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Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic

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Abstract. *Heracleum mantegazzianum*, a tall forb from the western Caucasus invaded several different habitats in the Czech Republic. The relation between invasion success and type of recipient habitat was studied in the Slavkovský les hilly ridge, Czech Republic. The vegetation of 14 habitat types occurring in an area of ca. 25 km^2 was analysed using phytosociological relevés, and the invasion success of *Heracleum* (in terms of number of localities, area covered and proportion of available area occupied) was recorded separately in each of them. Site conditions were expressed indirectly using Ellenberg indicator values. The hypothesis tested was that *Heracleum* spreads in the majority of vegetation types regardless of the properties of the recipient vegetation.

Community invasibility appeared to be affected by site conditions and the composition of the recipient vegetation. The species is not found in acidic habitats. Disturbed habitats with good possibilities of dispersal for *Heracleum* seeds are more easily invaded. Communities with a higher proportion of phanerophytes and of species with CS (Competitive/Stress-tolerating) strategy were more resistant to invasion. The invasion success was bigger in sites with increased possibilities of spread for *Heracleum* diaspores. Communities invaded by *Heracleum* had a lower species diversity and a higher indicator value for nitrogen than not-invaded stands. It appears that species contributing to community resistance against invasion of *Heracleum*, or capable of persisting in *Heracleum*-invaded stands, have similar ecological requirements but a different life strategy to the invader.

Keywords: Alien plant species; Community invasibility; Landscape section; Plant trait; Site condition; Species diversity; Strategy.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Since Elton's (1958) classic study, biological invasions have been receiving increasing attention (Pyšek 1995) and in the last decades they have become one of the most attractive research fields in ecology (Drake & Mooney 1989; di Castri et al. 1990; Lodge 1993). While the process itself represents a serious threat to native species, it also provides us with an unparallelled opportunity for ecological studies (Vitousek et al. 1987). Many of those studies have focused upon the history and dynamics of invading species at various hierarchical levels. Rejmánek (1989) and Kornaś (1990) provided reviews of many of these studies and references to particular case studies. However, invading species and target communities cannot be studied independently because the species-community interactions are what determine the outcome of invasion.

Recently, the most rapid progress in this field seems to be associated with a shift in focus to the critical interactions of invader and target community (Crawley 1987; Rejmánek 1989; Hester & Hobbs 1992; Lodge 1993; DeFerrari & Naiman 1994). Moreover, progress in the ecological study of invasions appears to be essential for understanding what determines the dynamics of ecological communities (Lodge 1993).

Invasive species are not only able to affect the structure and function of an ecosystem (Versfeld & van Wilgen 1986; Witkowski 1991; Vitousek & Walker 1989; Vitousek 1990) but can also reduce the biodiversity of communities and landscapes, both at the local and regional scales. They may cause considerable problems in landscape management (de Waal et al. 1994) and nature conservation (Usher 1988).

The present study is aimed at analysing the effect of the type of recipient vegetation on the invasion of *Heracleum mantegazzianum*, an alien species from Asia and one of the most noxious European alien weeds (Pyšek 1991, 1994; de Waal et al. 1994). The hypothesis tested here is that, owing to its biological and ecological properties, *Heracleum* is capable of entering the majority of vegetation types in the landscape regardless of the properties of the recipient vegetation.

Material and Methods

Research area and habitats studied

The study area is located in the Slavkovský les hilly ridge (western Bohemia, Czech Republic) in the surroundings of the village of Prameny, 11 km east of the town of Horní Slavkov (50° 09' N, 12° 48' E). The geological substrate consists of Palaeozoic granite; the area is situated at an altitude of 600 - 650 m a.s.l. and has a moderately moist climate with a mean annual temperature of 5 - 6 °C and an annual precipitation of 650 mm (Vesecký et al. 1957). Originally, the area was covered by acidophilous beech and oak forests (Mikyška 1972). At present, the landscape is managed moderately intensively; it is used mostly for silvicultural and agricultural purposes, including cattle breeding. The following habitat types were distinguished in an area of ca. 25 km^2 – listed according to the proportion of the area they cover which is given in parentheses. A summary of the species composition is presented in App. 1. Ecological characteristics of the habitat types studied are given in Table 1.

Spruce forests (28.9 %). Forest plantations with spruce as the main component of the tree layer.

Mown meadows (19.5 %). Mesophilous meadows used for hay and mown twice a year.

Pastures (15.8 %). Used for cattle grazing.

Moist grasslands (13.0 %). Sites in the vicinity of water courses, some of them periodically flooded.

Fields (6.1 %). Arable land used for plantations of fodder and corn. This habitat type was excluded from the data analysis because expressing its vegetation characteristics in the way used for other habitats could be misleading due to the variety of crops cultivated.

Urban sites (4.5 %). Most of the area of the village of Prameny harbours vegetation of various successional ages occurring in man-made sites.

Dry grasslands (3.7 %). Relatively thermophilous sites on south-exposed slopes, often on rock outcrops.

Road ditches (3.3 %). Representatives located in open areas, further called ‘sunny ditches’ (1.7 %) and those shaded by neighbouring vegetation, called ‘shaded ditches’ (1.6 %) were treated separately.

Water courses (2.3 %). Sites along the brook flowing through the village and along small streamlets in the open landscape.

Forest margins (1.1 %). Ecotonal zones between forests and adjacent vegetation, mostly meadows, pastures and arable land.

Birch woodlands (0.7 %). Patches of deciduous or mixed forests with birch and pine forming the tree layer.

Willow scrub (0.6 %). Moist sites, periodically flooded, with willows forming the shrub layer.

Road verges (0.5 %). Verges of smaller roads and paths in the open landscape are included.

Peat bogs (0.02 %). Acid, *Sphagnum*-dominated habitats.

Study species

Heracleum mantegazzianum (*Apiaceae*) is a monocarpic perennial with a thick taproot, a stout stem attaining 5.5 m height, large pinnate leaves (up to 3 m long) and usually 7 - 10 umbels bearing oval-elliptical, broadly winged fruits 9 - 11 mm in size (Tutin et al. 1964-1980). The species spreads exclusively by seed, and its seed production per plant may reach several tens of thousands (Neiland 1986; Brondegaard 1990). In the study area, the species germinates in early spring (April), the flowering period starts in May, fruits appear in July and are shed from September onwards.

The species is native to the western Caucasus where it occurs in the upper forest belt of the southern slopes, mainly in meadows, clearings and forest margins (Mladenova 1950). It was introduced in the 19th century into the Czech Republic, as well as in other European countries (Lundström 1984; de Waal et al. 1994). See further Pyšek (1991) for the historical dynamics of the distribution of the species in the area, and Pyšek (1994) for an analysis of the ecology of its invasion. There are two main reasons for the efforts in the Czech Republic and elsewhere in Europe to eradicate the species from infested areas (Williamson & Forbes 1982; de Waal et al. 1994): (1) the replacement of native vegetation – the consequences of which have been discussed by Pyšek (1991) – and (2) injuries to the human skin caused by phototoxic substances (Drever & Hunter 1970). In the study area, *Heracleum* rapidly attains dominance in invaded communities, with a cover of 50 -100 %. Part of the competitive superiority of *Heracleum mantegazzianum* – the largest forb in central Europe – over other plants is ascribed to its huge size and its ability to shade the surrounding vegetation with its huge ground leaves. The large seed-set (Neiland 1986; Brondegaard 1990) with dispersal promoted by water, wind and human-related factors (Jehlík & Lhotská 1970) also contributes to its rapid spread into various vegetation types.

Sampling

Field research was conducted in 1992. Vegetation was sampled using Braun-Blanquet’s seven-point scale 5, 4, 3, 2, 1, + and *r* (e.g. Westhoff & van der Maarel 1978). Five relevés were made in each habitat type. The size of the sample plot was 5 m × 5 m, except in those

Table 1. Characteristics of habitats in the study area and overview of their invasion by *Heracleum mantegazzianum*. Ellenberg indicator values were used to characterize site conditions: light (L), moisture (M), nitrogen (N), and soil reaction (R). Total number of species recorded (S-tot), mean species number per relevé (S-mean), and species diversity (Shannon index *H*') are presented as community characteristics. Habitats which are disturbed by human activities (DIST) and those in which dispersal of diaspores of *Heracleum* is probably promoted (DISP) are indicated by 'yes'. Total number of *Heracleum* occurrences recorded, total area occupied by it in a given habitat type, and habitat saturation were taken as invasion measures. Habitat saturation was expressed as the ratio between the area occupied by *Heracleum* in a particular habitat type and total area covered by that habitat in the study area. Areas in m^2. Habitats are listed according to their availability in the landscape section studied.

	Ecological characteristics						Community characteristics			Habitat area available	Invasion success		
	L	M	N	R	DIST	DISP	S-tot	S-mean	*H'*		Number of records	Area occupied	Habitat saturation
Spruce forests	5.4	5.8	3.8	2.9			25	10.0	1.28	594750	0	0	0.00
Mown meadows	6.9	5.9	5.8	5.3	yes[1]		20	9.0	1.15	400500	0	0	0.00
Pastures	7.0	5.4	6.4	5.7	yes[2]		41	15.4	1.20	325000	35	12718	0.04
Moist grassland	6.9	6.5	4.9	5.5			42	15.0	1.40	266850	28	5833	0.02
Urban sites	6.9	5.6	6.7	6.6	yes[3]	yes	47	14.2	1.18	93500	66	11745	0.13
Dry grasslands	7.3	5.0	3.9	6.1			49	16.0	1.55	76950	13	1764	0.02
Water courses	6.8	6.9	6.2	6.2		yes	61	17.6	1.52	47400	65	18020	0.38
Sunny ditches	6.9	5.4	6.9	6.7	yes[1]	yes	28	9.4	1.10	35800	107	15789	0.44
Shaded ditches	6.8	5.9	7.0	6.5	yes[1]	yes	27	8.6	1.02	32060	95	10164	0.32
Forest margins	6.4	5.6	6.1	5.2			21	9.0	0.98	22760	13	1788	0.08
Birch woodlands	6.4	5.3	4.2	4.5			31	12.4	1.34	15250	0	0	0.00
Willow scrub	7.0	6.4	6.1	5.8			39	13.3	1.23	11400	17	3499	0.31
Path margins	7.3	5.5	5.9	6.1		yes	36	10.8	1.12	10000	9	4036	0.40
Peat bogs	6.5	6.6	2.8	3.0			21	11.3	1.48	500	0	0	0.00

[1]mowing; [2]grazing; [3]various kinds of disturbance

habitats in which the linear character of the vegetation made it impossible; in these cases, a total area of 25 m^2 was considered. In total, 70 relevés were made in not-invaded vegetation. In those habitats into which the invasion by *Heracleum* was observed, corresponding relevés were made in invaded stands (50 in total, so that the total number of relevés was 120). Where possible, the patches of *Heracleum* surrounded by not-invaded vegetation were selected, and the respective pairs of relevés (representing the invaded and not-invaded vegetation of a given habitat type) were formed by the invaded stand and adjacent not-invaded one. In this way 50 pairs of relevés were obtained. This approach was further justified by comparison of aerial photographs taken in the 1980s with those from a recent date, which show a gradual increase of *Heracleum* at the expense of not-invaded vegetation (P. Pyšek unpubl.).

To express the habitat availability in the landscape, five transects, each 200 m wide (covering the same area in which the vegetation survey was conducted), were made running from the village of Prameny 0.5 - 2.5 km into different directions (the record of *Heracleum* most distant from the village was taken as the beginning of the transect). Along these transects, the area covered by each habitat type was estimated.

Occurrences of *Heracleum* including both solitary plants and developed stands were recorded in each habitat type and the area covered by the species was estimated in the latter case. The following measures were used to express the invasion success (understood here as the extent of spread into the target vegetation) of *Heracleum* in each habitat type: (a) number of records, (b) area occupied (obtained by summing up the sizes of particular stands; the value of 1 m^2 was taken for solitary plants), and (c) the ratio between the area occupied by *Heracleum* and the area covered by the given habitat type in the area studied (this ratio is further referred to as habitat saturation).

Data analysis

Species dominance/abundance values were transformed to a 1 - 7 numerical scale and used in this form for multivariate analysis. Canonical Correspondence Analysis (ter Braak 1987, 1988) with all species present in a relevé was used to analyse the data from not-invaded vegetation. Invasibility (understood as the ability of *Heracleum* to enter the given vegetation type) was used as a predictor variable (coded as 1 for the relevés made in those habitat types which were found invasible, i.e. in which the invasion by *Heracleum* was observed). In order to investigate the relationship between invasibility and other potentially relevant factors, two other nominal variables were included (Table 1): (1) disturbance – coded as 1 for habitat types significantly disturbed by human activities including grazing , and (2)

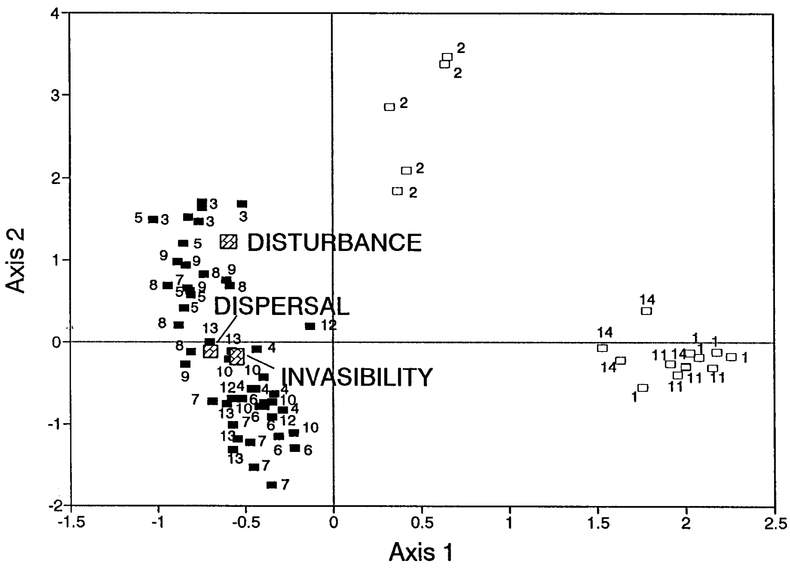

Fig. 1. CCA ordination diagram referring to not-invaded vegetation in the study area. Habitats (listed according to their availability in the landscape section studied):

1 - Spruce forests;
2 - Mown meadows;
3 - Pastures;
4 - Moist grasslands;
5 - Urban sites;
6 - Dry grasslands;
7 - Water courses;
8 - Sunny ditches;
9 - Shaded ditches;
10 - Forest margins;
11 - Birch woodland;
12 - Willow scrub;
13 - Path margins;
14 - Peat bogs.

Centroids are indicated by hatched squares. Habitats potentially invasible are shown as filled squares, those into which invasion was not observed are shown as empty squares.

dispersal possibilities – coded 1 for habitats in which transport of *Heracleum* seeds by water and humans could be suggested (see Pyšek (1994) and 0 for the others.

Site conditions were not measured directly but expressed using Ellenberg indicator values for light, moisture, nitrogen and soil reaction (Ellenberg et al. 1991). Weighted average values were calculated for each relevé using the transformed values of the Braun-Blanquet scale as species weights – 5 ⇒ 7, 4 ⇒ 6, 3 ⇒ 5, 2 ⇒ 4, 1 ⇒ 3, + ⇒ 2, *r* ⇒ 1. An average value from the relevés made in not-invaded vegetation of a given habitat type was adopted as its characteristic.

In the same way, the proportions of particular life forms (Raunkiaer's system as taken from Mueller-Dombois & Ellenberg 1974) and life strategies (Grime 1979; Grime et al. 1988) were calculated for each relevé and habitat type. Those life forms and strategies whose representatives occurred only in a very low number of relevés – chamaephytes in 5, S (Stress-tolerating) strategy in seven, SR (Stress-tolerating/Ruderal) and R (Ruderal) strategies in three each, or whose contribution did not exceed 15 % in any of the relevés – therophytes, CR (Competitive/Ruderal, strategy) were excluded from the analysis.

Species diversity of a relevé was measured as number of species *S* and Shannon index *H'* ($\log_e$ base, see e.g. Peet 1974); *H'* was calculated on the basis of cover % data derived from the Braun-Blanquet scale values as follows: 5 ⇒ 87.5 %, 4 ⇒ 62.5%, 3 ⇒ 37.5%, 2 ⇒ 15%, 1 ⇒ 2.5%, + ⇒ 1, *r* ⇒ 0.1.

In addition to CCA the data were analysed with multiple regression (Sokal & Rohlf 1981).

Results

Factors affecting community invasibility

Fig. 1 displays CCA results using data from not-invaded vegetation of the study area. The first axis ($\lambda_1 = 0.75$) separates invasible vegetation types from those in which the invasion was not observed and accounted for 56.7 % of the species-environment relation in the data set (Table 2). A Monte Carlo permutation test for the first axis was highly significant ($P < 0.001$). The second axis ($\lambda_2 = 0.34$) was associated with disturbance (Table 2).

To evaluate the factors responsible for the position of relevés on the ordination axis that is related to the vulnerability of a community to invasion, a CCA was performed using invasibility as the only explanatory variable and disturbance and dispersal possibilities as covariables. Sample scores on the first ordination axis, which may be taken as a measure of invasibility, were

Table 2. Summary of the results of the CCA ordination. Cumulative percentage variance of the species-environment relations and inter-set correlations of environmental variables with axes are shown. See text for details.

Axis	1	2
Eigenvalue	0.75	0.31
Cumulative % variance	56.7	79.7
Variable:		
Invasibility	– 0.93	– 0.23
Disturbance	– 0.40	0.80
Dispersal possibilities	– 0.51	– 0.08

Table 3. Relationship between vegetation characteristics and its vulnerability to invasion. Site conditions (expressed as mean Ellenberg indicator values), vegetation composition (characterized by proportional contribution of particular life forms and life strategies), disturbance and dispersal possibilities (coded as 0 or 1) were expressed for each relevé (n = 70) and used as predictors of invasibility (see text for details). Significant predictors, as selected by a forward stepwise multiple regression, are shown and signs of their correlation with invasibility are given.

Predictor	*P*-value	Sign
Light	0.0117	+
Reaction	0.0004	+
Dispersal	< 0.0001	+
Disturbance	< 0.0001	+
Phanerophytes	0.0114	-
CS-strategy	0.0008	-

subjected to a multiple regression using site conditions and plant traits as predictors (Table 3). Invasibility was positively associated with light and soil reaction indicator values and negatively with the proportion of phanerophytes and CS-strategists. It was also encouraged by disturbance and possibilities for dispersal of *Heracleum* seed (Table 3). The regression model was highly significant ($F_{6,60}$ = 32.49, P < 0.0001) and the predictors accounted for 74.1 % of the variability in the invasibility scores.

Factors affecting the extent of invasion

The extent of invasion expressed as habitat saturation was subjected to a multiple regression using site conditions (nitrogen, soil reaction), proportion of hemicryptophytes, phanerophytes, C- and CS-strategy, and disturbance and dispersal possibilities (coded 0 and 1, see Table 1) as predictors. A stepwise multiple regression (forward selection) was used because of mutual correlation of the predictors. The possibility of dispersal for *Heracleum* diaspores turned out to be the only significant predictor (P < 0.001) and explained 61.6 % of variability in habitat saturation. The regression model was highly significant ($F_{1,12}$ = 21.89; P < 0.001).

Comparison of invaded and not-invaded vegetation

In total, 141 species were recorded in relevés made in not-invaded vegetation. Of these, 73 (51.7 %) also occurred in adjacent invaded stands and 68 (48.2 %) were not present in invaded stands. 11 species which were not present in not-invaded vegetation appeared in stands invaded by *Heracleum* so that the total number of species present in *Heracleum*-dominated vegetation was 84. In terms of the total number of species, invaded vegetation supported 40.5 % less species than not-invaded vegetation.

The vegetation invaded by *Heracleum* had a lower species diversity (mean ± s.d: H'= 0.52 ± 0.35, n = 50) and mean species number per relevé (S = 7.46 ± 3.17) compared to corresponding not-invaded stands (H'= 1.22 ± 0.42, S = 12.80 ± 5.08) and the differences were highly significant in a paired t-test (t = 9.00 and 6.16, respectively, P < 0.001). Only a few species occurred in *Heracleum* stands with at least a frequency of 20 %: *Urtica dioica* (0.56) *Anthriscus sylvestris* (0.46), *Alopecurus pratensis* (0.34), *Dactylis glomerata* (0.30), *Elymus repens* (0.28), *Cirsium arvense* (0.22), *Lupinus polyphyllus* (0.22), and *Tanacetum vulgare* (0.20).

The species present in the 50 relevés made in *Heracleum*-invaded vegetation had higher indicator values for nitrogen (mean ± s.d = 5.9 ± 1.9, n = 84, species quantities not considered) than species from corresponding not-invaded stands (5.2 ± 2.2, n = 144) and the difference was significant (Kruskall-Wallis test, P < 0.05). No significant differences between both groups were found with respect to indicator values for moisture, nitrogen and light (Kruskall-Wallis test) or for life forms (χ^2 = 2.14, P = 0.54, d.f. = 3) and life strategies (χ^2 = 1.11, P = 0.77, d.f. = 3).

Discussion

It is increasingly recognized that the characteristics of a target community are as important to the fate and impact of an introduction of an exotic species as the characteristics of the invader itself (Drake & Williamson 1986; Rejmánek 1989; Ramakrishnan & Vitousek 1989; Lodge 1993). In the present study, community vulnerability to invasion was analysed at two levels: (a) whether the invader is able to enter the community (i.e. the community invasibility), and (b) whether it is able to spread in a given vegetation type (i.e. the extent of invasion). Considering site conditions, open habitats, i.e. those supporting a high proportion of light-demanding species, are highly invasible because (1) the competition from resident species is reduced (Crawley 1987), and (2) these species are not able to compete after being shaded by plants of *Heracleum mantegazzianum*. This species is not found in acid habitats such as peat bogs, birch woodlands or spruce forests. This offers some support for the view that plant communities in extreme environments are less susceptible to invasions (Rejmánek 1989).

The invasibility was also related to the characteristics of the recipient vegetation. The communities with a large proportion of phanerophytes appear to be less susceptible to invasion. Considering life strategies, communities that are more resistant against invasion of *Heracleum* have a large proportion of plants with a CS (Competitive/Stress-tolerating) strategy. Examples are *Calluna vulgaris, Deschampsia flexuosa, Dryopteris dilatata, Festuca rupicola, Molinia caerulea* and *Vaccinium* spp. Tolerance of shade, low nutrient level and/or acidity are presumably the main reasons for species with this type of strategy being able to resist *Heracleum* invasion. However, in view of the fact that CS-species are linked with acid habitats, it seems more likely that HERACLEUM prefers non-acid conditions than that it is prevented from invading the habitat by CS-strategists.

Habitat saturation is obviously the best measure of invasion success because it takes habitat availability in the area into account and thus expresses the real level of infestation in a more precise way than the number of records or area occupied. The habitat saturation is strongly affected by dispersal possibilities, i.e. it is higher in habitats in which an encouraged spread of *Heracleum* diaspores can be suggested. No significant effect of site conditions and vegetation characteristics was found in the present data-set. This may be taken as an indication that the degree to which *Heracleum* spread is limited by recipient vegetation may actually be rather low (Pyšek 1994). There are, however, other factors that can have an impact on the invasion success such as successional age (Rejmánek 1989; DeFerrari & Naiman 1994) or biomass of the resident vegetation (Peart & Foint 1985). Although these were not analysed in the present study (because of the impossibility of assessing *post hoc* the former and because of the technical difficulties linked with the latter), the absence of *Heracleum* from spruce forests, birch woodlands and peat bogs indicates that such factors might be relevant to the present data.

Heracleum represents an example of an invader which is successful in a wide range of central-European habitats (Pyšek 1994; Pyšek & Prach 1993). Some of the habitat characteristics suggested to favour the success of a species as an invader (Lodge 1993) are fulfilled by *Heracleum*, namely a reasonable climatic match with the species' native habitats, and an absence of herbivory (Harcombe et al. 1993). Unlike the majority of Czech alien species, it had been able to spread into semi-natural habitats in the country immediately after its introduction (Pyšek 1994); it is normally suggested that only a small fraction of aliens are successful in semi-natural, successionally advanced vegetation (Williams 1985; Rejmánek 1989) and, if so, their establishment is usually preceded by establishment in man-made habitats (Kornaś 1990).

Comparison of not-invaded and *Heracleum*-invaded communities shows that nitrophilous species are better represented in the latter. Although the majority of successful invasions appear not to alter large-scale ecosystem properties in any clear way (Vitousek 1990), there is evidence for profound, post-invasion changes which can alter the composition and structure of invaded communities (Vivrette & Muller 1977; Vitousek 1990). Some studies have shown the enrichment of nutrient status of the site by the invasion of aliens (Vitousek & Walker 1989; Witkowski 1991; Hester & Hobbs 1992). In the case of *Heracleum*, a very large production of biomass which is easily decomposed during winter certainly increases the nutrient status of invaded sites.

The results obtained indicate that communities more vulnerable to invasion are composed of species with similar ecological requirements (at least with respect to nitrogen) and different life form and/or strategy compared to the invader. It appears that species possessing similar traits are less able to compete with such a strong competitor. *Heracleum* itself is a hemicryptophyte with a nitrogen indicator value of 8 (on a 9-degree scale; Ellenberg et al. 1991). It possesses some of the properties which are attributed to a successful invader (Baker 1965; Noble 1989; Roy 1990), especially a high Relative Growth Rate (the plants are able to grow up to 4-5 m in height from April to June and develop an extremely large leaf area), large seed set (up to 107 000 per single plant - J. Caffrey, pers. comm.) and effective seed dispersal (Pyšek 1991, 1994). Being a fast-growing monocarpic perennial with a rapid leaf turnover, it is a typical representative of the CR (Competitive/Ruderal) strategy type (Grime et al. 1988). Its extreme success as an invader may be explained by its combining traits that favour appearance in disturbed habitats (early production and dispersal) with those that allow overcoming biotic barriers when invading more complex, successionally advanced vegetation (Kornaś 1990; Richardson et al. 1990).

Both history and chance play important roles in biological invasions,with regard to both community assembly and invader appearance (Crawley 1987; Lodge 1993). It is even possible that each particular case of biological invasions may represent a single event. For these reasons, it is useful to analyse plant traits conditioning the success of each particular invader in relative terms, with reference to the particular vegetation it invades.

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App. 1. Species composition of the vegetation of particular habitat types studied. Frequency of occurrence is given for each species and those being dominant, i.e. reaching a cover of > 50 %, are indicated by D. Only species with at least 50 % frequency are shown.

Spruce forests: *Picea abies* 100D, *Deschampsia flexuosa* 100D, *Sorbus aucuparia* 80, *Dryopteris dilatata* 80, *Calamagrostis villosa* 80D, *Maianthemum bifolium* 60, *Rubus idaeus* 60.

Mown meadows: *Alopecurus pratensis* 100D, *Bistorta major* 100, *Sanguisorba officinalis* 100, *Lolium multiflorum* 80D, *Ranunculus acris* 80, *Juncus effusus* 60, *Poa pratensis* 60.

Pastures: *Dactylis glomerata* 100D, *Taraxacum officinale* 100, *Juncus conglomeratus* 80, *Alchemilla monticola* 80, *Poa pratensis* 60, *Plantago major* 60, *Trifolium pratense* 60, *Alopecurus pratensis* 60D, *Aegopodium podagraria* 60, *Geum urbanum* 60, *Urtica dioica* 60.

Moist grasslands: *Alopecurus pratensis* 100D, *Deschampsia caespitosa* 80D, *Vicia cracca* 80, *Angelica sylvestris* 60D, *Cirsium palustre* 60, *Festuca rubra* 60, *Sanguisorba officinalis* 60, *Lathyrus pratensis* 60, *Galium uliginosum* 60.

Urban sites: *Tanacetum vulgare* 60D, *Urtica dioica* 60D, *Elymus repens* 60, *Dactylis glomerata* 60, *Aegopodium podagraria* 60D, *Alopecurus pratensis* 60, *Cirsium arvense* 60.

Dry grasslands: *Achillea millefolium* 100, *Campanula rotundifolia* 100, *Galium album* 100, *Festuca rupicola* 60D, *Agrostis capillaris* 60D, *Hypericum maculatum* 60, *Trifolium medium* 60.

Water courses: *Urtica dioica* 80D, *Angelica sylvestris* 80, *Phalaris arundinacea* 60D, *Filipendula ulmaria* 60D, *Epilobium angustifolium* 60, *Deschampsia caespitosa* 60, *Alopecurus pratensis* 60.

Road ditches - (a) Sunny ditches: *Urtica dioica* 80D, *Anthriscus sylvestris* 60D, *Dactylis glomerata* 60, *Heracleum sphondylium* 60; (b) Shaded ditches: *Anthriscus sylvestris* 100D, *Urtica dioica* 80D, *Elymus repens* 60D.

Forest margins: *Urtica dioica* 100D, *Senecio ovatus* 80D, *Rubus idaeus* 80, *Elymus repens* 80, *Anthriscus sylvestris* 80, *Dactylis glomerata* 60, *Lupinus polyphyllus* 60.

Birch woodlands: *Deschampsia flexuosa* 100D, *Betula pendula* 80D, *Pinus sylvestris* 80D, *Vaccinium myrtillus* 80D, *Calamagrostis villosa* 60D, *Campanula rotundifolia* 60, *Hieracium lachenalii* 60, *Silene vulgaris* 60, *Rubus idaeus* 60, *Sorbus aucuparia* 60.

Willow scrub: *Salix aurita* 100D, *Heracleum sphondylium* 80, *Alopecurus pratensis* 80, *Urtica dioica* 80, *Stellaria graminea* 60, *Filipendula ulmaria* 60, *Symphytum officinale* 60, *Angelica sylvestris* 60, *Dactylis glomerata* 60.

Path margins: *Agrostis stolonifera* 60D, *Achillea millefolium* 60, *Anthriscus sylvestris* 60, *Taraxacum officinale* 60.

Peat bogs: *Sphagnum* spp. 100D, *Bistorta major* 100, *Potentilla erecta* 100, *Molinia caerulea* 80D, *Sanguisorba officinalis* 80D, *Cirsium palustre* 60, *Nardus stricta* 60, *Calluna vulgaris* 60.