

## ANALYSIS AND DISTRIBUTIONAL PATTERNS OF THE INVASIVE FLORA IN A PROTECTED MOUNTAIN AREA – A CASE STUDY OF MEDVEDNICA NATURE PARK (CROATIA)

NINA VUKOVIĆ, ANITA BERNARDIĆ, TONI NIKOLIĆ,  
VLADIMIR HRŠAK, MIŠKO PLAZIBAT, SVEN D. JELASKA\*

Department of Botany, Faculty of Science, University of Zagreb  
Marulićev trg 20, 10000 Zagreb, Croatia

\* e-mail: sven@botanic.hr

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### ABSTRACT

In this paper we have analysed invasive flora of Medvednica Nature Park, Croatia with respect to their origins, life forms, systematic positions, types of seed dispersal, Ellenberg indicator values and spatial distributions using MTB 1/64 grid units for analyses. A total of 27 invasive plant species, belonging to 14 families, were recorded with Asteraceae being the most frequently occurring family. Therophytes were the most common life form, as is generally true of Croatian invasive plants; however, hemicryptophytes and geophytes were more frequent in Medvednica. Here, invasive plants originated mainly from both Americas with slightly lower portion in comparison to all Croatian invasive plants, while contrary was the case when comparing those originated from Asia. The most widespread species was *Erigeron annuus* (L.) Pers., and the species with the lowest occurrence were *Chamomilla suaveolens* (Pursh.) Rydb and *Datura innoxia* Mill. A multiple regression model explains 44% of the spatial variability in the invasive plants data per MTB 1/64 unit, using the number of all recorded plant species, the average elevation and the lengths of paths and roads as estimators. The latter two variables also had the most influence on the ordination axes in analyses of the spatial distribution of seed dispersal types present in each MTB 1/64 unit. Anemochory was the most frequent type of seed dispersal.

KEY WORDS: invasive alien plants, MTB grid, dispersal strategy, habitats, RDA, regression.

### INTRODUCTION

Introduction of alien plants into new environments is nowadays a large-scale phenomenon, accompanied by many adverse effects. Humans began intentional introductions in ancient history, mainly for cultivation of agricultural, horticultural or ornamental plants (Lambdon et al. 2008). Over time, as the human population experienced increased growth and development, intentional and unintentional introduction and spreading of alien plants were considerably enhanced by long-distance trade, travel and tourism; according to Lambdon et al. (2008), after 1800 A.D., the number of introduced species in Europe rapidly increased. After introduction, some introduced species have undergone the process of naturalisation, establishing self-replacing populations in the new environment. A subset of naturalised plants with 'special skills' (production of reproductive offspring, often in large numbers at considerable distances from parent plants, having the potential of spreading over a large area) became even better adapted, i.e. invasive (Richardson and Pyšek 2006).

The negative impact of invaders on native communities has been researched, debated and confirmed widely in the scientific community (Vilà et al. 2006; Hejda et al. 2009). Keeping in mind that invasive species can be highly aggressive, biological invasions are, along with habitat loss, considered to be one of the major threats to overall biodiversity (Genovesi and Shine 2003).

Considerable efforts have been made to prevent further invasions and to establish successful control over invasive species. Studies on biological invasions in the last few decades have examined the mechanisms and patterns of invasions, the roles of different factors in invasion success and the impacts of invasive species to resident species and communities (Lonsdale 1999; Lockwood et al. 2005; Richardson and Pyšek 2006; Vilà et al. 2006; Traveset et al. 2008; Hejda et al. 2009; Jarchow and Cook 2009). Global concern about invasive species and their possible negative impacts on biodiversity have, in some cases, induced investigations of invasive flora of nature reserves (Timmins and Williams 1991; Pyšek et al. 2002; Pyšek et al. 2003; Foxcroft et al. 2009). A large group of European scientists

has recently been involved in the most extensive study of alien organisms to date (DAISIE project, 2004-2008) in order to create an inventory of invasive species that threaten European natural environments (Lambdon et al. 2008).

Until recently, data on Croatian invasive plant species included mainly sporadic and/or accidental records concerning alien adventitious, neophyte, ruderal or weedy plants (Topić and Kusulja 1989; Trinajstić and Jasprica 1998; Cigić et al. 2003; Milović 2004). In the last few years, check-lists of invasive species have been made (Dobrović et al. 2005; Dobrović et al. 2006a), and a few national projects regarding alien flora were initiated, resulting in the development of the module «Allochthonous plants» and its integration into the existing Flora Croatica Database (Nikolić 2008). Finally, national standards for terminology and criteria for the treatment of alien flora were proposed (Mitić et al. 2008), and a preliminary check-list of invasive alien plant species with analyses of their family affiliations, life forms and origins was prepared (Boršić et al. 2008).

Other than this general national overview, distributional patterns and/or invasive species assemblages for some particular regions have not been analysed in detail until now. Mt. Medvednica, located on the very edge of the capital city with a Nature Park in its western part, has been a subject of interest to Croatian botanists for several decades (Bulić 1952; Egić 1978; Mihelj 1982; Hršak et al. 1999; Jelaska et al. 2003; Dobrović et al. 2006b, c; Mareković et al. 2009).

During that time, different studies have provided a large amount of data on the flora of Medvednica, making it possible to extract information on the occurrence of invasive plants. This study is intended to provide more detailed insight into the invasive plant species of Medvednica Nature Park, based on previous records. Our objectives were to determine (1) what invasive plant species occur in the park, (2) what is their current distribution in the park and (3) what are the main factors responsible for such distribution. The data and results could inform better park management regarding invasive species in the future.

## MATERIALS AND METHODS

### Study area

Mount Medvednica is situated in north-western Croatia, near the capital city, Zagreb (Fig. 1). Its lower parts are surrounded with populous areas – apart from Zagreb to the south (with one of the largest population densities in Croatia), there is the Hrvatsko Zagorje region to the north, a mainly rural area.

The massif is 42 km long and stretches from SW to NE, with an approximate width of 9 km, and its highest peak, Sljeme (1033 m), in its western part. The western part of the massif, encompassing 228.26 km<sup>2</sup>, was declared a Nature Park in 1981 by the Nature Protection Law. Its proxi-

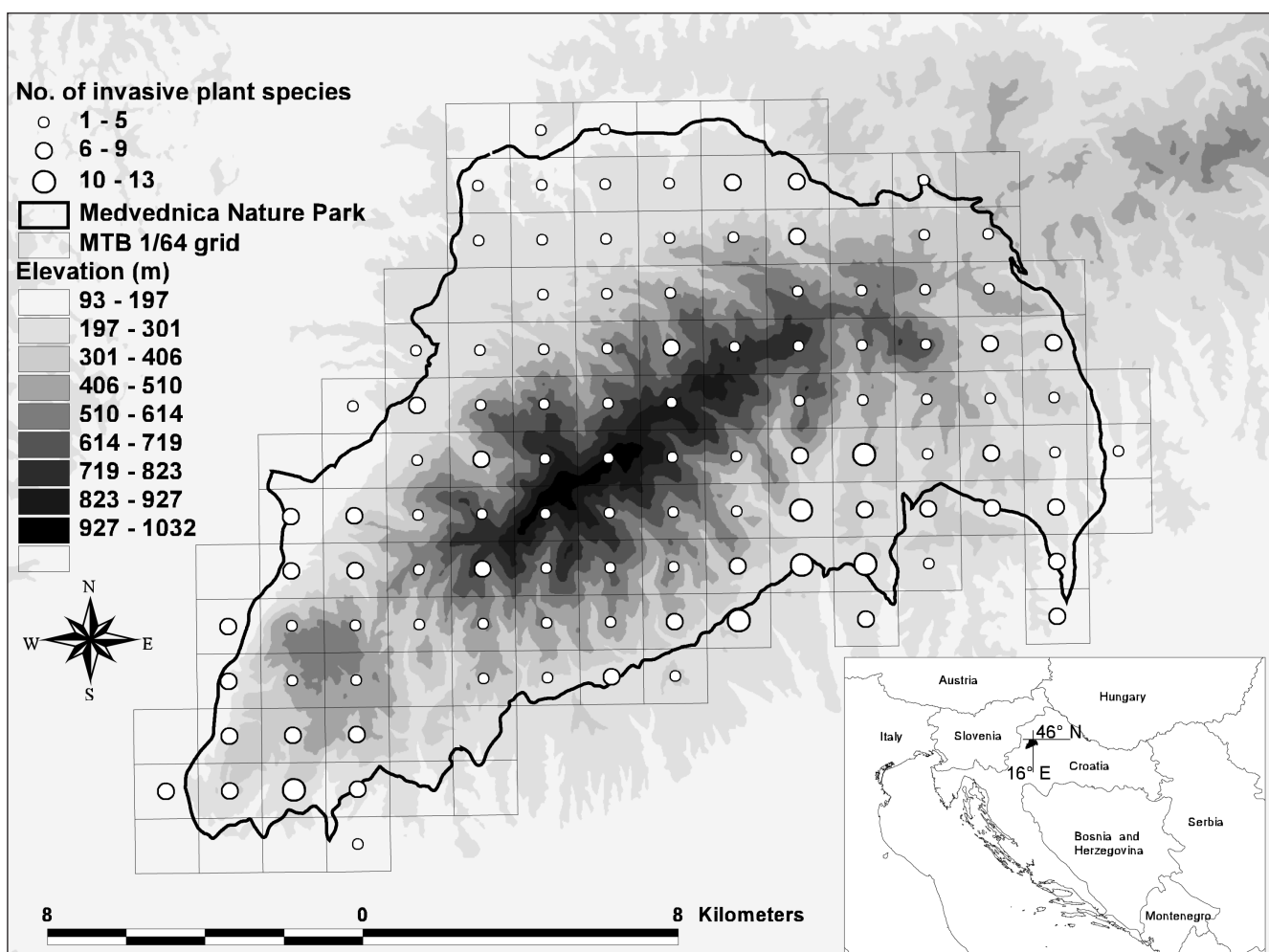


Fig. 1. Lower right corner – position of Medvednica Nature Park. Main map – MTB 1/64 grid. number of invasive plant species per MTB 1/64 unit and elevation.

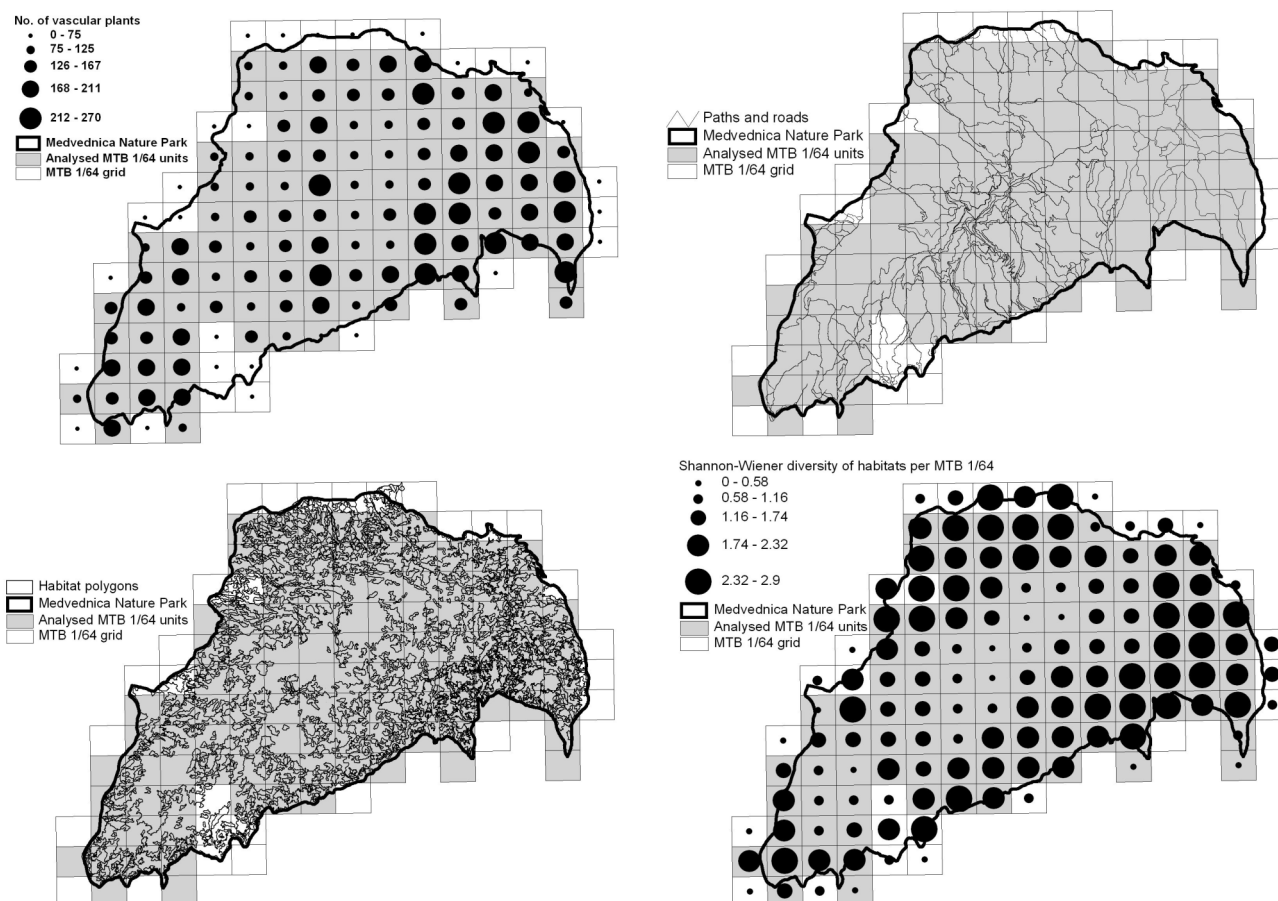


Fig. 2. Upper left corner – number of all recorded vascular plant species per MTB 1/64 unit; upper right corner – paths and roads in the Nature Park; lower left corner – polygon map of habitats; lower right corner – Shannon-Wiener index of habitat diversity per MTB 1/64 units.

mity to a large city and history of nature protection make this area a popular tourist destination with many visitors throughout the year.

Medvednica Nature park is mostly covered with woodland (63%), dominated by beech forests in the upper parts (Aremonio-Fagion (Ht 1938) Törek et al 1989 alliance), while the lower parts belong to Carpinion betuli Isll. 1932 alliance. Some areas are covered by azonal acidophilous and termophilous forests. Grasslands and anthropogenic habitats (cultivated land, settlements and roads) account for 6.1% and 30.3% of the area, respectively (Dobrović et al. 2006b). Besides botanists, Medvednica attracts other biologists as well (Maguire et al. 2002; Šerić Jelaska et al. 2007; Radović and Tepić 2009; Šerić Jelaska and Durbešić 2009) because of its high overall biodiversity despite strong anthropogenic influence.

Climate of the area is temperate continental. Local values of rainfall and temperature are mainly determined by elevation; hence, rainfall gets more abundant and temperature gets lower as elevation increases. In the upper parts of Medvednica, the mean annual rainfall is 1262 mm, and the mean annual temperature is 6.9°C (Dobrović et al. 2006b).

#### Data sources

Data on the plant species of Medvednica Nature Park were taken from the Flora Croatica Database (Nikolić 2008), and they originated from several published floristic papers (Marković-Gospodarić 1965; Gaži-Baskova 1978; Marković 1982; Mihelj 1982; Hulina 1984; Marković and

Lukač 1993; Pandža et al. 2001; Cigić et al. 2003; Milović 2004) and from unpublished field observations done in last decade and repositied in the database.

Spatial data on Medvednica Nature Park used in the analysis were as follows: elevation zonation (represented as 100 m zones), distribution of different habitat types (represented as polygons) and network of paths and roads. The entire area of the Nature Park was divided into a MTB (Meßtischblätter) grid subdivided into 1.5×1.45 km units (MTB 1/64), according to a proposed national standard (Nikolić et al. 1998). After spatial overlapping with the MTB 1/64 grid, the environmental characteristics of each MTB 1/64 unit were calculated, using the ArcView 3.3 (©ESRI) software (Fig. 2):

1. Mean elevation – expressed as the sum of the values of different elevation zones multiplied with their proportions in the area of the MTB 1/64 unit.

2. Habitat diversity – expressed as the Shannon-Wiener index of diversity (H), according to the following equation:

$$H = - \sum_{i=1}^s p_i \ln(p_i)$$

where  $s$  stands for the number of different habitats, and  $p_i$  stands for the proportion of each habitat within the MTB 1/64 unit.

3. Total number of habitat polygons – all polygons were included, even if several polygons of the same habitat were

present within the unit. This number was used as a simple measure of habitat fragmentation.

4. Total length of paths and roads – length of all road and paths per MTB 1/64 unit.

#### Data analysis

We analysed the taxonomy of the invasive flora of Medvednica Nature Park to determine the number of monocotyledonous and dicotyledonous species, as well as their family affiliations.

The portion of different life forms was determined using Raunkier's system (Raunkier 1934) as presented by Pignatti (1982) and Ellenberg et al. (1991). Different life forms were denoted with the following abbreviations: P – Phanerophytes, H – Hemicryptophytes, T – Therophytes, G – Geophytes.

The analysis of the geographic origins of invasive plants was based on data on their native range taken from Boršić et al. (2008). Species originating from different continents were designated by the following abbreviations: Am – the Americas (North and South), As – Asia, Af – Africa, EA – Eurasia.

The above data were compared to overall data for Croatian invasive flora. For the purpose of comparison, the Croatian data from Boršić et al. (2008) were adjusted in the following way, leading to a recalculation of proportions:

(1) Life form data were modified according to the available literature.

(2) Subspecies of *Erigeron annuus* (L.) Pers. were treated as one species, reducing the total number of invasive species to 62.

(3) A new category of origin (Mixed – originating from more than one continent) was introduced into the origin analysis.

In order to determine its preferred ecological conditions, each invasive species was assigned a set of indicator values (Ellenberg et al. 1991; Pignatti et al. 2005) describing its affinity toward different climatic factors (T – temperature, L – light, K – continentality) and soil characteristics (F – moisture, R – acidity, N – fertility, S – salinity). The means of the indicator values were used to indicate the average affinity of invasive flora towards different ecological conditions.

Finally, a total of 106 MTB 1/64 field units were included in the analysis of the distribution of flora within Medvednica Nature Park, out of which 102 units contained invasive plants. The data from the literature was geo-coded on the basis of the locality description and ascribed to the corresponding MTB 1/64 unit. The total number of species and the number of invasive species per unit were calculated. Units with scarce floristic information were excluded from the distribution analysis. However, one invasive species (*Datura innoxia* Mill.) was recorded only in one of the omitted units; this species was nevertheless included in the total list of invasive species and subjected to the analyses of taxonomy, life form, origin and ecological preferences.

Simple linear regression was used to analyse the correlation between the number of invasive species and the total number of species per unit. Multiple linear regression with the forward stepwise procedure (Hair et al. 1995) was used

TABLE 1. List of invasive species of Medvednica Nature Park with their family affiliations, life forms (T – Therophytes, H – Hemicryptophytes, G – Geophytes, P – Phanerophytes), origins (Am – the Americas, As – Asia, EA – Eurasia, Af – Africa), seed dispersal mechanisms (Au – autochory; Ae – anemochory; Hy – hydrochory; Zo – zoochory and At – anthropochory) and the number of MTB 1/64 units containing the species.

Species	Family	Lifeform	Origin	Chory	Units
<i>Ailanthus altissima</i> (Mill.) Swingle	Simaroubaceae	P	As	Ae	3
<i>Amaranthus retroflexus</i> L.	Amaranthaceae	T	Am	At	30
<i>Ambrosia artemisiifolia</i> L.	Asteraceae	T	Am	At	49
<i>Angelica archangelica</i> L.	Apiaceae	H	EA	Ae, Hy	5
<i>Artemisia verlotiorum</i> Lamotte	Asteraceae	H	As	Ae	2
<i>Asclepias syriaca</i> L.	Asclepiadaceae	G	Am	Ae	4
<i>Chamomilla suaveolens</i> (Pursh) Rydb.	Asteraceae	T	As Am	Zo	1
<i>Coryza canadensis</i> (L.) Cronquist	Asteraceae	T	Am	Ae	35
<i>Datura innoxia</i> Mill.	Solanaceae	T	Am	Ae, Zo	1
<i>Datura stramonium</i> L.	Solanaceae	T	Am	Ae, Zo	5
<i>Echinocystis lobata</i> (Michx.) Torr. et Gray	Cucurbitaceae	T	Am	Au, Hy	2
<i>Erigeron annuus</i> (L.) Pers.	Asteraceae	T	Am	Ae	93
<i>Galinsoga ciliata</i> (Raf.) S. F. Blake	Asteraceae	T	Am	Ae	26
<i>Galinsoga parviflora</i> Cav.	Asteraceae	T	Am	Ae, Zo	33
<i>Helianthus tuberosus</i> L.	Asteraceae	G	Am	Au, Hy	12
<i>Impatiens balfourii</i> Hooker f.	Balsaminaceae	T	As	Au	18
<i>Impatiens glandulifera</i> Royle	Balsaminaceae	T	As	Au, Hy, Zo	8
<i>Impatiens parviflora</i> DC.	Balsaminaceae	T	As	Au, Zo	6
<i>Juncus tenuis</i> Willd.	Juncaceae	H	Am	At, Zo	21
<i>Panicum capillare</i> L.	Poaceae	T	Am	At, Au, Zo	13
<i>Phytolacca americana</i> L.	Phytolaccaceae	G	Am	Zo	3
<i>Reynoutria japonica</i> Houtt.	Polygonaceae	G	As	At, Au	8
<i>Robinia pseudoacacia</i> L.	Fabaceae	P	Am	Au	83
<i>Solidago canadensis</i> L.	Asteraceae	H	Am	Ae, At, Au, Zo	5
<i>Solidago gigantea</i> Aiton	Asteraceae	H	Am	Ae, Zo	22
<i>Sorghum halepense</i> (L.) Pers.	Poaceae	H	Af As	Ae, At, Hy, Zo	9
<i>Veronica persica</i> Poir.	Scrophulariaceae	T	As	Au, Zo	39

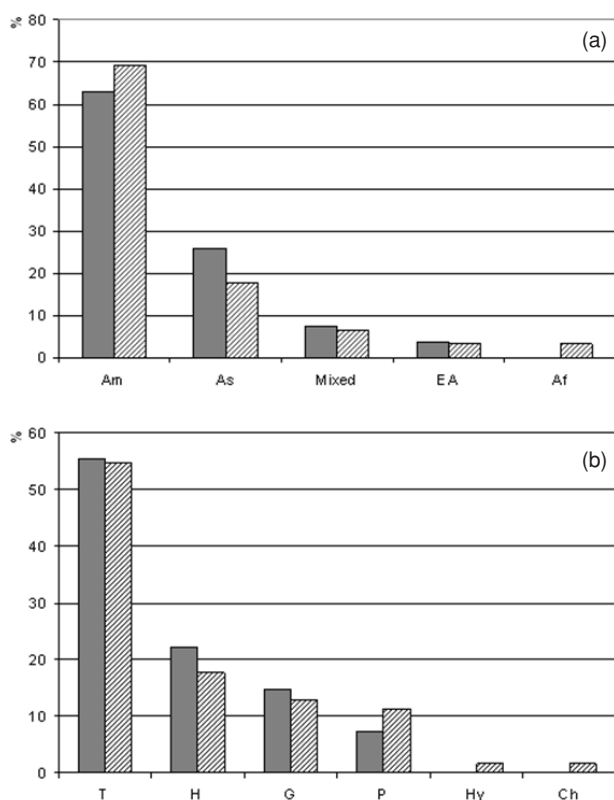


Fig. 3. Comparison between Medvednica Nature Park (solid bars) and Croatia (dashed bars). (a) – origin of invasive flora (Am – the Americas, As – Asia, Mixed – mixed origin, EA – Eurasia, Af – Africa); (b) – life form composition of invasive flora (T – Therophytes, H – Hemicryptophytes, G – Geophytes, P – Phanerophytes, Hy – Hydrophytes, Ch – Chamaephytes).

to analyse the correlation between the number of invasive species and environmental factors, and variables identified as non-significant were excluded from the final model.

We have analysed invasive species with respect to their seed dispersal strategies, based on data from the Flora Croatica Database (<http://hirc.botanic.hr/fcd> accessed on November 19th, 2009.). We have used the highest level classification that consists of the following five categories: Au – autochory; Ae – anemochory; Hy – hydrochory; Zo – zoochory and At – anthropochory. In cases where more than one dispersal type was assigned to a species, all types were counted in the calculation of the proportion of dispersal types in the Nature Park and in the MTB 1/64 units. To elucidate possible correlations between seed dispersal types and four environmental variables (elevation, length of paths and roads, Shannon-Wiener diversity index of habitats and number of polygons of that habitat) in the MTB 1/64 units we have employed constrained ordination using Redundancy Analyses (RDA) in the CANOCO 4.5 software (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003).

## RESULTS

### Species diversity

The study included a total of 27 invasive plant species of Medvednica Nature Park from 14 plant families (Table 1). The families with the most species were Asteraceae (37.0%), Balsaminaceae (11.1%), Poaceae (7.4%) and So-

lanaceae (7.4%). 88.9% of the invasive species are dicots s.l. (basal families, Magnoliids and Eudicots), and 11.1% are monocots. Analysis of life forms (Fig. 3) showed that therophytes are the most common (55.6%), followed by hemicryptophytes (22.2%), geophytes (14.8%) and phanaerophytes (7.4%). Analysis of their geographic origins (Fig. 3) has shown that most of the invasive flora in the park is native to North and/or South America (63.0%), followed by species originating from Asia (25.9%). Species introduced from Eurasia constitute 3.7%, while species originating from more than one continent (mixed origin) constitute 7.4%.

### Ellenberg bioindicator values

Ellenberg bioindicator values are presented in Table 2, and the mean values are used to indicate preferable climatic conditions and soil characteristics for invasive flora of Medvednica. The mean values for the amount of light and soil fertility have shown to be relatively high ( $\approx 7$ ).

### Distribution analysis

General distribution analysis has shown that most widespread invasive species in Medvednica Nature Park is *Erigeron annuus* (L.) Pers., recorded in 93 MTB 1/64 units, followed by *Robinia pseudoacacia* L., found in 83 units. Species with the lowest occurrences are *Artemisia verlotiorum* Lamotte and *Echinocystis lobata* (Michx.) Torr. et Gray, each recorded in 2 units, and *Chamomilla suaveolens* (Pursh.) Rydb. and *Datura innoxia* Mill., each with only one record and the latter being excluded from the statistical analysis as previously explained. The greatest numbers of invasive species per unit mostly occur in the lower areas of the south-western and eastern parts of the park.

Statistical analysis revealed some significant correlations between variables used in the analysis (Table 3). There was a significant positive correlation between the number of invaders and the overall floristic diversity, presented as the total number of species. Single factor analysis showed that the total number of species explained  $r^2=21\%$  of the variation in the number of invasive species ( $r=0.46$ ;  $p=0.000001$ ).

The results of the forward stepwise multiple regression are given in Table 4. The final model included elevation, length of paths and roads and total number of species, and it explained  $r^2=44\%$  of the variation in number of invasive species.

The most frequent dispersal strategies, according to the proportions in the invasive plant species check list, in Medvednica Nature Park were anemochory and zoochory (27% each), while the least frequent was hydrochory (10%). The two remaining dispersal strategies, autochory and anthropochory, were used by 21% and 15% of the invasive plant species, respectively. When analysing their frequencies in the MTB 1/64 units, the average frequency among all units was highest for anemochory (35%), followed by autochory (25%), zoochory (20%) and anthropochory (16%), while hydrochory accounted for the remaining 3%.

The first two ordination axes of the RDA (Fig. 4) explain only 7.6% of the variance in the species. That low value is not surprising given the fact that a portion of the seed dispersal strategies were analysed for a subset of the present

TABLE 2. Ellenberg indicator values for invasive flora of Medvednica Nature Park (L – light, T – temperature, K – continentality, F – moisture, R – acidity, N – fertility, S – salinity).

Species	L	T	K	F	R	N	S
<i>Ailanthus altissima</i> (Mill.) Swingle	8	8	2	5	7	8	0
<i>Amaranthus retroflexus</i> L.	8	7	6	4	7	7	1
<i>Ambrosia artemisiifolia</i> L.	9	7	–	4	8	6	0
<i>Angelica archangelica</i> L.	7	6	5	9	–	9	1
<i>Artemisia verlotiorum</i> Lamotte	9	6	3	6	7	8	0
<i>Asclepias syriaca</i> L.	7	7	4	6	5	4	0
<i>Chamomilla suaveolens</i> (Pursh) Rydb.	8	5	3	5	7	8	0
<i>Conyza canadensis</i> (L.) Cronquist	8	6	–	4	–	5	0
<i>Datura innoxia</i> Mill.	7	9	5	3	5	7	0
<i>Datura stramonium</i> L.	8	6	3	4	7	8	1
<i>Echinocystis lobata</i> (Michx.) Torr. et Gray	7	8	–	9	8	8	0
<i>Erigeron annuus</i> (L.) Pers.	7	6	–	6	–	8	0
<i>Galinsoga ciliata</i> (Raf.) S. F. Blake	7	6	4	4	6	7	0
<i>Galinsoga parviflora</i> Cav.	7	6	3	5	5	8	0
<i>Helianthus tuberosus</i> L.	8	7	–	6	7	8	0
<i>Impatiens balfourii</i> Hooker f.	5	5	5	6	5	7	0
<i>Impatiens glandulifera</i> Royle	5	7	2	8	7	7	0
<i>Impatiens parviflora</i> DC.	4	6	5	5	–	6	0
<i>Juncus tenuis</i> Willd.	6	6	3	6	5	5	0
<i>Panicum capillare</i> L.	6	8	5	3	4	3	0
<i>Phytolacca americana</i> L.	9	8	5	5	5	4	0
<i>Reynoutria japonica</i> Houtt.	8	6	2	8	5	7	0
<i>Robinia pseudoacacia</i> L.	5	6	4	4	–	8	0
<i>Solidago canadensis</i> L.	8	6	5	–	–	6	0
<i>Solidago gigantea</i> Aiton	8	6	5	6	–	7	0
<i>Sorghum halepense</i> (L.) Pers.	8	7	–	6	7	7	0
<i>Veronica persica</i> Poir.	6	–	3	5	7	7	0
<b>Mean value</b>	<b>7.15</b>	<b>6.58</b>	<b>3.90</b>	<b>5.46</b>	<b>6.20</b>	<b>6.78</b>	<b>0.11</b>

TABLE 3. Cross-correlations of the number of invasive species and the total number of species with environmental factors for 106 MTB 1/64 units (No. inv. – number of invasive species, No. sp. – total number of species, Mean elev. – mean elevation, Hab. div. – habitat diversity, Hab. poly. – number of habitat polygons, Km – total length of paths and roads). Significant correlations ( $p < 0.05$ ) are in bold.

	No. inv.	No. sp.	Mean elev.	Hab. div.	Hab. poly.	Km
No. inv.	1 p=0	<b>0.4615</b> <b>p=0.000</b>	<b>-0.5083</b> <b>p=0.000</b>	<b>0.294</b> <b>p=0.002</b>	0.1564 p=0.109	-0.0841 p=0.391
No. sp.		1 p=0	-0.1777 p=0.068	<b>0.2404</b> <b>p=0.013</b>	<b>0.2471</b> <b>p=0.011</b>	0.0124 p=0.899
Mean elev.			1 p=0	<b>-0.4229</b> <b>p=0.000</b>	-0.3266 <b>p=0.001</b>	<b>0.5829</b> <b>p=0.000</b>
Hab. div.				1 p=0	<b>0.8663</b> <b>p=0.00</b>	-0.1757 p=0.072
Hab. poly.					1 p=0	<b>-0.2249</b> <b>p=0.02</b>
Km						1 p=0

flora. Much more interesting is that the first two axes in the species-environment data analysis explained 98.2% of the variance in the fitted “species” data (i. e. seed dispersal strategy) with respect to the environmental variables. The average elevation mostly influenced the first ordination axis, while the length of paths and roads and the average elevation mostly influenced the second axis (Table 5). From the RDA biplot (Fig. 4), it can be seen that the proportion of invasive species with anemochory increases with increasing elevation, and the proportion with anthropochory increases with increasing lengths of paths and ro-

ads. Autochorous plants were more frequent where higher habitat fragmentation occurred, as were hydrochorous invasive plants that were, furthermore, limited to the lower parts of the Nature Park.

## DISCUSSION

In comparison to the whole of Croatia (modified from Boršić et al. 2008), the invasive flora of Medvednica Nature Park shows similar family affiliations, compositions of

TABLE 4. Regression model of the number of invasive plants in the study area, developed with forward stepwise procedure from five independent variables (Mean elev. – mean elevation, No. sp. – total number of species, Km – total length of paths and roads).

R=0.6664 R <sup>2</sup> =0.4442 F(3,102)=27.171 p<0.00000 Std. Error of estimate: 2.2288				
	Coefficients B	Std. Err. of B	t(102)	p-level
Intercept	4.619533	7.042714	4.43030	0.000024
Mean elev.	-0.010310	0.001611	-6.39879	0.000000
No. sp.	0.022026	0.004741	4.64556	0.000010
Km	0.232700	0.082333	2.82632	0.005667

life forms and origins. The invasive flora of Croatia comprises 62 species from 27 families, and the most represented families are also Asteraceae (32.3%), Poaceae (11.3%), Solanaceae (6.5%) and Balsaminaceae (4.8%). An extensive study of alien flora of Europe (Lambdon et al. 2008) has shown that the families Asteraceae and Poaceae, highly radiated families with weedy tendencies, have provided the greatest number of alien plants to Europe. The same study provided a list of the 150 most widespread alien plants in Europe, containing 22 out of the 27 invaders of Medvednica Nature Park. Moreover, the species with the highest occurrences in Europe as aliens (i.e. *Conyza canadensis*, *Datura stramonium*, *Amaranthus retroflexus*, *Galinsoga parviflora* and *Helianthus tuberosus*) are present in the park.

In Croatia (Fig. 3), most invaders are therophytes (54.8%), followed by hemicryptophytes (17.7%), geophytes (12.9%), phanerophytes (11.3%), hydrophytes and chamaephytes (1.6% each). The predominance of therophytes, also noted in some other studies of non-indigenous species (Silva and Smith 2005), can be explained by the fact that they are annual plants that produce large numbers of easily transmitted seeds, enabling fast and successful reproduction and dispersal. These traits are already recognised as important factors in plant invasiveness (Richardson and Pyšek 2006). Data on the origin of the invasive species of Medvednica show similarity to those for Croatian invasive flora; the invasive flora of Medvednica consists of 69.4% American species, 17.7% Asian species, 6.5% spe-

TABLE 5. A summary of the redundancy analyses of 106 MTB 1/64 units, seed dispersal types and 4 environmental variables, with results of the Monte Carlo permutation test of significance for the first and all canonical axes. In lower part of the table, canonical coefficients for standardised variables on first four axes are shown (Elev – mean elevation; Km – total length of paths and roads; Shannon – Shannon-Wiener index of diversity of habitats; Habpoly – number of habitats polygons).

Axes	1	2	3	4	Total variance
Eigenvalues	0.067	0.009	0.001	0.000	1.000
Species-environment correlations	0.360	0.159	0.092	0.112	
Cumulative percentage variance of					
Species data	6.7	7.6	7.7	7.7	
Species-environment relation	87.1	98.2	99.4	100	
Sum of all eigenvalues					
Sum of all canonical eigenvalues					1.000
Summary of Monte Carlo test					0.077
Test of significance of first canonical axes: eigenvalue=0.067. F-ratio=6.983. P=0.018					
Test of significance of all canonical axes: trace=0.077. F-ratio=2.025. P=0.032					
Canonical coefficients for standardized variables					
Axes	1	2	3	4	
Km	0.069	-1.069	0.638	-0.404	
Elev	0.917	0.99	-0.343	-0.193	
Shannon	0.167	0.095	-1.722	-1.282	
Habpoly	-0.281	0.455	-1.972	0.334	

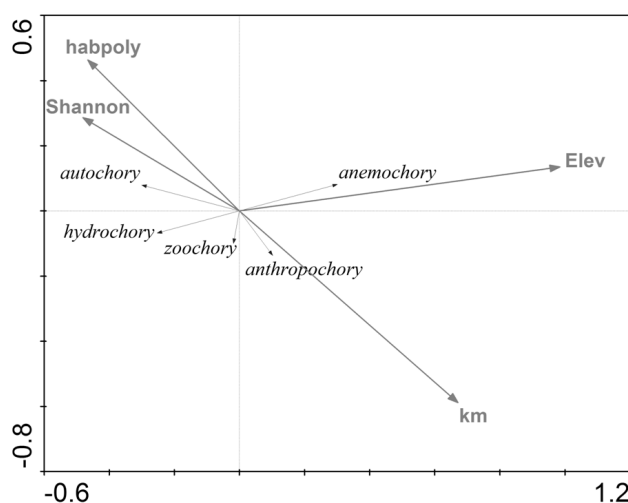


Fig. 4. Biplot of seed dispersal types and environmental variables after redundancy analyses on the first (X) and second (Y) ordination axes (Elev – average elevation, km – length of paths and roads, Shannon – Shannon-Wiener index of diversity of habitats, habpoly – number of habitats polygons).

cies of mixed origin, 3.2% African species and 3.2% Eurasian species (Fig. 3).

#### Bioindicator values

A set of bioindicator values generally describes the ecological preferences of a species in terms of some climatic factors and soil characteristics. In this study, the values show that the plant invaders of Medvednica Nature Park prefer full sunlight but also tolerate reduced amounts of light, up to 70% of full sunlight. Given that Medvednica is a predominantly forested area and that alien species tend to occur more frequently in areas adjacent to 'closed' vegetation (i. e. greater canopy closure, Alexander et al. 2009b), this could point to the importance of habitat fragmentation (i. e. forest opening) as a factor from which invaders benefit. The temperature tolerance data show that the invaders grow in moderately warm to warm habitats, and the continentality data describe them as suboceanic species that can tolerate some marine influence but are more land-oriented.

Considering those facts, the geographic location and climate of Mt. Medvednica seem to provide favourable conditions for this group of plants. Moreover, these plants prefer moderate soil moisture, avoiding wet or frequently-drained soils; they grow in neutral environments but can tolerate slightly acid or slightly alkaline soils, conditions commonly found on Mt. Medvednica. The indicator value for soil fertility shows that invaders often choose nitrogen-rich (human-influenced) habitats, provided in this case by land cultivation, urbanisation and recreational activities. As expected, the indicator value for salinity describes invasive species as not tolerant of salinity.

The ecological niche of invasive species of Medvednica Nature Park, as interpreted here, should not be taken as a single pointer to which areas, in terms of ecological conditions, these plants readily inhabit or avoid, as bioindicator values were obtained by observing species-environment relationships in a certain range and niches could differ between ranges (e. g. climatic niches in the native vs introduced ranges, Beaumont et al. 2009).

### *Species distribution*

Invasive plant species can be found almost everywhere in Medvednica Nature Park, probably because of the intensive human influence it has undergone through the years. The position of the park on the very edge of the capital city makes it a very popular and frequently visited tourist destination. Different studies of alien flora (Silva and Smith 2005; Chytrý et al. 2008; Lambdon et al. 2008) have shown that alien plants readily inhabit disturbed habitats with high human use, such as industrial and ruderal habitats, arable land, gardens and parks, where disturbance might be the key for their establishment and naturalisation (Pyšek et al. 2002). Furthermore, introduction of non-indigenous species is largely human-induced (Stohlgren et al. 2006), with humans having a key role in the intensity of propagule pressure (Lockwood et al. 2005). Propagule pressure can be influenced by medium- and large-scale disturbances, such as logging, prescribed burning or livestock grazing (Stapanian et al. 1998) and by small-scale disturbances, such as horseback riding, as pointed out by Törn et al. (2009). Accordingly, the areas most populated with invasive species have been shown to be the fringe areas of Medvednica Nature Park, especially its southern parts. A study of grasses of the park (Mareković et al. 2009) also showed that cultivated, ruderal and weedy grasses mostly occur in the same parts.

It has previously been reported that the richness of non-indigenous flora positively correlates with the richness of native flora (Timmins and Williams 1991; Lonsdale 1999; Pyšek et al. 2002; Silva and Smith 2005; Stohlgren et al. 2006), showing that species-rich areas tend to be more invaded than species-poor areas. A greater richness of flora indicates greater habitat diversity, and more habitat types offer more solutions for invasive plants (Lonsdale 1999). Our results confirm this theory, showing that both the total number of species ( $r=0.24$ ;  $p=0.013$ ) and the number of invasive species ( $r=0.29$ ;  $p=0.002$ ) are positively correlated with habitat diversity. The importance of habitat diversity could increase over time, as species might gradually develop preferences for a greater range of habitats, like in some cases of *Ambrosia artemisiifolia* invasion (Lavoie et al. 2007; Essl et al. 2009).

The total number of species, to a certain extent, reflects the level of exploration of an area; therefore, a greater number of species implies that there has been more thorough research in that area. Logically, with improvement in our investigation efforts the number of invasive species recorded also tends to increase.

A significant negative correlation ( $r=-0.51$ ;  $p=0.000$ ) between the number of invasive species and the mean elevation could be explained in several ways. The increase in elevation on Mt. Medvednica results in fewer available habitat types, as seen from Table 3, followed by a reduction in the number of invasive plants. Also, higher elevations are less populated; thus, the diversity of human pressures that increase disturbance and/or propagule pressure (e.g. urbanisation, land cultivation, gardening) is reduced. The number of invaders might also be affected by climatic conditions, and lower temperatures at higher elevations could lead to less successful establishment of invasive species. For example, it has been shown that the current distribution of *Ambrosia artemisiifolia* in Austria is strongly linked to temperature (Essl et al. 2009) and that the species is generally more widespread in areas with slightly warmer climates. In general, the invasive flora of Medvednica Nature Park mostly comprises species inhabiting temperate regions with moderate climates. A shift toward greater bioindicator values for temperature (Table 2) shows the affinity of invaders for a warm environment, resulting in lesser performance of invaders along the temperature gradient. On the other hand, the limitations in elevational distribution of aliens is not dependent on their status of temperature affinity, since these species seem equally capable of adapting to changing climatic conditions in their native and introduced ranges (Alexander et al. 2009a, b; Poll et al. 2009). Any attempt to fully explain correlation of invaders with temperature should take all these factors into consideration.

There is a logical presumption that the invasion process may be facilitated by the existence of a network of paths and roads (Christen and Matlack 2006; Lavoie et al. 2007; Jørgensen and Kollmann, 2009). Roadsides are somewhat disturbed and nutrient-rich habitats, especially sites like parking areas, waste areas or rest areas. Also, roads provide a constant flow of vectors (e.g. visitors and vehicles), which act as conduits for the dispersal of alien species and ease their spread and establishment (Timmins and Williams 1991). These facts account for the greater frequency of aliens near the roads and the decline in occurrence of aliens with increasing distance from roadsides (Alexander et al. 2009b).

When observed separately, the correlation between the length of paths and roads and the number of invasive species was not significant (Table 3); however, they appeared to be positively correlated ( $r=0.23$ ;  $p=0.005667$ ) after their inclusion in the final multiple regression model (Table 4).

The results of RDA analyses have shown that there is an obvious influence of environmental factors on the frequency of different types of seed dispersal. While the positive correlation of anthropochorous species with the lengths of paths and roads is expected and logical, as is the correlation between anemochorous plants and higher elevations, the higher frequency of autochorous plants in more fragmented landscapes should be tested further. For that purpose a more detailed classification should be used because the main classifications used here include different seed dispersal distances (Vittoz and Engler 2007). Furthermore,



even within a particular subtype of seed dispersal there might be some differences in dispersal efficiency, as shown by Parolin (2006) in the case of ombrohydrochorous plants. Even the spatial position and age of seed-producing plants are important (Harris et al. 2009) for the success of invasions. Spatial position might correlate with the level of habitat fragmentation if in more fragmented landscapes plants from the core could participate more efficiently in further invasions. Fabiszewski and Brej (2008) have shown reproductive success of *Impatiens glandulifera* and *Reynoutria japonica* as crucial for their invasiveness, while Perglova et al. (2009) shown in four *Impatiens* species that seed and seedling traits could significantly affect the potential invasiveness of particular species.

The trends observed on Mt. Medvednica should be checked and compared in the future with other central-European mountains where there is higher human impact and hence a higher level of habitat fragmentation in their lower parts, as already observed in the neighbouring Žumberak-Samoborsko gorje Nature Park (Jelaska et al. 2005).

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