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ABSTRACT

Ambrosia psilostachya (Asteraceae) is a perennial ragweed native to North and Central America, introduced to Europe at the end of nineteenth century. Likely to have been accidentally introduced, the species spread in several countries. For a long time, its invasion history has been overlooked mainly due the frequent misidentifications with other ragweeds, mostly with *A. maritima*, the only species of the genus *Ambrosia* native to the Old World. This study reconstructs the invasion history of *A. psilostachya* in Italy through an extensive review of herbarium specimens, literature and field data. According to our research, *A. psilostachya* was probably introduced to Italy in the first half of nineteenth century, but the first record in the wild dates back to the beginning of twentieth century on the Tyrrhenian coastline. Over the years, *A. psilostachya* spread along the peninsula becoming common along rivers and coastal dunes, especially in habitats characterized by sandy soils. Its massive occurrence along sandy coastal systems should be considered an urgent call to investigate this species and its impacts more deeply. The species could represent a relevant threat to native flora especially on sandy soils as well as to human health due to its allergenic pollen.

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Introduction

Biological invasions are an increasing issue at a global level (Seebens et al. 2017; Pyšek et al. 2020; Daly et al. 2023). Invasive alien species are a major component of global change (Essl et al. 2020), causing severe negative impacts on native biodiversity and ecosystem functioning (Bellard et al. 2016; Blackburn et al. 2019; Rai and Singh 2020; Dueñas et al. 2021), frequently affecting also the economy and human health (Calabrese et al. 2015; Schindler et al. 2015; Diagne et al. 2022).

In this regard, *Ambrosia* L. (Asteraceae) is globally considered a problematic genus (Smith et al. 2013; Makra et al. 2015; Montagnani et al. 2017). Species, commonly called ragweeds, are mostly native to North America. With the help of human-mediated vectors, species such as *A. artemisiifolia* L. (common ragweed) spread almost all over the world (Essl et al. 2015), becoming invasive alien species of global concern (Schaffner et al. 2020; Montagnani et al. 2023). Generally, the main problem with ragweeds regards their allergenic potential, due to a highly volatile pollen causing severe symptoms (e.g. hay fever, dermatitis) to sensitive persons, and a consequent relevant expenditure at the sanitary level (Montagnani et al. 2023). Moreover, major economic losses in agriculture are associated to several species that are crop weeds (e.g. *A. artemisiifolia*, *A. confertiflora* DC. and *A. trifida* L.) (Essl et al. 2015; Yair et al. 2019; Chauvel et al. 2021). In the roster of alien ragweeds, *A. psilostachya* DC. (Western or perennial ragweed) is a globally widespread species, occurring in all continents (except Antarctica). Its native range spans from northern Mexico to the USA (almost all states) and the southern provinces of Canada (Strother 2006). It is a perennial plant, typical of tallgrass prairies of the American Great Plains (Reece et al. 2004), where it is also a weed in pastures and rangelands, favoured by overgrazing and fire (Funderburg et al. 2014). It is a pioneer, sand-loving species adapted to xeric and, preferentially, sunny conditions (even if it also lives under the canopy of open woodlands) (Montagnani et al. 2017). Furthermore, it is resistant to high salt and metal concentration in soils (Rivera-Becerril et al. 2013). All these characteristics contribute to making *A. psilostachya* an opportunistic plant which can easily colonize synanthropic habitats as well as natural and semi-natural environments exposed to a certain degree of human disturbance. Coherently, in Europe, *A. psilostachya* is reported to colonize anthropogenic herb stands (e.g. along road verges, urban wastelands), agricultural contexts (e.g. fallows, recently abandoned fields and field margins, vineyards) as well as dry sandy grasslands also on alluvial soils, river banks, coastal dunes and, occasionally, sandy shores (Weeda 2010; Del Vecchio et al. 2015; Fried et al. 2015; Ardenghi and Polani 2016; Dines and Pearman 2020; Verloove 2023). The perennating plagiotropic creeping roots are the key organs that allow *A. psilostachya* to live and spread in stressful conditions, also thanks to the physiological integration among connected ramets and to mychorrizal fungi (Salzman 1985; Rivera-Becerril et al. 2013). Root and belowground shoot fragments, rather than fruits, are likely to be key propagules in the dispersal of *A. psilostachya* and vegetative reproduction by root sprouts represent the prevailing reproductive strategy, ensuring a rapid spread of the species once established (Bassett and Crompton 1975; Karrer et al. 2023).

In addition to the release of allergenic pollen and its negative impacts as weed in crops and pastures (Montagnani et al. 2017, 2023), another highly alarming aspect is represented by its ability to colonize and spread in coastal sandy dune plant communities, which poses a risk to native flora and habitats of conservation concern (Del Vecchio et al. 2015; Fried et al. 2015).

In spite of the high risk represented by the spreading of this species, to date *A. psilostachya* has been poorly studied (Karrer et al. 2023). Probably this is primarily due to the frequent misidentifications with other congeners: *A. psilostachya* is frequently confused with *A. artemisiifolia*, occasionally *A. tenuifolia* (Karrer et al. 2021) or *A. maritima* L., which is currently considered the only ragweed native to Europe and the Mediterranean Basin, scarcely known due to its extreme rarity (Orsenigo et al. 2017; Karrer et al. 2023). Identification issues are mainly due to the lack of reliable identification keys in former times but also to the morphological variability of the species. These critical issues contributed to overlook the invasion of *A. psilostachya* (Karrer et al. 2023), with genuine inaccuracies about its distribution, despite recent taxonomic clarifications (Karrer et al. 2016, 2021; Karrer and Guarino 2018, 2019). In Europe, *A. psilostachya* has been introduced to many countries (Montagnani et al. 2017) and, while in several areas of central and northern Europe it failed to establish after initial introduction (e.g. Austria, Hungary, Denmark, Estonia, Finland, Norway), in southern Europe it is currently in expansion (Karrer et al. 2023; Lozano et al. 2024). In this regard, in Italy, the species occurs in many regions (Galasso et al. 2018, 2024), advancing especially along rivers (Pignatti et al. 2017) and becoming very common in coastal habitats also in sites of conservation interest (Del Vecchio et al. 2015; Giulio et al. 2021; de Francesco et al. 2022). Being an opportunistic species, *A. psilostachya* especially colonizes disturbed areas and distinguishing negative impacts due to its spread from those related to human disturbance (e.g. trampling) could be often tricky. In costal dunes, *A. psilostachya* would take advantage of disturbance to thrive where native species cannot, replacing the most sensitive taxa (Del Vecchio et al. 2015). Although studies about impacts are few and results contrasting (Fried et al. 2015; Sohrabi et al. 2021), the high spreading ability of the species requires a precautionary approach. In fact, especially in a country such as Italy, characterized by a huge coastal natural heritage already under pressure due to long-lasting severe anthropogenic transformation (Prisco et al. 2016), the species poses a potential serious threat to coastal flora and ecosystems. So, based on extensive herbarium revisions as well as field and literature data collection, in the present study, we reconstruct for the first time the invasion history of *A. psilostachya* in Italy from its early introduction until today, covering more than one century. Together with a geography-based timeline of invasion, the spectrum of environments progressively colonized by the species is also given. Records are based on reliable sources, as we matched a wide revision of herbarium specimens with field data collected by expert botanists and consistent bibliography. This *a posteriori* analysis sheds light on the first invasion phases of *A. psilostachya* in Italy and can contribute to understand the key mechanisms underlying the spread of this species, providing useful information to its monitoring and effective management.

Materials and methods

Data collection and specimen identification

We examined herbarium specimens referred to the *Ambrosia* genus in Italy from the main Italian herbaria and important European herbaria. The list of consulted public herbaria is reported in Table S1. In addition to the herbarium data, field data were collected by authors involved in the present work and scientific and grey literature mentioning the target species was analyzed. Moreover, data regarding *A. psilostachya* collected by Gentili et al. (2017) and Karrer et al. (2023) were also integrated. Localities lacking geographic coordinates were georeferenced basing on toponyms reported in IGM (Italian Military Geographic Institute) database available on Geoportale Nazionale (http://www.pcn.minambiente.it/viewer/) or Google Maps and Google Earth platforms. Duplicates (records with the same coordinates and year of collection) were maintained only when different localities were associated to the same geographic coordinates (e.g. when coordinates correspond to the centroid of a grid that includes more sites).

As previously said, *A. psilostachya* can be frequently confused with other congeners and issues can arise when dealing with incomplete and old herbarium specimens. In the present work we integrated the key to *Ambrosia* species in Flora of North America by Strother (http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=101325; accessed 29 August 2023) with the most recent identification keys deriving from a wide analysis of European herbaria and field specimens (Karrer et al. 2016, 2021; Karrer and Guarino 2018, 2019). Considering that misidentification frequently occurs with *A. artemisiifolia* (annual) and *A. maritima* (annual or short-lived perennial), whose belowground organ is a taproot, *A. psilostachya* can be easily identified if the belowground organs are well documented. Moreover, the leaves represent a quite reliable morphological trait to be considered for identification; they are arranged proximally opposite and distally alternate. *A. psilostachya* leaf blades are characterized as pinnatifid (1-pinnate compound) or pinnatopartite (rarely entire, i.e. uppermost stem leaves and leaves of individuals in shade) with lobes linear and widely connected, often sharpened to the tip. Petioles are either missing or very short (not longer than 25 mm) and broadly winged. Leaves are densely hairy on both the abaxial and adaxial side and coloured somewhat greyish-green (slightly darker green on the adaxial surface). Fruits (1-seeded achene enclosed in a bur) have few (1–6) or none lateral blunt spines; however, the general variability of diaspores in the genus can be misleading. The herbarium specimens identified as *A. psilostachya* are reported in Table S2. In order to ease the identification of revised specimens in herbarium collections, for each record the following details are provided: (1) code of herbarium, reported in accordance to Index Herbariorum (2024); (2) accession number/barcode of herbarium specimen (when available) (3) previous and revised identification of specimen, (4) locality (as reported in herbarium specimen label), (5) date of collection, (6) notes (e.g. collectors, previous revisions).

Classification of colonized environments

Based on field observations and information obtained from herbarium specimens and bibliographic data, for each record of occurrence of *A. psilostachya* "in the wild" (i.e. not cultivated, outside confined environments such as gardens), the colonized environment has been categorized according to the following classification:

- *Beach and costal dunes*: coastal environments from sandy dunes to beaches; in addition, retrodunal pine woods on sandy soil are included in this category;
- *Rivers and waterbodies*: banks of lentic and lotic water systems;
- *Other natural and semi-natural environments*: grasslands, fallows and open woods (generally ecotonal environments);
- *Country matrix*: farms and little towns in the countryside in an agricultural-dominated landscape;
- *Railways*: railroad yards and stations;
- *Roads*: verges of linear infrastructures not strictly related to agricultural or urban contexts;
- *Urban matrix*: towns and cities;
- *Wasteland*: unmanaged areas in quarries or industrial contexts as well as abandoned fields (e.g. allotments interested by working sites).

On a 20-years basis, an analysis of the frequencies of *A. psilostachya* records in the above-mentioned environments along the timeline of invasion was done.

Distribution and areas of first introduction

In a Geographic Information System (GIS) environment, using QGIS version 3.28 "Firenze" software (QGIS Association, http://www.qgis.org), the distribution map of *A. psilostachya* in Italy was obtained, considering the period from the first introduction to the most recent records.

In the SAGA GIS application, we used the IDW (Inverse Distance Weighting) method to interpolate the spatial distribution of the year of record of *A. psilostachya* in an area, in order to highlight the areas of first introduction (resolution: 1 km; power: 2). The IDW method is a deterministic method where the unknown point values are estimated with a weighted average of the values available at the known points; this algorithm generates a map from vector point data by inverse distance squared weighting and uses numerical approximation (weighted averaging) techniques (Duarte et al. 2015). To correctly identify the areas of first introduction, among all those where *A. psilostachya* was found repeatedly for more than one year, only the oldest record was selected for the analysis. Furthermore, in order to avoid incorrect inferences of the time of introduction in areas where the species is absent, the analysis was scaled only on those areas where *A. psilostachya* could potentially be present (even if not surveyed), delimited within a radius of 50 km from each record of the species.

Results

Data collection

Among a total of 1,133 collected records, 917 were attributed to sites of occurrence of *Ambrosia psilostachya*.

In particular, we examined 437 herbarium specimens labelled as *Ambro*sia sp. pl. collected from 1804 to 2018, plus the examination of the Aldrovandi herbarium (BOLO) in which specimens dating back to the turn of the 16th and 17th centuries are conserved. In total, 221 specimens have been identified as *A. psilostachya*. Thirty-three percent of herbarium specimens attributed to *A. psilostachya* were erroneously or incompletely (e.g. *Ambrosia* sp.) identified in the past. Of these, the majority was confused with *A. maritima* (77%), while misidentifications with *A. artemisiifolia* were much less frequent (just three cases). In most cases, *A. psilostachya* was identified as another species, and only in one case *A. artemisiifolia* was misidentified as *A. psilostachya*. Overall, 529 records came from field observations by co-authors involved in the present work. Then, 167 records were extrapolated from bibliographic sources, databases and online floras published from the first decades of the twentieth century onwards. Total records corresponding to *A. psilostachya* listed by sources are reported in Table 1.

Distribution of *A. psilostachya* in Italy

Occurrences of *A. psilostachya* are mainly distributed in northern (Piemonte, Liguria, Lombardia, Trento Autonomous Province, Emilia-Romagna, Veneto, Friuli Venezia Giulia) and central Italy (Toscana, Lazio, Abruzzo, Marche, Umbria) while only eight records refer to southern Italy, with only one record in Calabria and three and four in Molise and Puglia, respectively (Figure 1). However, the presence of the species has not been recently confirmed in Lazio, coherently to Lucchese (2018) and Umbria (last observations in the 1970s). Other uncertain cases regard: Liguria, where the species has not been recently recorded since the 1990s, but its occurrence should be verified especially at the borders with Toscana (where it has been recorded along the Parmignola river in 2012–2013; Ciccarelli et al. 2014) and Piemonte (1994 at Piana Crixia, Savona) and Trento Autonomous Province, where the species has been no longer found in spite of quite recent records (2004).

Table 1. Number of analyzed records from different sources and number of occurrences corresponding to *Ambrosia psilostachya*.

Source	Collected records	*A. psilostachya* occurrences
Herbaria	437	221
Field observations	529	529
Literature and on line databases	167	167
Total	1133	917

Three main clusters of records can be identified on a geographical basis: the Tyrrhenian cluster including records from Liguria to northern Toscana, the Padana cluster grouping records distributed in the Po Plain, along Po River and connected watercourses, and the Adriatic cluster formed by records distributed almost continuously along the Adriatic coast from Trieste and the Marano and Grado Lagoon to the northern part of the Gargano peninsula. According to biogeographic regions (as defined by the map from the European Environment Agency, available at http://www.eea.europa.eu/), *A. psilostachya* is mainly concentrated in the Continental region and secondarily in the Mediterranean one, while in the Alpine region the occurrences are more sporadic.

Invasion history of *A. psilostachya* in Italy

In the following paragraph, the source of the datum is indicated only for records extrapolated from the literature; differently, when no reference is reported, it is implied that the record was derived from herbarium collections and Table S2 needs to be checked for details.

The oldest record of *A. psilostachya* corresponds to an herbarium specimen dating back to 1842: it is from the herbarium of Pisa (PI) and it was identified as "*A. heterophylla* Muhl. ex Willd." (synonym of *A. polystachya* DC.) after the collection in an unidentified botanical garden in Veneto region (NE Italy), as reported in the label ("in Hort. botanico veneto"). This record has not been included in our analysis as it cannot be excluded that the species was cultivated. More than six decades after, *A. psilostachya* was found in the wild: indeed, in 1909, it was collected as *A. maritima* in northern Toscana, in a locality (Quercioli) in the inland of Massa (Massa-Carrara), not far from the coast. After this, in 1923, *A. psilostachya* was collected again in Massa-Carrara (locality Fossola), few kilometres from the first record site. In the period from 1909 to 1927, the only records of *A. psilostachya* are reported for this area of northern Toscana, mostly in Massa-Carrara but also in Viareggio (Lucca). As the 1930s approached, *A. psilostachya* was found in new southward areas of Toscana (Livorno province), mainly on the sandy beachside or along coastal roads, but also northwards, as new occurrences in Liguria and Piemonte region (NW Italy) were found. In Liguria, from 1929 on the species was found in Genova: initially along the urban shoreline and then along the Polcevera and, secondarily, Bisagno rivers. Other sites were identified westwards in 1934, in the inner areas nearby Varazze (Savona). In Piemonte, the first records date back to 1931 in the Langhe sector (Castiglione Falletto, Cuneo), where the species was collected and studied by Prof. Ferdinando Vignolo-Lutati (1935), who published the first study on the genus *Ambrosia* in Italy, trying to unravel the complicated identification of taxa.

Then, in 1940 *A. psilostachya* made its appearance on the Adriatic coast. Specifically, it was recorded in central Italy, Marche, between Pesaro and Fosso Sejore (Pesaro-Urbino) where it will be repeatedly found in following decades, from the end of 1950s onwards (Viegi et al. 2003).

Figure 1. Distribution of *Ambrosia psilostachya* in Italy with confirmed (green) and not confirmed (grey) occurrences. The map at bottom left reports the acronym of Italian administrative regions (ABR: Abruzzo; BAS: Basilicata; CAL: Calabria; CAM: Campania; EMR: Emilia – Romagna; FVG: Friuli Venezia Giulia; LAZ: Lazio; LIG: Liguria; LOM: Lombardia; MAR: Marche; MOL: Molise; PIE: Piemonte; PUG: Puglia; SAR: Sardegna; SIC: Sicilia; TOS: Toscana; TAA: Trentino alto adige; UMB: Umbria; VDA: Valle d'Aosta; VEN: Veneto).

After the Second World War, during the 1940s, *A. psilostachya* appeared in the Po Plain and in the Pre-Alpine area. It ephemerally appeared in Lombardia, firstly in Varese (1946) and subsequently in Milano (1949), in both cases along railroads or in railway yards. In 1947, it was firstly recorded in Emilia-Romagna, in Parma, along the homonymous stream. In the same period, it was first recorded on the northern Adriatic coast, in Friuli Venezia Giulia (1946, Riva Lunga di Monfalcone, Gorizia) (Cohrs 1953) and, in 1949, it was repeatedly found in Veneto in Jesolo (Venezia) on the beachside and in areas near the Piave river and the Laguna Veneta. In the same year, *A. psilostachya* was found also more southward on the beach of Roseto degli Abruzzi (Teramo).

In the 20 years between 1950 and 1970, the records along the Adriatic coast multiplied: especially in the 1950s, *A. psilostachya* was found both on the coast and in inner areas in Abruzzo (e.g. Basciano on the central Apennines at 400 m a.s.l.), and during the 1960s, as anticipated, it was frequently recorded along the coast of Marche (Viegi et al. 2003). In 1956, the species was firstly recorded along the Po River in Emilia Romagna (Piacenza). In this period, it also appeared in two big cities where today its occurrence is no longer confirmed: in 1954, its presence was reported along the urban roads in changing areas in Torino (Piazza Marmolada and surroundings), where the species has been noticed until 1977; finally, in 1964, *A. psilostachya* was found in Roma (Pineto area) where its presence is confirmed only until 1972.

From 1970 to the end of the '80s, the records of *A. psilostachya* are scattered along the Italian peninsula, with a major concentration in the administrative region of Piemonte and on the northern Apennines (Piana Crixia, Savona). During this period, *A. psilostachya* was recorded in the alpine zone, on the western Alps in 1972 (Venaus – Susa Valley, Torino) (Mondino G.P. *personal observation*). It was also observed in the Po Delta area (between the provinces of Rovigo and Ferrara) and new occurrences nearby Venezia (Punta Sabbioni) were added.

From the 1990s onwards, *A. psilostachya* has been repeatedly found in the Po Plain and tributaries, where recent records are the majority, as well as along the Adriatic coasts. In this period, *A. psilostachya* was found for the first time in southern Italy. In 1990, it firstly appeared on the coasts of Molise, in Termoli (Campobasso), while a few years later, in 1999, it was found in Puglia, both in the northern part (Gargano promontory) in Schiapparo (Lesina, Foggia) and southern part in Torre Guaceto (Brindisi). Finally, in 2013, for the first time, the species was found in Calabria, at the estuary of Fiumara dell'Amendolea (Reggio Calabria), a region where it is currently naturalized (Spampinato et al. 2022).

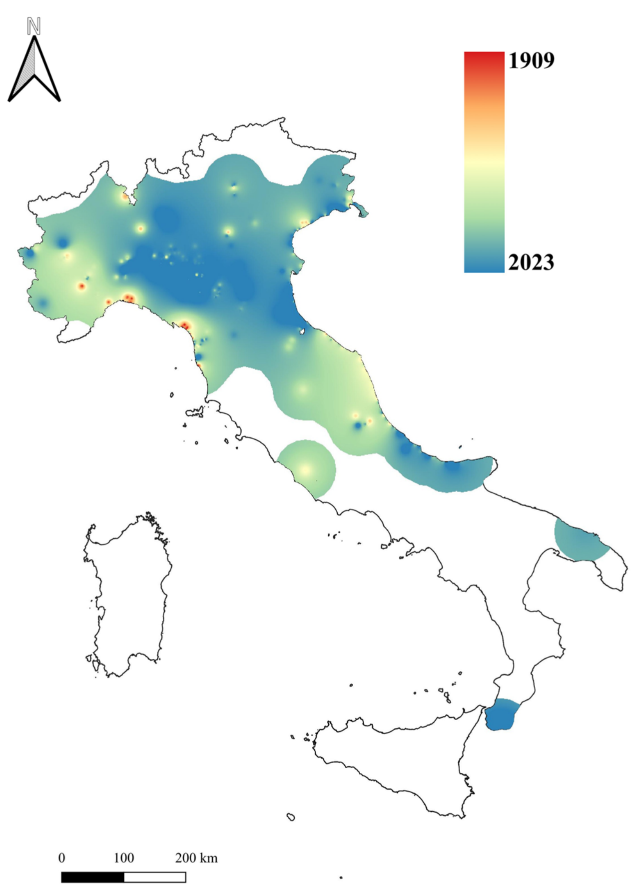

Figure 2. Areas of introduction of *Ambrosia psilostachya* in Italy.

Based on the interpolation of the year of collection (only for plants found in the wild), the map in Figure 2 gives a general and summarizing overview of the areas of first introduction of *A. psilostachya*, in a colour scale that goes from red, indicating the oldest records, to blue for the most recent ones. The map highlights as the areas of oldest occurrence of *A. psilostachya* the northern Tyrrhenian coast, specifically northern Toscana and Genova, and secondarily southern Piemonte, on the hillside of Castiglione Falletto.

Colonized environments

Beyond the first collection in a botanical garden, until 1932, *A. psilostachya* collections were clustered nearby coastal settlements (sometimes in rural areas not far from the coast as the first record of the species in northern Toscana), while since 1933 it started to be found also in inner areas in little towns in the countryside. Until the beginning of 1940, it was frequently found along roads, on beaches and secondarily along rivers (Figure 3). The majority of these environments were associated to coastal or country settlements: road verges tight between built-up areas and beaches or crossing country towns, beaches neighbouring coastal settlements, watercourses flowing across country contexts close to urban areas. In this period, only in one case *A. psilostachya* was not found close to settlements but, however, in a narrow coastal valley in the Mediterranean maquis crossed by railways and road bridges (Botro di Calignania, Livorno). As shown in Figure 3, only after 1940 *A. psilostachya* started colonizing new types of environments, even if marginally: in fact, especially between 1940 and 1960, it was collected along urban roads in big cities (e.g. Torino, Roma) and several times along railroads and in railway yards (e.g. Milano, Varese, Verona), contexts where the species usually resulted to be ephemeral. Later, *A. psilostachya* was found in other human-shaped environments classified as "wasteland" due to null or very low level of management: abandoned lots nearby or inside industrial sites, unmanaged areas in quarries or abandoned fields are example of environments where the species has been sporadically found in more recent times (from 1980 onwards). Regarding natural or semi–natural environments, from the 1950s onwards, *A. psilostachya* was observed also in grasslands (usually in quite disturbed contexts) and woods (open woods or nearby paths crossing the woods); more recently it has been found also in open habitats on the Maritime Alps (valley floor of Vallone dell'Arma, Cuneo). However, other natural/semi-natural or human-shaped environments not ascribable to river or other waterbodies and beach-dune systems remained secondary during the colonization of Italy by *A. psilostachya*: as reported in Figure 3, from the past to today the species became frequent along rivers and coasts, where it currently colonizes coastal dune systems, beaches (even sometimes between the shoreline and the shifting dunes) and retrodunal pine woods. Field observations and data reported on herbarium labels indicate that the species is very often associated to sandy soils.

Considering the entire time span in which it spread, *A. psilostachya* has been found from sea level up to 1,400 m a.s.l. as it occurs from the coasts to Alpine valley floors.

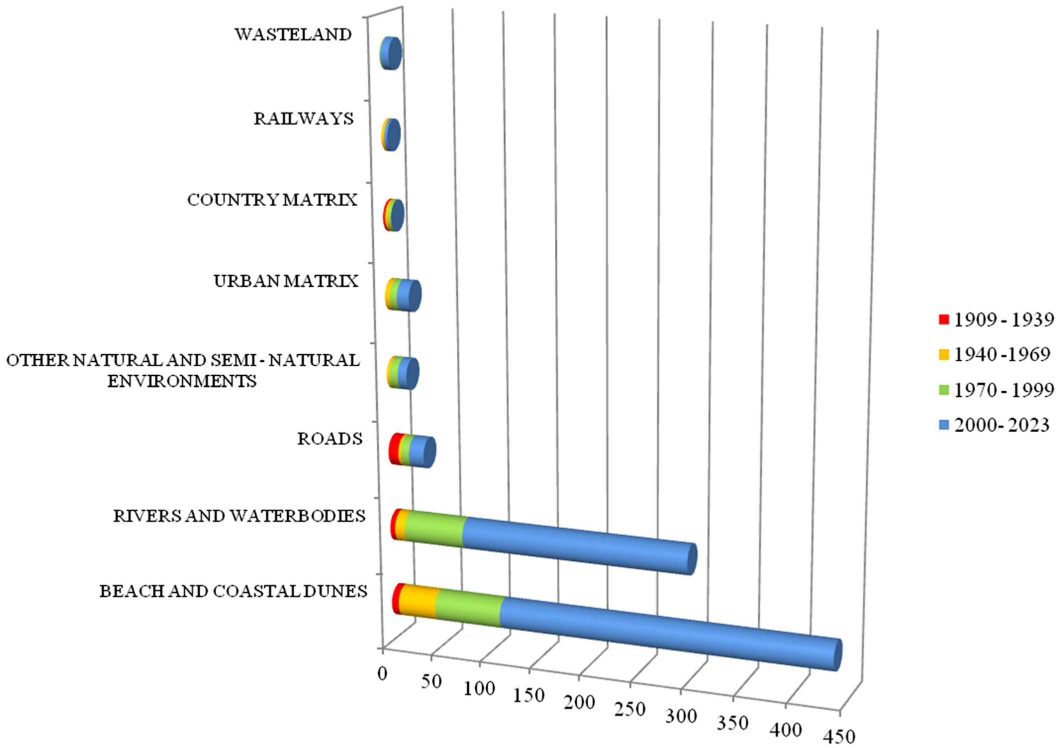

Figure 3. Types of environments colonized by *Ambrosia psilostachya* along the timeline of invasion in Italy. Number of records collected in each time span (*x*-axis) are reported for each type of environment (*y*-axis).

Discussion

The present investigation, based on a considerable and reliable amount of data collected from herbaria, expert botanists and literature, allowed to map the distribution and invasion history of *Ambrosia psilostachya* in Italy in a time span of more than one century. New information and insights were obtained about this overlooked North American ragweed, which is quite silently gaining ground in Europe and in other continents.

Invasion history of A. psilostachya in Italy: first introductions

We found that the first evidence of introduction of *A. psilostachya* to Italy dates back to 1842 in a botanical garden in Veneto, which could be the Padua Botanical Garden, even though no other information is available to confirm the localization. If this record is considered, Italy may be considered the first European country where *A. psilostachya* has been introduced, before Great Britain (1880), France (1891) and Germany (1894) (Montagnani et al. 2017; Karrer et al. 2023). Before 1842, *A. psilostachya* could be listed in botanical garden collections, for example under the synonym of *A. peruviana* DC. (Tenore 1813), but actually the analysis of available specimens did not confirm the identification. Botanical gardens are known to play a key role in the first introduction of alien plants and their subsequent "escape" in the wild (van Kleunen et al. 2018; Ni and Hulme 2021), but it is not known whether the species was an accidental occurrence or a cultivated plant in the garden. In favour of the latter hypothesis, it is important to highlight that also other ragweeds have been cultivated in botanical gardens since the end of the eighteenth century such as *A. artemisiifolia*, *A. maritima*, *A. peruviana* All. and *A. trifida* (Allioni 1770–1773; Essl et al. 2015; Gentili et al. 2017). In this regard, also *A. psilostachya* could have been imported from North America as medicinal plant used in traditional medicine by Indigenous peoples of the Americas (Montagnani et al. 2017). However, the first record of *A. psilostachya* in the wild seems not to be related to botanical gardens and it is far from Veneto.

In fact, after more than sixty years, in 1909, the species was found surely as spontaneous in northern Toscana, likely to be the first area of introduction in the wild of *A. psilostachya* (Figure 2), where the plant found suitable conditions to thrive over the years and up to now (Figure 1). Accordingly, in Italy, the first record in the wild is earlier than found in earlier studies (previously, the first introduction was dated 1924; Karrer et al. 2023). The presence of ports already active at the beginning of the twentieth century (Marina di Carrara and Viareggio) and an extended sandy coast might have played a crucial role in the introduction and spread of the species in this area. Ports are an important gateway of accidental introduction of alien species (Tordoni et al. 2017; Yu et al. 2020). So, once cargos containing contaminated lots of vegetables (e.g. potatoes; Montagnani et al. 2017; Karrer et al. 2023) or cereals have been unloaded from the ships, *A. psilostachya* could have "escaped", finding suitable transitory conditions in the port area (Ikeda et al. 2022) or in nearby beaches (*A. psilostachya* was found in 1927 and 1930 in beaches not far from the ports of Marina di Carrara and Viareggio, respectively). Even if the northern Toscana ports were not particularly dedicated to the grain commerce (mainly addressed to Carrara's marble trade and elite tourism), the transit of food or grain shipments cannot be excluded. The potential relevance of ports in the introduction of *A. psilostachya* to Italy seems to be supported also by the early presence of the species in Genova, an important port city addressed to the international trade of different commodities (grains and vegetables included), and in the surroundings of Livorno, another historical city port (Figure 2).

Invasion history of A. psilostachya in Italy: secondary introduction and spread

If ports might have been the gateway of introduction to Italy, then *A. psilostachya* arrived to novel areas probably thanks to diversified unintentional pathways. For example, its early occurrence in inner areas (e.g. in northern Toscana and valleys near Genova, Langhe hillside in southern Piemonte) might be the result of the use of commodities contaminated by viable propagules of *A. psilostachya*. The unintentional introduction as contaminants is an effective pathway of introduction and spread of alien species at world level (Cossu et al. 2020; Montagnani et al. 2023). In Europe, the importance of this pathway is known also for *A. artemisiifolia* (Essl et al. 2015), contaminant of agricultural commodities which became a relevant crop weed. The same vector can be assumed for *A. psilostachya,* even if it rarely occurs in crop fields (Karrer et al. 2023) and, also in the present analysis, in agricultural areas it has never been found in crops, but mostly along field margins or ruderal sites nearby roads (e.g. in Castiglione Falletto and Varazze). This could be related to ecological reasons (e.g. lack of suitable edaphic conditions) or maybe the species was a contaminant of grains and vegetables not for planting in fields but for food consumption (human food, livestock feed or industrial products; Cossu et al. 2020). This would be coherent with its early presence also in inner areas not characterized by a large-scale agriculture where the rural matrix was mixed with small-size manufactures at that time (e.g. Polcevera valley in Genova, Quercioli and Pontecimato in Massa-Carrara). The hypothesis that contaminated commodities from North America were largely used in northwestern Italy is supported also by the early occurrence of other North American congeners in the same areas: *A. artemisiifolia* has been firstly found in southern Piemonte (in 1902 in Alba, a few kilometres from Castiglione Falletto) and in the 1930s in Liguria along the Polcevera river (Gentili et al. 2017), where also *A. trifida* was found (Montagnani, unpublished data).

After 1943, unintentional introductions and secondary spread of *A. psilostachya* likely increased with the arrival of the "Allied troops" for the Italian Campaign of the U.S. Army (1943–1945) during the Second World War. The role of military movements of U.S. troops has already been identified as a promoting factor in the introduction and spread of *A. psilostachya* in other parts of the world, as in Australia and Belgium (Parsons and Cuthbertson 2001; Verloove 2023), as well for *A. artemisiifolia* (Chauvel et al. 2006) and *A. trifida* (Ardenghi and Polani 2016). Specifically, *A. psilostachya* could have been transported as contaminant of commodities as well as a "hitchhiker" on both civil and military vehicles and machineries, embedded in soils attached to wheels, tracks, etc. (Montagnani et al. 2017). This would have contributed to the introduction/spread of *A. psilostachya* both on the countryside (Ardenghi and Polani 2016) and in urban areas. In particular, at the end of the 1940s, the occurrence of *A. psilostachya* in railway yards (Varese, Milano) and big cities (Torino) could be caused by the passage of the U.S. troops or the transportation and depots of military cargoes. Maybe also urban cultivations for food supply in "war gardens" (Rusciano et al. 2017) could have contributed to the introduction of *A. psilostachya* to cities. In urban areas, the species probably benefitted from the presence of ephemeral "post war" suitable conditions that disappeared with the reconstruction of cities.

All these vectors are likely to be relevant to the introduction of *A. psilostachya* in Italy that probably resulted from events occurring at different times and in different areas, coherently to genetic data collected by Karrer et al. (2023). Some of these factors (e.g. introduction as contaminant of commodities) may keep on being active and progressively contributed to new introductions or new sites of occurrence. In this regard, also natural vectors could have played a role: the distribution of *A. psilostachya* in the Po Plain along the Po River and its tributaries (Figure 1) is an evident result of an effective hydrochorous dispersal of seeds or fragments of roots along watercourses (Montagnani et al. 2017; Karrer et al. 2023). Along coasts, again natural vectors can be responsible of the long-distance dispersal of the species: sea currents and waves could have transported the viable propagules of *A. psilostachya* over very long distances (Karrer et al. 2023) as also reported for other invasive alien species (e.g. *Carpobrotus edulis* (L.) N.E.Br.; Souza-Alonso et al. 2020), even if the effectiveness of this vector has yet to be demonstrated. However, considering the massive spread along the northern Toscana coast and especially along the Adriatic coast from the 1960s onwards (Figure 2), it seems clear that *A. psilostachya* has been strongly promoted by factors related to urbanization specifically along coasts. Since the beginning of the twentieth century, but especially after the Second World War, Italian coasts were subjected to deep changes, due to city and infrastructure construction as well as tourism development (Malavasi et al. 2013; Romano et al. 2017). Thanks to its ruderal behaviour and its ability to thrive in xeric conditions on sandy soils, *A. psilostachya* successfully took advantage of the coastal changes of the last 70 years. It occurred along roads as well as near settlements also at the beachside, while the colonization of more natural coastal areas (e.g. in Veneto) seems subsequent (Figure 3). Roads (including the construction phase) and vehicles (cars, but also working machineries) could have contributed to its dispersal along the coast and elsewhere, as demonstrated for its congeners *A. artemisiifolia* and *A. trifida* (Vitalos and Karrer 2009; Karrer 2014; Rauschert et al. 2017; Lemke et al. 2021; Son et al. 2024), together with the direct or indirect movement of contaminated sandy soils (Karrer et al. 2023). In consideration of the massive horizontal spreading of the roots also in small areas (35 m of root system excavated in few square meters; Montagnani C. *personal observation*), contaminated soils can be a highly relevant source of viable propagules. These factors can be locally relevant, but they can also act at wider scale: Karrer et al. (2023) supposed that the dispersal of the species over very long distances (170 km) can be ascribed to contaminated vehicles used for construction of infrastructure along beaches. Moreover, the presence of roads seemed to contribute to the introduction of *A. psilostachya* not only at sea level but also to Alpine valleys. Albeit sporadically, from the 1970s to recent times (2014), *A. psilostachya* has been found in the western Alps in Vallone dell'Arma (Cuneo) and Val Susa (Torino). Along the valley floor, both valleys are crossed by a road and a highway, respectively. It is known that roads promote the introduction and invasion of alien plant species from the lowlands to the alpine zone (Lembrechts et al. 2014) and this could be an alarming element as *A. psilostachya* can obviously resist cold winter conditions (Montagnani et al. 2017; Karrer et al. 2023) and become a threat to riverine habitats and grasslands in natural areas of conservation concern.

Our study highlighted the marked tendency of the species to become more and more frequent in natural and semi-natural environments (even if under different levels of human or natural disturbance), especially along rivers and coastal dune systems (Figure 3). Our findings are coherent with Karrer et al. (2023) who indicate that *A. psilostachya* is frequent in such natural habitats in Europe. Other studies highlighted that this species is much more common in ruderal habitats and cultivated environments than in semi-natural environments (e.g. France), but this could be due to analyses carried out in sites of late colonization (Fried et al. 2015). Despite the lack of comprehensive investigation into the potential negative impacts, this justifies the concern about the threat of *A. psilostachya* to habitats of conservation interest particularly in coastal areas (Del Vecchio et al. 2015).

The distribution of A. psilostachya in Italy

As result of repeated events of introduction and spread, in Italy *A. psilostachya* has invaded 15 out of 20 administrative regions, as it was never recorded in Valle d'Aosta, Campania, Basilicata, Sicilia and Sardegna, coherently to Galasso et al. (2024). North and central Adriatic coasts and the central part of Po Plain are the most invaded areas, together with the northern Toscana coasts. The very sporadic occurrence of *A. psilostachya* in southern Italy and in the central and southern Tyrrhenian coasts, where suitable habitats occur (e.g. extensive sandy shorelines), could be related to the lack of suitable climatic conditions. However, *A. psilostachya* is likely to be adapted also to warmer and drier climates as those characterizing the southern Mediterranean areas (Blasi et al. 2014). In this regard, predictive models indicate that *A. psilostachya* can expand its range also in warmer and drier conditions forecasted under future climate change scenarios (Rasmussen et al. 2017; Xian et al. 2023). So, the absence of the species could be related also to a lack of vectors of introduction and spread to certain areas of southern Italy especially in the past. In this area, the magnitude of international trades *via* ports was lower (Corbino 1923) (even if present, as in Naples, for example) especially if compared to northwestern Italy where the species was firstly found (Lupo 2010) and agricultural importations from North America had a minor impact (Bevilacqua 1989; Federico et al. 2011). At the beginning of twentieth century, the internal transport of goods by rail in the south of Italy was low as compared to the rest of the country (Mortara 1913) and the process of urbanization and infrastructure building was delayed in many areas (Fiorini et al. 2019). Especially at the beginning of invasion, these factors may have resulted in lowering (or halting) the propagule pressure *via* formerly cited pathways of introduction and spread of the species. In more recent times, also the distance from the Italian core distribution of *A. psilostachya* could have played a role in preventing its massive introduction southward. However, a boost to its introduction may have come from the landing and long stationing of U.S. troops during WWII also in regions where *A. psilostachya* has never been found (e.g. Campania, Sicilia). In consideration of all these elements, further investigations should be done to clarify the absence of *A. psilostachya* in many southern regions where environments suitable to the species are not lacking.

Conclusions

To sum up, it is important to highlight that over the course of a little more than one century, *A. psilostachya* has become quite a widespread invasive alien species in Italy. From early introductions in northwestern Italy, it gradually spread to other areas. Ports seem to have been relevant points of accidental introduction. Subsequently both human-mediated and natural vectors have been relevant vectors of dispersal. Disturbance and vectors related to especially linear infrastructures, coastal changes due to urbanization and tourism created the right conditions for an opportunistic ruderal species, such as *A. psilostachya*, to spread.

Its massive occurrence along sandy coastal systems should be considered an urgent call to investigate more deeply this species and an early sign of alarm for as yet not invaded coastal ecosystems. In this sense, further investigations about its potential negative impacts to native biodiversity and its proclivity to spread southwards, where the species is sporadic until now, should be done in order to prevent the colonization of areas of conservation interest that have not yet been invaded. Attention should also be paid to alpine areas, where it has occasionally been recorded. Furthermore, it should be underlined that *A. psilostachya* colonizes "popular" environments, such as beaches, where its allergenic impacts can be severe. Together with an increase in knowledge, it is desirable to rapidly implement early warning systems and management measures to contain the spread of the species at a national level.

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