



Plant invasion as an emerging challenge for the conservation of heritage sites: the spread of ornamental trees on ancient monuments in Rome, Italy

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Abstract Cultural heritage sites such as historical or sacred areas provide suitable habitats for plants and play an important role in nature conservation, particularly in human-modified contexts such as urban environments. However, such sites also provide opportunities for the spread of invasive species, whose impact on monuments has been raising growing concerns. The aim of this study was to investigate the patterns of distribution and spread of invasive plants in heritage areas, taking the city of Rome as an example. We focused on woody species as they pose the greatest threat to the conservation of monuments, owing to the detrimental effects of their root system. We analysed changes in the diversity and traits of native and non-native flora growing on the walls of 26 ancient sites that have been surveyed repeatedly since the 1940s. We found that the diversity of the native flora has steadily decreased, while there has been an increase in non-native, larger and more damaging species. The introduced species that have expanded most are ornamental wind- or bird-dispersed trees, which represent a major management problem as their propagules can reach the upper sections of the monuments, where they become more difficult to control. The most widespread and damaging of such species is *Ailanthus altissima*, which has recently been

included among the invasive species of European Union concern (EU Regulation 2019/1262). Our findings show that plant invasion is an emerging challenge for the conservation of heritage sites and needs to be prioritized for management to prevent future expansion.

Keywords *Ailanthus altissima* · Biodeterioration · EU regulation on invasive alien species · Impacts · Ornamental horticulture · Urban flora

Introduction

Culturally protected sites, such as monumental or sacred sites, play an important role in nature conservation throughout the world (Bhagwat and Rutte 2006; Verschuuren et al. 2010; Gao et al. 2013; Frascaroli et al. 2016; Woods et al. 2017), particularly when they are located in environments that have been markedly modified by man, such as agricultural landscapes (Frosch and Deil 2011). In cities, they are even more crucial (Jackson and Ormsby 2017) because they become part of a network of green spaces such as parks (Nielsen et al. 2014) and road verges (Rupprecht and Byrne 2014; Säumel et al. 2016) that can deliver numerous ecosystem services and play a key role in the conservation of urban biodiversity (Shwartz et al. 2014; Kowarik et al. 2016; Planchuelo et al. 2019).

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Numerous cities throughout the world contain cultural heritage sites that have been protected from urban development and have become important components of the urban green infrastructure (Gopal et al. 2019). The reasons for protecting these cultural areas vary according to the specific value of the site, which depends on whether they are of historic, artistic or religious importance. However, as the expansion and densification of cities continue, these areas are becoming increasingly valuable on account of their habitat and biodiversity functions. Larger sites can, owing to their size, heterogeneity and moderate human-mediated disturbance, provide key habitat for a wide range of plants and wildlife, and therefore harbour a rich diversity of species, which often even exceed that found in more intact natural elements of the urban green, such as remnant forests and urban parks (Kowarik et al. 2016). Since parts of these structures, such as the tops of high monuments and walls, are difficult and expensive to access to man, some sites also provide a refuge for relict populations of species of high conservation value, which have become rare in the surrounding rural environments (Shwartz et al. 2014; Ives et al. 2016). Smaller sites also form a key part of the urban green infrastructure and enhance biodiversity by creating a series of green patches in the urban mosaic or by providing habitat continuity and improving connectivity within the urban ecological network when they stretch over considerable distances in built-up areas, as in the case of ancient city walls (Shwartz et al. 2013).

On account of this connectivity and of their vicinity to propagule sources and human-mediated disturbance, urban heritage sites also provide opportunities for the establishment and spread of invasive plants. Until recently this was not considered to be a significant economic or environmental problem because the majority of the non-native species that grow spontaneously within heritage areas tend to be confined to the most disturbed habitats, such as trampled areas and paths, which have a low conservation value and are successfully controlled by means of ordinary mowing and clearing procedures (Celesti-Grapow and Blasi 2004; Cicinelli et al. 2018). However, when they grow on, or close to monuments, introduced plants can, like native plants, seriously threaten their conservation (Caneva et al. 2006; Cicinelli et al. 2020). In fact, vascular plants can inflict severe damage on buildings and structures,

largely due to their roots, which induce both chemical and mechanical forms of deterioration (Cutler and Richardson 1989; Caneva et al. 2008). Moreover, the recent acceleration of biological invasions in a wide range of habitats worldwide (Seebens et al. 2017), particularly in urban and human-made habitats, where invasion success is facilitated by high levels of disturbance and the high-intensity planting of introduced species (Pyšek et al. 2010a, 2010b; Kowarik 2011; Gaertner et al. 2016; Cadotte et al. 2017; Kühn et al. 2017) has also affected heritage sites, and the spread and impact of some species on monuments has become a source of increasing concern (Caneva et al. 2009; Casella and Vurro 2013; Minissale and Scian-drello 2017).

Rome, one of the largest and most populated cities in southern Europe, represents an ideal case study to investigate these issues because it has an exceptionally long history of plant species introductions and a rich body of botanical documentation, which spans the last four centuries and is often focused on the flora of ancient sites. Although introduced plants have been considered to play a very minor role in the flora of these sites, the expansion and impact of some invasive species in recent decades has increasingly threatened their conservation.

A number of studies have been conducted on the impact of other taxonomic groups, such as fungi, lichens and bryophytes, on the biodeterioration of stone monuments (Salvadori and Casanova 2016; Warscheid and Braams 2000) and advances have been made in our knowledge of the plant cover of archaeological areas (Ceschin et al. 2016) particularly of the most noxious native species, such as ivy (*Hedera helix* L., Bartoli et al. 2017). However, a gap in research on non-native flora growing in heritage sites remains. Specific studies are needed to shed more light on this emerging trend and to implement effective management strategies.

As a contribution to this little-investigated field of research, we studied the vascular flora growing on the ancient walls of Rome to analyze trends in the patterns of native and non-native plant species richness and spread in heritage sites over time. We focused on woody species because they are among the main plant invaders worldwide (Richardson and Rejmánek 2011; van Wilgen and Richardson 2014), they are considered the most harmful invasive species in urban systems (Potgieter et al 2017) and they pose the greatest threat

to the conservation of monuments, whether they grow on them or in their vicinity, owing to the detrimental effects of their extended root system (Lisci et al. 2003; Motti and Stinca 2011).

Here we present an analysis of the woody flora growing on the walls of ancient sites in Rome that have been surveyed repeatedly since the mid-1940s. We aimed to explore changes in native and non-native flora richness and traits such as size and growth form, which are key components in determining the damage potential of the species and, consequently, their potential impact on monuments. We also aimed to investigate the introduction history and dispersal strategies of non-native species as drivers of invasion success, as well as to identify the major invasive species, i.e. those that have changed most and those that are currently most widespread on the monuments.

Materials and methods

Study area

We analysed the vascular flora recorded on the walls of 26 heritage sites in the city of Rome, Italy.

The Rome metropolitan region, which is located in the centre of the Mediterranean (41°54'N, 12°29'E), has a population of 2,750,000 inhabitants within an area of 1287 km². The urban area covers approximately 345 km² and is enclosed in a suburban matrix of agricultural, semi-natural and built-up areas (Capotorti et al. 2013).

The climate is sub-Mediterranean and the natural vegetation consists of deciduous or mixed oak woodland. The current landscape is very heterogenous owing to the natural lithomorphological complexity of the area and to the long history of human impact, which spans almost three millennia and has produced a large variety of habitats and vegetation types. The Rome metropolitan region contains a rich flora that consists of 1649 species, the majority of which (86.2%) are native to Italy while the remainder (13.8%) are introduced species (Celesti-Grapow et al. 2013). Approximately 1300 species, 15% of which are woody, occur in the urban area, which is characterized by a high richness of tree and shrub species from natural vegetation, that grow spontaneously, prevalently in patches of natural forests and in man-made parks in the vicinity of the city centre.

Innumerable heritage sites of outstanding art-historical and archaeological significance are scattered throughout the metropolitan area of Rome. Some major sites (e.g. the Colosseum, the Caracalla Baths and the Roman Forum) cover large areas, other remains are very small, but still of outstanding art-historical and archaeological importance, such as fragments of walls dating back to the sixth century BC.

Owing to their high degree of environmental heterogeneity and to different management practices, these sites support a rich diversity of wild, mainly native, plants (Ceschin et al. 2016). Ancient walls are the most common host environment of the flora in these sites. These walls often support a greater abundance of plants than any other area in the heritage site, largely because they are the parts from which it is most difficult to remove vegetation. Plants colonise a variety of habitats provided by the vertical walls and horizontal tops of the sites, with highly diverse ecological conditions resulting from differences in factors such as inclination, exposure, moisture, building materials, age of the construction and type of management (Lisci and Pacini 1993).

In recent centuries, the heritage sites in Rome have been subjected to increasingly intense management efforts aimed at clearing the plant cover. After having been in a state of abandonment and covered by large amounts of vegetation for hundreds of years, preservation and restoration efforts gradually began in the early nineteenth century and increased in the twentieth century, becoming increasingly intense in the last decades (Caneva et al. 2003). The sites are now periodically managed by removing the vegetation cover, largely by means of mechanical weed control methods based on mowing. Weeding operations are generic actions that do not distinguish between invasive species and non-invasive species; specific actions targeted at invasive species are not carried out. The frequency of weeding operations varies greatly depending on the sites. In some major tourist areas they take place on a weekly basis in the peak growing season (April–July) so to allow the visitors to have an unimpeded view of the sights. In other sites, such as in those containing ancient walls, they are carried out far less frequently and for reasons such as safety, e.g. owing to the risk of falling branches or because road signs have been covered by the vegetation (SABAP 2020).

The total removal of all deteriogen agents (i.e. any agents that result in the deterioration of man-made constructions), including mosses and lichens, is infrequent owing to the high costs involved, and problems related, among other things, to the use of specific chemicals designed not to damage the sites, as well as to the difficulties encountered in reaching the highest parts of the monuments (Caneva et al. 2008). The number of more thorough interventions has increased in the last two decades thanks to the organization of special cultural events in Rome that have provided the financial support required to carry them out.

Selection of the sites and data survey

All the selected sites are located in the historic centre of Rome, which has been included among the UNESCO world heritage sites on account of its outstanding artistic value (WHC UNESCO 1990). The sites, which are integrated within the urban fabric, include some archaeological remains of great importance, such as the Colosseum, fortifications built over the centuries (e.g. city walls dating from different periods), a monumental cemetery and some old religious buildings associated with the Vatican City (Fig. 1).

The 26 sites were chosen from a larger sample of 40 sites surveyed by the Roman botanist Anzalone (1951) after the Second World War, between 1946 and 1950.



Fig. 1 Examples of the sites and of the plants studied in the historic centre of Rome, Italy. The invasive tree *Ailanthus altissima* growing close to the Colosseum (left). The native shrub *Capparis spinosa*, growing on the remaining arch of the

Pons Aemilius, the oldest Roman stone bridge on the river Tiber (top right). Damage inflicted to heritage sites by the roots of *Ailanthus altissima* (bottom right). Photographed by J. Grapow

We surveyed the same sites three times in 1988–1990, 1994–1995 and 2004–2005 (hereafter referred to as 1990, 1995 and 2005) within different research projects that were either specifically dedicated to the flora of archaeological sites or to the overall urban flora of Rome (Celesti-Grapow 1995; Celesti-Grapow et al. 2006, 2013), often by exploiting platforms and scaffolding being used for restoration purposes that allowed us to study areas that cannot normally be accessed. The different sites were surveyed with the same sampling procedure as that used by Anzalone (1951) and at least once in each of the main vegetative seasons of the flora of Rome, i.e. spring/early season (March–April), spring/summer main season (May to July) and summer/autumn late season (September to October).

Like Anzalone (1951), we only recorded the flora growing on the monuments (i.e. on the vertical walls and tops) or at their base. We used occurrence records as they represent the first essential piece of information for monitoring invasive species, particularly their range expansion (Latombe et al. 2017).

We surveyed the same sites, using the same sampling procedure, a fourth time during the spring of 2016–2019. Of the 40 sites first investigated by Anzalone (1951), we excluded from our most recent survey (hereafter referred to as 2019) those sites that are located outside the city centre because the land use and level of urbanization in their immediate surroundings have greatly changed over the decades. This has led to a deep transformation of the sites, which means they cannot be detected accurately or be surveyed by means of the same sampling methods, which is essential if comparisons are to be made between the past and present situations. By contrast, the city centre, which has been densely built-up and almost continually inhabited for more than two millennia, has not undergone such marked rural-to-urban transformations since the time of Anzalone's surveys.

We also excluded some sites that could no longer be accessed closely enough to be able to survey their flora. Other sites had already been excluded from our previous surveys conducted between 1988 and 2005 as their location could not be clearly identified on the basis of the original description provided by Anzalone (1951).

Compilation of the dataset

We compiled a dataset of the woody flora, containing the presence and absence scores of all woody species (i.e. including both phanerophytes and chamaephytes according to Raunkiaer's 1905 system of classification of life forms), recorded in the 26 historical sites from Anzalone (1951) and from our own survey campaigns (1990, 1995, 2005 and 2019). As mentioned earlier, we concentrated on woody species not only because they are considered among the most harmful invasive plants worldwide (van Wilgen and Richardson 2014), but, above all, because they are the species that inflict by far the most damage on human constructions such as buildings, walls and monuments owing to the large size and secondary diametric growth of the roots (Lisci et al. 2003; Motti and Stinca 2011).

For each species, we provided information (1) on plant form, i.e. tree, shrub, dwarf shrub (the latter including Raunkiaer's (1905) life forms chamaephytes and nanophanerophytes) or vine as it is considered to be related to the potential damaging capacity of the plants, with trees being the most damaging species and dwarf shrubs the least (Signorini 1996; Caneva et al. 2008; Motti and Stinca 2011), and (2) on the height of the species as a proxy for the size of the plant, as larger plants are considered to cause the most severe damage on human artifacts owing above all to their more extended root systems and greater weight (Caneva et al. 2006). These data were gathered from the flora of Italy (Pignatti 2017–2019). We also provided each species with (3) the Hazard Index (HI), with values ranging from 0 to 10. This index, which is attributed to vascular species on the basis of (i) life form (ii) invasiveness and vigour and (iii) capacity of vegetative reproduction and type of root system, is used to estimate the potential of a species to damage buildings (for details, see Signorini 1996; Motti and Stinca 2011; Motti and Bonanomi 2018).

To analyse the spread of invasive species, for the non-native flora we added the information on dispersal strategies and introduction pathways, which is crucial for the management of plant invasions (Pergl et al. 2017; Sádlo et al. 2018). Therefore, for each non-native species, we also used the database of the flora of Rome (Celesti-Grapow 1995) to extract some additional information on:

- (1) Main dispersal mode, referring to transport of diaspores by different vectors (Kleyer et al. 2008; Pérez-Harguindeguy et al. 2013; Sádlo et al. 2018), divided according to the following categories: autochory (self-dispersal), dispersal by birds, by humans, by insects, by mammals, by water and by wind.
- (2) Pathway of introduction. A general framework for classifying introduction pathways of alien species has been developed by Hulme et al. (2008) and implemented by the UN Convention on Biological Diversity (CBD 2014). In our study, we classified the species according to their pathway of introduction in Italy and adopted the following subcategories (we use here the original names of the categories, for details on the framework and its categories see Hulme et al. 2008; CBD 2014): erosion control such as windbreaks and hedges; landscape improvement in the wild (within the release category); agriculture, botanical garden, forestry, horticulture, ornamental purpose other than horticulture (within the escape category); contaminant of nursery material and seed contaminant (within the contaminant category).

Data analysis

For the 26 sites used in this study, we separately tested for compositional differences in the native and non-native flora between the five sampling dates (1950, 1990, 1995, 2005 and 2019) using one-way non-parametric multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001) and the Jaccard dissimilarity coefficient for presence and absence data.

All calculations were performed using the program PAST (freely available at: <http://folk.uio.no/ohammer/past>) and 9999 permutations. To visualize changes in the floristic composition of the native and non-native flora between the five sampling dates, we applied a principal coordinate analysis (PCoA) to the Jaccard dissimilarities between sampling units (see Legendre and Legendre 1998).

For each of the 130 sampling units (i.e. 26 sites \times 5 sampling dates), we calculated the mean value of the hazard index and the maximum plant height by averaging the values of all species present in each

sampling unit. We also calculated, for each sampling unit, the proportion of species (native or non-native) belonging to the four plant forms: tree, shrub, dwarf shrub or vine. For the non-native flora we also added the proportion of non-native species belonging to the different introduction pathways and dispersal modes used in this study. For all these quantitative variables, we separately tested for differences between the five sampling dates using traditional one-way ANOVA and 9999 permutations.

Results

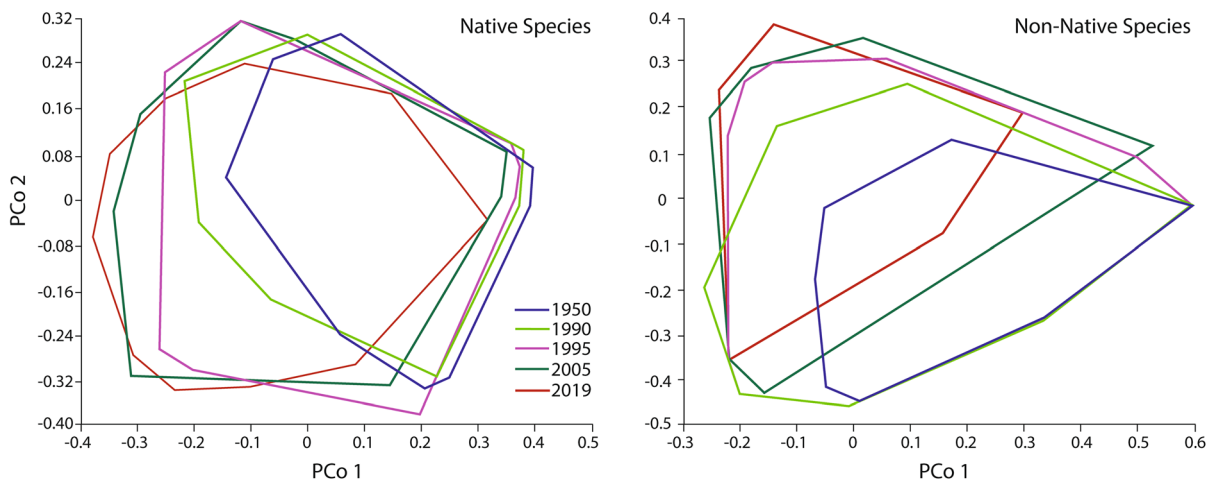
A total of 119 woody species, 35 (29.4%) of which are non-native, were detected on the walls of the 26 heritage sites in all 5 samplings from 1951 to 2019; 27 of these species are trees, 55 shrubs, 20 dwarf shrubs and 17 vines. The current wall flora of the 26 sites (2019 survey) contains 84 woody species, 35 (41.7%) of which are non-native. The number of species in the flora varies considerably from site to site; the richest is the Palatine hill, where a total of 34 woody species were recorded in the latest survey (2019). All the recorded non-native species escaped from cultivation; the majority of these (19 species) were introduced for ornamental purposes.

Although the overall richness remains substantially unchanged, as shown in Table 1 and Fig. 2, the floristic composition of both the native and non-native species groups significantly changed across the sampling dates, with a substantial decrease in native species (533 occurrences in 1950 vs. 216 in 2019) and a corresponding increase in non-native species (30 occurrences in 1950 vs. 224 in 2019). The non-native species whose numbers increased most are: *Acer negundo* L. (1 occurrence in 1950 vs. 16 in 2019), *Ailanthus altissima* (Mill.) Swingle (5 vs. 22), *Ligustrum lucidum* W.T.Aiton (1 vs. 15), *Lonicera japonica* Thunb. (2 vs. 11), *Parthenocissus quinquefolia* (L.) Planch. (2 vs. 15), *Platanus hispanica* Mill. ex Münchh. (0 vs. 12) and *Robinia pseudoacacia* L. (3 vs. 16); these are also the species that are currently most widespread in the 26 sites.

The results of traditional one-way ANOVA further showed that the mean sample values for plant height ($F = 16.63$, $p < 0.0001$; 9999 permutations), the hazard index ($F = 20.17$, $p < 0.0001$) and the relative proportion of trees ($F = 25.75$, $p < 0.0001$)

Table 1 *P*-values of the pairwise tests for compositional differences in the native flora (above, white cells; overall *F* statistic = 1.876, *p* = 0.0002) and non-native flora (below, grey cells; *F* = 2.659, *p* < 0.0001) between the five sampling dates

		Native flora				
		1950	1990	1995	2005	2019
Non-native flora	1950		0.6219	0.0708	0.0002	0.0001
	1990	0.0597		0.9986	0.2468	0.0017
	1995	0.0007	0.9956		0.8378	0.0235
	2005	0.0001	0.0102	0.2232		0.5321
	2019	0.0001	0.0001	0.0002	0.8733	

**Fig. 2** Two-dimensional principal coordinate analysis (PCoA) of the 130 sampling units (i.e. 26 sites \times 5 sampling dates) analysed in this study showing the convex hulls of the five

significantly increased over time, whereas the relative proportion of shrubs ($F = 4.51$, $p < 0.0018$) significantly decreased (Table 2). By contrast, the proportions of the remaining plant life forms did not differ significantly between the different sampling dates at $p < 0.05$.

When non-native species alone were considered, the analysis of variance highlighted a significant increase in the relative proportion of species introduced for ornamental purposes ($F = 9.91$, $p < 0.0001$) and of those dispersed by birds ($F = 4.51$, $p < 0.0017$) and by wind ($F = 3.24$, $p < 0.0154$; Table 2). All other introduction pathways and dispersal modes (strategies) did not differ significantly between the sampling dates at $p < 0.05$.

sampling dates. For the ordination, we used the Jaccard dissimilarity coefficient for presence and absence data

Discussion

Patterns of species richness

Despite the major environmental changes that have taken place in the surrounding metropolitan area, i.e. the progressive increase in urbanization, and the constant removal of vegetation resulting from management procedures, the overall woody plant diversity of the heritage sites in Rome has not changed significantly in the last 70 years. By contrast, the floristic composition has changed, with a decline in the richness of native species and an increase in the richness of non-native species. Moreover, this trend has been associated with a significant increase in those traits (e.g. size) that allow the flora to inflict more damage on monuments.

Table 2 Mean values for plant height, hazard index (see text) and relative proportion of trees and shrubs, relative proportion of non-native ornamental species and relative proportion of bird-dispersed and wind-dispersed non-native species for the five sampling dates investigated in this study

	1950	1990	1995	2005	2019
<i>All species (native and non-native)</i>					
Maximum plant height (m)	5.342 ^a	5.856 ^{ab}	6.551 ^{bc}	7.609 ^{cd}	8.469 ^d
Hazard Index [1–10]	4.403 ^a	4.576 ^{ab}	4.781 ^{bc}	5.095 ^{cd}	5.347 ^d
Relative proportion of trees (%)	5.758 ^a	11.351 ^b	14.877 ^b	23.818 ^c	31.751 ^c
Relative proportion of shrubs (%)	42.015 ^a	35.064 ^{ab}	34.525 ^b	30.887 ^b	26.871 ^b
<i>Non-native species only</i>					
Relative proportion of ornamental species (%)	63.333 ^a	69.880 ^b	73.684 ^b	78.035 ^b	77.679 ^b
Relative proportion of bird-dispersed species (%)	20 ^a	25.301 ^{ab}	28.070 ^{ab}	32.948 ^b	33.928 ^b
Relative proportion of wind-dispersed species (%)	36.667 ^a	42.168 ^a	42.982 ^{ab}	44.508 ^{ab}	42.411 ^{ab}

Pairwise comparisons were performed using one-way permutational ANOVA (9999 permutations). For each variable, different letters indicate significant statistical differences in the pairwise comparisons at $p < 0.05$. Holm-adjusted data for multiple comparisons

The results in Table 1 and Fig. 2 show that native and non-native woody species have responded in contrasting ways to the environmental changes that have occurred in the city since the 1940s and to direct management activities. A decrease in native plant species diversity associated with an increase in non-native plant species diversity along with increasing urbanisation is a well-known pattern that has been reported both in Rome (Celesti-Grapow et al. 2006) and in other cities in the world (Sukopp 2004; Kühn and Klotz 2006; Zhao et al. 2006; Aronson et al. 2015; Štajerová et al. 2017).

The loss of native woody species was somewhat predictable in our study sites, as it is related not only to the densification of the surrounding urban matrix but also to the continual clearing of the walls for management purposes. The vegetation that colonized the sites was repeatedly removed in the years in which we conducted our surveys, particularly over the last two decades, as part of standard management procedures aimed at the conservation of the monuments and at removing vegetation to allow visitors to gain a better view of them (SABAP 2020).

Greater management efforts and the environmental changes that have taken place in the city appear instead to have had a positive effect on the non-native woody flora, whose species diversity has increased since the 1940s. The overall increase in non-native species richness over time and/or along a gradient of increasing human impact is a well-known trend in urban and human-made habitats (Pyšek 1998; Pyšek

et al 2010a), where the establishment and spread of the introduced flora are promoted by disturbance and by the widespread availability of propagules from cultivated plants (Pyšek et al. 2010b; Kowarik 2011; Gaertner et al. 2016; Cadotte et al. 2017; Kühn et al. 2017). This increase is, however, a new finding in our study area. Although some studies have previously reported the presence of a few particularly harmful non-native species, such as *Ailanthus altissima* and *Robinia pseudacacia*, thereby highlighting the fact that some non-native trees are potentially detrimental to the monuments and recommending that they be monitored and controlled (Celesti and Blasi 2004; Caneva et al. 2009), such cases were considered to be sporadic. Until quite recently non-native plant species were not reported to be establishing successfully on ancient monuments and were thus considered to play a minor role in the flora on ruins where native plants have always thrived. Indeed, culturally important sites have generally been considered hot spots of native species diversity (Ricotta et al. 2001), refuges for local rare or endemic species and important sites for the conservation of natural vegetation, especially within cities (Minissale and Sciandrello 2017; Gopal et al. 2019). This increase undoubtedly constitutes an alarming threat to the conservation of monuments and possibly even to the conservation of the city's biodiversity.

Changes in species life form, size and deteriogen potential

Management efforts are probably one of the main causes underlying the relative decrease in shrub species in the period considered (Table 2). The shrub species that have declined most belong to the Mediterranean natural maquis, i.e. the evergreen shrub vegetation of the Mediterranean region. Similarly, when Caneva et al. (2003) compared the lists of the flora of the Colosseum published over the past four centuries, they found a general decrease in the numbers of native shrubs species of Mediterranean maquis, especially in those belonging to the most mature stages of succession that were colonizing the horizontal top of walls and ruins.

It is remarkable that the proportion of dwarf shrubs in the flora has not changed significantly over time. The vast majority of these species are evergreen native plants from natural rocky habitats, such as the caper (*Capparis spinosa* L., Fig. 1), that have found an analogue to their natural habitat in the city walls (Lundholm and Richardson 2010; Kowarik et al. 2016). These species are the most typical components of the wall flora of Rome, where they are widespread and abundant in the sites we analysed and on ancient walls throughout the city centre.

The relative proportions of trees have, on the other hand, steadily increased over time (Table 2). This is an unusual pattern in the wall flora. Native trees had until recently always been very scarce on walls even though some, such as laurel (*Laurus nobilis* L.) and Holm oak (*Quercus ilex* L.), had been extensively planted in the city centre and thus provided abundant sources of seeds.

The increase in the number of trees in the study area as well as the higher number of woody species with a greater deteriogen potential over time are trends that should arouse concern. In urban areas, trees have been shown to exert serious impacts on buildings and infrastructures (Fig. 1) owing to their great weight, extensive root systems and, most importantly, their secondary diametric root growth, which can seriously damage paved surfaces, walls and monuments and require costly measures if they are to be eradicated (Potgieter et al. 2019b).

The important role of tall alien trees as the invasive species that exert the most negative impacts in urban contexts has been repeatedly highlighted (McLean

et al. 2017; Potgieter et al. 2019a). Indeed large size, and specifically plant height, is one of the major predictors of the capacity of non-native plants to spread and become invasive (Pyšek et al. 2012) as well as one of the main reasons for why non-native trees are among the most widespread and harmful invasive species worldwide (Bucharova and van Kleunen 2009; Richardson and Rejmánek 2011; Pyšek et al. 2014; Rejmánek 2014).

Changes in the introduction history and dispersal strategies of the non-native flora

The preference of humans for peculiar plant traits has caused an increase in the proportion of non-native trees in urban areas following the introduction of ornamental species that have escaped from cultivation (Potgieter et al. 2017). In recent years, several studies have highlighted the importance of the introduction pathways and of the dispersal strategies on the invasion success of non-native species, (Essl et al. 2015; Pergl et al. 2017; Sádlo et al. 2018), and in particular trees (Donaldson et al. 2014). In our study area, the proportion of ornamentals in the non-native flora grew over time, thus confirming the importance of ornamental horticulture as the main introduction pathway of invasive plants (Dehnen-Schmutz et al. 2007; Hulme et al. 2018; van Kleunen et al. 2018), particularly in urban areas (Kowarik 2005; Kowarik et al. 2013; McLean et al. 2017; Padayachee et al. 2017; Petřík et al. 2019).

As regards the dispersal modes, the proportion of trees dispersed by birds and wind in the flora within the study area also grew over time. In urban areas, anemochory and ornithochory are common dispersal modes (Lososová et al. 2006), and fruit type was found to be related to the success of woody non-native plants (Aronson et al. 2007). Indeed, wind- and bird-dispersed propagules are efficiently transported to the highest parts of monuments, where control measures such as mowing are both difficult and costly. A case in point is the Colosseum, which is 57 m high and whose uppermost sections have been cleared of plants only thanks to exceptional restoration sponsorships (Caneva et al. 2003; Tod's for Colosseum 2017).

Although human-mediated dispersal can play an important role in the spread of plants in man-made sites, the species composition in the area considered in this study is unlikely to have been affected by visitors

to the sites because humans do not act as dispersal vectors of the woody species we analysed, as instead happens for some herbaceous species that are transported, for example, on the shoes or clothing of humans.

Most widespread and emerging species and management challenges

The aforementioned trends are confirmed by findings showing that within our study area the most relevant non-native species, i.e. those whose numbers have increased most since the 1940s and that are currently most widespread on monuments, are all plants introduced as ornamentals and dispersed by wind or birds. These species are prevalently trees, such as *Acer negundo*, *Ailanthus altissima* (Fig. 1), *Ligustrum lucidum*, *Platanus hispanica* and *Robinia pseudoacacia*, that have been planted along roads and in city parks. As propagule pressure and planting intensity are important correlates of invasion success of non-native species, particularly of trees (Pyšek et al. 2009; Feng et al. 2016), these findings may prove useful for the prioritization of management efforts in cities and for the management of urban green spaces (Potgieter et al. 2018), as they highlight the need to avoid using ornamentals of wind- and bird-dispersed trees that were shown both to be invasive and to have the potential to grow on and to deteriorate man-made constructions i.e., *Ailanthus altissima*, *Acer negundo* and *Ligustrum lucidum*.

Among the most relevant non-native plants there are also a few ornamental vine species, the most rapidly increasing and widespread of which is *Parthenocissus quinquefolia*; these species tend, however, to be planted in private residential gardens, where they are widely used as covering for shelters and fences. Indeed, climbing plants are very common in densely built-up urban areas because they take up little room in small courtyards and they grow well in pots on roof gardens. When they escape cultivation, some climbers are considered to severely threaten the conservation of ancient monuments because they can establish successfully on walls and form a dense cover. However, the impact of climbers on the conservation of monuments is still debated: while they are blamed for damaging monuments, some are also considered to provide a certain degree of protection for the remains

they cover (Viles et al. 2011; Kowarik et al. 2016; Bartoli et al. 2017).

Although most of the widespread species mentioned above are widely cultivated throughout the metropolitan area of Rome, they are neither common nor abundant in the wild. The only widespread invasive species that grow spontaneously in the city are *Ailanthus altissima* and *Robinia pseudoacacia* (Celesti-Grapow 1995). These trees are also the two most widespread woody species in the non-native flora of Italy, with *Ailanthus altissima* being the only woody species classified as invasive in every Italian administrative region (Galasso et al. 2018).

Ailanthus altissima (Fig. 1) is a tree that typically invades urban areas and has become one of the most common alien trees in urban land in Europe as well as other countries in the rest of the world (Kowarik and Sämel 2007; Kowarik et al. 2013; Sladonja et al. 2015; Sladonja and Poljuha 2018).

In the sites we analysed, the presence of *Ailanthus altissima* has constantly increased over the decades, from five sites in 1950, to 11 in 1990, 13 in 1995, 19 in 2005 and 22 currently. Moreover, unlike most other non-native trees, which are usually represented by a single or few individuals, *Ailanthus altissima* often becomes very abundant and reach high cover on the monuments. In Rome, this tree is found throughout the metropolitan area, where it forms dense stands in different habitat types, preferentially colonising abandoned land and roadsides. *Ailanthus altissima* is the only non-native species of the flora in Rome to be acknowledged to exert a highly significant negative impact (Celesti-Grapow et al. 2013), by infrastructural damage resulting from an aggressive root system (Almeida et al. 1994; Motti and Stinca 2011; Casella and Vurro 2013), particularly on the city's historical heritage, i.e. ancient monuments and archaeological remains.

The main features that make this early successional tree so successful are its adaptation to wall habitats, tolerance to urban conditions, efficient reproduction and dispersal and difficult management (Kowarik and Sämel 2007; Constán-Nava et al. 2010; Badalamenti et al. 2012; Wickert et al. 2017). Its winged, wind-dispersed samaras are efficiently transported to the highest parts of the monuments from where it can further spread vegetatively. Standard management procedures, which mainly consists in cutting the plant at its base, stimulate resprouting and increase overall

density of *Ailanthus altissima* stands (Burch and Zedaker 2003).

The impacts of this species in a wide range of habitats have resulted in it recently being added to the European Union List of Invasive Alien Species of Union concern (EU Regulation 2019/1262). This list includes species that are subject to restrictions and measures set out in the European Union Regulation on Invasive Alien Species (EU Regulation 1143/2014, European Union 2014) and is the core instrument of the Regulation (Genovesi et al. 2015). Despite this, scientific evidence on the impacts of *Ailanthus altissima* is still scarce. Our results confirm the need (i) to carry out more thorough investigations into the impacts of this species, which is considered one of the main flagship invaders in Europe (Nentwig et al. 2018), and (ii) to include the control of *Ailanthus altissima* among the priorities in management actions in urban systems not only at the local and national scales but in other countries worldwide.

Management challenges, future research and conclusions

Our results show that the invasion of non-native harmful species has steadily progressed in recent decades despite management efforts aimed at suppressing the vegetation covering the monuments. The recent spread of some invasive trees on heritage sites represents a new finding and an emerging challenge for the conservation of such areas.

This is a highly complex problem, particularly when these species are located in urban systems. In addition to the conflict of values that typically affects urban green spaces (Pickett et al. 2001; Kowarik 2011; Gaertner et al. 2017b; Saloman Cavin and Kull 2017; Potgieter et al. 2019b), such as the need to choose between urban development and nature conservation (Dearborn and Kark 2010) or to decide whether to use native or non-native species (Sjöman et al. 2016), heritage sites introduce further specific challenges, such as the need to choose between the protection of monuments and the conservation of biodiversity.

Indeed, some monumental areas are not only important components of the urban biodiversity but are also of considerable global value (e.g. world cultural heritage sites) as well as of great national

socio-economic importance for a number of sectors (e.g. the tourist industry).

Further open questions in the current debate on the management of plants on heritage sites regard whether some species, rather than being a cause of biodeterioration, actually provide a certain degree of bioprotection for monuments by acting as a barrier against weathering and thermal stress and by reducing erosion (Viles et al. 2011; Kowarik et al. 2016; Salvadori and Casanova 2016). It should also be borne in mind that some management actions can inflict considerable damage on monuments. This is not, however, the case in our study area, in which the removal methods are aimed at hindering the development of a dense plant cover and the succession towards more mature stages and are, consequently, mainly limited to mowing and cutting at the base of the plant.

Another issue that is related to invasive species on heritage sites is the cultural connections that people have with plants, particularly in cities (Gaertner et al. 2016, 2017a). Examples include tensions with the local inhabitants that often arise when trees are to be removed (Dickie et al. 2014) and the positive perception of inhabitants who may appreciate the iconic value of the plants covering the monuments.

All these reasons also show that management of invasive plants in culturally protected sites, especially when located in urban areas, is considerably more complex than that of invasive plants in agricultural areas, where most traditional management methods have originated (Pearson and Ortega 2009), and cannot consist in the mere removal of the target species, that may even result in an increase of secondary invaders (see Pearson et al. 2016).

Despite the complexity of this problem, we believe that the expansion of invasive species needs to be urgently addressed because it shows no signs of slowing. Further research and interventions, including specific monitoring and control campaigns, need to be implemented to prevent future invasions. New management strategies need to be developed by integrating multidisciplinary approaches that take into account the wide range of interests involved in heritage sites, including first and foremost the conservation of the monuments themselves. All in all, we believe that culturally protected sites provide an opportunity to gain new insights into the management of plant invasions, particularly in urban systems.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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