and in September (0.613 mg/g FW). Carotenoid level trends showed similar seasonal variation, although on average significantly lower. Abiotic drivers and plant adaptability to environmental conditions, including intensified light and temperature intensity in the summer period, appear to drive these observed patterns. Furthermore, in the submerged photosynthetic pinnately dissected structures, chlorophyll a and b content varied seasonally and increasingly differed from that in the buoyant foliage with growth, being 1.2–2.0 times lower in August compared with that in rosette leaves (Ishimaru et al., 1996).

6.5.2 | Aeration

The water caltrop may cope with poorly oxygenated conditions (i.e. hypoxic or even anoxic), which can be common in the water bodies it inhabits (see Section 4; Menegus et al., 1992). An experimental study assessing the impact of oxygen level on the development and metabolism of *T. natans* revealed that seeds germinated, and seedlings displayed growth under hypoxic as well as anoxic circumstances. However, seedling development was restricted to hypocotyl and macrocotyledon petiole (see Section 8.3 for terminology) elongation as shoot buds remained quiescent until oxygen became available (Menegus et al., 1992). An alcoholic fermentation system sustained the anaerobic growth of *Trapa* seedlings, in which the ethanol fermentation rate amounted to 21.2 µmol ($g FW^{-1} h^{-1}$). In addition to the high ethanol synthesis rates, the highly anoxia-tolerant plants showed little carboxylic acid production when exposed to anoxia and lactate-to-succinate ratios below one, confirming the coupling of high alcoholic fermentation rates and little accumulation of lactate in highly anoxia-tolerant plant seedlings (Menegus et al., 1992).

As an adaptation to the submerged environment, *Trapa* additionally employs aerenchyma, that is large intercellular space that

facilitates internal gas exchange (Jung et al., 2008). The hypocotyl has nonexistent to minimal air space (Seago et al., 2016), but Jung et al. (2008) noted honeycomb aerenchyma formed via schizogeny in the adventitious roots and shoot of *Trapa*. Well-developed air cavities have also been found in the spongy tissue of floating leaf lamina and petioles (Brown, 1880; Nedukha & Kordyum, 2016), whereas the aerenchyma in the inflated as opposed to the thin region of the petioles enclosed larger irregular air chambers (Bercu, 2004). Seago et al. (2016) have found aerenchyma to arise not only by schizogeny but also by expansigeny, a process in which intercellular spaces grow into lacunae through cell division and cell expansion (Seago et al., 2005), for instance, in floating leaf laminae, petioles, roots, first stolon internodes and peduncles. Collectively, the authors emphasize the presence of air space in tissues close to the air–water interface.

6.5.3 | Mineral nutrition

Trapa growth in natural water bodies may be limited by nitrogen availability, as nitrogen flux has been shown to increase net production as well as rosette and leaf size, whereas the maximum biomass amounted to 487 g dry mass m^{-2} in the most nitrogen-enriched tank (Tsuchiya & Iwakuma, 1993). Interestingly, a 3-year study in Lake Grand-Lieu, France, showed that *Trapa* accumulated high levels of nitrogen (2.17%–3.10%) and phosphorus (0.330%–0.580%) annually, but plant nutrient stocks did not always reflect variation in external water nutrient loading, suggesting that nutrient-enriched sediments compensated for varying water nutrient input. This indicates that *Trapa* may not be limited by low water nutrient inflow (Marion & Paillisson, 2003). Bolpagni et al. (2006) additionally emphasized the importance of sediments as a significant nutrient source in small shallow water bodies with low nutrient levels in the water column, observing that large amounts of inorganic nitrogen and phosphorus assimilated by the water caltrop were of sedimentary origin. A study on *T. maximowiczii* (syn. *T. natans* var. *quadricaudata*, Table S2) in Lake Taihu, China by Li et al. (2010) showed that eutrophication of water (especially phosphorus) and nutrient accumulation in sediment both contribute to increased water caltrop productivity. More specifically, high water nitrogen and phosphorus concentrations increased plant dry mass, dry mass of anchoring roots and aquatic roots as well as rosette diameter, while water enrichment with phosphorus further enlarged plant dry mass and fruit number. Nutrient-rich sediment resulted in increased plant height, plant dry weight, aquatic and anchoring root dry weight and maximum rosette diameter (Li et al., 2010). A positive effect of sediment fertilization has also been observed by Bogucki et al. (1980) and Arima et al. (1992), whereas Li et al. (2010) suggest that increased water fertility may be less important compared with enlarged sediment nutrient availability. The collective findings emphasize the critical role of nutrient availability in both water and sediments in influencing water caltrop performance dynamics.

6.6 | Biochemical data

The water caltrop is of considerable human interest as a crop due to its biochemical attributes (Zhu, 2016). Starch is the major constituent of the *Trapa* fruit, amounting to more than 80% of kernel dry weight, which is why the water caltrop seed is much appreciated as a food source (Chiang et al., 2009; Karg, 2006; Zhu, 2016). As stated by the FAO/WHO standard, the water caltrop is also a reasonable protein source (Zhu, 2016). While Singh et al. (2010) have determined 1.87% of total protein content (wet basis), protein contents in kernels may reach around 4.4% in fresh fruit (Alfasane et al., 2011). Other studies certify the water caltrop to have 6%–7% protein content in kernels on a dry basis (Zhu, 2016), 10.80% in dry fruit (Alfasane et al., 2011) and 15%–20% proteins in air-dried kernels (Janković, 1973 as cited in Borojevic, 2009). Chiang et al. (2009) also observed that water caltrop varieties contain large quantities of amino acids, which proved to surpass the FAO/WHO reference, with Glu, Asp and Arg being the major amino acids, in descending order. Air-dried kernels contain around 7% fat (Janković, 1973 as cited in Borojevic, 2009), though according to Zhu (2016) and Singh et al. (2010), the water caltrop kernel is not a substantial lipid source, with lipid content being only 0.5%–0.6% (dry basis) and 0.36% (wet basis). Alfasane et al. (2011) detected 0.65% and 1.85% fat in fresh and dry fruit, reinforcing its significance as a dietary commodity. In addition, dried air kernel contains 3% sugars (Janković, 1973 as cited in Borojevic, 2009), while sugar amounts to 4.80%–5.63% on a wet basis (Babu & Dwivedi, 2012; Singh et al., 2010). Water caltrop fruit additionally has a high quantity of vitamins (such as vitamins A, B, C and E), (essential) minerals and ions (e.g. Ca, K, Na and Zn), dietary fibres and many other phytochemical compounds (Adkar et al., 2014; Zhu, 2016). Fresh and dried *T. bispinosa* (syn. *T. natans* var. *bispinosa*, Table S2) seeds contain 116 and 355 kcal of energy per 100 g, respectively (Alfasane et al., 2011). Nevertheless, the biochemical attributes of *T. natans* var. *bispinosa* plant fruit kernel appear to vary significantly when gathered in different sites (Babu & Dwivedi, 2012).

7 | PHENOLOGY

The water caltrop is an annual, completing its life cycle in 1 year (Groth et al., 1996). Across its range, the vegetative period, meaning the time between germination and decay, usually lasts from April/May to September/October, that is for 5–7 months (Apinis, 1967; Galanti et al., 1990; Poudel et al., 2023; Villa et al., 2018; Xu et al., 2014). The length of the vegetative growth period can vary from year to year within the same water body (Kunii, 1988b). In northern Italy, southern Germany and Japan, in early spring (late March to late April), when favourable conditions occur, the seeds break dormancy and germinate within 4–5 days (Karg, 2006; Kuluev et al., 2018), whereas the majority of seeds from Croatian populations germinates within the first week (Phartyal et al., 2018). Hypocotyl development as well

as stem succession and elongation take place until the submerged rosettes reach the water surface by mid-May to early June (Caspar & Krausch, 1981; Romo & Galanti, 1998; Villa et al., 2018). Submerged leaves on the stem are generally replaced after approximately 2 weeks by adventitious structures (Groth et al., 1996). Aquatic roots are well-grown by the onset of July, thereafter root and submerged stem biomass stay stable (Romo & Galanti, 1998). From the end of June until early September, plants attain high coverage, display maximum growth (e.g. in terms of rosette diameter) and seasonal above-water growth reaches its peak, with an observed LAI ranging from 0.95 to 2.3 $m^2 m^{-2}$ (Arima, Hoque, et al., 1999; Caspar & Krausch, 1981; Kiviat & Beecher, 1991; Kunii & Maeda, 1982; Pinardi et al., 2018; Poudel et al., 2023; Villa et al., 2018). Flowers are absent in the early growth period (Poudel et al., 2023). For instance, in Lake Upkankul in Russia, flowering was detected only after 40–45 days (Kuluev et al., 2018). Flowers of Central European, North American and Japanese populations usually bloom from June to September (Caspar & Krausch, 1981; Countryman, 1978; Karg, 2006; Kiviat, 1993; Kunii & Maeda, 1982). Fruits begin to appear around 1–2 weeks after flowers (Kuluev et al., 2018; Poudel et al., 2023), maturing a month after initiation (Countryman, 1978). Fruit development lasts from mid-July into October in Europe and the United States (Borojevic, 2009; Hummel & Kiviat, 2004; Huss et al., 2023; Kiviat, 1993; Seago et al., 2016). Mature fruits are then released from the peduncles when ripe and sink to the sediment (Karg, 2006). Flowers and fruits occur in various developmental stages and sizes simultaneously (Figures 3 and 4). Around late summer or autumn, rosette leaf colour already changes from green to purple-brown or red (Caspar & Krausch, 1981; Karg, 2006). *Trapa* canopy decays and the number of flowers and fruits per plant declines from September onwards, but both flowering and fructification may last until plant senescence in late fall (October to December), at the latest until frost completely disintegrates the vegetative matter (Countryman, 1978; Galanti et al., 1990; Hummel & Findlay, 2006; Huss et al., 2023; Kiviat, 1993; Kunii & Maeda, 1982; Poudel et al., 2023).

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Flower buds arise from axillary growth in young nodes close to the shoot apex, in the axils of younger leaves (Figure 3b,h; Arima, Daigoho, et al., 1999). They first emerge around 5 to 6 weeks after seed germination and the development of the inconspicuous flowers from buds takes c. 10–14 days (Boylen & Methé, 1991). The flower stalk extends gradually and then rapidly (Figure 3b,i) so that the bud comes into flowering above the water surface (Figure 3a,g). Solitary flowers with white or light pink petals, up to 1 cm in size (Figure 3c–e,j–l), are formed successively. Sepals are the first to develop, followed by stamens, petals and carpels (Sinjushin, 2018). While the taxonomic descriptions commonly recognize *Trapa* to have radially symmetric flowers, a recent revisit of floral structure and development by Sinjushin (2018) recognizes *Trapa* to have 'disymmetric' flowers with the formula $K_{(2+2)}C_4A_{2+2}G_{(2)}$. According to this study, the flowers consist of four valvate sepals in two dimerous whorls making up the calyx, four petals making up the corolla, four stamens arranged in two dimerous whorls and a semi-inferior ovary consisting of two completely fused carpels and a style with capitate stigma (Graham & Graham, 2014; Jäggi, 1883; Sinjushin, 2018).

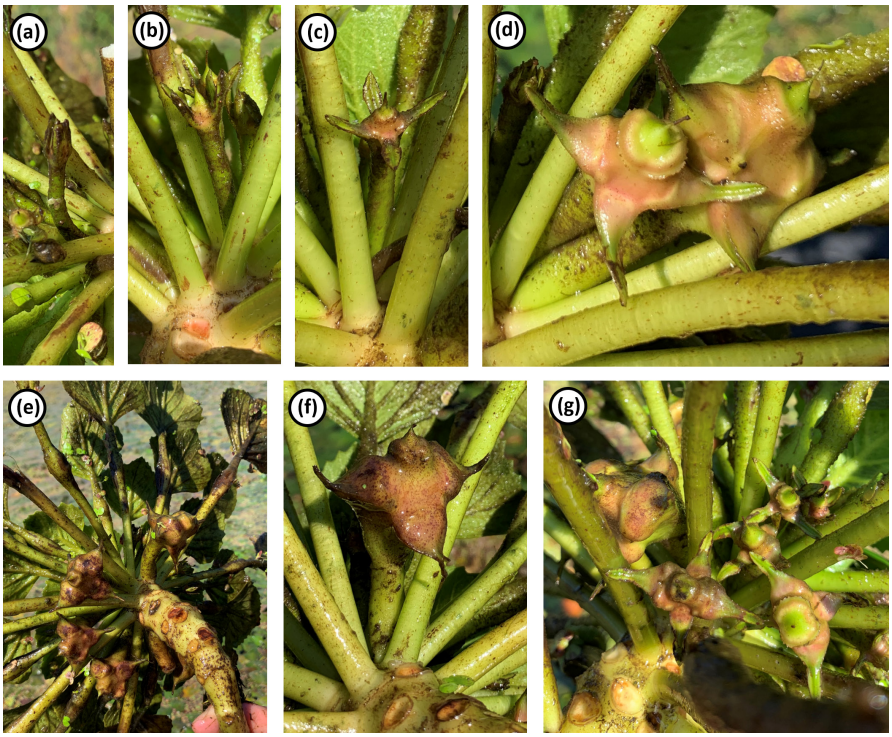


FIGURE 4 *Trapa* fructification succession in German population found in Rußheimer-Altrhein Elisabethenwört oxbow lake. (a–d) Sepal transitioning into horns and peduncle base thickening. (e–f) Darkened, ripe fruit(s) with intact exocarp attached to rosette underside through peduncles with scars of seceded peduncles or petioles along the upper stem. (g) Simultaneous presence of several successional stages of fructification. Photographs by Natalie Palm.

After remaining above the water surface during anthesis for a brief time period (approximately 24 h), the flower closes and the flower stalk bends down and submerges again (Figure 3f,m; Arima, Daigoho, et al., 1999; Karg, 2006). The number of flowers per plant correlates strongly with degree-days for both air and water and calendar days (Poudel et al., 2023).

Several insects visit *Trapa* flowers. However, pollination often occurs successfully even in emasculated buds and flowers excluded from alleged pollinators, suggesting the prevalence of self-pollination and possible apomixis (Kadono & Schneider, 1986). Entomophily thus appears to play a minor role, and insect visitors are only considered incidental pollinators, though they may assist with indirect autogamy when moving within the flower (Kadono & Schneider, 1986). The rather low amount of simultaneously blooming small ephemeral *Trapa* flowers with low merism (minimum number of organs) further hints towards a self-pollinating strategy, which is distinct from that of the closest *Trapa* relatives, which are tropical trees of the genera *Lagerstroemia*, *Sonneratia* and *Duabanga* that have cross-pollination adapted large, showy flowers (Sinjushin, 2018). Self-pollination thus appears to be the primary mode of reproduction and may be completed before the complete opening of petals, as the elongated filaments and anthers reach, touch and pollinate the capitate stigma (i.e. direct autogamy favoured by positioning and orientation of floral organs; Arima, Daigoho, et al., 1999; Kadono & Schneider, 1986). This ability would allow the water caltrop to self-pollinate when pollinators are scarce or not available (Arima, Daigoho, et al., 1999; Sinjushin, 2018), suggesting that the breeding system is an unlikely limiting factor concerning pollination (Razanajatovo et al., 2016; van Kleunen & Johnson, 2007). The dominance of self-pollination may contribute to the different fruit morphology patterns observed between *Trapa* populations (Kadono, 1987). However, a high degree of inbreeding has been reported as a consequence of autogamy in *Trapa* populations (Li et al., 2017). The researchers detected low levels of genetic diversity in *Trapa* taxa and explained it based on the annual life cycle that may convey reduced resilience to habitat deterioration because of genetic bottlenecks and inbreeding eroding the genetic diversity. Therefore, the water caltrop's evolutionary capacity to deal with constantly changing environments may be reduced (Li et al., 2017).

8.2 | Hybrids

Identifying and analysing hybridization among water caltrop taxa is a challenging task (Kim et al., 2010). Intermediate fruit forms between taxa varying in morphological parameters (e.g. horn number and shape) have been ascribed to frequent hybridization in the genus (Staszkiewicz & Wojcicki, 1978). However, taxonomic challenges arise owing to the restricted number of morphological diagnostic attributes (Kim et al., 2010). Hence, several studies additionally relied on studying genetic variation. Artyukhin et al. (2019a), Kim et al. (2010) and Takano and Kadono (2005) have provided information supporting the existence of intrageneric hybridization. For instance, the hybrid origin of *T. japonica* (syn. *T. natans* var. *bispinosa*, Table S2) as well as amphiploid taxa within the '*T. japonica*' group were revealed and *T. maximowiczii* (syn. *T. natans* var. *quadricaudata*, Table S2) plants have been found to potentially be hybrids. In contrast, based on a study of natural populations and a culture experiment, Nakano (1913) as cited in Kadono and Schneider (1986) doubted that apparent intermediate forms originated from hybridization. The contingent observation of cross-pollination (together with the main pollination mode of self-pollination and realizable apomixis), as observed in a study by Kadono and Schneider (1986), supports this view (Kadono, 1987). Additionally, despite obvious morphological differences in fruits, no instances of hybridization among *Trapa* taxa were detected in a recent study by Li et al. (2017), which was based on assessing the genetic relationship and diversity among *Trapa* taxa. However, the authors emphasize that observations so far are focused on only a few *Trapa* taxa. Therefore, additional analyses should be executed to comprehend the source of *Trapa* morphological diversity, incorporating the assessment of breeding systems of other *Trapa* taxa together with molecular methodology (Kadono & Schneider, 1986).

8.3 | Seed production and dispersal

Once the flowers are pollinated, the peduncle (i.e. flower stalk) bends downwards, the androecium and corolla abscise, one of two locules together with its ovule aborts, and the development of an unilocular, one-seeded fruit occurs below the water surface (Figure 4; Agrawal & Ram, 1995; Cook, 1990; Countryman, 1978; Hegi, 1926; Hummel & Kiviat, 2004; Kadono & Schneider, 1986; Les & Mehrhoff, 1999; Sinjushin, 2018; Zetter & Ferguson, 2001). The calyx persists, as the sepals fuse with the ovary at their base, harden and develop together with the ovary to the fruit (Jäggi, 1883). Though commonly referred to as a 'nut', the fully developed fruit is a drupe, which is exclusive to *Trapa* in the Lythraceae (Graham & Graham, 2014). Lacking a typical mesocarp (so far not documented in the existing literature), the drupe consists of a soft, fleshy, evanescent, short-lived exocarp that deteriorates over time to expose the endocarp (Borojevic, 2009; Groth et al., 1996; Huss et al., 2023). During endocarp maturation, substantial biochemical changes in terms of impregnation of cell walls with gallotannins and lignin elicit the dark-brown, hard and persistent features that enhance seed protection (Huss et al., 2023). The endocarp exhibits two lower spines (sometimes one or both nonexistent, commonly of a smaller size) developing from abaxial as well as adaxial sepals and two upper larger spines generated by lateral sepals, all armed with recurved barbs (Arima, Daigoho, et al., 1999; Borojevic, 2009; Frey et al., 2017; Huss et al., 2023; Jäggi, 1883; Powles, 2006; Sinjushin, 2018). The fruit apex may give rise to a short protrusion, also called 'crown', which may be more or less pronounced or not present at all (Chorak et al., 2019; Kadono, 1987). Its opening, also called terminal pore, or 'coronary disk' (Sinjushin, 2018), resulting from style abscission (Gleason & Cronquist, 1991), may be closed by a cover and a wreath of radially

arranged bristles (Jäggi, 1883). This adaptation to the aquatic environment allows for constant seed hydration in water, while facilitating outward movement of the radicle (see Section 8.5; Figure 6) and simultaneously restricting penetration of disruptive elements such as small soil particles into the fruit (Huss et al., 2023). Located within the endocarp, the mature seed (c. 1.0–2.0 cm long, 1.0–2.0 cm wide; Graham & Graham, 2014) lacks an endosperm but contains two unequal cotyledons (Borojevic, 2009; Ghosh, 1954; Tutin et al., 1968). One, large, starchy and functional, is withheld in the fruit, while its stalk, also called cotyledonary mid-piece or macrocotyledon petiole, protrudes from the fruit. The other, small, scale-like and abortive, arises from the fruit apex through the stylar canal pore as it is borne on the hypocotyl (Arima et al., 1990; Caspar & Krausch, 1981; Chen et al., 2007; Cook, 1990; Philomena & Shah, 1985). Fruit morphology strongly varies between *Trapa* infraspecifics. Fruits are c. 1.0–3.0 cm long, 1.0–5.0 cm wide and 0.5–3.0 cm thick (Kadono, 1987; Suriyagoda et al., 2007). The fresh weight of well-ripened fruits ranges from 0.9 to 11.2 g and the dry mass amounts to c. 2.1 g (Arima, Hoque, et al., 1999; Kiviat & Beecher, 1991). Intraspecific *Trapa* comparisons have demonstrated that each water caltrop plant may potentially generate up to 113 productive rosettes, and each rosette can produce up to 19 fruits (Suriyagoda et al., 2007). The propagule production rate is influenced by population dynamics based on prevalent environmental conditions (Powles, 2006). For instance, the number of fruits produced per plant strongly correlates with degree-days for both air and water and calendar days (Poudel et al., 2023).

Like other aquatic plants that produce few heavy seeds for adaptation to constant surroundings, where persistence is of greater importance than dispersal, *T. natans* does not rely on wind dispersal (anemochory). Instead, it produces fruits of a large size that are up to 20% denser than water (Cook, 1985; Hummel & Kiviat, 2004; Kunii, 1988b; Kurihara & Ikusima, 1991; Vuorela & Aalto, 1982). After having been released from the rotting peduncle of the adult plant at maturity, the detached fruits normally rapidly sink to the bottom of the sediment due to their weight and the dispersal distance is hence limited (Figure 5; Kadono, 1987; Kiviat, 1993; Les & Mehrhoff, 1999; Miki, 1952). Once the fruit has dropped to the bottom sediment, it is usually held in place and rarely detaches from the sediment again. However, water currents may be influential in this respect (Les & Mehrhoff, 1999). In lentic habitats, for example in the enclosed, disconnected water bodies with stagnant water that it commonly inhabits in Europe, seed dispersal through hydrochory may be restricted to areas close to parent plants (Kadono, 1987; Meschede, 1910; Nishihiro et al., 2014; Vuorela & Aalto, 1982), though fruit transport to other sites may be promoted by floods (Walusiak et al., 2024). In contrast, within lotic water bodies that are not enclosed, such as the slowly flowing waterways it commonly inhabits, detached seeds may spread along the direction of flow and can settle at sites far from the parent plant (Nishihiro et al., 2014). Additionally, buoyant rosettes with still attached nonmature fruits may be ripped out of the sediments completely or disconnected from their bottom part (Hook, 1977; Jäggi, 1883). There they may drift away downstream, being able to survive in a loosened, detached manner and even produce mature seeds on the way, dropping the fruits in other sites than those in which they were originally produced by their parent plants (Groth et al., 1996; Kiviat, 1993; Meschede, 1910).

Apart from short-distance transport through hydrochory, the propagules may be equipped for dispersal over longer distances (Kunii, 1988b; Powles, 2006; Schofield & Bunting, 2005). The barbed hooks of the propagule may serve as an adhesive device in animal dispersal, that is epizoochory, for instance, through attachment to feathers or fur (Frey et al., 2017; Kunii, 1988b; Nishihiro et al., 2014). Indeed, though sometimes extended transport by animals is regarded to be unlikely due to large fruit size and weight, as well as seed sensitivity to desiccation (see Section 8.4), the diaspores have

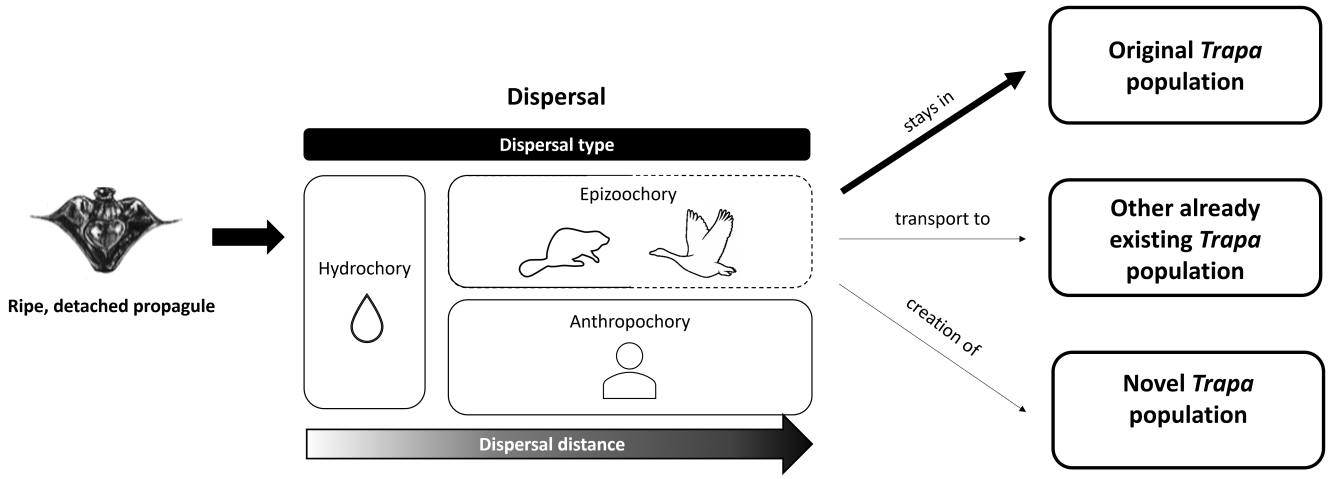


FIGURE 5 Multiple *Trapa* dispersal mechanisms together with associated transport distances and the resulting probability of *Trapa* propagules either remaining within the original population or being carried elsewhere, meaning to another already existing or new *Trapa* population.

been observed to be attached to plumage or fur of animals present in water bodies inhabited by the water caltrop (Cook, 1990; Jäggi, 1883; Les & Mehrhoff, 1999; Powles, 2006). Water-visiting birds (Baade et al., 1987; Karg, 2006; Kunii, 1988b) like ducks and geese (Kiviat, 1993; Poudel et al., 2023) or mammals like muskrats (Les & Mehrhoff, 1999), beavers (Brockmann-Jerosch, 1913; Flenley et al., 1975; Hegi, 1926; Karg, 2006) and otters (Karg, 2006) have been suggested to be relevant dispersal vectors (Theoharides & Dukes, 2007). Epizoochory thus appears to be a key mechanism for intermediate and long-distance dispersal. As has been observed for other aquatic plant species, megafauna extinction and low availability or lack of suitable epizoochoric dispersal agents have thus (partly) been suggested to explain the recent decrease in the size, number and extent of native *Trapa* populations (Barnosky, 2008; Flenley et al., 1975; Hegi, 1926). These restricted natural epizoochoric dispersal abilities, together with limited hydrochory, can hinder the introduction of fruits to water bodies outside the parent plant water body, limiting introduction to novel sites and the chance to exchange genes with other already existing populations, and may favour the persistence of diaspores in parent plant water bodies (Figure 5), which may be subject to significantly altering habitat conditions and hence may no longer prove to be suitable (Kadono, 1987; Meschede, 1910; Nishihiro et al., 2014). Nevertheless, scientific evidence for relevant epizoochoric dispersal agents and their efficacy in dispersing the water caltrop (e.g. quantification of the number of propagules dispersed) still needs to be provided to estimate whether and to what extent restoration of dispersal agents may promote *Trapa* conservation. Considering the great variability in the fruit morphological properties of different *Trapa* genotypes will allow a more accurate estimation of their dispersal success, as they may influence the attachment potential. This will enable us to further contribute to studies that have reported the natural dispersal abilities of *Trapa* to be limited and have attributed them to be responsible for the heterogeneous distribution of the floating-leaved plant (Nishihiro et al., 2014). Interestingly, in its non-native range in the northeastern United States, the rapid spread of *Trapa* has been suggested to be related to epizoochoric dispersal (Poudel et al., 2023), also warranting further studies in this respect.

Artificial dispersal by humans (anthropochory) may complement the natural dispersal mechanisms of the water caltrop as an intermediate and long-distance dispersal mechanism (Brockmann-Jerosch, 1913; Cook, 1985; Jäggi, 1883; Karg, 2006; Les & Mehrhoff, 1999), and there is wide speculation that its range was strongly influenced by its utility to humans (see Section 10.4; Gams, 1927 as cited in Frey et al., 2017; Hegi, 1926; Lansdown, 2019). For example, it has been proposed that the wide distribution in its native range during the Holocene was encouraged by people who cultivated it for use as food, medicine or as ornamental aquatic plant across Europe (Brockmann-Jerosch, 1913; Karg, 2006; Pemberton, 1999; Renfrew, 1973). Abandonment of anthropogenic use of *Trapa* may have reduced the likelihood of deliberate anthropochory, and also the unintentional long-distance diaspore transport as people came less and less in contact with the aquatic plant species (Brockmann-Jerosch, 1913; Flenley et al., 1975; Frey et al., 2017; Hegi, 1926; Jäggi, 1883; Roman & Darling, 2007). Additionally, *T. natans* was deliberately anthropogenically introduced to North America, initiating its non-native range expansion (see Sections 10.3 and 11.2; Mikulyuk & Nault, 2009). There, unintentional anthropochory is not uncommon, as fruits can incidentally stick to human attire, outdoor recreation gear such as outboard motor propellers, nets, wooden boats and other vessels (Countryman, 1978; Hummel & Kiviat, 2004; Kiviat, 1993). Outreach and educational initiatives aim to raise public awareness regarding the unintentional and intentional movement of *Trapa* (Maryland Sea Grant College, 2002).

Collectively, the various *Trapa* dispersal mechanisms, namely hydrochory, epizoochory and anthropochory, are widely acknowledged. Nevertheless, their specific contributions to the distribution pattern, for instance in terms of realistic transport distance and propagule transport frequency, remain inadequately investigated, making it difficult to estimate the extent to which propagules remain in their original population or are being transported to another already existing or new *Trapa* population. Further studies on *Trapa* dispersal are thus justified, especially concerning propagule characteristics in this context, to fully understand the contrasting occurrence trends observed between its native and non-native range.

8.4 | Viability of seeds: Germination

Non-dormant (i.e. dormancy broken through cold stratification but not germinating) *T. natans* seeds are desiccation sensitive and fail to withstand even a short drying period (~36 h) as they are subsequently not capable of germination (Phartyal et al., 2018). Though the majority of aquatic macrophytes have been characterized to have orthodox, that is desiccation tolerant, seeds (Hay et al., 2000), the seeds of *T. natans* have thus been seen to be recalcitrant in terms of their desiccation sensitivity (Martin & Uhler, 1939 as cited in Les & Mehrhoff, 1999; Muenscher, 1936; Phartyal et al., 2018). The existence of the terminal pore likely accelerates the drying process of the seed once situated outside of water (Huss et al., 2023).

The seeds of *T. natans* collected in Croatia have been further shown to be recalcitrant of temperate origin, meaning that they tolerated storage temperatures below 5°C in an experimental study (Phartyal et al., 2018). Specifically, short exposure (c. 24 h) to freezing temperatures as low as −12°C was not lethal and did not lead to a marked reduction in seed viability (Phartyal et al., 2018). The authors emphasize that it still needs to be revealed whether seeds of (sub-) tropical origin are equally sensitive to low temperature and drying out or whether they differ in this respect (Phartyal et al., 2018). Strikingly, non-dormant water caltrop fruits stored at a freezing temperature in water for 35 days have been found to not germinate at all and lose complete viability (Rector et al., 2015). Together with the finding that seeds under simulated drawdown subjected to a fluctuating refrigerating/freezing temperature persisted well (>70%;

Rector et al., 2015), these observations indicate a seed's capacity to tolerate freezing, dependent on the duration of exposure (Phartyal et al., 2018).

Seeds require a minimum period of 9–30 weeks of cold moist stratification (while overwintering in the sediment of the water body), then usually break dormancy in the spring season (in April and May), under normal spring daylength conditions, once water temperatures reach 10°C or warmer, as the rotting of the bristle-bordered terminal fruit pore is initiated and the seed germinates; the seed begins to germinate within 4 weeks (Apinis, 1967; Countryman, 1978; Cozza et al., 1994; Galanti et al., 1990; Kunii, 1988a; Kurihara & Ikusima, 1991; Madsen, 1990; Mazumdar, 1985; Mikhaylova, Artyukhin, Panfilova, et al., 2021; Muenscher, 1936, 1944; Phartyal et al., 2018; Vuorela & Aalto, 1982). Under laboratory conditions, the maximum or final germination rate was not affected by temperature, but, at warmer temperatures, seed germination was more synchronized and occurred more quickly (Kurihara & Ikusima, 1991). Generally, seeds appear to be capable of germinating under the broad range of environmental conditions to which they are exposed in their aquatic habitat, such as light and darkness, constant and alternating temperature, as well as oxic and hypoxia (Phartyal et al., 2018). Although the seeds are highly sensitive to desiccation, the broad distribution range may be ascribed to the wide seed germination niche of the aquatic species (Phartyal et al., 2018). Uniform and high seed germination of 80%–100%, coupled with the abundant seed set (see Section 8.3), significantly enhances the potential for *T. natans* to establish at one location (Galanti et al., 1990; Kurihara & Ikusima, 1991; Madsen, 1990; Phartyal et al., 2018).

Interestingly, while a certain number of seeds break dormancy and germinate in the spring following fruit production, and most seeds germinate within the first 2 years, a fraction (17%–50%), remains dormant in the sediment for prolonged periods and accumulates over time and generates a persistent seed bank (Hoque et al., 2009; Kunii, 1988a; Methé et al., 1993; Nohara, 1993). Buried seed reserves have been rated as an essential adaptation for the maintenance of *T. natans* var. *japonica* stands and play an important role in population dynamics, contributing to the stability of stands in times in which disturbances (e.g. strong water current and wave action in the context of typhoons) are present (Kurihara & Ikusima, 1991). The maximum duration of seed dormancy has been reported variably in the literature. A dormancy of above 2 years was reported, potentially reaching 9 years or more (Kunii, 1988a; Uchida, 1973 as cited in Nohara, 1993). However, dormancies for a period of 10–50 years have been suggested by Hegi (1926) and Hummel and Kiviat (2004).

8.5 | Seedling morphology

Once the hypocotyl with a radicle at its tip has emerged from the pore at the fruit apex (Chen et al., 2007), it displays negative geotropism by bending upward in a spiral shape and becoming elongated. It is milk-white after emergence. It remains white in some cases but may also discolour and turn light green when it reaches a few centimetres in length, whereas, at the same time, the elongation slows down. When elongated to approximately 5 cm, the petiole of the macrocotyledon emerges from the pore and pushes up the hypocotyl through elongation. The deeper the water, the greater the length of the hypocotyl and macrocotyledon petiole (Arima et al., 1990; Miki, 1959; Philomena & Shah, 1985). The macrocotyledon petiole is connected to the hypocotyl by the cotyledonary node (Arima et al., 1990). The upper side of the node is covered by a lip-shaped, ligulate small cotyledon, that protects the stem(s) that will later emerge (Agrawal & Ram, 1995; Arima et al., 1990). The cotyledonary sheath borne at the tip of the macrocotyledon petiole provides further protection (Philomena & Shah, 1985). A prominent bulge grows underneath the small cotyledon at the cotyledonary node indicating the imminent development of the plumule (Agrawal & Ram, 1995; Muenscher, 1944). The small cotyledon curves upward and facilitates the emergence of the plumule (Agrawal & Ram, 1995). Hypocotyl curvature is initiated as the radicle becomes positively geotropic. A succession of second and third shoots takes place and roots showing heterorhizy develop around the hypocotyl (see Section 6.1). At the basal part of the hypocotyl, geotropic roots establish and grow in the soil, while the roots emerging from the part between the basal part and the end of the hypocotyl elongate towards the water surface (see Section 6.1.3; Arima et al., 1990; Mirani et al., 2012; Philomena & Shah, 1985). Seedling morphology is shown in Figure 6.

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

A geographic survey of natural enemies of *Trapa* conducted in northeast Asia and western Europe identified several insects that feed on the plant. Among the most damaging herbivores are two leaf beetles (Chrysomelidae) of the genus *Galerucella* (Pemberton, 1999). In Asia, *Galerucella birmanica* Jacoby feeds on the plant and is sometimes managed with insecticides by farmers wanting to protect their *Trapa* crop. In Europe and North America, *Galerucella nymphaeae* L. attacks *Trapa*. An undetermined species of *Galerucella* also appears to attack *Trapa* in Africa (Simmons & Blossey, 2023). Though *G. birmanica* and *G. nymphaeae* are very similar to each other in terms of the life cycle, appearance and feeding manner, whereas adults and larvae feed on the plant leaf lamina, they differ regarding their host specificity and damaging effect. Of the two, *G. birmanica* is a *Trapa* specialist and is currently being evaluated as a potential biological control agent for *Trapa* in North America (see Section 11.2; Simmons & Blossey, 2023). Additionally, two weevils (Curculionidae), *Nanophyes japonica* Roelofs and an unidentified *Nanophyes* species were observed to attack the floating petioles and leaf foliage, such that the leaf ageing process and weevil development appear to be synchronized, implying a strong specialization to the host compared with the other observed natural enemies. While these were found in Asia, adults, larvae and pupae of the

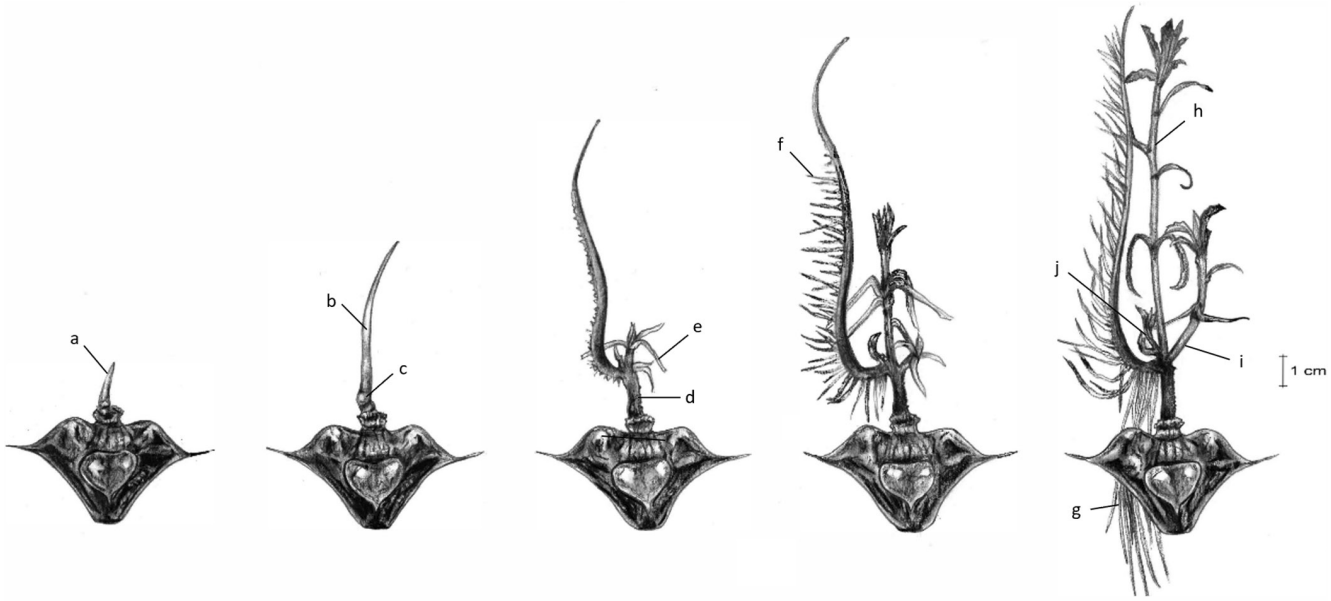


FIGURE 6 Germinated seedlings of *T. natans* at 2, 4, 8, 10 and 15 days, from left to right, respectively. a—radicle, b—hypocotyl, c—plumule, d—macrocotyledon petiole, e—linear leaf, f—'water' root, g—'underground' root, h–j—first, second and third primary shoot. Illustration by Paula Olías Garcia.

small weevil *Bagous rufimanus* Hoffman were found in Europe, located in the fruit epidermis, peduncle and stem, eliciting low feeding damage. Filter-feeding larvae of at least one and probably additional nonbiting midge species (Chironomus spp., Chironomidae) were observed in petiole floats. The polyphagous aphid *Rhopalosiphum nymphaeae* L. (Aphididae) is an agricultural pest to cultivated water caltrop, consuming the leaves. The leaf hopper *Macrosteles purpurata* Kuoh and Lu (Cicadellidae) also feeds on the respective foliage, and an additional undetermined blue-grey leafhopper has been seen in some localities, though neither appears to be harmful nor a *Trapa* specialist. The armyworm *Spodoptera litura* Fab. (Noctuidae), which is a major pest in cultivated *Trapa*, was identified to feed on plant leaves. An unknown leaf miner was observed inside some plant foliage. At least three species of snout moths (Pyralidae) were detected in northeast Asia, whereas *Nymphula interruptalis* (Pryer) was the most detrimental, because of the consumption of and consequent mortality of the central bud, which stopped further growth. Similar observations of larvae of *Nymphula* sp. were made in Europe (e.g. in France and Poland). *Paraponyx vittalis* (Bremer) was also common at times. Additionally, snails (for instance, *Radix auricularia* L. among unknown snails) were observed to periodically damage *Trapa* plants, also living off many unrelated plants. Released cercariae of the fluke *Fasciolopsis buski* (Lankester) encyst in aquatic plants such as *Trapa* (Keiser & Utzinger, 2009). Raw or insufficiently cooked water caltrop used for human consumption may thus convey fluke-associated intestinal, food-borne trematode infection, namely fasciolopsiasis (Keiser & Utzinger, 2009; Sadun & Maiphoom, 1953 as cited in Zhu, 2016). Therefore, water caltrop as an aquatic product should be carefully processed and cooked before consumption by humans to hinder infestation (Zhu, 2016).

In addition to invertebrates, several mammal species, which in part can withstand the fruit spines and break open the endocarp, have been observed to feed on *T. natans* (Kiviat, 1993). Of these, several rodents appear to feed on *Trapa* (Pemberton, 1999). Norway rats (*Rattus norvegicus*), beavers (*Castor canadensis*), nutria (*Myocastor coypus*), muskrats (*Ondatra zibethicus*), eastern chipmunks (*Tamias striatus*) and red (*Tamiasciurus hudsonicus*) and grey (*Sciurus carolinensis*) squirrels were detected or are assumed to consume the reproductive (e.g. fruits) and/or vegetative parts (e.g. core of the rosette) of the plant. Additionally, white-tailed deer (*Odocoileus virginianus*) browse on the vegetative matter of *Trapa* (Hummel & Kiviat, 2004; Kiviat, 1993; Pemberton, 1999). Previous studies have also mentioned consumption by swans (Bolender, 2010).

9.2 | Plant parasites and diseases

9.2.1 | Higher plant parasites

None reported.

9.2.2 | Fungi

Fungi associated with water caltrop have also been detected in the survey by Pemberton (1999), including species from the Ascomycota phylum such as *Cercospora* sp. and *Botrytis cinerea*, as well as *Sclerotium rolfsii* from the Basidiomycota phylum. These were observed to infest the leaves or the whole plant. Additionally, *Bipolaris tetramera* (Ascomycota) damages *Trapa*.

9.2.3 | Bacteria

None reported.

9.2.4 | Viruses

An unknown virus has been reported to occur in China (Pemberton, 1999).

10 | HISTORY

10.1 | Taxonomic history

Although the plant is easily identified (Countryman, 1978), the taxonomy of the genus *Trapa* is complex and far from clear (Bilz et al., 2011; Li et al., 2017; Sun et al., 2020). Discussions on family association have been dynamic (Zetter & Ferguson, 2001). Previously, *Trapa* was variously placed within the families of Onagraceae and Lythraceae (Cronquist, 1981 and Fassett, 1957 as cited in Pemberton, 2002; Graham et al., 1993; Takhtajan, 1997 as cited in Graham et al., 1998), or sufficiently distinct to constitute a separate family (i.e. Trapaceae, syn. Hydrocaryaceae) due to its unique morphological, embryological, anatomical and palynological features (Cook, 1990; Cook et al., 1974; Erdtman, 1986; Ghosh, 1954; Hutchinson, 1969; Miki, 1959; Muenscher, 1944; Nandy et al., 2018; Tutin et al., 1968). Modern molecular evidence places *Trapa* within Lythraceae and the order Myrtales (Graham et al., 1998, 2005; Sun et al., 2020; The Angiosperm Phylogeny Group, 1998).

The distinction of varieties or separate species within *Trapa* is still debated (Apinis, 1967; Ding & Jin, 2020; Frey et al., 2017). For example, the genus has been previously reported to contain up to 20, 30 or 70 distinguishable species (Cook, 1990; Cook et al., 1974; Iamonico, 2013; Muenscher, 1944; Vassiljev, 1949 as cited in Ding & Jin, 2020). Other studies have mentioned its common recognition as a genus encompassing *T. natans* as one single species, for instance, comprised of two varieties, namely *T. natans* var. *natans* and *T. natans* var. *bispinosa* (Hummel & Kiviat, 2004; Tutin et al., 1968) or comprising two polymorphic species (Chen et al., 2007). Alternative authors have recognized more than two species and multiple types, forms or varieties (Ding & Jin, 2020; Glück, 1936 as cited in Vuorela & Aalto, 1982; WCVP, 2023). One reason for the ongoing confusion may lie in the classification system. Taxonomic identification based on vegetative morphology (such as leaf size, shape and petiole swelling) appears to be of low value (Fan et al., 2016), and while plant systematics traditionally classifies plants based on morphological flower characteristics, *Trapa* infraspecifics have been mainly categorized by fruit morphology (Borojevic, 2009; Fan et al., 2016; Li et al., 2017). A selection of morphological fruit properties has been identified to be especially useful in this respect (Ding & Jin, 2020; Fan et al., 2016); however, the large variation in fruit morphology (for instance, the size, mass, number, position and shape of spines and protuberances) has contributed to taxonomic uncertainty (Fan et al., 2022; Lam et al., 2024). Researchers have varied in their treatment of principal diagnostic fruit characters as there is a lack of taxonomic standards, and it is unclear whether the morphological variation of fruits is due to phenotypic plasticity or adaptive divergence between populations, varieties or species (Chorak et al., 2019; Fan et al., 2022; Frey et al., 2017; Graham, 2013; Hegi, 1926; Kadono, 1987; Kim et al., 2010; Lam et al., 2024; Li et al., 2017; Takano & Kadono, 2005; Tutin et al., 1968; Vuorela & Aalto, 1982).

A narrow species approach in *Trapa* may be of low ecological worth (Apinis, 1967), and the presently simplified taxonomic investigation may not account for the true genetic diversity of the genus (Frey et al., 2017; Li et al., 2017). A worldwide taxonomic revision appears to be necessary to resolve the taxonomy and avoid Linnaean gaps and biased Red List categorizations in this genus, as so far taxonomic uncertainties complicate the interpretation of population trends, survival risk assessment, and hence evaluation of *Trapa* conservation status (Frey et al., 2017; Kozlowski, 2008; Lansdown, 2019; Sun et al., 2020; Zhu, 2016). Previously rarely exploited standardized molecular methods have proven useful in this respect and advancements in molecular marker development for studying *Trapa* phylogeny now include allozymes, rapid amplification of cDNA ends, chloroplast insertion or deletion, nuclear single sequence repeats and amplified fragment length polymorphisms (Lam et al., 2024). These have been increasingly utilized to assess phylogenetic relationships in the *Trapa* genus and reveal the extent to which morphological fruit properties reflect genotypic differentiation, to enhance our understanding of the large variation in fruit morphology and its taxonomic significance (Chorak et al., 2019; Fan et al., 2024; Kim et al., 2010; Li et al., 2017; Takano & Kadono, 2005). Indeed, evolutionary relationships within *Trapa* align with morphological features (Fan et al., 2024). For instance, phylogenetic studies based on chloroplast genomes and amplified fragment length polymorphisms revealed the division of the *Trapa* genus into two evolutionary branches, one small- and another large-seeded, with the latter being clustered based on geographical origin or seed properties (Fan et al., 2021, 2022). Additionally, the cryptically introduced two-horned *Trapa* taxon found in the northeastern United States, and most closely related to *T. bispinosa* Roxb. var *iinumai* Nakano (accepted synonym unknown in Table S2), has been identified to be morphologically (e.g. crown lacking, leaf underside reddish, pink petals, pink petioles; see Figure 3g–m) and genetically different from the previously recognized four-horned *Trapa* taxon with white flowers (Chorak et al., 2019; Fan et al., 2024). Both invasive taxa appear to belong to different clusters of the previously mentioned large-seeded *Trapa* branch (Fan et al., 2024). An intensified taxonomic examination of the genus across its entire range using genetic and morphological characteristics would complement the existing knowledge base for making effective decisions about regionally appropriate *Trapa* management in its native range (e.g. treatment of infraspecific taxa as different conservation units, Fan et al., 2022, 2024; Frey et al., 2017), and would potentially allow for identifying further *Trapa* taxa in their non-native range. This is especially

important information, as different invasive genotypes may behave differently, for instance in terms of phenology (Chorak et al., 2019; Dodd & Schad, 2021), which is why new introduction(s) of the water caltrop or extant populations need to be assessed concerning potentially variable responses to control measures (Chorak et al., 2019; Dodd et al., 2021, 2022). Phylogenetic research may thus enhance *Trapa* management in its invaded range and prevent further range expansion (Fan et al., 2024).

10.2 | Native range history

Thanks to the unique flowers, fruit hulls, seeds and pollen grains produced by *T. natans* that do not decay, sites that contain *Trapa* remains have been analysed and with the help of macrofossils such as fruit remains as well as fossil pollen grains, it has been possible to reconstruct the occurrence of the water caltrop in its native prehistoric distribution range (Karg, 2006; Korhola & Tikkanen, 1997). Collections of fossil fruits and pollen grains of *Trapa* are extensive and various representatives of *Trapa* have been described by palaeobotanists (Graham, 2013). While before and during the Palaeolithic no plant findings could be detected, *T. natans* has been noted to have occurred during Mesolithic and Neolithic times as well as thereafter (Filipović & Tasić, 2012; Hopf, 1957; Karg, 2006; Rimantienė, 1992). Though it is a challenging task to have a comprehensive overview of all *Trapa* fossil occurrences, a literature review suggests that over 70 fossil species are recognized to date to have been present in Europe, Asia and North America during the Neogene, displaying rapid diversification in terms of morphology and geography of the genus throughout that time (Aung et al., 2021; Graham, 2013). Seventeen Japanese species, 16 Russian and 16 European species were described from the Neogene (Aung et al., 2021). The oldest so far discovered *Trapa* species were recorded in the Upper Cretaceous and Senon periods in North America; however, only a few species were detected (Apinis, 1967; Hegi, 1926). Remains of plant macrofossils and pollen originating from various localities hence provide evidence for a broad, diverse Holocene distribution (Karg, 2006).

Compared with its tertiary (interglacial and postglacial) distribution, *T. natans* over time became distributed in a relatively sporadic, scattered and disjunct manner and is rare or has become extinct in some regions (Apinis, 1967; Artyukhin et al., 2019a; Frey et al., 2017; Hegi, 1926; Karg, 2006; Lansdown, 2019). In North America, in the Miocene only two species were sparsely represented, and in the Pliocene only one which progressively disappeared at the beginning of the Pleistocene so that the North American distribution range was gradually lost at the end of the tertiary and is now extinct (Apinis, 1967; Hegi, 1926). Also, in deposits of the Pliocene and Pleistocene in Europe, the fruit type diversity decreased notably (Gregor, 1982 and Mai, 1985 as cited in Graham, 2013). *Trapa* was present in Britain in the Holocene until 4200 years ago (Flenley et al., 1975; Schofield & Bunting, 2005), commonly occurred as far north as the coast in south-west Finland in a shallow, eutrophic, small lake until 2500 BP (Korhola & Tikkanen, 1997), and, until 1915, continued to exist along its northern border in southern Sweden (Jonsell & Karlsson, 2010 as cited in Graham, 2013). Its Northern distribution range has receded, with extinction in Sweden (POWO, 2023) and *Trapa* populations continuously decrease in continental Europe (Borojevic, 2009; Graham, 2013; Hegi, 1926; Jäggi, 1883; Karg, 2006; Lewandowska et al., 2019). For instance, between 1950 and 1990, the number of populations decreased from 14 to two in the Upper Rhine Plain of Baden-Württemberg, one of the former main distribution areas of *Trapa* in Germany (Bolender, 2010). Since the beginning of the 19th century, in the Insubric region, more than half (52%) of the described water caltrop stands have faced extinction, indicating increasing fragmentation of *Trapa* populations and enlarged isolation in local populations (Frey et al., 2017). It nowadays is extinct in Spain (POWO, 2023). All in all, the paleoecologic fossil pollen and macrofossil remains as well as neoecological data thus demonstrate *Trapa* to have been more widely distributed during interglacial and postglacial times than today, and the distribution range continues to decline (Hegi, 1926).

It is important to keep in mind that, of course, insights on (pre) historical occurrence dynamics are limited by the number of work-intensive paleolimnological studies. More exhaustive information on the distribution dynamics from other regions is necessary to get an overall impression of *Trapa* population size, distribution and trends. For example, although the water caltrop today occurs in Africa, a fossil record of *Trapa* is not available for the continent, potentially due to biased fossil collections (Aung et al., 2021; Xing et al., 2016). Population trend data will have to be collected from points throughout its range to ensure that the European trend is not an indicator of a global decline (Lansdown, 2019). However, the accuracy of information on tempo-spatial occurrence dynamics is obscured by taxonomic uncertainty (see Section 10.1; Lansdown, 2019).

Manifold environmental factors may be driving the decrease in *T. natans* in Europe (Lansdown, 2019). Based on *Trapa* temperature preferences (see Section 2.1), prehistoric and historic climatic fluctuations may explain some of the population dynamics. Fossil pollen and macrofossil studies focusing on European countries indicate that favourable conditions were provided for *T. natans* and many other thermophilous species (e.g. *Ceratophyllum submersum*, *Najas flexilis*, *N. marina*, *N. minor* and *N. tenuissima*) due to increased warmth and dryness during the Holocene Climatic Optimum (9000–5000 cal. year BP), which is why these were observed to expand northwards during early and middle Holocene. The water caltrop has even been declared to be an indicator of the thermal maximum. Nevertheless, climatic conditions deteriorated towards the end of the Subboreal and start of the Subatlantic periods of the late Holocene and are known to have contributed to the downward trend of many plant species. A shift from continental to oceanic conditions (which means lower summer temperatures and increased precipitation) took place. These altered climatic conditions may also have led to the extinction of the thermophilic *Trapa* populations at their former northern European boundary (Ahlqvist, 2007; Alhonen, 1964; Borojevic, 2009; Donner, 1995 and Hintikka, 1963 as cited in Korhola & Tikkanen, 1997; Flenley et al., 1975; Godwin, 1956; Godwin, 1975,

Lang, 1994 and Szafer, 1954 as cited in Lewandowska et al., 2019; Hegi, 1926; Jäggi, 1883; Magyari et al., 2008; Malmström, 1920; Miotk-Szpiganowicz & Gałka, 2009; Samuelsson, 1934; Schofield & Bunting, 2005; Wanner et al., 2008). Additionally, alterations in habitat availability and local water body conditions may cause declines in populations. These changes include infilling (terrestrialization) due to vegetation succession, nutrient level alterations caused by oligotrophication or prolonged hypereutrophication, acidification, water depletion through dehumidification or desiccation, modifications of the physical environment through activities such as drainage and dredging, (spring) floods and competition with other plants (Alhonen, 1964; Apinis, 1967; Borojevic, 2009; Frey et al., 2017; Gaillard & Birks, 2007; Hegi, 1926; Jäggi, 1883; Karg, 2006; Korhola & Tikkanen, 1997; Lansdown, 2019; Larocque-Tobler & Pla-Rabès, 2015; Lewandowska et al., 2019; Mikhaylova, Artyukhin, Panfilova, et al., 2021; Samuelsson, 1934; Schofield & Bunting, 2005; Villa et al., 2018; Vuorela & Aalto, 1982). At the same time, human overuse may have promoted the disappearance of the water caltrop at some locations (see Section 10.4.1), while alternative research has related the reduction or disappearance of the aquatic macrophyte to land reclamation and urban expansion (Tornadore et al., 2000). Loss of formerly established habitats due to altered environmental conditions, as a common cause of *Trapa* decline (Lansdown, 2019), could be compensated for by exploiting new suitable available sites. However, although several dispersal mechanisms exist, the dispersal abilities of *Trapa* are limited and may be responsible for the heterogeneous distribution of the floating-leaved plant (see Section 8.3; Meschede, 1910; Nishihiro et al., 2014). Nevertheless, it has not become apparent which factors play a larger and smaller role in shaping the occurrence dynamics of *T. natans* (Lansdown, 2019).

10.3 | Non-native range history

According to Cook (1985), the majority of aquatic plants have become more widespread as man has become mobile. In the context of its invasion in North America, *Trapa* indeed mostly benefited from the fact that it is a food crop as well as an ornamental and medicinal aquatic plant species, which increased the likelihood of intentional transport to non-native environments through humans (Hummel & Kiviat, 2004; Maryland Sea Grant College, 2002). Despite warnings, the water caltrop was introduced to North America during the 19th century (Brown, 1880; Les & Mehrhoff, 1999). According to Eaton (1947) and Mills et al. (1993), it was first introduced to Concord (Massachusetts) before 1859, although specimen notes in the archives of the New England Botanical Club suggest that the date is erroneous and was meant to be 1879 (Les & Mehrhoff, 1999). Other earliest records suggest that the water caltrop was first introduced to North America in 1874 (Countryman, 1978). In 1877, the water caltrop was grown at Harvard University in Asa Gray's Botanical Garden (Cambridge, Massachusetts; Borojevic, 2009). In 1879, it was first observed in the local wild close to Fresh Pond (Countryman, 1978). Though it was first suspected that it escaped from cultivation, a gardener at the Cambridge Botanical Garden was discovered to have deliberately inserted *Trapa* at Fresh Pond and some additional ponds close by (Countryman, 1970, 1978; Davenport, 1879). Because, at the time, the infestation potential of the water caltrop was commonly underestimated, Davenport (1879) did not consider *Trapa* to be an aggressive aquatic nuisance plant species and distributed seeds from Fresh Pond to his friend M. Pratt (of Concord, Massachusetts). Together, they placed plant material in a pond close to the Sudbury River and later on G. E. Davenport suspected that Pratt further distributed it, as a plant of *T. natans* collected from a pond in Concord, likely originated from material disseminated by his friend (Davenport, 1879). The water caltrop was further discovered in 1886 in the Concord River (in the Town of Concord, Massachusetts), with populations exploding aggressively and eventually spanning approximately 40 ha and it became a noxious weed in the Sudbury River (Burk et al., 1976; Bye, 1974 as cited in Countryman, 1978; Eaton, 1947; Mills et al., 1993). Simultaneously, a Polish Catholic priest visited Europe in the 1880s as a plant enthusiast and took along seeds that he had collected before coming to Schenectady (New York). He transplanted these into Sander's Lake (Scotia, New York, now known as Collins Lake) in 1884, and in 1886, it was stated that these displayed luxurious growth (Wibbe, 1886). The water caltrop escaped from Collins Lake during a flooding event into the nearby Mohawk River via Collins Creek and became well established there as early as 1920 and by 1934 the estimated cover amounted to 405–486 ha (Muenscher, 1937, and Winne, 1950 as cited in Hummel & Kiviat, 2004). *Trapa* expanded downstream and by the late 1930s reached the Hudson River at the city of Cohoes (Countryman, 1978; Muenscher, 1937, and Winne, 1950 as cited in Hummel & Kiviat, 2004). In 1952, the total infestation in New York State spanned around 1416 ha (Greeley, 1965). From Massachusetts and New York, the water caltrop spread further, despite intensive management campaigns against *Trapa* in the 20th century comprising huge efforts over decades, for instance at Lake Champlain (Vermont) and the Potomac River flowing into the Chesapeake Bay (Virginia/Maryland; Hook, 1977; Naylor, 2003). Presently, *Trapa* is found in 10 other northeastern states of the United States (in Connecticut, Delaware, Maine, Maryland, New Hampshire, New Jersey, Pennsylvania, Rhode Island, Vermont and Virginia) and since 1998 it is also present in southwestern Quebec, Canada, just north of the United States–Canada border (Borojevic, 2009; Pfingsten et al., 2021; POWO, 2023). It is also present in the District of Columbia (POWO, 2023). Prospectively, there is indication that *Trapa*, as a major invader, will spread even farther within the US and Canada, as its potential range may not be yet fully exploited, likely also due to climate change, and the warmer habitat preference of the thermophilic aquatic macrophyte (see Section 2.1), as well as more suitable local site conditions and habitat availability (Ding & Blossey, 2005b; Marković et al., 2015; Pemberton, 2002; USDA, 2016). For instance, as nutrients are continuously supplied to water bodies in North America due to cultivation and urbanization, *T. natans* is likely to flourish (Marković et al., 2015; Powles, 2006). Beyond the introduction of *T. natans* to North America, the water

caltrop is also commonly acknowledged to have been introduced to Australia (see Introduction), but information in this respect is scarce.

10.4 | Usage

10.4.1 | Food production

Ethnohistoric and archaeological evidence on *T. natans* (e.g. fossil pollen and macrofossils) suggests that the water caltrop may have constituted diets of prehistoric humans in northern Europe (e.g. in Latvia, Lithuania and Montenegro) from 5000 BC onwards (Borojevic, 2009; Mikulyuk & Nault, 2009; Vuorela & Aalto, 1982). Interestingly, the debate whether *Trapa* was merely gathered from natural populations or intentionally cultivated is ongoing. On the one hand, evidence has been provided that there were no private family stands of *Trapa* that were managed, encouraged or cultivated, indicating that plant material was merely gathered from naturally occurring *Trapa* populations by people living in prehistoric settlements (Borojevic, 2009; Rimantiené, 1992; Zvelebil & Dolukhanov, 1991). On the contrary, there is an indication that *Trapa* was a formerly used crop, especially due to its occurrence in artificial water bodies close to anthropogenic settlements such as fishponds and town moats, likely originating from intentional introductions through humans (Brockmann-Jerosch, 1913; Frey et al., 2017; Ozola et al., 2010; Zvelebil & Dolukhanov, 1991).

Although it is not clear to what extent the balance was between occasional collection and deliberate production, it has been proven that prehistoric humans prepared this food plant (Zvelebil & Dolukhanov, 1991). Evidence in this respect is mainly based on relicts of subfossil water caltrop occurring near signs of prehistoric humans (Alhonen, 1996 and Valovirta, 1957 as cited in Ahlqvist, 2007). For example, *Trapa* fruits have been found in a Swedish peat bog in earthenware from Neolithic times (Brockmann-Jerosch, 1913), while in Germany (Karg, 2006), Latvia (Ozola et al., 2010), Finland (Vuorela & Aalto, 1982), Serbia (Filipović & Tasić, 2012) and Slovenia (Tolar et al., 2011) partially charred *Trapa* remains, such as shell (endocarp) parts, horns and bristles, were found during archaeological excavations around the degraded remains of former hearths of dwellings. Wooden mallets (used to split or break the fruits) with *Trapa* shells entrenched in their working surfaces have also been found in many settlements (Vankino, 1970 as cited in Rimantiené, 1992; Zvelebil & Dolukhanov, 1991). Until 1880 AD, it was common practice to purchase water caltrop at many markets across Europe (Brockmann-Jerosch, 1913; Jäggi, 1883). Though the raw fruits may also be consumed fresh (Borojevic, 2009), for instance, in Northern Italy (Milan), fruits were often sold (similar to chestnuts) in a roasted manner (Brockmann-Jerosch, 1913), likely because they were easier to crack and peel (as the woody endocarp becomes fragile), became more flavoursome and could be preserved for several weeks (Karg, 2006). Alternatively, the mid-European folk ate the water caltrop fruits like chestnuts, by cleaning, cooking, drying and grinding them into flour (Borojevic, 2009; Brockmann-Jerosch, 1913; Rimantiené, 1992). The water caltrop appears to have served as a flour substitute for people lacking cereal cultivation and supplemented the normal diet for those who grew cereals, such as Swiss and Austrian residents in the Neolithic (Coles & Coles, 1989 as cited in Ahlqvist, 2007). Especially in times of cereal crop failure and/or in times when poor people could not afford alternatives, it became a significant dietary component, with the flour of the dried kernel also being used for baking (Borojevic, 2009; Brockmann-Jerosch, 1913; Karg, 2006). Water caltrop not only served as a staple food for humans but also appears to have served as animal feed, for instance for pigs (Borojevic, 2009).

Although previous research has shown that *T. natans* has been an important supplement to the nutrition of pre-(historic) mankind in Europe (Karg, 2006), the water caltrop was merely consumed by humans until the onset of the 20th century (Brockmann-Jerosch, 1914, as cited in Karg, 2006). It became less important over time and today '*Trapa* is a forgotten crop in Europe', apparently not due to a decrease in plants, but because of human migration from the villages or perhaps replacement by other cereals (Borojevic, 2009). At the same time, extensive culture as well as overexploitation of *Trapa* by humans, due to excessive harvesting by fruit collectors, may have promoted the disappearance of water caltrop at some locations (Dong et al., 2013; Frey et al., 2017; Hegi, 1926; Korhola & Tikkanen, 1997; Malmström, 1920; Samuelsson, 1934).

In Asia, *Trapa* has been and continues to be an important food crop for humans. Prehistoric remains of *Trapa* taxa have been found. For instance, remains of water caltrop were detected at 21 Neolithic sites along the Lower Yangtze River Valley in China, suggesting that water caltrop was domesticated and cultivated as an important non-cereal crop by 7000 BP. Genotypes were deliberately selected for their large fruit size and shape (Borojevic, 2009; Guo et al., 2017). Lu et al. (2022) reported the first domestication of water caltrop in the Yangtze River Valley by 6300 BP, with selection favouring enlarged fruits and more vigorous adventitious root systems. Concurrently, a recent study provides further evidence of 6000 years of artificial selection in domesticated *T. bispinosa* (syn. *T. natans* var. *bispinosa*, Table S2), evincing larger seed size and reduced capsule thickness (Lam et al., 2024). Thus, water caltrop was a calorie source that nourished early agriculturalists in eastern Asia (Lu et al., 2022).

Interestingly, it is still considered an important crop in Asia today and continues to be commercially grown, whereas yields in traditional culture range from 600 to 650 kg/ha. With the application of inorganic fertilizers and pest control measures, yields were as high as 4000–4800 kg/ha (Ahmad & Singh, 1998; Borojevic, 2009). Yield depends on the cultivated *Trapa* infraspecific and its domestication degree (Lam et al., 2024). Harvested *Trapa* material is sold fresh on pond banks or at inland markets (Borojevic, 2009) or cleaned, skinned, cut up and wrapped before being commercially retailed in hotels, restaurants or elsewhere (Singh et al., 2008). It is widely consumed not only in China but also in Thailand (*krajub* fruit), India (*singhara* fruit in Hindi) and other Asian countries for the edible kernel of its fruits and also for its leaves and stems that are consumed in a raw manner or cooked as vegetables (Arima, Hoque, et al., 1999; Babu & Dwivedi, 2012; Borojevic, 2009; Chen et al., 2007; Graham, 2013;

Hoque et al., 2009; Lu et al., 2022; Pemberton, 1999; Tulyathan et al., 2005; Zhu, 2016). The seed is usually eaten raw, roasted or boiled (Hoque et al., 2009). Because the hardness of the endocarp makes it difficult to skin the fruit and extract the internal white kernel, a common preparation method for *Trapa* fruits is steaming, since it softens the external cover, while cooking the internal flesh (Tulyathan et al., 2005). The edible white flesh is appreciated not only for its physicochemical characteristics but also for its sensory quality (Jankovic, 1973 as cited in Borojevic, 2009). Being recognized as a cereal substitute and consumed as grain food (Babu & Dwivedi, 2012), the fruit flesh is usually consumed by humans as a snack or ingredient in other dishes (Tulyathan et al., 2005). It is used in meals as a thickening agent in sauces and soups (Chiang et al., 2009), in preparing curry (Hoque et al., 2009), dried to make flour to prepare bread (for instance in chapatti or puris) and in manifold sweet dishes (Hoque et al., 2009; Singh et al., 2010, 2011). It is also integrated into beverages, for example in tea, brewing liquor and wine (Hoque et al., 2009).

Despite its lengthy cultivation history and use as a crop, there is an indication that the water caltrop is an under-used crop in the food industry and would require further attention from food processors (Singh et al., 2010). For instance, so far water caltrop flour has been incorporated into food products such as cookies (Bala et al., 2015; Singh et al., 2011), muffins (Krishnaiya et al., 2016) and noodles (Yadav et al., 2014) through blending with other types of flour. The development of novel food products seems promising and its use as a gluten-free alternative has not been fully taken advantage of potentially revealing unexploited potential (Tulyathan et al., 2005; Zhu, 2016). Making use of its crop potential can partly combat global food issues and may help to exploit the increasing water levels caused by global warming in some regions (Babu & Dwivedi, 2012). Additionally, integrative research on supposedly non-linkable *Trapa* aspects, such as its invasion, conservation and multipurpose crop use, is limited but may assist in adequately approaching the exploitation of the usefulness of the aquatic macrophyte in combination with conservation efforts as well as combat measures (Hummel & Kiviat, 2004). For instance, an assessment of the human food potential of *Trapa* is still pending in its invasive range (Hummel & Kiviat, 2004).

10.4.2 | Phytoremediation

To restore polluted wetlands, several aquatic plant species such as *Azolla pinnata*, *Eichhornia crassipes*, *Ceratophyllum demersum*, *Lemna minor*, *Phragmites australis*, *Pistia stratiotes*, *Potamogeton nodosus*, *Sagittaria latifolia and Typha latifolia*, have been exploited for phytoremediation purposes, meaning efficient plant utilization for the removal, detoxification or immobilization of environmental pollutants (Ansari et al., 2020; Petrovic & Krivokapic, 2020; UNEP, 2021). Also, the water caltrop has promising characteristics such as rapid growth capacity, large biomass accumulation, extensive root system development in water and sediment and is easily cultivable (Petrovic & Krivokapic, 2020; Xu et al., 2020). Also because of its presumed pollutant tolerance (see Section 2.2), *T. natans* has thus been extensively researched concerning its ability to eliminate (heavy) metals and metalloids from contaminated waters (Alam & Hoque, 2017; Kumar & Chopra, 2018) including antimony, arsenic, cadmium, chromium, copper, iron, lead, manganese, molybdenum and zinc (Babu et al., 2011, 2013; Baldisserotto et al., 2004, 2007, 2010, 2013; Baruah et al., 2014, 2021; Bauddh et al., 2015; Kumar et al., 2002; Petrovic & Krivokapic, 2020; Rai & Sinha, 2000). The water caltrop has been proven to be effective in this respect (Kumar & Chopra, 2018), whereas the impact of sulphate and chloride on the viability of *Trapa* remains unaddressed, rendering it a promising area for further research (Mikhaylova, Artyukhin, Panfilova, et al., 2021). Nevertheless, despite the advantages of *Trapa* for phytoremediation, its efficient uptake capacity may have adverse consequences. The detected accumulation of metals in edible parts is a potential limiting factor for using the water caltrop as a crop (Rai & Sinha, 2000). More prudent cultivation practices and consumption, for example using unpolluted water bodies for plant cultivation, boiling kernel before consumption, as well as removing the 'tapetum' from fruits, may assist in meeting food health standards (Rai & Sinha, 2000). Permissible tolerance limits are yet to be determined (Rai & Sinha, 2000).

Due to its ability to efficiently capture mineral nutrients (see Section 4), *Trapa*'s nutrient uptake capacity has been investigated (Chandra et al., 2013; Galanti & Guilizzoni, 1985; Kumar & Chopra, 2018). Xu et al. (2020) determined absorption contribution rates that amount to 36.9% and 34.5% of total nitrogen and total phosphorus, respectively. For effective cleaning, aquatic macrophyte biomass must be extracted from the water bodies after absorption of the nutrients (Xu et al., 2020). Biomanipulation experiments conducted in this respect have shown that artificial extraction of *T. natans* may markedly improve the local water quality in the vegetative period (Yuan et al., 2021). For example, in China, in an area in which *Trapa* was repeatedly removed, total and dissolved nitrogen as well as phosphorus were much lower, compared with the *Trapa* zone. Within a long-term harvesting project in Italy, annual harvesting of around half of the total water caltrop cover led to the extraction of about 70 kg $year^{-1}$ of phosphorus, 38 t $year^{-1}$ of organic matter and 1 t $year^{-1}$ of nitrogen, thereby improving water quality and decreasing eutrophication (Galanti et al., 1990). Also, if *Trapa* remains within the systems, high nutrient removal rates have been observed. In oxygen-depleted beds of *T. natans*, compared with those of *Vallisneria*, increased microbial activities that remove inorganic nitrogen and generate significant amounts of gaseous nitrogen result in enhanced denitrification and thus permanent loss of nitrogen from the ecosystems (Caraco & Cole, 2002; Tall et al., 2011). The beds extracted 70%–100% of total nitrogen retained in a Hudson River section during the summer months, and accounted for 25% of annual nitrogen removal, although they only occupy 2.7% of the total tidal Hudson area and are active only 3 months per year. Consequently, *T. natans* may positively influence the whole ecosystem function and perform an essential ecosystem service. Furthermore, in a more controlled setting, the removal rates

of NH^{4+}–N, NO^{3-}–N, NO^{2-}–N, total nitrogen and total phosphorus from wastewater, amounted to 99.47%, 95.83%, 85.17%, 83.73%, 88.72%, respectively (Xu et al., 2020).

10.4.3 | Other

In addition to serving as a food source and as a means of phytoremediation, *Trapa* has been used in ancient European, Chinese and Indian medicinal practices and knowledge of traditional medicine has provided the foundation for investigating the health benefits of *T. natans* in modern times (Banu et al., 2023; Jäggi, 1883; Lim, 2013; Zhu, 2016). Because of several medicinal properties, such as antioxidant, antimicrobial, antiviral, analgesic and anti-inflammatory activities, the plant species is of medicinal importance (Lim, 2013). The water caltrop has also been attributed religious and cultural significance, and the fruits have, for instance, been used to manufacture rosaries in Europe or as prayer offerings during rituals in the Chinese Chou dynasty (Ahmad & Singh, 1998; Hegi, 1926; Hoque et al., 2009; Jäggi, 1883; Lim, 2013). The macrophyte has also been used for ornamental purposes, for instance, as a decorative aquatic plant in ponds (Naylor, 2003).

11 | CONSERVATION AND MANAGEMENT

11.1 | Conservation measures

Although some stands of the Trapetum natantis Müller et Gors 1969 association (see Section 3) are still preserved, for instance in the Danube Delta in Romania and the Upper Rhine Area in Germany, in several countries in Europe, such as Poland, the phytocoenoses of Trapetum natantis Müller et Görs 1960 have retreated from their originally present natural water bodies. They have therefore been nationally allocated to the rare, threatened aquatic plant communities that are in danger of extinction (Klosowski, 1995; Rennwald, 2000). Direct interventions in populations and biocoenoses (namely mechanical influences as an indirect effect of use through, for instance, water sport, navigation and direct intentional weed removal) and halt of traditional utilization, as well as change (e.g. water regime, drainage, eutrophication, pollution by poisonous chemicals and waste products) and destruction (e.g. waterway construction, creation of artificial water bodies, infilling) of sites, are among the discernible risk factors. If these factors continue to have an effect, significant transformations may occur within the next one to two decades, leading to fragmented or degraded states that are increasingly difficult to identify, or even resulting in the complete loss of the community (Rennwald, 2000). This is especially detrimental since in addition to *T. natans*, some of the associated species (e.g. *Marsilea quadrifolia*, *Nymphaea alba and Salvinia natans*) are also macrophytes of conservation concern (Valchev et al., 2006). However, promisingly, plant associations of Trapetum natantis have a brief regeneration time of 3–10 years, even arising from single plants (Jusik et al., 2023).

Due to its wide native range, *T. natans* itself is classified as 'Least Concern' according to the global IUCN Red List, although the authors of the report acknowledge that the status of the species may be more positive than is actually the case (Lansdown, 2019). Accordingly, no global conservation actions are necessary to date, although resolving taxonomic uncertainty could give a different impression. According to the regional European Red List, water caltrop is classified as a 'Near Threatened' macrophyte and is protected under the Bern Convention, being listed in Annex I (Bilz et al., 2011). In several European countries, for instance, in Germany and Poland, where many previous occurrences have been degraded to a few remnant populations of small extent, *T. natans* has been listed on the red list partly as 'Greatly Endangered' and is protected as a rare species by federal acts for the protection of nature (Bolender, 2010; Marković et al., 2015; Mikhaylova, Artyukhin, Panfilova, et al., 2021). Because of adverse population trends, associated high loss rates and evident extinction in some countries (see Section 10.2), researchers have appealed for the conservation of wild *Trapa* populations, especially because extinction of any population would substantially decrease total genetic diversity (Li et al., 2017).

Several conservation areas have been established on a local spatial scale in European countries to safeguard the aquatic plant species (Hay et al., 2000). Since one of the common causes of *Trapa* decline is the loss and degradation of habitats (see Section 10.2; Lansdown, 2019; Walusiak et al., 2024), habitat restoration has been a common measure (Jusik et al., 2023) and opportunities herein should be continuously identified (Walusiak et al., 2024). Additionally, due to great adaptation potential to varied conditions (Artyukhin et al., 2019a), the water caltrop has been reintroduced to former habitats despite criticism of being scientifically unjustified (Didukh, 2010; Jusik et al., 2023). For instance, the LIFE-Nature project 'Living Rhine floodplain near Karlsruhe' (European Commission, 2021), a study among others funded by the European Union, was initiated for re-establishing *Trapa* populations in the former main distribution area in Germany. The aim was to secure the existence of the strongly endangered aquatic plant species. From 2004 to 2010, 3500 fruits were extracted annually from a source population and transferred to eight former sites. Unfortunately, though the water bodies had been categorized as suitable, based on various criteria (such as high summer temperatures, a present sludge layer and appropriate water–chemical–biological location factors), it soon became evident that the main influential factors guaranteeing a satisfactory development of *T. natans* could only be estimated to a limited extent. Flooding events with low water temperature, competing macrophytes, consumption by swans, and low water incidents were identified as unpredictable risk factors and thus limited success in reintroduction sites (Bolender, 2010). Similarly, reintroduction attempts in Russia and Ukraine were unsuccessful in most cases, though the outcomes have been variable (Didukh, 2010; Kashin et al., 2016; Mikhaylova, Artyukhin, Panfilova, et al., 2021; Smieja & Ledwon, 2013) and in several cases, reintroduction attempts have been successful (Parkhomenko et al., 2022). The water caltrop has also been introduced to novel sites, though

this measure is disputed and introduction attempts have been unsuccessful for the most part (Artyukhin et al., 2019b; Didukh, 2010; Jusik et al., 2023; Mikhaylova, Artyukhin, Panfilova, et al., 2021).

As adequate species distribution knowledge is essential for identifying its conservation status (Marcer et al., 2013; Walusiak et al., 2024), it is recommended to generally monitor current natural water caltrop populations throughout the distribution range and do so on an ongoing basis (Didukh, 2010; Lansdown, 2019; Merzlikin & Savitsky, 2021; Pinardi et al., 2021; Walusiak et al., 2024). When analysing the actual distribution and its change, the whole spectrum of environmental drivers should be taken into account (Jusik et al., 2023), to assist in the identification of favourable and potentially disruptive factors, to account for these in conservation practices in advance. Satellite-derived products have been used and may continuously assist in large-scale monitoring of temporal and spatial variation in key plant and environmental variables, without intervention, as well as before and after any intervention, for instance, in reintroduction and introduction or habitat restoration projects, to assess the efficacy of restoration work (Pinardi et al., 2018, 2021). In addition, in light of global change, species management and conservation approaches should aim to recognize prospective alterations in habitat suitability (Walusiak et al., 2024). For instance, despite the reported declining trends until the 21st century, current evidence from the past 20 years suggests a notable increase in the presence of *T. natans* populations in some European countries, such as Italy (Pinardi et al., 2021), Serbia (Marković et al., 2015), Ukraine (Merzlikin & Savitsky, 2021) and Poland (Jusik et al., 2023), including recolonization of historical localities (Walusiak et al., 2024). These patterns could partly be explained by high water temperatures. Concurrently, a recent modelling study suggests greater habitat suitability for *T. natans* in the northern European range under scenarios of global warming (Walusiak et al., 2024). The authors thus recommend the revaluation of the conservation status of *T. natans* (Walusiak et al., 2024). Nevertheless, it is a challenge to forecast the future of the water caltrop, because climate change can adversely affect habitat suitability and cause a reduction in *T. natans* populations (see Section 5.3; Jusik et al., 2023; Schneider-Binder, 2021).

In addition to in situ conservation, ex situ may be performed, for instance, in the form of seed banking (i.e. storage of seeds dried to a low moisture content at low temperature to maintain viability for many decades), however, this does not apply to *T. natans* thanks to its recalcitrant seed and non-orthodox seed storage behaviour (Hay et al., 2000). Alternatively, zoological parks, botanical gardens and aquariums can maintain cultures of the water caltrop, although decreased population size may elicit inbreeding within the seed bank and inbreeding depression may lead to decreased fitness (Aparicio & Guisande, 1997; Nishihiro et al., 2009). Due to the apparent genetic diversity of *Trapa* taxa and populations within a taxon, plant material should be grown or preserved in a segregated manner based on taxonomic group and geographic origin (Li et al., 2017), whereas it may also be necessary to distinguish natural and anthropogenically influenced *Trapa* populations (Frey et al., 2017).

11.2 | Management: Problematic and control methods

Multiple issues and challenges arise when non-native species that have been introduced to areas outside their endemic range naturalize (Chandra & Gerhardt, 2008). The aggressive growth habit of the water caltrop, together with the associated altered environmental conditions, may not only result in severe suppression of aquatic vegetation (see Section 4) but also have detrimental effects on adjacent fauna in the atmosphere, water body and sediment. For instance, birds have become entangled in *Trapa* beds while diving for prey (Connor, 1978) and invertebrate density, biomass, abundance, taxonomic composition as well as size class distribution may be altered, in turn impacting resident fish communities (Cattaneo et al., 1998; Feldman, 2001; Kornijów et al., 2010; Strayer et al., 2003; Tessier et al., 2004). This is why *T. natans* in some parts of its native range but mainly in its non-native distribution area is considered a noxious aquatic macrophyte (Barber, 2010; Cattaneo et al., 1998; Countryman, 1978; Feldman, 2001; Hummel & Kiviat, 2004; Kornijów et al., 2010; Methé et al., 1993; Strayer et al., 2003; Tessier et al., 2004). Aside from the drastic modifications in freshwater ecosystems, the water caltrop adversely affects anthropogenic activities such as navigation and recreation (Hummel & Kiviat, 2004). Human activities which require open water, such as boating, swimming, fishing and waterfowl hunting may not be performed due to the non-penetrable plant layer (Bering et al., 2013; Countryman, 1978; Hook, 1977; Naylor, 2003). Furthermore, risks to human health have been identified. Severe injuries have been reported after people have stepped on the sharp, barbed spine tips of nut hulls (occasionally even penetrating shoes), breaking off in the skin and causing painful wounds and infections (Countryman, 1978; Jäggi, 1883; Naylor, 2003). Water caltrop stands are also assumed to have contributed to the death of people by drowning after these were swept into and subsequently entangled in the plants (Bonopartis, 2001 as cited in Hummel & Kiviat, 2004). Because of these negative ecological, economic and social consequences associated with the aquatic macrophyte, significant research effort in its non-native range has been put into managing the invasive aquatic plant species and identifying efficient control methods.

In attempts of elimination, drainage of water bodies has been exploited as a rather radical method to combat aggressive aquatic plant growth, though this is only an option when one does not care about influencing the ecosystem as a whole (Burk et al., 1976; Les & Mehrhoff, 1999). Also, it may not always be effective as diaspores have, for instance, previously been observed to overcome short- and long-term dry periods due to coverage by moist substrate (see Section 5.3).

Promoting community participation, especially hand harvesting by uprooting plants and removing these has been employed (Naylor, 2003; Waterfield et al., 2010). While hand pulling may be effective in small populations, mechanical harvesting has been more efficient for large-scale control of water caltrop, especially in

clogged waterways (Hook, 1977). By the early 1990s, *T. natans* populations had been combatted with the help of mechanical harvesting (Crow & Hellquist, 2006), and evidence has been provided that an airboat cutting programme prevented a significant amount of new fruit production, while reducing vigour in terms of leaf size and number, as well as in terms of a number of buds and (pollinated) flowers (Methé et al., 1993). Mechanical *Trapa* removal may also increase the productivity of the entire aquatic plant community and enhance the gradual recovery of submersed macrophytes due to improved water quality (Yuan et al., 2021). *Trapa* mechanical harvesting and corresponding removal of potentially recyclable nutrient quantity, which would otherwise be released during decomposition, may be optimized when timing it as macrophyte biomass peaks in late summer, but before fructification, while being attentive to plant regrowth (Galanti et al., 1990).

Simultaneously, not only physical but also chemical control measures have been exploited, especially in large infested areas (Hook, 1977). Various herbicides, such as 2,4-dichlorophenoxy acetic acid (2,4-D) and triclopyr, have been used to combat water caltrop infestations, having been sprayed by helicopters, boats or by hand from canoes (Countryman, 1978; Greeley, 1960, 1965; Hook, 1977; Poovey & Getsinger, 2007). Challenges are related to partly restricted site accessibility, a relatively short spray season with daily wind and weather alterations, timing and speed of application as well as substance drift (Hook, 1977). Additionally, although chemical control measures have been proven to be efficient in decreasing *Trapa* abundance, application in concentrations required for effective control may negatively affect native aquatic flora and fauna. Due to these potential negative impacts and adverse public perception, chemical control is now seen as a last resort. However, herbicides have been checked and partially judged as safe for use by federal and state agencies (Hook, 1977; Hummel & Kiviat, 2004; Maryland Sea Grant College, 2002; Naylor, 2003; USDA, 2016).

In the non-native range, fewer natural enemies can allow introduced aquatic plant species to prioritize competitiveness over investment in defence mechanisms against herbivores (i.e. enemy escape hypothesis or evolution of increased competitive ability hypothesis; Blossey & Nötzold, 1995; Keane & Crawley, 2002). Following the assumption that this hypothesis applies to *T. natans*, and to reduce maintenance in perpetuity, minimize economic costs, enhance long-term suppression and make use of less destructive control methods (in terms of side effects), research pursued in the past has explored biological control possibilities to combat the further spread of water caltrop and suppress it (Ding et al., 2006a, 2006c; Ding & Blossey, 2005a; Mikulyuk & Nault, 2009; O'Neill, 2006; Pemberton, 1999, 2002). Several studies have been carried out in this respect, making use of natural enemies of *T. natans* from Europe and Asia that originate from climates comparable to those from infested areas in North America (Naylor, 2003). Research has focused on the promising leaf beetle *Galerucella birmanica* (Chrysomelidae, Coleoptera). It has been observed to be able to severely decrease the biomass and reproductive efforts of *T. natans*, highly prefers the water caltrop, and has a narrow host range as the fundamental host spectrum includes only one other species aside from the focal macrophyte *T. natans* (Ahmad & Singh, 1998; Ding et al., 2006a, 2006b; Simmons & Blossey, 2023). *G. birmanica* would pose a demographic risk to *T. natans* populations and can result in a rapid and severe decrease in population growth rate (Blossey et al., 2018). Also, other potential biological control agents, such as weevils like *Nanophyes japonica* (Curculionidae, Coleoptera), the water lily aphid *Rhopalosiphum nymphaeae* (Aphididae, Hemiptera), snout moths such as *Nymphula interruptalis* (Lepidoptera, Pyralidae/Crambidae) as well as larvae from nonbiting midges of *Chironomus* sp. (Chironomidae, Diptera) have been investigated for their host specificity and whether they are sufficiently damaging. However, either narrow specialists were not sufficiently damaging or very damaging organisms were too polyphagous (Jana et al., 2019; Mustafa et al., 2016; Naylor, 2003; Pemberton, 1995, 1999, 2002).

Given the absence of a single effective control method, an integrated approach combining various water caltrop suppression methods is currently considered most suitable for managing water caltrop infestations (Naylor, 2003; Pinardi et al., 2011; Poovey & Getsinger, 2007; Villa et al., 2017; Waterfield et al., 2010). In future, exploration of the most effective combinations of existing control methods together with the development of novel approaches can enhance control efforts. For instance, ultrasound tested in controlled experiments shows potential for application in water caltrop management, although further research and technical advances are needed before field applications can proceed (Wu & Wu, 2006, 2007). Also, dredging has been proposed as a management strategy to reduce sediment build-up and mitigate water caltrop overgrowth (Li et al., 2010). Reducing nutrient and other pollutant input to improve water quality should also reduce productivity and thus facilitate the management of extensive *Trapa* beds linked to anthropogenic eutrophication, especially in the non-native range (Frey et al., 2017; Kiviat, 1993). For effective control, the measures should be applied before the onset of fruit formation (Hook, 1977; Poudel et al., 2023) and repeated within the season or from year to year (Galanti et al., 1990; Hook, 1977).

12 | GLOBAL HETEROGENEITY

A large variation in the vegetative and reproductive attributes of *T. natans* has been documented worldwide (Arima, Hoque, et al., 1999; Suriyagoda et al., 2007). Suriyagoda et al. (2007) assessed the growth and fruit yield of 17 water caltrop lines sampled in southern Europe and Asia. European lines originating from high latitudes developed fewer rosettes per unit area, had a low canopy density, flowered earlier, displayed earlier life cycle completion, and were prone to producing a larger number of smaller fruits per rosette, though the number of fruits per m^2 was nevertheless lower. A higher rosette density was detected in all Asian lines. The yield was higher in the lines originating from China compared with the other lines due to larger fruits, regardless of the reduced fruit count per rosette. The Chinese and Indian lines had similar yield performance. Lines from Korea and Japan generated a greater amount of small fruits

per unit of area. Both the fruit size and shape (i.e. height, width and spines) showed great variability, causing physical damage and handling problems during fruit harvest and processing. The vegetative growth attributes and yield performance of several Asian (Japanese and Chinese) *T. natans* lines have additionally been investigated by Arima, Hoque, et al. (1999). Big Chinese fruit lines developed buoyant leaves earlier, had higher foliage formation rates and maintained them longer compared with the Japanese lines. Despite a higher number of rosettes, Japan's small fruit lines had the shortest growing period. The large water caltrop fruit lines were more productive than the medium or small fruit lines. The fruit yield and fresh weight of well-ripened fruit were 1–5 g and 250–400 g m^{-2} for the small-fruited lines, 5–10 g and 600 g m^{-2} for the medium-fruited lines and greater than 10 g and 600–1000 g m^{-2} for the large-fruited lines, respectively. With decreasing fruit size of the lines, the number of fruits per m^2 increased. While altogether these studies already document a huge variation in the productivity of water caltrop in its native range, investigations on intraspecific variation from lines and populations of various native (as well as non-native) countries so far not included will be necessary to get a comprehensive overview.

AUTHOR CONTRIBUTIONS

Natalie Palm authored the initial draft, incorporated edits and finalized the manuscript. Andreas H. Schweiger and Jürgen Franzaring provided supervision throughout the writing process and contributed to enhancing previous iterations of the manuscript.

ACKNOWLEDGEMENTS

This study was financially supported by the Anton & Petra Ehrmann Stiftung Research Training Group Water–People–Agriculture (WPA) associated with the University of Hohenheim. The authors thank Paula Olías Garcia for illustrating. We are grateful to Bernd Blossey and Wade Simmons, who have contributed their time and scientific intellect when giving advice on enhancing a previous manuscript draft. We are thankful for the constructive feedback provided by all editors and reviewers, including Erik Kiviat (kiviat@bard.edu). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14372.

DATA AVAILABILITY STATEMENT

Data are available from the figshare repository: https://doi.org/10.6084/m9.figshare.26132035.v1 (Palm et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Overview of accepted *Trapa* L. species with synonyms and synonym type. Data extracted from POWO (2023).

Table S2: Overview of accepted *Trapa natans* L. varieties with synonyms and synonym type. Data extracted from POWO (2023).

How to cite this article: Palm, N., Franzaring, J., & Schweiger, A. H. (2024). International Biological Flora: *Trapa natans*. *Journal of Ecology*, *112*, 2386–2420. https://doi.org/10.1111/1365-2745.14372