BIODIVERSITY RESEARCH

Determinants of native and alien species richness in the urban flora of Rome

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ABSTRACT

Until now, analytical studies on European urban floras have mostly concentrated on the central and north-western parts of the continent. In this paper, factors determining species richness of urban flora were studied for the city of Rome, Italy, based on a comprehensive floristic survey carried out between 1985 and 1994, and updated in 2005. All species were recorded in grid cells of 1.6 km² and classified into native and alien (the latter divided into archaeophytes and neophytes). The grids were classified with respect to the prevailing habitat type, area available to vegetation, level of disturbance and geographical position within the city. Data were analysed using minimal adequate models. Total species number was determined by habitat and its interaction with position on the north-west gradient; other variables explained much less variance. Holding other variables constant, the average species number per grid cell was highest in archaeological sites and parks, followed by woodlands and rivers, and grasslands and recent developments. Residential areas and the historical centre were poorest in species number. Towards the north of the city, species richness in corresponding habitats increases because of higher landscape heterogeneity and closer association with diaspore pools in the surroundings. Native species make up on average 84% of the total species numbers, and trends opposite to those for the total number of species were found for the proportional representation of aliens. The occurrence of alien and native species in the flora of Rome is driven by similar factors, but factors that increase representation of aliens decrease that of natives and vice versa. The representation of neophytes and native species in grid cells was easier to explain (74% of variation accounted for) than that of archaeophytes (27%); this result reflects that in terms of ecology and response to factors, archaeophytes take an intermediate position between native plants and neophytes. Proportional representation of neophytes decreased with increasing area available to vegetation, reflecting that semi-natural vegetation is better developed where less fragmented.

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INTRODUCTION

Urban ecology has a long history and has developed rapidly over the last few decades (see Sukopp, 2002 for an historical overview). Numerous studies have investigated plant communities of human settlements at a variety of scales in Central Europe. We now have a good understanding of the factors structuring vegetation composition in such sites (Kowarik, 1990; Wittig, 2002; Pyšek *et al.*, 2004a). Intensive research on urban floras of large cities in central and northern Europe has been also carried out (Burton, 1983; Klotz, 1987; Landolt, 2000; Godefroid, 2001; Chocholoušková & Pyšek, 2003), and complete species lists were produced for a number of cities in the second half of the 20th century; Pyšek (1993) gives a list of 77 cities in Europe for which the number of species has been reported up to the 1990s. This interest in urban floras can be attributed to the fact that cities are remarkably rich in species because of a high habitat diversity (Gilbert, 1989) and enrichment by alien species (Pyšek, 1998). Outside Europe, urbanization and its consequences have been intensively studied in North America (McKinney, 2002, 2006).

Plant species richness in cities is usually greater than in surrounding areas (Sukopp & Werner, 1983; Pyšek & Pyšek, 1990; Kühn *et al.*, 2004), and cities may harbour biodiversity hot spots and natural areas of a high wildlife value. The high diversity

of urban landscapes, resulting from variable land use, create a great variety of ecological conditions for plants (Gilbert, 1989). Conservation of biological diversity thus represents an important objective not only in nature reserves and semi-natural areas, but has also become vital in areas where human activity is most intense. In cities, nature conservation is of a special significance, because it has unique implications for social and community life, public health and human well-being (McKinney, 2002).

As in other human-made or heavily disturbed habitats, the total species richness in cities results from the presence of two groups of species, native and alien, the richness of which need not be driven by the same factors (Pyšek *et al.*, 2005). For 54 cities, information existed in the 1990s on how alien species contribute to the overall floristic diversity (Pyšek, 1998). They are generally over-represented in urban centres compared to the rest of the city and surrounding countryside (Chocholoušková & Pyšek, 2003) because cities are the main centres of their introduction and spread (Kowarik, 1990), and the establishment of aliens is favoured by human activities and disturbances (Hobbs & Huenneke, 1992; Davis *et al.*, 2000).

However, compared to the more northerly located parts of Europe, relatively little attention has been paid to urban floras in the Mediterranean Basin (Gavilan *et al.*, 1993; De Natale & La Valva, 2000; Dana *et al.*, 2002; Krigas & Kokkini, 2002; Pateli *et al.*, 2002; Chronopoulos & Christodoulakis, 2003). The city of Rome is an exception in this respect, because its natural landscape and wildlife have been studied in detail for a very long time. Historical documentation of plant species includes sources dating back to ancient Rome, as well as medieval illuminated manuscripts adopting pre-Linnaean nomenclature. The first botanical studies on Roman flora, the compilation of a list of plants growing inside the Colosseum, appeared in the 17th century (Panaroli, 1643). More recently, a distribution atlas of the flora (Celesti-Grapow, 1995), phytosociological overviews (Fanelli, 2002) and maps of actual vegetation related to environmental variables such as climate, geology and geomorphology (Blasi *et al.*, 2001, 2005) were produced. These studies indicated remarkable species richness and existence of diversity hot spots, not only in residual woodland and semi-natural areas surviving within zones of urban development, but also in archaeological sites and parks found in the very city centre (Ricotta *et al.*, 2001).

Regarding alien species, Rome constitutes a unique study subject because of (1) early floristic documentation, (2) continuous ancient human presence testified since the Lower Pleistocene, resulting in (3) long history of species introductions. Plants were first spread by the inhabitants of the numerous Iron Age sites found in the area, then by the Etruscan and Latin populations who settled there around the 9th century BC, as well as throughout Roman times, in particular via the far-flung trade routes of the Roman Empire. To this day, the widespread presence of gardens and parks dating from different historical periods and the intense turnover of goods and people from throughout the world (approximately 6 million tourists a year) make the introduction of new species still very much an ongoing process.

The present paper analyses the urban flora of the city of Rome and asks the following questions: What are the roles of habitat type, area available to vegetation and level of disturbance in determining the species richness within a city? What drives the proportion of alien species in the city flora and do the determinants of species richness differ among native and alien species? To what extent does the floristic composition depend on the spatial structure of urban environment, and what is the role of geographical position within the city relative to the above factors?

METHODS

Study area

The city of Rome (41°54′ N, 12°29′ E) extends over an area of *c.* 300 km². Unlike most urban areas of the world, the population of Rome has decreased over recent decades, declining in the whole municipality area (1272 km²) from 2.8 million in 1981 to 2.5 million residents in 2005. In spite of this, the city is still in a phase of marked urban expansion, which started in 1870 when Rome became the capital of Italy. This development has occurred mainly towards the south-east where the topography is more favourable. Hence, the flat eastern and south-eastern sectors of the city are more densely built than western north-western sectors, where open spaces are more numerous.

The urban landscape in Rome is very heterogeneous, both in terms of geography (climate, geology, soil, morphology) and land use (Blasi *et al.*, 2005). The climate is a moderate Mediterranean one, with an average annual temperature of 15.1 °C and average annual rainfall of 839 mm, although the city's location between the Tyrrhenian coast and the Apennine Mountains creates a south-west–north-east gradient of climate variation from the typical Mediterranean to temperate (Blasi, 1994). The geological substrate consists of a mixture of sandy, clayey or volcanic hills and plateaus, alluvial valleys and fluvial terraces (Arnoldus-Huyzendveld *et al.*, 1997).

The spontaneous vegetation consists of a variety of urban plant communities in the most densely built-up sites, and a mosaic of pastures, grasslands and fallow land in urban fringes. The city is surrounded mostly by agricultural land, which makes up 62% of the Roman municipality area. Notwithstanding the long-lasting human impact, spanning over more than 2700 years, residual fragments of ancient woodland with intensive wildlife still occur within the city limits. The survival of these fragments is the result of topography (they cover slopes too steep for urban development) or ownership (up to the mid-20th century they were included in private reserves generally used for hunting, and some were recently designated as nature reserves). Patches of such semi-natural woods are only found in the western and north-western sectors of the city, and are connected with more extensive woods in the surroundings. They consist of a variety of mixed-oak communities with a ground woodland flora rich in rare, threatened or endangered taxa. The most widespread are deciduous stands dominated by *Quercus cerris* on volcanic soils and by *Quercus pubescens* on less mature soils, and evergreen woods dominated by *Quercus suber* on sand and by *Quercus ilex* on the steepest slopes. There are also a few impoverished remains

of the deciduous *Quercus robur* forest that once covered the alluvial plains. Seminatural rocky vegetation develops on tufa escarpments, mainly occurring in the north, and rupestrian vegetation extends from these, to ancient walls, ruins and the remains of Roman aqueducts. Patches of spontaneous secondary woodland and Mediterranean shrubland commonly develop on steep escarpments and at unmanaged margins of parks and archaeological sites.

Floating-leaved, submerged and bank side vegetation is widespread along the banks of the Tiber River, its main tributary Aniene, and a network of minor watercourses. Fragments of riparian woods with *Salix alba*, *Populus alba*, *Populus nigra*, and *Alnus glutinosa*, which are common in the northern courses of the rivers, are gradually replaced by sparse trees as the rivers flow southward through the city (Blasi *et al.*, 1995).

Research and data

A comprehensive survey of the flora of Rome was carried out between 1985 and 1994. This research covered all habitats within the political borders of the city: both new, artificial sites created during urban development, and semi-natural and rural sites that became included in the urban spread. The distribution in the wild (outside cultivation) of vascular species was recorded in grid cells of 1.6 km^2 in size (for more details on the sampling protocol, see Menichetti *et al.*, 1987). Historical records from herbaria and literature were reviewed and only taxa found later than 1985 were included, making up the total inventory of 1285 taxa (Celesti-Grapow, 1995). In recent years, changes to the Roman flora have been constantly recorded. For the present study, the inventory was revised and updated and currently totals 1293 species of spontaneously occurring vascular plants.

In each grid cell ($n = 190$), the total number of species was recorded. Following the definitions of Richardson *et al.* (2000) and Pyšek *et al.* (2004b), all native species, naturalized species (alien species that have established self-maintaining populations) and casual aliens (whose populations are not self-sustaining so they rely on repeated propagule introductions for their persistence) were considered. Species were divided according to their status (see Pyšek *et al.*, 2004b for definitions) into native ($n = 1063$), archaeophytes ($n = 70$) and neophytes ($n = 160$). The classification of individual taxa followed Saccardo (1909), Viegi *et al.* (1974) and Pignatti (1982).

For each cell, the following variables were recorded, taken from the *Atlas of the flora of Rome* (Celesti-Grapow, 1995), from the *Land Cover and Vegetation maps of the Roman municipality* (Blasi *et al.*, 2001) and completed by a field survey:
(1) area available for vegetation expressed as the percentage of the cell area that is not built up (further referred to as 'area');
(2) prevailing habitat type, classified into (i) rivers; (ii) woodlands; (iii) large city parks; (iv) grasslands, pastures and abandoned fields (the latter mostly have a grass cover so they were included in this group); (v) archaeological sites with spontaneous vegetation among the ruins or covering them; (vi) recent housing, industrial and commercial developments where buildings alternate with unused allotments and wasteland; (vii) residential areas with spontaneous vegetation in small parks, gardens, flower beds and around the base of street trees; and (viii) historical centre, built up to a large extent, with spontaneous vegetation along roadsides, in trampled, paved and parking areas and on walls;
(3) disturbance level expressed on a semi-quantitative scale; the cells were classified into four groups of intensity and frequency of human disturbances. Disturbance was evaluated according to the hemeroby concept of Kowarik (1990) and Chronopoulos & Christodoulakis (2000), adapted to the study area. Because of the heterogeneity of the relatively large mapping units (1.6 km^2), the 10 levels of the original scale (H0 to H9) were reduced to five. None of the cells was attributed to the lowest levels of human disturbance (corresponding to H0 and H1 on the hemeroby scale of Kowarik, 1990), thus only four out of the possible five levels were recorded.
(4) geographical location within the city, expressed with respect to the city centre (centreness, coded 1–16), south–north gradient (northernness, −7 to +7) and east–west gradient (westernness, −7 to +7). A cell with zero coordinates is located at the very centre of the city, the one with the highest values of the parameters (e.g. 16, −7, −7) on its north-westernmost margin.

Statistical analysis

For analysis of the total species richness and proportion of aliens, the total number of species, proportion of archaeophytes and that of neophytes were the response variables, whereas geographical location (northernness, westernness and centreness), disturbance level and available area were covariates, and habitat types with eight levels (rivers, woodlands, parks, grasslands, archaeological sites, recent developments, residential areas and historical centre) were factors.

The total numbers of species were square rooted (e.g. Sokal & Rohlf, 1995: pp. 415–417) and the data evaluated assuming normal distribution of errors and identity link function. Proportions of archaeophytes and neophytes were analysed by specifying binomial errors and logit link function. Data for the response variable were stored in two vectors: one to identify the number of archaeophytes or neophytes, and the second the total number of species (the latter giving a binomial denominator; Crawley, 1993: pp. 267–278). To prevent the logits of archaeophytes or neophytes that were estimated from small sample of the total number of species from having an undue influence, logits were weighted by the total number of species in each sample. Over-dispersion of binomial errors was checked by comparing residual deviance with residual degrees of freedom (Crawley, 1993: p. 273). For analysis of the relationship between native and alien species richness (NAR), the square rooted numbers of archaeophytes or neophytes were the response variables, and the standardized numbers of native species were added to the above variables as a covariate. The data were analysed assuming normal distribution of errors and identity link function.

Before the analyses, covariates were checked for the most appropriate transformation by plotting the response variables against the covariates. The fitted models were checked by plotting standardized residuals against fitted values, and by normal

probability plots (Crawley, 1993). Because the explanatory variables were measured on different scales, they were standardized to zero mean and unit variance, to achieve their comparable influence. The standardization thus enabled direct comparisons of their effects because larger regression slopes directly indicated larger effects than smaller ones. Using the standardized values, collinearity was checked by a matrix of correlation coefficients, and then by calculating tolerance values, using the regression of the explanatory variable in question against all the remaining explanatory variables in the model (Quinn & Keough, 2002: p. 128).

Data were analysed with GLIM (version 4) (Francis *et al.*, 1994), separately for (1) the total number of species, the proportion of (2) archaeophytes and (3) neophytes, and after adding the number of native species as a covariate, for the number of (4) archaeophytes and (5) neophytes. Each model included the factor habitat, all the covariates, the interaction of each covariate with each level of the factor and all the possible interactions among covariates, except mutual interactions among the geographical location (northernness, westernness, centreness). The aim of each analysis was to determine the minimal adequate model (see Appendix S1 in Supplementary Material). In the minimal adequate model, all explanatory variables (factors and covariates) were significantly ($P < 0.05$) different from zero and from one another, and all non-significant explanatory variables were removed. This was achieved by a step-wise process of model simplification, beginning with the maximal model (containing all factors, interactions and covariates that might be of interest), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model), and retention of significant terms (Pyšek *et al.*, 2005). To prevent biases to the model structures caused by correlation between variables, model simplifications were made by a backward elimination from the maximal models using step-wise analysis of deviance tables (Crawley, 1993: pp. 192–197). The results were thus not affected by the order in which the explanatory variables were removed in the step-wise process of model simplification.

Significant explanatory variables in the minimal adequate models are termed net effects, because each describes the effect of the explanatory variable in question, holding the other significant explanatory variables constant. Consequently, each minimal adequate model gives an estimate of the relationship between the response variable and each of the explanatory variables, adjusting

for each of the remaining significant explanatory variables in the model (e.g. Quinn & Keough, 2002: pp. 114–119). As a result, the value of each parameter of the minimal adequate model describing the net effect can differ from a marginal effect of this explanatory variable, which does not take into account the effects of the other explanatory variables.

Significant differences among net effects of individual habitats were evaluated by the least square differences among means (LSD tests, e.g. Sokal & Rohlf, 1995: p. 243), using the standard errors of these differences from the minimal adequate models. The covariates in analyses assuming normal distribution of errors and identity link function that had common slope on all levels of the factor habitat were visualized as an added variable, or partial regression plots (see Appendix S2 in Supplementary Material), following the procedure suggested by Quinn & Keough (2002: p. 126) for the ordinary least square regression. Each of these plots is a scatter plot between two sets of residuals of the minimal adequate model, with the fitted slope corresponding to the partial regression slope of the response variable on the covariate in the minimal adequate model. Following Quinn & Keough (2002: pp. 131), analyses of interactions among covariates were made using centred variables, i.e. variables rescaled by subtracting their mean from each observation. Significant interactions between two covariates were further examined by simple slopes of the models at varying values of the interacted variables (see Appendix S3 in Supplementary Material) using simple slopes of one variable on another for three specific values of the changing variable: its mean, and mean plus and minus its sample standard deviation (Quinn & Keough, 2002: pp. 131–133).

RESULTS

Species richness

The minimal adequate model of the total number of species was highly significant ($F = 35.66$; d.f. = 14, 175; $P < 0.00001$) and had a very high explanatory power ($r^2 = 0.74$). This model indicated a significant effect of habitats and their interaction with northernness, and a significant effect of disturbance and two geographical coordinates, westernness and centreness (Table 1).

Habitats ($r^2 = 0.15$) and its interaction with northernness ($r^2 = 0.07$) explained most variance. Holding constant the

Table 1 Significance of explanatory variables in minimal adequate models of the total species number and of the proportional representation of aliens. The factor habitat is in italics, other parameters are covariates

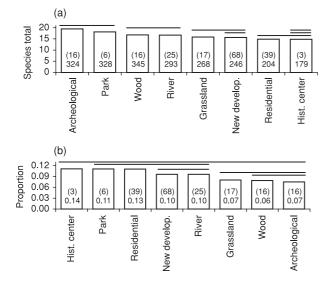| Explanatory variables	Total number of species			Proportion of archaeophytes			Proportion of neophytes		
	F	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P
Habitat	14.60	7, 182	< 0.00001	—	—	—	47.13	7	< 0.00001
(*Habitat*) × (northernness)	10.97	4, 179	< 0.00001	—	—	—	—	—	—
Disturbance	16.21	1, 176	0.00008	14.01	1	0.0002	7.852	1	0.005
Westernness	17.89	1, 176	0.0004	8.355	1	0.004	12.27	1	0.0005
Centreness	5.497	1, 176	0.02	—	—	—	—	—	—
Available area	—	—	—	—	—	—	10.03	1	0.001

Figure 1 Total number of species (a) and proportional representation of neophytes (b) in individual habitats. Bars (square root transformed in (a)) describe net effects, with the other significant explanatory variables held constant. Figures in parentheses inside the bars are sample sizes. The other figures inside the bars are marginal effects, i.e. those not taking into account the effect of the other significant explanatory variables of the minimal adequate models, and are equal to the average number of species (a) and the average proportional representation of neophytes (b) in individual habitats. Lines above the bars show groups of habitats not significantly different in LSD tests.
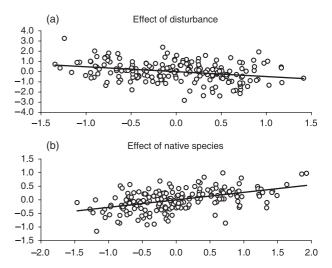

Figure 2 Partial regression plot (Appendix 2) for the net effect of disturbance on the total number of species (a) and for the effect of native species on the number of archaeophytes (b). Significances of the slopes are in Table 1 and their values in Table 2.

interaction of habitats with northernness and the effects of disturbance, westernness and centreness, the average species number was highest in archaeological sites and parks, followed by woodlands and rivers, and grasslands and recent developments. Residential areas and historical centre were poorest in species (bearing in mind that only three cells were examined in the latter, Fig. 1a). The net effect of interaction with northernness significantly increased species richness in archaeological and newly developed sites, rives and woodlands (Table 2).

The other significant explanatory variables, i.e. disturbance, westernness and centreness, explained less variance than habitats and their interactions with northernness. Holding all the other explanatory variables constant, the net effect of westernness ($r^2 = 0.03$) increased species richness, whereas the centreness ($r^2 = 0.01$) had an opposite effect (Table 2).

The negative net effect of disturbance ($r^2 = 0.02$; Table 2) indicates that holding all the other significant explanatory variables constant, species richness decreases in more disturbed habitats (Fig. 2a).

Proportional representation of alien species

The minimal adequate model of the proportional representation of neophytes (Table 1) had the same, very high explanatory power ($r^2 = 0.74$; $\chi^2 = 298.1$; d.f. = 10; $P \ll 0.00001$), as that for the total number of species. Most variance was explained by

Table 2 Significant ($P < 0.05$) regression slopes ± standard errors in the minimal adequate models of the total species number and of the proportional representation of aliens. The slopes are standardized and express relative effects of individual parameters. Factor levels of habitat are in italics, other parameters are covariates

Explanatory variables	Regression slope ± standard error		
	Total number of species	Proportion of archaeophytes	Proportion of neophytes
(*Archeological*) × (nothernness)	1.59 ± 0.60	—	—
(*New develop*) × (nothernness)	0.318 ± 0.120	—	—
(*River*) × (nothernness)	1.08 ± 0.22	—	—
(*Woodland*) × (nothernness)	0.468 ± 0.236	—	—
Disturbance	−0.480 ± 0.119	0.105 ± 0.028	0.0745 ± 0.027
Westernness	0.343 ± 0.081	−0.0809 ± 0.028	−0.059 ± 0.017
Centreness	−0.288 ± 0.12	—	—
Available area	—	—	−0.0787 ± 0.025

Table 3 Simple slopes of the number of neophytes against native species for different values of nothernness (centred values) in grassland and river habitats

Nothernness	Grassland				Riparian			
	Estimate	Standard error	F	P	Estimate	Standard error	F	P
Mean minus standard deviation	−0.00877	0.00384	5.22	0.04	0.0128	0.0032	16.17	0.0006
Mean plus standard deviation	0.00770	0.00438	3.09	0.1	−0.00024	0.0023	0.011	0.9

habitats ($r^2 = 0.12$), and much less by westernness ($r^2 = 0.03$), available area ($r^2 = 0.02$) and disturbance ($r^2 = 0.02$).

The minimal adequate model of the proportional representation of archaeophytes (Table 1) had much lower explanatory power ($r^2 = 0.27$; $\chi^2 = 28.84$; d.f. = 2; $P < 0.00001$) than the two previous models and only two variables had a significant effect. The largest proportion of variance ($r^2 = 0.13$) was explained by disturbance, and 8% by westernness.

The net effects of disturbance and westernness on the representation of both groups of alien species were opposite to the effects of these variables on the total number of species. Disturbance increased and westernness decreased the proportional representation of both neophytes and archaeophytes (Table 2).

In addition to these common effects for both alien groups, if habitat, disturbance and westernness are held constant, the net effect of available area caused a decrease in the proportional representation of neophytes (Table 2).

Similar to the net effects of disturbance and westernness, the net effect of habitat on the proportional representation of neophytes followed a different pattern from that found for the total number of species. The ranking of habitats according to the proportional representation of neophytes (Fig. 1b) is nearly opposite to that based on their total species richness (Fig. 1a). For instance, neophytes were most represented in the historical centre, which had the lowest total number of species, and the reverse was true for archaeological sites. Overall, the ranks of the net effects of the total number of species and of the representation of neophytes in the individual habitats were negatively correlated, and this relationship was marginally significant (Spearman's correlation coefficient $r_s = -0.62$, $P = 0.1$).

Relationship between native and alien species

The model for the number of archaeophytes, with the number of native species added as a covariate, yielded similar results as that for their proportion ($F = 23.82$; d.f. = 3, 186; $P < 0.00001$; $r^2 = 0.28$). Holding the effects of disturbance and westernness constant, there was very strong positive relationship between the number of archaeophytes and that of native species ($F = 58.18$; d.f. = 1, 187; $P < 0.0001$; $r^2 = 0.23$; Fig. 2b).

The model for the number of neophytes also mimicked the results of that for their proportions, including a high explanatory power ($F = 15.33$; d.f. = 23, 166; $P < 0.00001$; $r^2 = 0.68$). However, unlike in archaeophytes, the effect of native species was only

indirect and rather complex, manifested through interactions with habitat and northernness (model details not presented). If not affected by northernness, the significant relationships between neophytes and native species were all positive. Native species had the strongest effect on the number of neophytes in riverside habitats (0.653 ± 0.117), followed by parks (slope 0.611 ± 0.256) and archaeological sites (0.584 ± 0.229) and the weakest in recently developed areas (0.129 ± 0.068). However, the relationship was non-significant in woodlands, residential areas and historical centre.

In riparian and grassland habitats, the relationship between neophytes and native species was affected by northernness. In the former habitat, native species had a strong positive effect ($F = 16.17$; d.f. = 1, 22; $P = 0.0006$) only at low values of northernness (mean northernness minus standard deviation in Table 3) but not so at high values.

Conversely, in grasslands, the effect of native species on neophytes was negative ($F = 5.22$; d.f. = 1, 14; $P = 0.04$) at low values of northernness (mean northernness minus standard deviation, Table 3), and marginally positive (mean northernness plus standard deviation, Table 3) only at its high values ($F = 3.09$; d.f. = 1, 14; $P = 0.1$).

DISCUSSION

Habitats as main determinants of species richness

Habitat and its interaction with northernness explained most variance in species richness. The overwhelming effect of habitat on species richness has been long recognized not only in urban environments (Sukopp, 2002; Wittig, 2002; Pyšek et al., 2004a), although its net effect relative to other factors has been rarely determined (Pyšek et al., 2002, 2004a). The ranking of habitats according to species richness suggests that both more natural-like sites, such as riverbanks and woodlands, and typical human-made urban habitats, such as archaeological sites and grasslands in particular, can harbour considerable species richness. As in most ancient cities, history plays an important role; a positive relationship between settlement/buildings age and plant species composition was reported (Saarisalo-Taubert, 1963; Aey, 1990; Zerbe et al., 2003). In our data, it is difficult to relate the age of buildings to species richness unequivocally, but archaeological sites, which are richest in species (Fig. 1), are indeed the oldest, from Roman times. It is nevertheless impossible to separate possible effect of age from that of habitat heterogeneity in archaeological

sites. On the contrary, some species-poor habitats such as residential sites and new developments are rather young, with the majority of buildings originating from 1950 to 1970s and from the 1970 to the 1980s onwards, respectively. It needs to be stressed that the described pattern in habitat species richness refers to the net effect of habitats, unbiased by the effect of other environmental variables (see Pyšek *et al.*, 2002, 2005). This may partly explain the contrasting results of other studies; for example residential areas in many North American cities are reported to be highly species rich (McKinney, 2002, 2006).

The results confirm previous findings about extreme floristic richness of archaeological sites (Celesti-Grapow & Blasi, 2003, 2004). There is also an additional aspect to this phenomenon; plant diversity is conserved in these sites and brought into the very heart of the city, causing a peculiar pattern with hot spots of species richness in the centre, found in many Italian historical cities (Celesti-Grapow *et al.*, 2001). One of the main explanations of the remarkable species richness in archaeological sites is their within-habitat heterogeneity. They consist of a great diversity of microhabitats, creating a wide variety of ecological conditions for plants, from wet, dark and cool in excavations to extremely xeric, irradiated and hot on top of walls. Furthermore, there is a diversity of substrates as a result of the remnants from different historical periods and different degree of their conservation.

North and south are different: geographical gradients explain the pattern in species richness

The net effect of the habitat interacting with northernness means that towards the north of the city, species richness in some of the habitats increases. Archaeological sites, newly developed areas, riverbanks and woodlands in the north are richer in species than corresponding habitats in the south. Here the landscape heterogeneity (Pyšek, 1993) seems to be the most sensible explanation, together with availability of diaspore sources. In the northern/north-western sectors of the city, geological heterogeneity led to variable geomorphology, lithology, vegetation and land use (Blasi *et al.*, 2005). The relatively more homogeneous flat landscape in the south/south-east promoted human exploitation, at first with pastures and agriculture, later on with urbanization, leading to even higher homogeneity of the landscape. As a consequence, interconnected natural areas rich in wildlife were mainly preserved in the north and north-west, both within the city and outside the city limits. Vegetation in the north and north-west is therefore better connected with diaspore sources from the open landscape in the surroundings. Diaspore sources for native species (which make up most of the total number) are possible explanation for the higher richness of newly developed sites in the north, as well as for woodlands, which are scattered in the north and north-west, but totally absent from the south-east of the whole municipality (Celesti-Grapow & Fanelli, 1993). The vicinity of seed sources may be an explanation for this trend in archaeological sites too, because rocky habitats, which are the main seed sources for this habitat type, are also mainly found in the north.

The direction of the flow of Tiber from north to south also contributes to the above pattern. As the river flows through the city, hygrophilous species sensitive to human-induced disturbances and water pollution decrease at a rate that is faster than the corresponding increase in the number of species that are tolerant to sewage and pollution. Finally, the higher species richness in corresponding habitats in the north could be related to the climate, which is more temperate (Blasi & Michetti, 2001), thus less extreme in the north. Less summer drought might be particularly important in the more xeric conditions of urban sites such as those in the study area. Rome is located in a transition climatic zone, where slight differences in climate result in dramatically different vegetation (evergreen vs. deciduous forests; annual vs. perennial herbaceous vegetation).

The northernness is strongest but not the only spatially related determinant of plant species richness in Rome. Holding all other explanatory variables constant, the net effect of westernness increased species richness, whereas the centreness had an opposite effect. This means that the richness of the flora increases towards the west and with the distance from the city centre. These two spatial variables add only little to the explained variation but form a distinct pattern that is easy to interpret. The trend related to centreness is not surprising and has much support in European (Wittig, 2002; Chocholoušková & Pyšek, 2003; Pyšek *et al.*, 2004a) and American literature (McKinney, 2002, 2006); physical changes in metrics like human population density, road density, air and soil pollution temperature, rainfall, and soil characteristics strongly increase along the gradient towards the urban centre (McKinney, 2002). Nevertheless, it is interesting to note that the periphery-centre gradient in species richness was up to now not detected, for Rome, by rough estimates of floristic patterns because of the hot spots (parks, archaeological sites) located in the city centre. Only after net effects have been determined that the trend becomes obvious, indicating that Rome is not different from other large cities in this respect. The west-east gradient again needs to be interpreted with respect to the specific conditions within the city; it corresponds to increasing urbanization and decreasing heterogeneity. In addition, both gradients are also likely to be related to species pool in the surroundings and availability of diaspores; native species and archaeophytes have their major diaspore sources in natural areas and agricultural land, respectively, located west of the city.

Together, the analysis of geographical gradients codetermining species richness in Rome confirm the findings of classical botanical studies (e.g. Montelucci, 1953–1954), that pointed out to a higher species richness in the west and north-west compared to the east and south-east.

Disturbance as a fine-tuning mechanism of species richness in archaeological sites

The net effect of disturbance on species richness was negative, implying that more disturbed habitats harbour flora that is poorer in species. A similar response of species richness to disturbance was reported from Berlin (Kowarik, 1990) and Korean settlements (Kim *et al.*, 2002). This indicates that it is

'semi-natural' or 'semi-natural–like' sites that are most species-rich in Rome. Parks, woodlands and riverbanks fit well to this pattern; the only exception seems to be archaeological sites but they are only moderately disturbed (with a mean of 2.6 on the 4-degree disturbance scale, compared to 3.0 for newly developed sites, 3.5 for residential areas and 4.0 for the centre). However, parks, forests, riverbanks and archaeological sites are all habitats with an intermediate level of disturbance; minimally disturbed natural habitats are not found in Rome. At this intermediate level of disturbance, native species from natural habitats coexist with aliens.

Surprisingly, the net effect of disturbance explained only little variance ($r^2 = 0.02$); it is possible that the four levels used to express the disturbance are too coarse, as most grid cells fall at intermediate levels of disturbance. Nevertheless, the type and intensity of disturbance is another cause of the high species richness of archaeological sites. The disturbance there is moderate (intermediate) and mostly restricted to regular mowing to keep the ruins clear. Mowing prevents competitively strong Mediterranean grasses and forbs from achieving dominance and stops succession towards more developed, less species-rich stages. In addition, removal of dry biomass of tall herbs in the summer allows for the development of late summer and autumnal plants (Celesti-Grapow, 1995); interestingly, similar ruins outside Rome are covered by forest.

Within the range of the adopted scale, disturbance decreases species richness, but at the same time, it positively affects the proportions of both groups of aliens species, archaeophytes and neophytes. It appears that once the 'semi-natural habitats' in Rome are disturbed, their flora is enriched by aliens, yet their overall species richness decreases, because they lose rare species sensitive to disturbances. The increase in species richness with decreasing disturbance is the result of the addition of rare native species such as those tolerant to shade at woodland understorey, or those typical of oligotrophic habitats. This increase is much faster, probably the result of the larger species pool of native species, than the increase in aliens at higher disturbance levels.

Proportional representation of alien species: neophytes easy to explain, archaeophytes not so

Proportional representation of neophytes was, like the total number of species, best explained by the habitat, but that of archaeophytes was only determined by disturbance and westernness. The results also indicate that whereas the total species richness and proportion of neophytes was very easy to predict (74% of explained variation), it was much more difficult to do so for archaeophytes. Because there are 1063 native species accounting for 84.1% of the total species number (completed by 12.7% of neophytes and only 5.5% of archaeophytes), the trends described in previous discussions for the total number of species very closely mimic those that would be found, had the native species been analysed separately. Native species are finely tuned to natural conditions and the response of neophytes to important factors is rather straightforward, making the species richness of

both groups easier to predict. Archaeophytes, on the other hand, are something in-between; they do not reflect the subtle difference in environmental conditions as precisely as native species, because they have not been present in the region long enough to become perfectly adapted, but being present for several millennia makes them different from neophytes in terms of ecological demands and behaviour (Preston *et al.*, 2004; Pyšek *et al.*, 2004b, 2005).

In addition, archaeophytes are a heterogeneous group in terms of the degree of adaptation to local conditions, which may be supposed to be closely associated with the time of immigration (Pyšek & Jarošík, 2005). Some archaeophytes were found in Neolithic sites (Brilli-Cattarini in Viegi *et al.*, 2003), others probably came with Greek populations migrating westward some 2000 years BC. The majority, however, were imported into central Italy much more recently, mainly when Etruscan and Latin populations settled in the area at about 9th century BC, and during the far-flung trade in Roman times (Celesti-Grapow & Fanelli, 1993).

The pattern in Rome is therefore different from that reported by e.g. Deutschewitz *et al.* (2003), who found trends in the species richness of archaeophytes to be more similar to those of neophytes than of native species. Assumed evolution of many Mediterranean species, mainly annuals, with human disturbance (Pignatti, 1978; di Castri, 1990; Groves & di Castri, 1991; Naveh & Vernet, 1991) might be also true for archaeophytes introduced in ancient times.

That the trends in the total species numbers and proportional representation of native species are likely to be similar also explains why the effect of disturbance and westernness on the proportions of aliens were opposite to the effects of these variables on the total number of species. Towards more natural, peripheral, less disturbed, less urbanized sites, richness of native species increases, while proportions of aliens, particularly neophytes, decrease. It seems that the absolute numbers of both the native and the alien species (see succeeding discussions) are driven by the same external factors (namely heterogeneity) but the numbers of native species increase faster than those of aliens as a result of a larger species pool of natives (especially of rare species of natural habitats). This is also the reason why ranking of habitats according to the proportion of neophytes follows a pattern opposite to the ranking of habitats according to the total species richness. For instance, neophytes were most represented in the historical centre, which has the lowest total number of species, and the reverse was true for archaeological sites.

This result confirms that archaeological sites harbour surprisingly few alien species, as pointed out in the literature (Anzalone, 1951; Brandes, 1985; Lisci & Pacini, 1993; Krigas *et al.*, 1999; Celesti-Grapow & Blasi, 2004). The within-habitat heterogeneity typical of archaeological sites increases the number of aliens, yet their percentages are low because of the native species responding to increased habitat heterogeneity more efficiently. Archaeological sites are very rich in native vegetation of natural rocky habitats and Mediterranean scrub, typically developing later in succession on inaccessible, hence not frequently mown places (at the height of 30–50 m) or on neglected

places, not open to the public. This vegetation is made up almost exclusively of native species.

In addition to the previously mentioned effects, the net effect of available area caused a decrease in the proportional representation of neophytes. If there is enough space available to vegetation, native species are encouraged and the proportional representation of neophytes is lower. It is likely that larger available area translates into better possibilities for the development of less fragmented 'semi-natural' vegetation that is richer in species and represents a barrier to invasion by neophytes. Limited area, on the other hand, supports the formation of random assemblages of species where neophytes are less constrained by competition from native species. Consistently with the previously mentioned interpretation, archaeophytes behave as native species in this respect, as suggested by a non-significant effect of available area on their proportions. It needs to be taken into account that the 'available area' refers to the total area available in the whole 1.6-km^2 grid cell, whereas for vegetation, the size of single patches inside a cell is certainly more relevant. Nonetheless, 'smaller available area' in a cell generally corresponds to more fragmented patches within the cells, thus the total area is a reasonable indicator of the average patch size.

Relationship between native and alien species: what is good for native, is not good for aliens

No negative NAR relationships, that might indicate a direct competition between both groups, were detected. The only exception is grasslands, indicating that competition in grasslands might be particularly strong (see also Pyšek *et al.*, 2002). But in general, the relationships were positive or non-significant, as would be predicted by the theory for a scale like the one studied in this paper (Deutschewitz *et al.*, 2003; Kühn *et al.*, 2003; Chytrý *et al.*, 2005). This indicates that the same external factors affect both groups in the same way (Shea & Chesson, 2002).

Interestingly, NAR for archaeophytes is much stronger than that for neophytes and a direct one, indicating again that archaeophytes are more similar to native species than are neophytes (Kühn *et al.*, 2003). The Mediterranean Basin is special in that archaeophytes introduced a long time ago might have been subjected to the same evolutionary forces that drove many native apophytes to become adapted to human-made perturbations.

Unlike in archaeophytes, the relationship between native species and neophytes was indirect, manifested through interactions with habitat and northernness. In general, it tended to be positive and was strongest in riparian habitats, followed by parks and archaeological sites, whereas being very weak in recent developments and non-significant in woodlands, residential areas and historical centre. In riparian habitats and grasslands, NAR relationship depended on the position on the north–south gradient; as demonstrated in previous discussions, this is an important geographical determinant of the pattern of floristic richness in Rome.

Native and alien species relationships for neophytes are thus less consistent, indicating that they are relatively recent newcomers and their adaptation to individual habitats is still in progress, having proceeded further in some habitats than in others. Assuming that native species are well adapted to their environment, then the strength of the positive relationship between neophytes and native species in a particular habitat might be taken as indication of the degree of adaptation to local conditions. Using this as a criterion, the level of adaptation would be highest in riparian habitats, parks and archaeological sites, but low in newly developed areas, woodlands, residential areas and historical centre.

In riparian and grassland habitats, the relationship between neophytes and native species was affected by northernness. In riparian habitats, native species had a strong positive effect on neophytes only in the south, but not far to the north. This is because more than any other habitat, riverbanks differ from the north to the south. In the north, there are fragments of riparian woodlands and hygrophilous communities, leading to an increase in native species only and a negative NAR. To the south, the riverbanks get gradually heavily affected by urbanization and become poor in natural vegetation and enriched by neophytes. In grasslands, the NAR changed in the direction opposite to riparian habitats, because Mediterranean herbaceous vegetation is concentrated in the south and south-east. Towards suburbs in the north of the city, there is more heterogeneity and seed sources, thus both native and aliens increase. The south is dominated by grasslands and pastures of the Albani Hills (Menichetti & Petrella, 1986), which is extremely rich in native species; neophytes play a negligible role, hence the NAR is negative. These pastures have been continuously used since the Iron Age, creating long-term selection pressure for human-induced disturbances, making this type of Mediterranean vegetation less prone to invasions by aliens (Pignatti, 1978; di Castri, 1989, 1990; di Castri *et al.*, 1990; Groves & di Castri, 1991; Naveh & Vernet, 1991).

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SUPPLEMENTARY MATERIAL

The following materials are available online at http://www.blackwell-synergy.com/doi/abs/10.1111/j.1366-9516.2006.00282.x

Appendix S1. Minimal adequate model.

Appendix S2. Partial regression plot in the minimal adequate model.

Appendix S3. Calculation of simple slope in a model with significant interaction between two centred covariates.