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ORIGINAL PAPER

The invasion history of *Elodea canadensis* and *E. nuttallii* (Hydrocharitaceae) in Italy from herbarium accessions, field records and historical literature

Fabrizio Buldrini · Giovanna Pezzi · Martina Barbero · Alessandro Alessandrini · Lucia Amadei · Sebastiano Andreatta · Nicola Maria Giuseppe Ardenghi · Stefano Armiraglio · Simonetta Bagella · Rossano Bolpagni · Ilaria Bonini · Daniela Bouvet · Lisa Brancaleoni · Giuseppe Brundu · Massimo Buccheri · Gabriella Buffa · Simona Ceschin · Alessandro Chiarucci · Annalena Cogoni · Gianniantonio Domina · Luigi Forte · Riccardo Guarino · Leonardo Gubellini · Laura Guglielmone · Nicole Hofmann · Mauro Iberite · Lorenzo Lastrucci · Fernando Lucchese · Rossella Marcucci · Giacomo Mei · Umberto Mossetti · Juri Nascimbene · Nicodemo Giuseppe Passalacqua · Simonetta Peccenini · Filippo Prosser · Giovanni Repetto · Gabriele Rinaldi · Enrico Romani · Leonardo Rosati · Annalisa Santangelo · Anna Scoppola · Giovanni Spampinato · Adriano Stinca · Maria Tavano · Fulvio Tomsich Caruso · Roberta Vangelisti · Roberto Venanzoni · Marisa Vidali · Thomas Wilhalm · Francesco Zonca · Carla Lambertini

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Abstract We analysed the invasion history of two North American macrophytes (*Elodea canadensis* and *E. nuttallii*) in Italy, through an accurate census of all available herbarium and field records, dating between 1850 and 2019, and a rich literature collection describing the initial introduction and naturalisation phase that supports the results obtained by the occurrence records. *Elodea canadensis* arrived in Italy before 1866 and had two invasion phases, between the 1890s and 1920s and between the 1990s and 2000s; *E. nuttallii*, probably arrived in the 1970s, started invading in 2000 and the invasion is still ongoing. Botanical gardens and fish farming played a crucial role in dispersal and naturalisation of both species. The current invasion range of both species is centred in northern Italy, with scattered occurrences of *E. canadensis* in central and southern regions. River Po represents a dispersal barrier to the Mediterranean region and a strategic monitoring site to prevent the invasion in the peninsula. The study detects differences in the niches of the two species during the introduction and naturalisation phase and a habitat switch occurred after 1980 in *E. canadensis* and after 2000 in *E. nuttallii*, during their expansion phases. For *E. canadensis* the switch corresponds to the second invasion round. Further research can clarify whether the second invasion round is due to confusion of the recently introduced *E. nuttallii* with *E. canadensis*, to a cryptic introduction of a new genotype, to post-introduction evolution, or just to an increased scientific interest in biological invasions.

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F. Buldrini (✉) · G. Pezzi · M. Barbero · A. Chiarucci · J. Nascimbene
BIOME Lab - Dipartimento di Scienze Biologiche, Geologiche e Ambientali, Università di Bologna, Via Irnerio 42, 40126 Bologna, Italy
e-mail: fabrizio.buldrini@unibo.it

F. Buldrini · U. Mossetti
Sistema Museale di Ateneo, Università di Bologna, Via Irnerio 42, 40126 Bologna, Italy

A. Alessandrini
Istituto per i Beni Artistici, Culturali e Naturali della Regione Emilia-Romagna, Via Galliera 21, 40121 Bologna, Italy

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L. Amadei · R. Vangelisti
Herbarium Horti Pisani (PI) - Orto e Museo Botanico, Università di Pisa, Via L. Ghini 13, 56126 Pisa , Italy

S. Andreatta
Museo Civico di Storia Naturale di Verona, Piazza Arsenale 8, 37126 Verona, Italy

N. M. G. Ardenghi
Orto Botanico – Sistema Museale di Ateneo, Università degli Studi di Pavia, Via S. Epifanio 14, 27100 Pavia, Italy

S. Armiraglio
Museo Civico di Scienze Naturali di Brescia, Via A.F. Ozanam 4, 25128 Brescia, Italy

S. Bagella
Dipartimento di Scienze Chimiche, Fisiche, Matematiche e Naturali, Università degli Studi di Sassari, Via Piandanna 4, 07100 Sassari, Italy

R. Bolpagni
Dipartimento di Chimica, Scienze della Vita e della Sostenibilità Ambientale, Università degli Studi di Parma, Viale delle Scienze 11/a, 43124 Parma, Italy

I. Bonini
Museo Botanico - Dipartimento di Scienze della Vita, Università di Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

D. Bouvet · L. Guglielmone
Erbario - Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università degli Studi di Torino, Viale P.A. Mattioli 25, 10125 Turin, Italy

L. Brancaleoni
Dipartimento di Scienze dell'ambiente e della Prevenzione, Università degli Studi di Ferrara, Corso Ercole I d'Este 32, 44121 Ferrara, Italy

G. Brundu
Dipartimento di Agraria, Università degli Studi di Sassari, Viale Italia 39, 07100 Sassari, Italy

M. Buccheri
Museo Friulano di Storia Naturale, Via C. Gradenigo Sabbadini 22-32, 33100 Udine, Italy

G. Buffa
Dipartimento di Scienze Ambientali, Informatica e Statistica, Università Ca' Foscari Venezia, Via Torino 155, 30172 Venice, Italy

S. Ceschin · F. Lucchese
Dipartimento di Scienze, Università di Roma Tre, Viale G. Marconi 446, 00146 Rome, Italy

A. Cogoni
Dipartimento di Scienze della Vita e dell'Ambiente – Sezione Botanica, Herbarium CAG, Università degli Studi di Cagliari, Viale Sant'Ignazio da Laconi 13, 09123 Cagliari, Italy

G. Domina
Dipartimento di Scienze Agrarie, Alimentari e Forestali, Università degli Studi di Palermo, Viale delle Scienze, Edificio 4, 90128 Palermo, Italy

L. Forte
Dipartimento di Biologia - Museo Orto Botanico, Università degli Studi di Bari «Aldo Moro». Campus Universitario, Via Orabona 4, 70125 Bari, Italy

R. Guarino
Dipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche (STEBICEF), Università degli Studi di Palermo, Via Archirafi 20, 90123 Palermo, Italy

L. Gubellini · N. Hofmann
Centro Ricerche Floristiche Marche «A.J.B. Brilli-Cattarini», Via E. Barsanti 18, 61122 Pesaro, Italy

M. Iberite
Dipartimento di Biologia Ambientale, Sapienza Università di Roma, P.le A. Moro 5, 00185 Rome, Italy

L. Lastrucci
Museo di Storia Naturale dell'Università di Firenze – Collezioni di Botanica, Via G. La Pira 4, 50121 Florence, Italy

R. Marcucci
Museo Botanico-Erbario (PAD), Università di Padova, Via Orto Botanico 15, 35123 Padua, Italy

G. Mei
Dipartimento di Scienze Agroambientali e Territoriali, Università degli Studi di Bari «Aldo Moro», Via G. Amendola 165/A, 70126 Bari, Italy

N. G. Passalacqua
Dipartimento di Biologia, Ecologia e Scienze della Terra, Università della Calabria, Via P. Bucci, Cubo 4B, 87030 Arcavacata di Rende (CS), Italy

N. G. Passalacqua
Museo di Storia Naturale della Calabria ed Orto Botanico, Università della Calabria, Via Savinio loc. Polifunzionale, 87030 Arcavacata di Rende (CS), Italy

S. Peccenini
Dipartimento di Scienze della Terra, dell'Ambiente e della Vita, Università degli Studi di Genova, Corso Europa 26, 16132 Genoa, Italy

F. Prosser
Fondazione Museo Civico di Rovereto, Largo S. Caterina 41, 38068 Rovereto (TN), Italy

G. Repetto
Museo Civico Archeologico e di Scienze Naturali «Federico Eusebio», Via Vittorio Emanuele II 19, 12051 Alba (CN), Italy

G. Rinaldi · F. Zonca
Orto Botanico di Bergamo «Lorenzo Rota», Passaggio Torre d'Adalberto 2, 24129 Bergamo, Italy

E. Romani
Museo Civico di Storia Naturale di Piacenza, Via G.B. Scalabrini 107, 29121 Piacenza, Italy

L. Rosati
Scuola di Scienze Agrarie, Forestali, Alimentari e Ambientali, Università della Basilicata, Via dell'Ateneo Lucano 10, 85100 Potenza, Italy

A. Santangelo
Dipartimento di Biologia, Orto Botanico, Università degli Studi di Napoli Federico II, Via Foria 223, 80139 Naples, Italy

A. Scoppola
Dipartimento di Scienze Agrarie e Forestali, Università degli Studi della Tuscia, Via San Camillo de' Lellis s.n.c., 01100 Viterbo, Italy

G. Spampinato
Dipartimento di Agraria, Università Mediterranea di Reggio Calabria, Loc. Feo di Vito s.n.c., 89122 Reggio Calabria, Italy

A. Stinca
Dipartimento di Scienze e Tecnologie Ambientali, Biologiche e Farmaceutiche, Università della Campania Luigi Vanvitelli, Via A. Vivaldi 43, 81100 Caserta, Italy

M. Tavano
Museo Civico di Storia Naturale «Giacomo Doria», Via Brigata Liguria 9, 16121 Genoa, Italy

F. Tomsich Caruso
Museo Civico di Storia Naturale di Trieste, Via dei Tominz 4, 34139 Trieste, Italy

R. Venanzoni
Dipartimento di Chimica, Biologia e Biotecnologie, Università di Perugia, Via del Giochetto 6 (Edificio A), 06122 Perugia, Italy

M. Vidali
Dipartimento di Scienze della Vita, Università di Trieste, Via L. Giorgieri 5, 34127 Trieste, Italy

T. Wilhalm
Museo di Scienze Naturali dell'Alto Adige, Via Bottai 1, 39100 Bolzano, Italy

C. Lambertini
Dipartimento di Bioscienze, Università di Milano, Via G. Celoria 26, 20133 Milan, Italy

Introduction

Biological invasions are one of the great challenges that ecosystems are facing under a scenario of global climate change and increasing human pressure (Simberloff and Rejmánek 2012; Pyšek et al. 2020). This is especially true for freshwater ecosystems, which are among the most threatened of the Earth (Brundu 2015) and most affected by biological invasions (Pyšek et al. 2010; Bolpagni 2021). On a European scale, for example, out of 36 invasive plant species of European Union concern, 13 are hydro- or hygrophilous plants (EU Regulation no. 1143/2014; European Commission 2017, 2019). Aquatic invasions are associated with the almost total alteration of aquatic habitats and trophic conditions by human activities (Wärner et al. 2011; Brundu 2015): the most invaded areas are, in fact, the most economically developed and densely populated (Malavasi et al. 2018; Boscutti et al. 2022). Human pressure and disturbance provide windows of opportunity for which alien species are extremely competitive (Pyšek and Prach 1994; Pyšek et al. 1998; Brundu et al. 2012; Bolpagni 2021). Since 1945, the number and abundance of aquatic alien species have increased because of increased trade (mostly as ornamental and aquarium species, but also for scientific research and phytoremediation—Kay and Hoyle 2001; Brundu 2015), water eutrophication and global warming (Hussner 2009; Bolpagni et al. 2015; Lazzaro et al. 2020). Shifted species assemblages have profoundly modified aquatic biodiversity and ecosystem functioning in many European wetlands (Rodríguez-Merino et al. 2018).

Diversity changes in plant communities are generally well documented in herbarium collections, because the new incomers spark scientific interest for their systematic or environmental significance, especially in the early stage of invasion (Stinca et al. 2021; Spampinato et al. 2022). Herbaria are important sources of historical data, especially for ecosystems like wetlands that have undergone dramatic changes in the last centuries (Domina et al. 2020). Despite the many biases associated with opportunistic and non-systematic plant collections (Daru et al. 2018), herbaria can be considered as unique repositories of phytogeographical data and one of the most accurate data sources to reconstruct events that occurred in the past. Therefore, the role of herbarium records has widened in recent years, from

Fig. 1 Close-up of the terminal part of a sterile branch of *Elodea canadensis*. Note the leaves with apex obtuse or nearly rounded. Photograph taken by A. Moro—http://dryades.eu—, Madrisio (municipality of Fagagnana del Friuli), 23-04-2005. License CC BY-SA 4.0

Fig. 2 Close-up of the terminal part of a branch of *Elodea nuttalli*. Note the leaves linear-lanceolate, curved, with apex acute and nearly acuminate. Photograph taken by Andrea and Riccardo Truzzi—http://dryades.eu—, Civico Museo di Storia Naturale, Milano—La Flora Esotica Lombarda. License CC BY-SA 4.0

cataloging the diversity of life to documenting biodiversity changes (Muller 2016; Nualart et al. 2017; Lang et al. 2019) and tracing spatio-temporal invasion patterns (Lavoie 2013; Muller 2015).

Elodea canadensis Michx. (Hydrocharitaceae; Fig. 1) is a submersed macrophyte with a long invasion history in Europe, resulting in a large number of specimens in the European and Italian public herbaria. Its invasion history is particularly interesting because, about one century after its introduction, another closely related species, *E. nuttallii* (Planch.) H. St. John (Fig. 2), was recorded in Europe and has ever since competed with *E. canadensis* for the same habitat, and even outcompeted it in many of the habitats previously invaded by the latter (Simpson 1990; Erhard and Gross 2006; Greulich and Trémolières 2006; Zehnsdorf et al. 2015). The first records of these species in Europe date back to 1836 (Northern Ireland) for *E. canadensis* and 1939 (Belgium) for *E. nuttallii* (Wolff 1980; Simpson 1984). The more aggressive invasion by *E. nuttallii* suggests that *E. canadensis* invasion should be slowing down or even declining (post-invasion status), whereas *E. nuttalli* should be in a phase of exponential spread. *E. nuttallii* is in fact shortlisted among the invasive alien species of European Union concern for which early eradication and/or control are mandatory (European Commission 2017, 2019).

Both species are perennial rooting hydrophytes, native to stagnant to flowing freshwaters of North America. The leaf shape can distinguish them: from ovate to linear-oblong (occasionally linear-lanceolate) with apex broadly acute to obtuse in *E. canadensis*, linear or linear-lanceolate with apex narrowly acute to acuminate in *E. nuttallii* (Simpson 1988). Apart from these slight morphological differences, the two species have analogous ecological needs: there are no precise limits between the functional niches of *E. canadensis* and *E. nuttallii*, so that they were defined as true ecological redundants (Hérault et al. 2008; Bubíková et al. 2021). Both have fast growth and spreading ability, due to their exclusively vegetative propagation (only female individuals are known in Europe, see Walters 1980), and high phenotypic plasticity (Agrawal 2001; Hérault et al. 2008; Riis et al. 2010; Kočić et al. 2014), excellent qualities for invasive species. In Italy, two morphotypes are known for *E. nuttallii*, often co-occurring, and cases of intra-individual heterophylly were also reported; one morphotype has short and curved leaves, the other has long and flat or more or less twisted leaves (Banfi and Galasso 2010). In Europe, the latter was sometimes interpreted as a separate species, *E. callitrichoides* (Rich.) Casp. (e.g. Wolff 1980; Vanderpoorten et al. 2000), but morphological and genetic analyses demonstrated that these morphotypes are two different phenotypes of the same species, *E. nuttallii* (Vanderpoorten et al. 2000). This phenotypic variability confounds the taxonomy of the two *Elodea* species and contributes to their misidentification (cfr. Kočić et al. 2014 and references therein).

Because of their large and dense monospecific populations, *E. canadensis* and *E. nuttallii* are considered ecosystem-transforming species (Buccheri et al. 2019). Communities dominated or co-dominated by *E. canadensis* and/or *E. nuttalli* are included in the *Potametea pectinati* Klika in Klika & V. Novák 1941 syntaxonomic class, and represent about 10% of aquatic alien-dominated plant communities in Italy (cfr. Viciani et al. 2020; Castello et al. 2021).

The aim of this study was to reconstruct the invasion history, dynamics and current distribution of *E. canadensis* and *E. nuttallii* in Italy based on occurrences from herbarium specimens, field records and historical literature.

Since many new alien species are continuously arriving in Europe and Italy, we aimed at understanding a posteriori what happened in the first invasion phases of these two hydrophytes, to learn from past invasions how to interpret, monitor and manage current and future introductions of alien aquatic plant species.

Materials and methods

Data sources

Occurrence records of *E. canadensis* and *E. nuttallii* dating between 1850 and 2019 were collected from June 2019 to November 2020 from 41 independent sources, including 36 Italian herbaria owned by Italian universities or scientific museums and 4 private herbaria (hereafter mentioned as «herbarium records»; herbarium identification codes follow Thiers 2022). Additional data were collected from published sources (floristic checklists, local floras or other floristic records; hereafter «published records») and from unpublished floristic or vegetation data (observations, relevés etc.) collected in the field by the authors in the period 1990–2020 (hereafter «field records»).

Herbarium specimens were searched through the currently accepted names and their synonyms; in particular, for *E. canadensis* we searched for *Anacharis alsinastrum* Planch., *A. canadensis* (Michx.) Planch., *Elodea canadensis* Michx., *Philotria canadensis* (Michx.) Britton, while for *E. nuttalli* we searched for *Anacharis nuttallii* Planch. and *Philotria nuttallii* (Planch.) Rydb. Species identification was checked and corrected, whenever necessary, by the authors and herbarium curators.

In total, our database included 1131 records (877 of *E. canadensis*, 254 of *E. nuttallii*), of which 506 herbarium records, 584 published records and 41 field records (Supplementary material).

A parallel historical literature search, describing the introduction history of *E. canadensis* and *E. nuttallii* to Italy until their inclusion in the Italian flora, served as a reference to crosscheck introduction pathways, dates, and localities (hereafter «historical literature»). For *E. canadensis* we searched on Google Books (https://books.google.com) in October 2020, using the key words «*Elodea canadensis*» and the previously mentioned synonyms. We selected only Italian sources dating between 1850 and 1900. For *E. nuttalli*, that was introduced in more recent times, we also screened grey literature accompanying the first field records of the species in Italy, between 1985 and 2005.

Standardising and georeferencing data

For each occurrence record we retained the following information: coordinates (when available) and/or location (i.e. described locality), collection date, habitat and collector.

When coordinates were not available, the occurrences were georeferenced based on the locality description using *Google Hybrid* maps available in QGIS (Imagery 2021, © Google) and the toponym layer repository available on the Geoportale Nazionale (http://wms.pcn.minambiente.it/ogc?map=/ms_ogc/WMS_v1.3/Vettoriali/Toponimi_2011.map). If a locality corresponded to an administrative division (municipality, province, region), the coordinates were referred to the centroid of that unit. For this purpose, the ISTAT (National Institute of Statistics, www.istat.it) polygon layers of the administrative boundaries chronologically closest to the collection date of a record were used. ISTAT layers are available about every 10 years from 1861 to 2001 and every year from 2002 to today. Overall, for 632 records the coordinates were already available; for 314 records the coordinates were obtained by finding the locality using *Google Hybrid*; 170 records were referred to the centroid of the administrative unit: 109 to the municipality level, 48 to the province level, 13 to the region level. Only 14 records had no spatial data. The reference system used for all coordinate pairs was WGS84 (EPSG 4326). A radius was associated to each pair of coordinates in order to measure the uncertainty of a locality linked to the georeferencing procedure.

Concerning collection date, 755 records had a complete date (day, month and year), 52 had only month and year, 255 had only the year, 68 had no date.

After removing records missing spatial and/or temporal information, the final dataset consisted in 805 records of *E. canadensis* and 248 records of *E. nuttallii*.

Finally, habitat information derived from the herbarium specimen labels, which was reported in a wide range of formats, was classified into the following 13 habitat types: BAS (basins, fountains, troughs and small artificial water bodies with still water), BGA (botanical gardens), BOG (bogs and peatlands), CAN (artificial canals, including city canals, wastewater canals, agricultural ditches and any man-made canals with running water), LAK (natural lakes), MAR (marshes and swamps), PIS (pisciculture ponds), PON (natural ponds), RIV (natural rivers), RFI (rice pads and associated ditches), SPR (springs), WET (wet meadows, flooded forests) and OTH (other habitats, occasional in frequency or poorly described, like woodlands, fields, filtering systems, etc.).

Data analysis

Occurrence mapping

For each of the two *Elodea* species, we mapped the occurrence records in different time periods in order to observe different invasion phases. Four distribution maps were produced for *E. canadensis* (periods 1850–1900, 1901–1950, 1951–1980 and 1981–2019) and two for *E. nuttallii* (1980–2000 and 2001–2019).

In order to avoid redundancy and reduce the bias associated with different collection efforts in different areas, while maintaining spatial information (Antunes and Schamp 2017), the georeferenced records of each species were thinned by overlaying a grid and extracting only one record per grid-cell per year. For this purpose we used the Italian 177 cells of the 10 × 10 km grid by Cervellini et al. (2020), that follows the requirements of article 17 of the Habitats Directive (92/43/EEC). Each grid-cell is assigned to one European biogeographical region and indicates Nature 2000 habitats that it contains (Cervellini et al. 2020). We used gridded data for the period 2000–2019, to test differences between the two species in biogeographic distribution, habitats threatened by the occurrence of the species within the cell, and main land use. For land use we extrapolated the amount of urban and agricultural areas in cells where the two species occur or co-occur by intersecting the grid cells with the 2012 CORINE Land Cover layer (www.isprambiente.gov.it). Differences between agricultural and urban areas were tested between species with a one way-ANOVA (PAST 4.03; Hammer et al. 2001). Data mapping and spatial analysis were performed with QGIS version 3.12.2 (www.qgis.org).

Invasion curves

Invasion curves based on cumulative numbers of occurrence records over time can define three main invasion phases: lag, exponential growth and plateau (Pyšek and Prach 1993; Blackburn et al. 2011; Antunes and Schamp 2017). The temporal length of these three phases and the rate of spread, defined by the derivative of the curve, can vary from species to species (Crawford and Hoagland 2009; Antunes and Schamp 2017; Ceschin et al. 2018) and can be useful to understand, a posteriori, how invasions evolved. We used the thinned and gridded dataset of records to construct the invasion curves of *E. canadensis* and *E. nuttallii* in Italy and calculate the curve slope of their linear models.

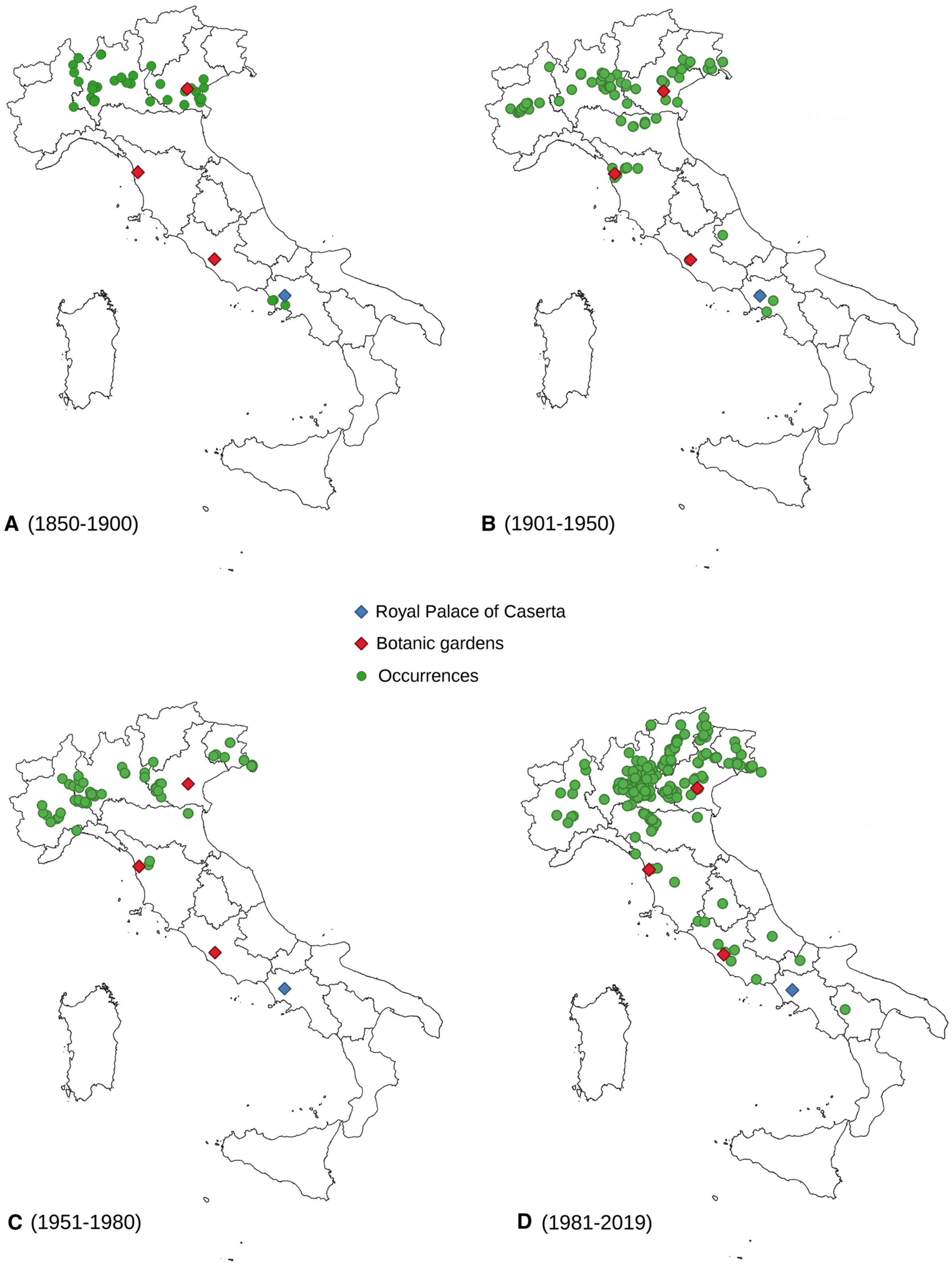
Results

Invasion history from occurrence records and historical literature

A herbarium specimen of *E. canadensis* with a hypothetical date (1880?) from the Province of Mantova in northern Italy (*Leg*. F. Masè, s.d., in MSPC; Table 1) might be the most ancient specimen on a national scale if the collection date could be confirmed. The first certain herbarium accessions are two samples of 1888 collected in northern Italy, around Lake Como (*Leg*. M. Longa, 7–1888, in FI; *Leg*. M. Longa, *det.*

Table 1 Herbarium specimens cited in the text. Collection places, original scientific names reported on the labels and a translation of the collection place description are also provided

Locality	Herbarium specimen citation	Translation
Province of Mantova, 1880?	*Leg*. F. Masè, s.d., in MSPC: «Casteldario (Mantova)», sub *Anacharis alsinastrum*	Municipality of Casteldario (province of Mantova)
Como Lake, 1888	*Leg*. M. Longa, 7–1888, in FI: «In aqua fluente et stagnante prope pagum Colico», sub *Elodea canadensis* Casp.	In running and stagnant waters near the village of Colico
	Leg. M. Longa, *det*. G. Camperio, 7–1888, in FI: «Colico, nei dintorni, in acqua corrente e stagnante», sub *Elodea canadensis* Rich	Colico and nearby water bodies, in running and stagnant waters
Pisa Botanic Garden, 1892	*Leg*. P. Pellegrini, 6–1892, in PI: «Orto Botanico Pisano»	Pisa Botanic Garden
Province of Padova, 1892	*Leg*. U. Ugolini, 1892, in PAD: «Fossi di Vanzo, Padova»	Ditches in Vanzo, [province of] Padova
Padova, 1894	*Leg*. Adr. Fiori, 6–1894, in FI: «Fossi entro Padova, inselvatichita», sub *Elodea canadensis* Michx	Naturalised in ditches within Padova town
Padova, 1895	*Leg*. L. Vaccari, 11–1895, in FI: «Orto Agrario Pat. fossi (Padova)», sub *Elodea canadensis* Rich	Agricultural Garden ditches (Padova)
Rome, 1899	*Leg*. E. Chiovenda, 23-5-1899, in BOLO: «Nelle vasche del R. Orto Botanico di Roma», sub *Elodea canadensis* Rich	In the ponds of the Royal Botanic Garden of Rome
Around Rome, 1901	*Leg*. E. Chiovenda, 17-9-1901, in BOLO: «Abbondantissima nel Collettore generale delle acque alte della bonifica di Maccarese», sub *Elodea canadensis* Rich	very abundant in the General drainage canal of the high waters in the land reclamation area of Maccarese (Rome)
Around Pisa, 1913	*Leg*. M. Savelli, 16-10-1913, in FI: «Pisa: abbondante nei fossi d'acqua lentamente scorrente mista a *Vallisneria spiralis* Linn. subito fuori dalla porta a Lucca lungo la via di S. Giuliano», sub *Anacharis canadensis* (Michx.) Planch	Pisa: abundant in the ditches of slowly flowing water, mixed with *V. spiralis* L., just out of the city door to Lucca along the road to S. Giuliano


A (1850-1900)
B (1901-1950)
Royal Palace of Caserta
Botanic gardens
Occurrences
C (1951-1980)
D (1981-2019)

◂**Fig. 3** Reconstruction based on herbarium records of the distribution of *Elodea canadensis* in different temporal ranges. Botanic gardens and the Royal Park of Caserta, in which, according to the literature, the species was cultivated, are also shown with red and blue diamonds respectively. NE is the Botanic Garden of Padova, W-centre is the Botanic Garden of Pisa and SW is the Botanic Garden of Rome

G. Camperio, 7–1888, in FI; Table 1). The first Italian published record that we could trace in the historical literature, documenting the occurrence of *E. canadensis* in the wild, dates back to 1873 (Goiran 1897: San Michele Extra, near Verona, northern Italy). However, for some years before 1873 the species had been the object of an intense samples' exchange for scientific research: in 1866 *E. canadensis* was sent to Mantova botanic garden, in 1867 it was introduced in the Botanic Garden of Padova and, shortly thereafter, it started naturalising in the Italian territory (Paglia 1879; Bozzi 1888; Banfi and Galasso 2010). The species was included in the Italian national flora in 1908 (Fiori and Paoletti 1896–1908). The historical literature shows that the species was present in Europe in the nineteenth century and was cited for the first time in Italian literature by Antonio Stoppani (1873), who reported a possible introduction to northern Europe from North America with timber rafts and documented the invasive spreading in European freshwater causing problems to river navigation. Between 1873 and 1908, the species was used in fish farming and its response to carbon and light was tested experimentally (Tolomei 1893). Some scientists even suggested its introduction in malarial wetlands (Gasperini 1890) as a natural remedy against mosquitoes (note that in Italy malaria was eradicated only in the 1950s).

The herbarium records show that in 1900 *E. canadensis* was already naturalised and widespread in northern Italy, while in the Mediterranean region it was cultivated in the Botanic Gardens of Pisa (*Leg.* P. Pellegrini, 6–1892, in PI) and Rome (*Leg.* E. Chiovenda, 23-5-1899, in BOLO) and occurred in canals nearby and fishponds of the Royal Palace of Caserta, in southern Italy (Fiori 1895; Fig. 3a). At the end of 1800 it was naturalised in ditches in the territory of Padova, in northern Italy: three herbarium specimens prove the occurrence of *E. canadensis* in the countryside ca. 25 km from Padova (*Leg.* U. Ugolini, 1892, in PAD), in town (*Leg.* Adr. Fiori, 6–1894, in FI), and in the ditches of Padova Agricultural Garden (*Leg.* L. Vaccari, 11–1895, in FI; Table 1). In the subsequent years the expansion was more intense in the continental (northern Italy) than in the Mediterranean region (Fig. 3b, c, d). Additional herbarium specimens come from new streams close to Padova Botanic Garden and the Royal Palace of Caserta (1901–1950, Fig. 3b) and from streams close to Pisa Botanic Garden (1901–2019, Fig. 3b, c, d). According to our reconstruction, the most aggressive invasion phase was in the period 1980–2019 (Fig. 3d), that counts 545 more herbarium records than in the period 1950–1980 (Fig. 3c). In the most recent map (1981–2019, Fig. 33333d) it is possible to identify long river stretches invaded by *E. canadensis* along the north–south valleys of big Italian rivers that originate in the Alps, and scattered occurrences in the Mediterranean region that cannot be obviously connected to botanic gardens or other sources.

The first Italian herbarium record of *E. nuttalli* dates back to 1989 and comes from the Lake Idro, in northern Italy; it is preserved at the Herbarium of Rovereto (ROV) and was first cited in the literature some years later (Desfayes 1995; Selvaggi and Dellavedova 2016). The species was subsequently observed in nearby areas (Zanotti 2000) and was included in the checklist of the Italian vascular flora in 2005 (Conti et al. 2005). In Italy, the introduction of *E. nuttallii* was due to the trade of ornamental species for artificial ponds and aquaria (Banfi and Galasso 2010). In other parts of Europe, the species was first found in Belgium in 1939, likely carried by migrating waterfowls (Verloove 2006); however, it is plausible that the species went unobserved for a long time, given the morphological and taxonomic similarity to *E. canadensis* (Walters 1980) and the presence of two different *E. canadensis* phenotypes (Banfi and Galasso 2010).

The invasion of *Elodea nuttallii* has been observed in northern Italy for the last 40 years (1980–2019). No occurrences were recorded in the Mediterranean biogeographic region of Italy so far (Fig. 4).

Invasion curves

Elodea canadensis invasion curve shows a lag phase from 1866 to 1892, an expansion phase from 1893 to 1923, and a plateau phase from 1925 to 1971 (Fig. 5). After this plateau, the curve has a second exponential rise, indicating a second phase of expansion from 1977 to today, suggesting that the invasion has not

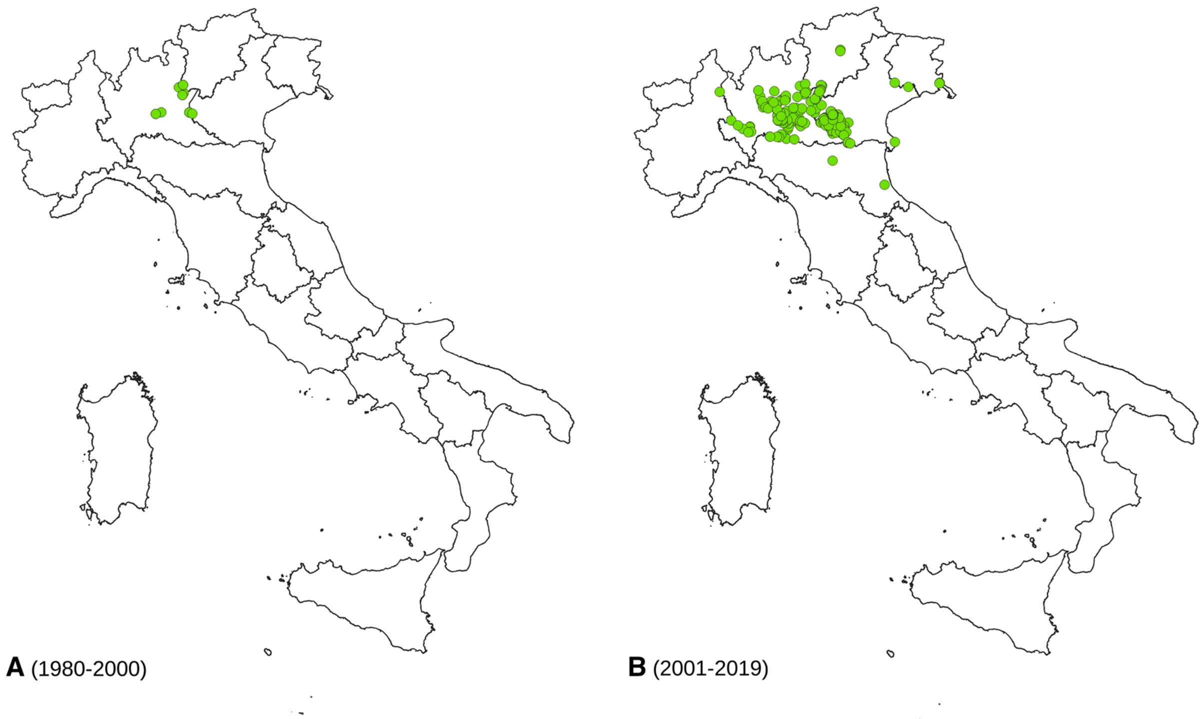


Fig. 4 Cumulative distribution of *Elodea nuttallii* records from 1980 to 2000 (**A**) and from 2001 to 2019 (**B**)

come to a halt yet. However, since 2005 the slope of this second expansion has become less steep, suggesting that the invasion is approaching the second plateau phase. The slope of the whole curve from 1866 to 2019 is quite moderate (angular coefficient of the trend line 3.03).

Elodea nuttallii had a lag phase between 1989 and 2000 and is still in the expansion phase (Fig. 5). The slope was most steep between 2000 and 2003 and the curve shows a breaking point around 2003, after which the expansion has been slowing down, suggesting that *E. nuttalli* is reaching the plateau phase too. The slope of the curve from 1989 to 2019 is quite steep (angular coefficient of the trend line 6.26). It has however to be noted that the cumulative record number remarkably differs between the two species: for *E. canadensis* it is 549, whereas for *E. nuttallii* it is only 152 (Fig. 5).

Biogeography and habitats

Both species occur in the Continental and Alpine biogeographic regions within Italy, although with notable differences in the number of occupied cells (the Continental region is more invaded than Alpine one). *E. nuttalli* occurs in the same grid cells as *E. canadensis* and only 3 cells are occupied by *E. nuttalli* alone. Only *E. canadensis* occurs in the Mediterranean region, and the number of cells occupied in the continental region in northern Italy is an order of magnitude higher than that of *E. nuttallii* (deduced by the number of cells assigned to continental, alpine and mediterranean biogeographic regions occupied by the two species).

Artificial canals (including ditches; habitat code CAN), streams (RIV) and lakes (LAK) are the most common water bodies where *E. canadensis* and *E. nuttallii* herbarium specimens were collected (Fig. 6). Until 1980, canals were the most frequent habitat for *E. canadensis* recorded in the herbarium dataset. However, from 1990 onwards the number of *E. canadensis* occurrence records from rivers and lakes increased considerably, with river records exceeding canal records in 2000–2010. *E. nuttallii* occurred almost exclusively in lakes until 2000, but in the subsequent decade it was most frequently

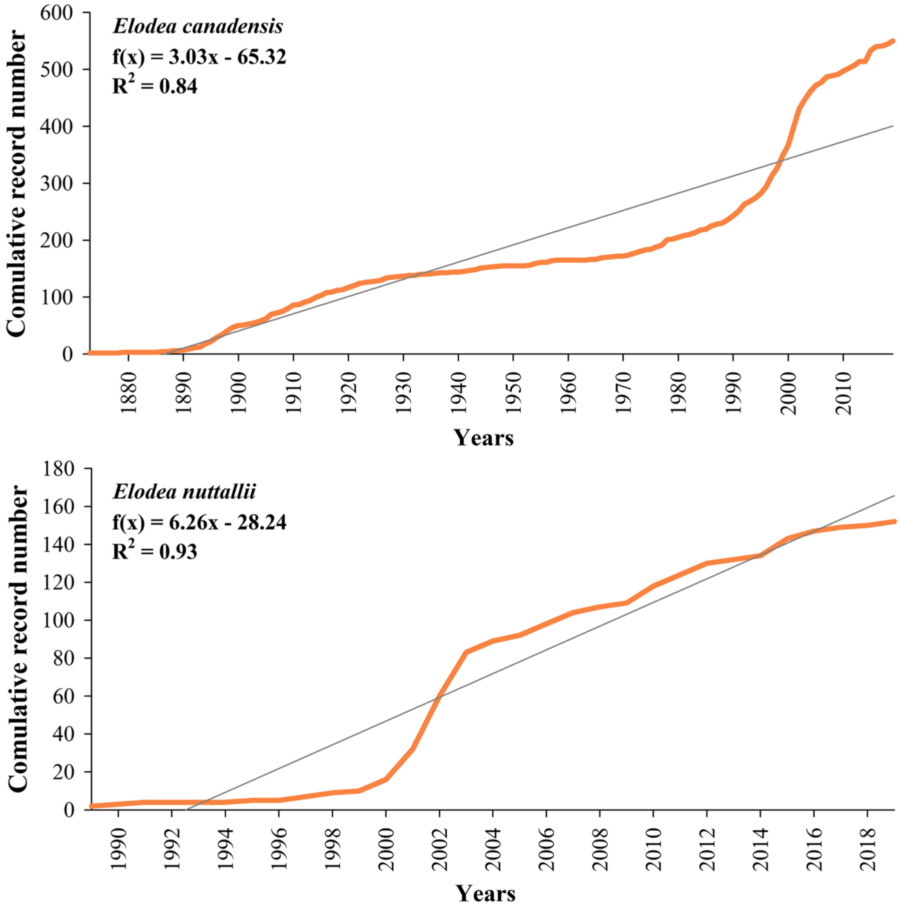


Fig. 5 Invasion curves of *Elodea canadensis* and *E. nuttallii* in Italy, based on herbarium records, published records and field records. Trend line and equation of the curve are also shown

recorded in canals and rivers. In the last 10 years, *E. canadensis* was mostly found in canals, whereas *E. nuttalli* in rivers, however differences in the number of occurrences among canals, rivers and lakes became less evident in both species.

Natura 2000 habitats (sensu Habitats Directive 92/43/EEC) that are more frequent within *Elodea* occurrence cells are 91E0* (Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior—Alno-Padion*, *Alnion incanae*, *Salicion albae*), 3260 (Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation) and 3150 (Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition*-type vegetation), both in the Continental and Alpine biogeographic regions (Fig. 7). Peat bogs (habitat 7230: Alkaline fens) and petrifying springs (habitat 7220*: Petrifying springs with tufa formation—*Cratoneurion*) are also frequent in *Elodea*-invaded cells in the Alpine region.

In the Mediterranean regions, the most frequent habitats in *Elodea*-invaded grid cells are 3140 (Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp.), 3150 (Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition*-type vegetation) and 3170* (Mediterranean temporary ponds).

Current land use in the grid cells where the two species occur is primarily agriculture (in over 50% of each grid cell) for both species. Urbanisation accounts for only about 8% in each grid cell for both species, nevertheless urbanisation percentage is significantly higher (about 14%, $P<0.001$) in cells where both species co-occur rather than in those where they occur alone (Fig. 8).

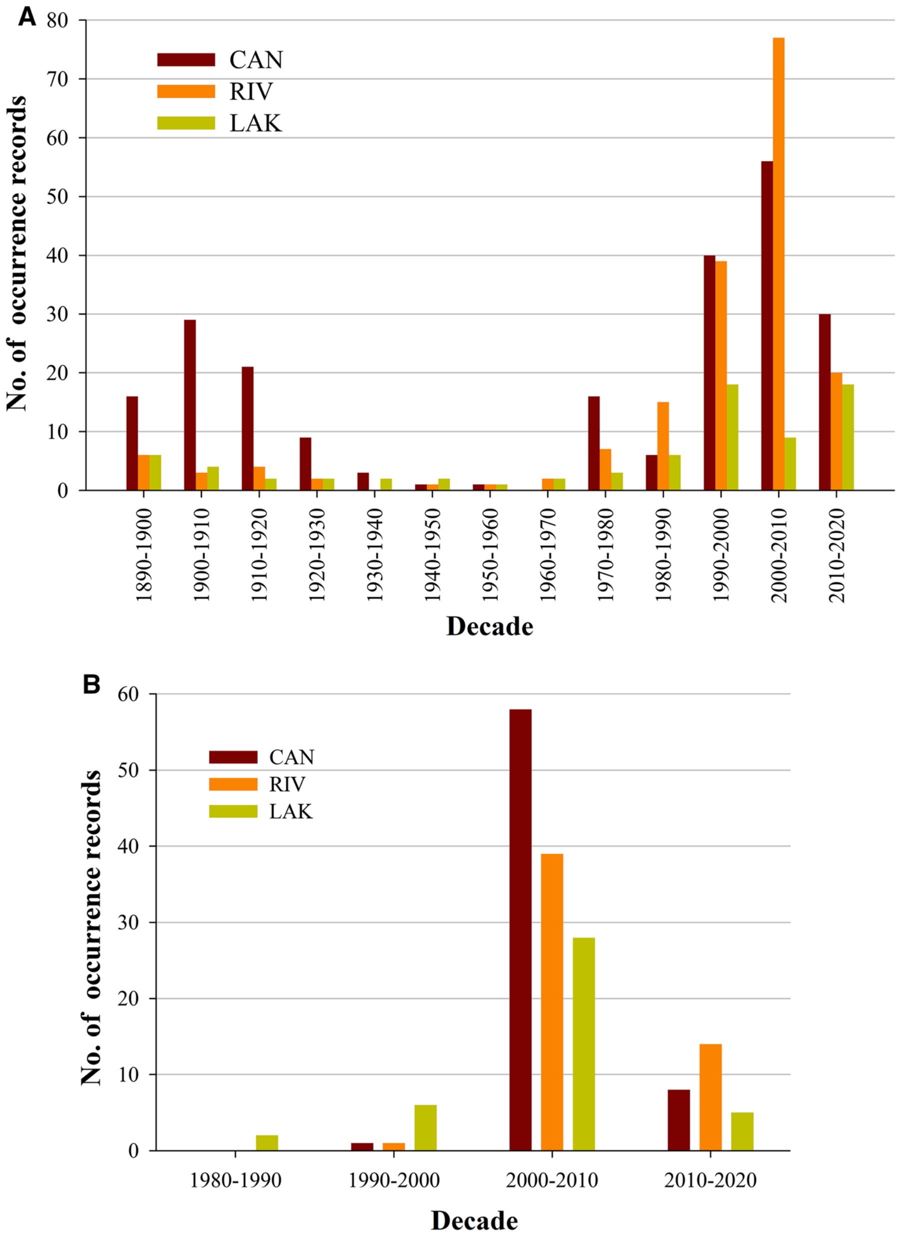


Fig. 6 Most frequent habitats of *Elodea canadensis* (**A**) and *E. nuttallii* **B** recorded in herbarium specimen labels. Abbreviations: CAN: canals, RIV: rivers, LAK: lakes

Discussion

Invasion history from occurrence records and historical literature

The first record of *E. canadensis* in Europe dates back to 1836 in the British Isles (Simpson 1984), whereas in Italy the species appeared 30 years later in parks and botanic gardens. The published records document the cultivation in the Botanic Garden of Mantova in 1866, in that of Padova in 1867, later in that of Pavia (Bozzi 1888; Banfi and Galasso 2010). In the same period, *E. canadensis* was already widespread in many parts of central Europe and was becoming so invasive that it was the most common alien aquatic species in Europe for a while (Erhard and Gross 2006; Zehnsdorf et al. 2015). The first ascertained Italian herbarium samples were collected in 1888 from northern Italy, that is the Italian area of first introduction and most impacted by the invasion.

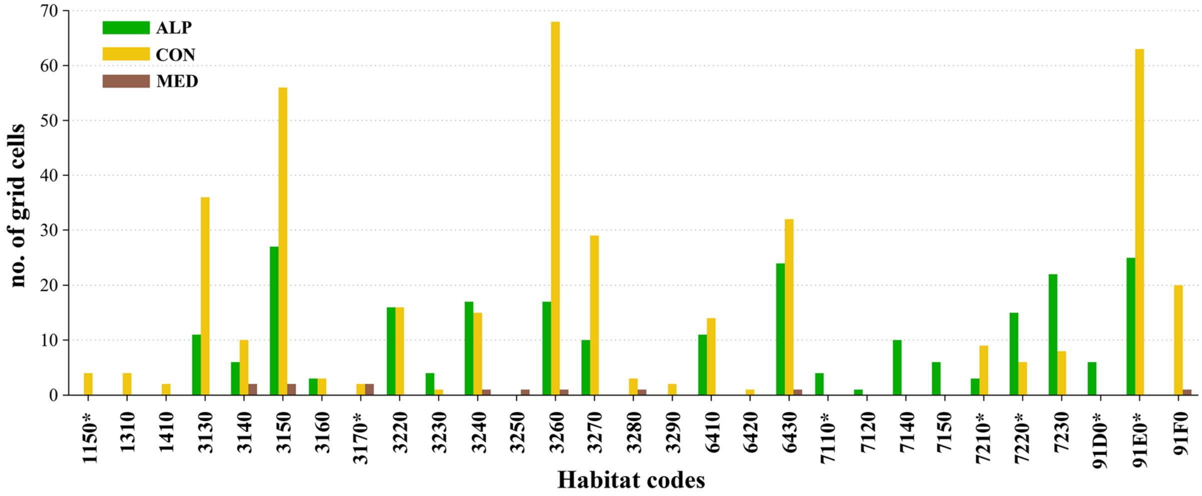


Fig. 7 Natura 2000 habitats in *Elodea canadensis* and *E. nuttallii* occurrence cells in the Alpine, Continental and Mediterranean biogeographic regions. Biogeographical regions: ALP: alpine, CON: continental, MED: Mediterranean. Explanation of habitat codes: 1150*: coastal lagoons, 1310: *Salicornia* and other annuals colonizing mud and sand, 1410: Mediterranean salt meadows (*Juncetalia maritimi*), 3130: Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoëto-Nanojuncetea*, 3140: Hard oligo-mesotrophic waters with benthic vegetation of *Chara* spp., 3150: Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition*-type vegetation, 3160: Natural dystrophic lakes and ponds, 3170*: Mediterranean temporary ponds, 3220: Alpine rivers and the herbaceous vegetation along their banks, 3230: Alpine rivers and their ligneous vegetation with *Myricaria germanica*, 3240: Alpine rivers and their ligneous vegetation with *Salix eleagnos*, 3250: Constantly flowing Mediterranean rivers with *Glaucium flavum*, 3260: Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation, 3270: Rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation, 3280: Constantly flowing Mediterranean rivers with *Paspalo-Agrostidion* species and hanging curtains of *Salix* and *Populus alba*, 3290: Intermittently flowing Mediterranean rivers of the *Paspalo-Agrostidion*, 6410: *Molinia* meadows on calcareous, peaty or clayey-siltladen soils (*Molinion caeruleae*), 6420: Mediterranean tall humid herb grasslands of the *Molinio-Holoschoenion*, 6430: Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels, 7110*: Active raised bogs, 7120: Degraded raised bogs still capable of natural regeneration, 7140: Transition mires and quaking bogs, 7150: Depressions on peat substrates of the *Rhynchosporion*, 7210*: Calcareous fens with *Cladium mariscus* and species of the *Caricion davallianae*, 7220*: Petrifying springs with tufa formation (*Cratoneurion*), 7230: Alkaline fens, 91D0*: Bog woodland, 91E0*: Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*), 91F0: Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmenion minoris*)

Up until 1890, in Italy *E. canadensis* was regarded as a useful plant for its ability to recover marshes from malaria, assist aquaculture and serve as a fertiliser (Quaglia and Soave 1886, 1889; Gasperini 1890); some authors even suggested its use to support the colonisation of Africa, where malaria fevers prevented Italian colonisers' success (Gasperini 1890). Even though it was already considered a water pest in Europe (Quaglia and Soave 1886), only in the last years of the nineteenth century the signs of an invasion began to be reported by the Italian botanists (Pasquale 1894, 1896; Fiori 1895), associated with the first local extinctions of rare native aquatic plant species (mainly in the families Haloragaceae, Hydrocharitaceae and Najadaceae; Cavara 1894). We can therefore assume that the species needed about 20–30 years to establish before starting invading new territories, as also shown by the invasion curve.

The initial spread affected principally northern Italy, with isolated occurrences in the centre and south. Escapes from botanic gardens probably played an important role in the spreading of *E. canadensis*, as already proposed by Fiori (1895), and as documented by our temporal distribution

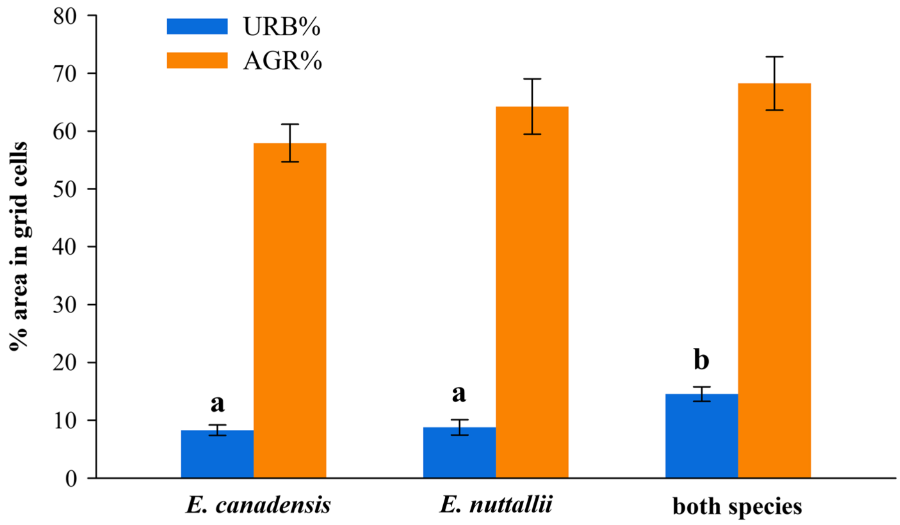


Fig. 8 Land use in *Elodea canadensis* and *E. nuttallii* occurrence cells: urbanisation and agriculture percentage per cell

maps in the areas surrounding the botanic gardens of Padova, Pisa and Rome (*Leg*. U. Ugolini, 1892, in PAD; *Leg*. Adr. Fiori, 6–1894, in FI; *Leg*. E. Chiovenda, 17-9-1901, in BOLO; *Leg*. M. Savelli, 16-10-1913, in FI). The Park of the Royal Palace in Caserta was probably another centre of spread for the invasion in southern Italy. *E. canadensis* was often introduced as an ornamental plant (Zehnsdorf et al. 2015) for fishponds or accidentally with exotic fishes (Thomson 1922) and quite likely it was also the case in the park of a Royal Palace.

Through the years, the expansion continued primarily in northern Italy. Occurrence records in central and southern regions between 1980 and 2019 (Fig. 3d) were, as expected, centred around the older records associated with the botanic gardens and the Royal Palace of Caserta, but also included occasional new occurrences in regions that previously were not affected by the invasion, suggesting invasion corridors from North to South Italy or new introductions.

Elodea nuttallii invasion took place in the last 40 years (1980–2020), without any records in central and southern Italy so far. As its ecological requirements are very similar to those of *E. canadensis* (Kočić et al. 2014; Zehnsdorf et al. 2015), its more limited distribution compared to that of *E. canadensis* might be related to time rather than ecology. Since the first record of *E. nuttallii* dates back to 1989, the species has spread for only 33 years in Italy, compared to the 160 years of *E. canadensis* invasion. The central part of northern Italy is the most invaded region; the occurrence in the rest of northern Italy is sporadic.

Like *E. canadensis*, *E. nuttallii* is a cold-temperate species that found its climate niche within the European continental biogeographic region, that in Italy roughly extends up to the northern Apennine watershed and follows the Apennines parallel to the Adriatic coasts for half of the peninsula (European Environment Agency 2017).

Invasion curves

Elodea canadensis has been in Italy at least since 1866, and showed two invasion phases: the first in the period 1890–1930 and the second, more aggressive, from around 1980 onwards. An unprecedented effort in the recording of biodiversity and invasive species after 1980 might have skewed the curve with an artifactual recent expansion phase (+33.3% accessions for *E. canadensis*, +894.7% for *E. nuttallii* compared to previous period; see Fig. 5). From the 1930s up to the end of the century, in Italy there was a general decrease in systematics studies, with a consequent decrease in herbarium accessions dating to that period. In addition, the Second World War imposed a forced stop to nearly all field activities, at least in the years 1940–1945, and the contemporary destructions caused by bombings led to the loss of some herbarium collections (see e.g. Taffetani 2012, pp. 734 and 743). All of this could have contributed to a further underestimation of the real presence of *E. canadensis* in Italy in the period 1930–1980. However, it should be noted that the second invasion round is accompanied by a switch in the habitat. In addition to canals, that were *E. canadensis* preferential habitat until 1970 (registered in the herbarium specimen labels), also rivers and lakes became important for the species after this period: in 2000–2010 the occurrences in rivers even exceeded those in canals (Fig. 6a). The colonisation of new habitats could be due to evolution which occurred post-introduction in the new range or to a cryptic invasion of a second genotype of *E. canadensis*. The trade of this species has never ceased and introductions of new, still undiscovered genetic lineages may have been overlooked. The new genotype, better adapted to eutrophication and the increasing temperatures of the early twenty-first century, would preferably have occupied eutrophic rivers and lakes, a hypothesis that can be confirmed by genetic analysis. In addition, the 1970s witnessed a massive use of pesticides and herbicides that depleted biodiversity in agricultural areas (Santini and Buldrini 2012): this phenomenon could have accounted for a reduced expansion of *E. canadensis* in canals in agricultural areas until the 1980s and the subsequent colonization of other water bodies (cfr. Bowmer et al. 1995; Glomski et al. 2005).

Other hypotheses concern the ability of *Elodea* spp. to thrive in stressed environments, that might have facilitated the expansion to new areas, and, not last, the initial misidentification of *E. nuttallii* with *E. canadensis* when it first appeared in Italy. The two species are morphologically very similar (Walters 1980; Vanderpoorten et al. 2000; Banfi and Galasso 2010) and the still imperfect knowledge of the newly arrived *E. nuttalli* could have induced various botanists to erroneously identify it as *E. canadensis*, causing an overestimation of the presence and spreading ability of the latter at the end of the twentieth century. Another still largely unexplored factor that might have had a role in the colonization of new habitats could be the co-occurrence of other invasive species, as documented for *E. nuttalli* in Ireland where patch extension was found to be positively correlated with the presence of *Dreissena polymorpha* Pallas, 1771 (Crane et al. 2022).

Biogeography and habitats

For both species, the invasion range in Italy is centred in the northern part, i.e. in the continental and Alpine biogeographical regions, with isolated occurrences of *E. canadensis* in central and southern Italy, i.e. in the Mediterranean region. Both species have never been recorded in Sardinia and Sicily and in the small islands around Italy (Celesti-Grapow et al. 2016). This fact is not surprising since the two species are native to northern America (Simpson 1984) and are typical of cold-temperate climates. Indeed, the trophic and thermic seasonal fluctuations in inland waterbodies could be the reason for the lower invasion pressure of *Elodea* species in the Mediterranean region compared to temperate ecosystems (Guarino et al. 2021). However, the complete absence (at least at the current state of the floristic knowledge) of *E. nuttallii* in the Mediterranean region suggests that the two species, even if regarded as ecological redundants (Hérault et al. 2008), have some different climatic requirements, with *E. nuttallii* being less thermophilous than *E. canadensis*. This fact was already reported by Pignatti et al. (2017–2019) and can also be observed in the habitats recorded for the first occurrences of the two species: mostly canals (i.e. shallow waters, with tendency to summer heating) for *E. canadensis*, from the beginning up to 1980; mostly lakes (i.e. deep, cold waters, with scarce or negligible summer heating) for *E. nuttallii*, from the introduction up to 2000. Variation in temperature-associated conditions could be more marked in waters at the margin of the temperate range. Irrespective of the species, a shift from the original habitat to other types of waterbodies has been evident in the last decades: this could be due to adaptation to the new environmental conditions (cfr. Allard 1988), or selection of the most resistant genotypes (Lambertini et al. 2010; Riis et al. 2010; Johnson and Munshi-South 2017), or simply the species had physical access to other habitats. Therefore, the distribution of *E. canadensis* and *E. nuttallii* might still change in coming years, especially in central and southern parts of Italy where the distribution range of these species is disjunct, and some areas are poorly investigated (Conti et al. 2016; Stinca et al. 2017; Rosati et al. 2020).

For the time being, the largest alluvial plain of Italy, i.e. the Po Plain, is the area with the highest number of records. The area is quite rich in permanent water bodies and one of the most impacted by human activities in Italy (Bolpagni et al. 2020). Here the probability of finding both species increases with increasing urbanisation and water exploitation independently of taxa (Fig. 8).

River Po crosses northern Italy from west to east and appears as an important barrier for the spread of *Elodea* species in the peninsula. This is likely because the Apennine catchments, south of River Po, have a torrential regime and undergo a long lean period (and even drought) during the summer months that reduces survival capacity and migration of aquatic species to the Mediterranean region. The Alpine catchments, on the contrary, are supplied by Alpine glaciers all year around, and although they may have lean periods in the summer, they never, or only exceptionally, experience drought. Despite the drought barrier, the risk of spreading of the two species south of River Po is high, since the artificial network of canals that brings irrigation water from River Po to the agricultural lands south of the river (Montanari et al. 2020, 2022) can provide dispersal corridors in the dry season. During summer, in fact, these canals are maintained full of water (Dallai et al. 2015; Montanari et al. 2020), and provide a suitable environment for the survival of both *Elodea* species exactly when natural watercourses undergo lean or drought. The risk, in the near future, of a mass spreading of the two species to the southern parts of the Po Plain, that at present are still not extensively invaded, is therefore very high, also considering the intensive management of the canal networks (mowing of the vegetation and dredging of the canals) and the more and more frequent flooding events that occur in this area. In addition to the obvious ecosystemic impact, an invasion in this area would have negative consequences for canal maintenance and effectiveness in draining rainwaters (hydrogeological risk is high in this region) and supplying irrigation water (cfr. Dallai et al. 2015). Monitoring *Elodea* and other invasive aquatic species in this area is therefore strategic to prevent invasions in the peninsula, as well as to plan eradication measures in advance that, in the case of *E. nuttallii*, are mandatory (EU Reg. 1143/2014). An option that should be considered is that of repristing occasional drought barriers that can interrupt the migration flow and have proved successful in containing these invasions for the past 100 years. In any case, given that eradication and control are obligatory for *E. nuttallii*, and were successful in other parts of Europe (Hoffmann et al. 2013; Garland et al. 2022), it is also possible (and desirable) that containment actions have a positive effect on the distribution of both species that largely occur in the same areas, thereby leading to a contraction, rather than an expansion, in the ranges of both species in the coming years.

Natura 2000 habitats that occur within *Elodea* occurrence records cells are the ones that are most threatened by the invasion of these species. Based on our field work, we can confirm that in the Po Plain both species frequently occur in habitats 3150 (Natural euthrophic lakes with *Magnopotamion* or *Hydrocharition*-type vegetation; see also Bolpagni 2013) and 3260 (Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation), as well as in temporary alluvial forests formed by the swollen rivers of the Alpine catchment, as detected by our study, often together with other invasive elodeids like *Egeria densa* (Planch.) Casp. (native to South America) and *Lagarosiphon major* (Ridl.) Moss (native to South Africa). Elodeas and alien species are one of the major threats for the conservation of Natura 2000 habitats in Italy, both aquatic and terrestrial (Lazzaro et al. 2020; Viciani et al. 2020).

Mediterranean habitats appear more resilient to *Elodea* invasion because of summer drought, but also because many rivers are dammed for the creation of water reservoirs, and artificial networks for drainage and irrigation are not as extended as in northern Italy. Nevertheless, there are various lakes (both natural and artificial) that provide suitable establishment sites to *E. canadensis* and *E. nuttallii*, in case of introduction in these zones. As a matter of fact, we have recently become aware of a few more lakes in internal areas of the peninsula where *E. canadensis* is currently present and could have occurred for a long time, like Lake Trasimeno in central Italy, where it has been known since the end of 1800 and whose presence could be linked to the various experiments of aquaculture that were discussed and performed in the 1880s (Ministero di Agricoltura, Industria e Commercio 1886, 1887). The distribution of *Elodea* species could therefore be wider in the Mediterranean region than documented by this study, and the invasion risk should not be underestimated even in this area.

Conclusions

This study reconstructed the invasion history of *E. canadensis* and *E. nuttallii* in Italy, two aquatic pests that occur in large parts of Eurasia. Herbarium specimens, occurrence records and historical literature provided insight into the introduction history and dynamics of two invasions by two closely related species. With this information we could identify a strategic area where to address monitoring and management, for the prevention of further spreading. The study also provides new perspectives on the invasion process of plant species. To the best of our knowledge, this is the first study that resolves the initial invasion phase of a plant species with such a detail, especially for *E. canadensis*. Interestingly, in the nineteenth century the introduction pathways were not very different from those of today, i.e. deliberate human introduction (fish farming, botanic garden collections and applied research then, as documented by this study, aquarium and ornamental plants trade, living collections, cultivation, scientific research and phytoremediation today—Kay and Hoyle 2001; Hulme 2011; Brundu 2015; van Kleunen et al. 2018a, 2018b).

Compared to the invasion curve of *E. nuttalli* introduced 100 years later in the same area, *E. canadensis* had a longer lag phase and a less steep expansion in the first invasion round between 1890 and 1930. The steepness (i.e. spread rate) of the second expansion phase was, instead, more similar to that of *E. nuttallii* invasion occurring in the same period 1990–2005. *E. canadensis* invasion curve also shows that invasions can have more than one expansion phase as previously suggested (Pyšek and Prach 1993). More research is necessary to corroborate this new finding, i.e. to assess the evolutionary change that was recorded by these occurrence records.

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Authors contributions All authors contributed to the study conception and design. Data collection was performed by all authors and coordinated by FB, material preparation and analysis were performed by MB, CL, GP and FB. The first draft of the manuscript was written by FB, GP and CL and all authors critically read, amended and commented the first version of the manuscript, contributing validly to data interpretation. All authors read and approved the final manuscript.

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Data availability All data generated or analysed during this study are included in this published article (and its supplementary information files).

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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