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Invasion patterns of *Heracleum mantegazzianum* in Germany on the regional and landscape scales

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Summary

Heracleum mantegazzianum Somm. et Lev. is an invasive tall forb in Europe with implications for human health (photo-dermatitis), recreational and economic interests, and local biodiversity. This paper presents invasion patterns of the species in Germany on the regional and landscape scales and assesses the species' impacts on native habitats. We conducted a survey addressing the nature conservation authorities of all 440 German districts and carried out our own field studies in the most heavily invaded landscapes in Germany. The survey indicated that *H. mantegazzianum* is present and perceived as a potentially dangerous invader in about two-thirds of German districts, while actual or short-term hazards can be assumed for only about 15% of districts. The latter were concentrated in the natural geographic region 'western low mountain ranges'. In the field studies, dominant stands of *H. mantegazzianum*, which bear the highest potential for adverse effects on native biodiversity, accounted for 36% of all large stands of the species. Invasion success was highest in abandoned grasslands, grassland and field margins, and corresponding tall-forb stands. The saturation (% area covered) of these preferred habitats with *H. mantegazzianum* was 8.7%. The invasion percentage (% area invaded) was 18.5%. In conclusion, our results suggest that today *H. mantegazzianum* has only moderate impacts on the regional and landscape scales even in most heavily invaded regions of Germany.

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Introduction

The umbelliferous tall forb *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) is one of the most prominent invasive species in Central Europe today. It was introduced from its native

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range in the Western Greater Caucasus to botanic and private gardens in several European countries in the 19th century (e.g. Kowarik, 2003; Ochsmann, 1996; Wyse Jackson, 1989). During the 20th century the species became a popular ornamental plant (Kobylka, 1977; Lundström, 1984; Pyšek, 1991; Sheldon, 1982) and was also propagated as a bee plant (Adolphi, 1995; Zander, 1930). Hence, the species has been widely dispersed by humans (gardeners and bee keepers) which substantially enhanced its spread (Pyšek, 1991). *H. mantegazzianum* has repeatedly escaped cultivation since its introduction (Ochsmann, 1996) but a massive spread has been observed in several European countries only from the 1950s onwards (e.g. Czech Republic: Pyšek, 1991; Germany: Ochsmann, 1996; Great Britain: Clegg & Grace, 1974; Tiley et al., 1996; Wade et al., 1997). Today, *H. mantegazzianum* is widespread in Germany and occupies at least 57% of grid cells in the national floristic map (German National Floristic Database, 'Datenbank Gefäßpflanzen'; www.floraweb.de).

H. mantegazzianum has serious health implications for humans due to phyto-photo-dermatitis caused by furocoumarins (syn. furanocoumarins) contained in the sap of the plant (Drever & Hunter, 1970; Jaspersen-Schib et al., 1996; Lagey et al., 1995). Further, it conflicts with recreational and economic interests, e.g. by obstruction of trails and riverbanks (Tiley & Philp, 1994), and may lead to serious erosion of riverbanks (Caffrey, 1994). Moreover, it can reduce local biodiversity (alpha diversity) by outcompeting native plant species (Lundström, 1984; Manchester & Bullock, 2000; Pyšek & Pyšek, 1995; Thiele & Otte, 2007). Therefore, *H. mantegazzianum* is commonly regarded as a problem plant that provokes costly and tedious control actions. The total annual costs due to health impacts and management of the species in Germany were estimated as ca. €12 million (Reinhardt et al., 2003).

As monetary resources are frequently limited, it is necessary for managers to decide which invasive species and populations to control in the first place and which ones to control later or leave alone (Hiebert, 1997). In order to take sound and sensible decisions, managers are in need of information on the impacts of invasive species. However, rigorous assessments of imminent impacts from non-indigenous species have rarely been conducted (Byers et al., 2002; Parker et al., 1999).

On a geographical scale, impacts can be quantified by: (i) the range size of an invader; (ii) its abundance per unit area across that range; and (iii) the size of the effect per individual or per biomass unit (Parker et al., 1999). It is reasonable,

for impact assessment, to try to narrow down the total non-indigenous range of a species to regions where the species actually has spread and increased in abundance after introduction, i.e. where it is an 'invasive species' (sensu e.g. Kolar & Lodge, 2001). Concerning the abundance of invasive plant species, dominant stands, which *H. mantegazzianum* is able to build up, will have especially severe effects on recipient habitats. Therefore, the proportion of stands that attain dominance appears to be a useful additional measure. Furthermore, better precision in assessing impacts will be achieved if the available area of potentially suitable habitats is taken into account. Finally, different types of invaded habitats should be distinguished in any assessment of impacts because abundances and effects might vary with habitat type.

The aim of our study was to assess the impacts of *H. mantegazzianum* on native habitats at the regional and landscape scales. Our objectives were to:

- (1) assess the large-scale pattern of *H. mantegazzianum* invasion throughout Germany and to identify regions where the species is 'invasive';
- (2) record the distribution and abundance of the species in the most heavily invaded landscapes with regard to different habitat types;
- (3) calculate the area-corrected relative invasion – invasion percentages (i.e. % habitat area invaded) and habitat saturation (i.e. % habitat area covered by *H. mantegazzianum*) – for each invaded habitat type and, finally;
- (4) assess present impacts and to make a prognosis for the species' potential to threaten regional biodiversity.

Methods

Germany-wide survey

In 2001, a survey on *H. mantegazzianum* was conducted by addressing questionnaires to the nature conservation authorities of all 440 German districts ('Landkreise') and cities independent from a district administration ('kreisfreie Städte'). The questionnaire asked for information on habitat types invaded by the species (default list provided), occurrences in nature reserves (yes, no), protected habitat types (which ones?), and whether inventories of the species had been carried out. For each habitat type addressees were asked to estimate the frequency class of *H. mantegazzianum* (absent,

rare, occasional, common) and maximum spatial extent of single stands of the species (up to 100 m², >100–1000 m², >1000 m²).

The received data were used to create a ranking of districts by invasion intensity which was assessed by summing up weights allocated to estimated frequency classes and maximum stand sizes, with higher frequencies and larger stand sizes receiving higher weights. Extra points were awarded for each protected habitat type reported to be invaded and inventories of *H. mantegazzianum* carried out. Index values derived from this summation were categorised into four classes of invasion intensity: species absent, low, medium, and high invasion intensity. The first class contained zero values only, while the latter were derived by dividing the range of non-zero values into three equal intervals.

Locating and mapping of study areas

For our own field research, study areas were defined as landscape sections of 1 × 1 km² which had to meet the criterion of containing at least three stands of the species. This criterion was set in order to: (i) avoid marginally infested landscape containing only isolated and maybe 'accidental' stands; (ii) add objectivity to the sampling procedure (all encountered areas meeting the require-

ments were surveyed); and (iii) enable efficient data recording.

The 35 most heavily invaded districts (and independent cities), based on the Germany-wide survey, were chosen as potential study regions and their nature conservation authorities were asked to send copies of topographic maps (1:10,000–1:25,000) depicting known *H. mantegazzianum* stands. Maps were received from 33 districts of which 22 seemed to have suitable study areas. Altogether, 30 potential study areas were scrutinised on field excursions and, finally, 20 proved to meet the requirements defined above. These study areas, which were distributed over 14 districts in seven German states, were surveyed in the summer seasons of 2002 or 2003. State, district, grid coordinates, and altitude of study areas are given in Table 1.

Within each study area all stands of *H. mantegazzianum* were mapped by means of a GPS system (sub-meter accuracy). Stands smaller than 25 m² or narrower than 1 m were mapped as points or lines, respectively. Larger and wider stands, here referred to as 'large stands', were mapped as polygons categorised into dominant stands (dense stands) and open stands. The criterion for dominance was *H. mantegazzianum* cover exceeding 50% of the total surface area of the stand. Abundances of *H. mantegazzianum* and the percentage of reproductive individuals were estimated

Table 1. State, district, grid coordinates, and altitudes of study areas

No.	State	District ('Landkreis')	Grid east	Grid north	Altitude (m a.s.l.)
1	Rhineland-Palatinate	Altenkirchen	3410.500	5623.000	160
2	Rhineland-Palatinate	Ahrweiler	2588.300	5594.500	135–175
3	North Rhine-Westphalia	Ennepe-Ruhr-Kreis	2593.800	5696.400	85
4	North Rhine-Westphalia	Euskirchen	2545.800	5595.000	470–490
5	North Rhine-Westphalia	Euskirchen	2535.500	5589.000	590
6	Bavaria	Freising	4465.500	5362.500	480–500
7	Bavaria	Garmisch-Partenkirchen	4430.200	5270.000	865
8	Bavaria	Garmisch-Partenkirchen	4443.500	5253.500	930
9	Lower Saxony	Göttingen	3552.500	5710.500	235
10	North Rhine-Westphalia	Hagen	3396.700	5687.000	145–195
11	North Rhine-Westphalia	Hagen	2600.100	5695.500	90
12	North Rhine-Westphalia	Hagen	3397.000	5689.800	260–290
13	Hesse	Kassel	3529.200	5684.000	270–305
14	Hesse	Lahn-Dill-Kreis	3467.000	5595.500	260
15	North Rhine-Westphalia	Olpe	3421.500	5664.500	255–275
16	Thuringia	Wartburgkreis	3569.500	5620.500	325–350
17	Hesse	Waldeck-Frankenberg	3488.300	5668.500	260
18	Hesse	Waldeck-Frankenberg	3477.800	5655.500	325–345
19	Hesse	Waldeck-Frankenberg	3487.500	5661.200	260–310
20	Saarland	St. Wendel	2589.000	5482.100	360–395

Coordinates represent the south-western corner of study areas (each 1 × 1 km²) according to the German geodetic system ('Gauß-Krüger'). If the altitudinal range of plots in a study area is less than 20 m, average values are supplied, otherwise the lowest and highest value of investigated plots.

(not taking into account seedlings and juveniles with only primary leaves) and habitat types were recorded for all point-like, linear, and large stands. GPS data were imported to ArcView GIS 3.2 (©Environmental Systems Research Institute, Inc.) for quantitative analysis. The total number of individuals of *H. mantegazzianum* was calculated from abundance estimates and number, length, or area of the respective stand types.

Measurement of invasion percentages and habitat saturation

Invasion percentage was defined here as the ratio between the area of *H. mantegazzianum* stands and the total area of the respective habitat type within the study areas. Habitat saturation was defined as the ratio of the area covered by *H. mantegazzianum* plants within the stands and the total area of the habitat type (cf. Pyšek & Pyšek, 1995). As the cover percentages of *H. mantegazzianum* are mostly lower than 100%, the habitat saturation is lower than the invasion percentage. The spatial extent of potential habitats was assessed by interpreting digital aerial orthophotos of the study areas. All areas with sufficient extent to allow for adequate precision of area measurement from the images were mapped as polygons in ArcView GIS and for each habitat type the area sum was calculated. Patches insufficient in size and fringes narrower than about 5 m in nature were not mapped separately but subsumed to neighbouring areas. The habitat types which could be discerned by interpretation of aerial images are listed and described in Table 2.

Table 2. Habitat types and other land-cover types which could be discerned in the interpretation of aerial images

Habitat type	Key traits
Abandoned grasslands, margins of grasslands and fields, and tall-forb stands	More or less nutrient rich sites which have not been subject to regular land use in recent years and which feature herbaceous vegetation (mostly dominated by grasses and sometimes dominated by tall forbs)
Open riverbanks	Unshaded riverbanks with herbaceous vegetation
Shaded riverbanks	Riverbanks shaded by tree lines, copses, or forests
Table 2. (continued)	
Habitat type	Key traits
Open railwaysides	Unshaded railwaysides (verges, embankments) with herbaceous vegetation
Shaded railwaysides	Railwaysides (verges, embankments) shaded by tree lines, copses, or forests
Open roadsides	Unshaded roadsides (verges, embankments) with herbaceous vegetation
Shaded roadsides	Roadsides (verges, embankments) shaded by tree lines, copses, or forests
Woodlands	Copse, tree-dominated wasteland, afforested sites, and scrubland
Ruderal areas	Heavily disturbed sites, such as sand pits, rotovated areas, etc.
Managed grasslands	More or less nutrient rich meadows and pastures which are used agriculturally on a regular basis
Forest margins and fringes	Ecotonal zone between forest and adjacent vegetation and the outermost 10 m of the forest itself
Housing areas	Areas of coherent plots used for housing
Garden plots	Gardens outside settlements
Nutrient-poor grasslands	Low-intensity meadows or pastures at rather nutrient poor sites
Industrial and business areas	Areas of coherent plots of industry or business use
Amenity grassland	Lawns in parks, sports complexes, etc.
Straw meadows	Wet meadows on poor substrates which are mown once per year in late summer or autumn
Lakes	Water body of lakes and ponds
Streets	Tarmacked area of streets
Railway tracks	Rails and their gravel bed
Rivers	Water body of rivers

Abandoned grasslands, margins of grasslands and fields, and tall-forb stands had to be combined into one category due to methodological constraints related to the interpretation of aerial images. The area of forest margins was determined by creating 10 m buffer zones inside the forest polygons. Point-like and linear stands at fringes of woodlands and scrublands were included into the category 'woodlands' while stands at forest fringes were included into 'forest margins and fringes'.

The area of large stands of *H. mantegazzianum* within a particular habitat type was measured by intersecting polygons mapped by GPS in the field with the interpretation of aerial images. The area covered by point-like and linear stands was calculated from abundance estimates, length (in the case of linear stands), and percentage of reproductive individuals under the assumption that the area covered by each individual alone is on average 1 m² for reproductive individuals and 0.1 m² for vegetative individuals.

Results

Germany-wide survey

In total, 309 (70.2%) of the 440 questionnaires were returned. Of these, 300 stated that *H. mantegazzianum* was present in the district area (68.2% of the total, 97% of returns). Occurrences in nature reserves were mentioned by 50% of the districts that had replied and denied by 26%, while the remaining made no statement. About 40% reported protected habitat types to be invaded. Among these were, most frequently, natural riversides and wet grasslands and, occasionally or rarely, alluvial forests, alder swamp forests, calcareous and acidic fens, lakeshores, terrestrial reed stands, and nutrient-poor (chalk) grasslands. Inventories of *H. mantegazzianum* stands had been carried out in at least 21% of the districts (48% 'no inventories', 31% 'no statement') and 3.7% indicated (without being asked) that management action had been undertaken.

There were significant differences of *H. mantegazzianum* frequency estimates between habitat types (Kruskal-Wallis ANOVA: $p < 0.001$). *H. mantegazzianum* occurred most frequently on 'riverbanks and ditches' and 'road verges and paths' (tested by Mann-Whitney *U*-tests with Bonferroni adjustment). Intermediate frequencies were exhibited by 'ruderal areas', 'forest margins and fringes', and 'gardens and parks', while 'fallow fields and abandoned grasslands', 'railway tracks and stations', and 'low-intensity grasslands' were men-

tioned noticeably less frequently. The species was least frequently reported from high-intensity grasslands.

Also concerning the maximum extent of single stands of *H. mantegazzianum* there were significant differences between habitat types (Kruskal-Wallis ANOVA: $p < 0.001$). Stands of the species most frequently reached very large extent of coverage ($> 1000 \text{ m}^2$) in 'riverbanks and ditches', 'ruderal areas', and 'fallow fields and abandoned grasslands', whereas the maximum extent of stands was significantly smaller in 'road verges and path', 'gardens and parks', 'railway tracks and stations', and 'high-intensity grasslands' (Mann-Whitney *U*-tests with Bonferroni adjustment). 'Forest margins and fringes' and 'low-intensity grasslands' did not differ significantly in stand size from all the other habitat types.

On the basis of index values of invasion intensity nine districts (3% of returns) were classified as 'high', 57 (18%) as 'medium', and 234 (76%) as 'low' while in another nine districts *H. mantegazzianum* was absent. Figure 1 shows that the particular classes were not evenly distributed over Germany. There was a significant accumulation of 'medium' and 'high' levels of invasion intensity in the mid-western parts of Germany (Mann-Whitney *U*-test: $p < 0.001$) which mostly coincided with the natural geographic region 'western low mountain ranges'. In the regions 'Alps' and the 'foothills of the Alps' ('Alpenvorland'), there was a slight accumulation of 'medium' invasion intensity, suggesting a secondary focus. In contrast, in the 'north-eastern lowlands', districts without *H. mantegazzianum* occurrences or 'low' invasion intensity prevailed, except for Berlin and two districts of 'medium' and 'high' level where giant *Heracleum* sp. were tested as a fodder crops in the 1960s and subsequently spread into the wild. However, these test plants, at least in the district 'Oder-Spree', were reported to be *Heracleum sosnowskyi* (Zimmermann, 1966). Throughout the remaining parts of Germany, the 'north-western lowlands' and 'south-western low mountain ranges', invasion intensity was predominantly 'low', interspersed with few instances of 'medium' level.

Field investigations

The study areas were primarily situated in the focal region 'western low mountain ranges' (16 out of 20 study areas). They covered a total area of 2000 ha (20 km²) and contained 233 large stands of *H. mantegazzianum* of which 36% were dominant stands. Altogether, the stands occupied an area of

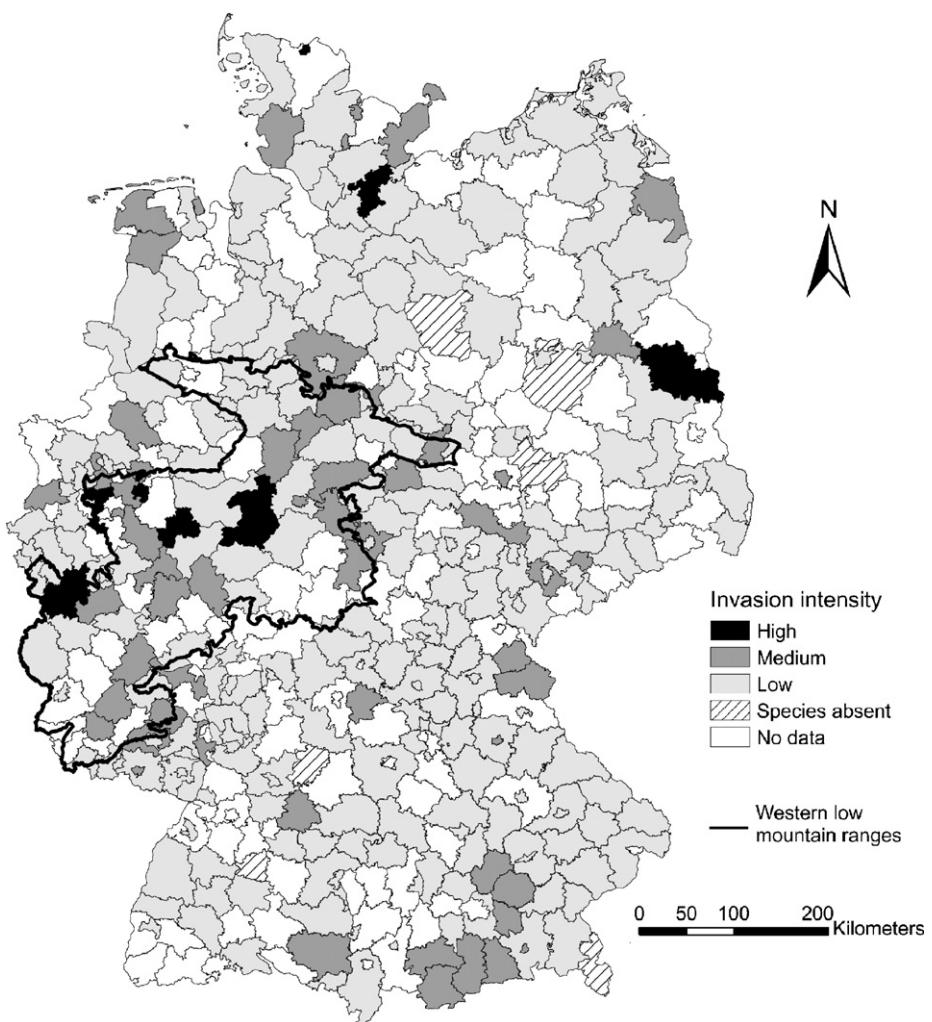


Figure 1. Map of *Heracleum mantegazzianum* Somm. et Lev. invasion intensity in districts of Germany. Classification of invasion intensity was based on a Germany-wide survey addressed to 440 district conservation authorities in 2001. The line signature delineates the natural geographic region 'western low mountain ranges' which represents a focal region of *H. mantegazzianum* invasion.

16.4 ha (0.8% of the total study area). Open stands (11.8 ha) generally prevailed over dominant ones (4.6 ha). With both stand types, sizes of single stands between 100 and 1000 m² occurred most frequently (145 stands) while stands larger than 1000 m² were in the minority (32).

Apart from large stands, occurrences of *H. mantegazzianum* were frequently found in the form of linear and point-like structures not suited for mapping of spatial extent. Linear structures bearing *H. mantegazzianum* were found in 16 out of 20 study areas and amounted to a length of between 30 and 2121 m per study area. Point-like stands were found in all study areas with absolute frequencies of between 2 and 57 per study area. The number of stands per category declined from point-like (322), over linear (185), and open (148)

to dominant (85), while the number of individuals per category exhibited the opposite pattern (6921; 12,690; 53,979; 126,687 individuals per category, respectively) with 63% of all individuals accumulated in dominant large stands.

Figure 2 shows the absolute frequencies of *H. mantegazzianum* incidences per habitat type found during the field surveys of 2002 and 2003. In accordance with the questionnaire survey, roadsides and embankments of rivers and ditches showed high frequencies regardless of being open or shaded by trees. Also margins and fringes of forests, woodlands, and scrublands were frequently infested by *H. mantegazzianum*, while this species occurred less commonly in ruderal areas and on railwaysides. In contrast to the questionnaire survey, abandoned grasslands were among the

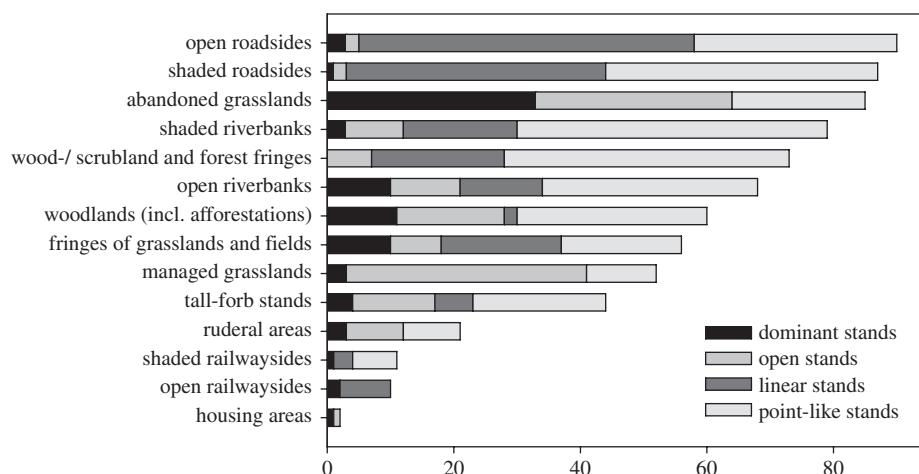


Figure 2. Absolute frequencies of *Heracleum mantegazzianum* Somm. et Lev. incidences found during field surveys of different habitat types in 2002 and 2003. Signatures separate different stand types of *H. mantegazzianum* (point-like stands, linear stands, large open stands, large dominant stands).

commonest habitat types of *H. mantegazzianum* and the species was even found in managed grasslands quite regularly. Furthermore, the species occurred with intermediate frequencies in woodlands (coppices, tree-dominated wasteland and afforested sites), at margins of grasslands and fields and in tall-forb stands at disused sites (this habitat type had not been included in the Germany-wide questionnaire survey). The percentage of dominant stands among all large stands varied with habitat type and was especially high (above 50%) for open roadsides, abandoned grasslands, and margins of grasslands and fields. Protected habitat types were almost completely absent in the field records except for two sites featuring abandoned and slightly wet grasslands, and some occurrences in alluvial forests which, however, did not contain Red List species (Thiele & Otte, 2006).

The highest invasion percentage (18.5%) was found for abandoned grasslands, margins of grasslands and fields, and tall-forb stands (which had to be combined into one category) followed by open riverbanks (13.8%), open railwaysides (9.7%), ruderal areas (5.8%), and open roadsides (3.4%). The remaining invaded habitat types showed invasion percentages of about 2% or less. Due to their lesser frequency and spatial extent dominant stands contributed considerably less to the invasion percentages than open stands (Table 3). Contributions of point-like and linear stands to invasion percentage and habitat saturation were negligible throughout. The highest habitat saturation (8.7%) was again found for abandoned grasslands, margins of grasslands and fields, and tall-forb stands.

Discussion

Perception and extent of *H. mantegazzianum* invasion in Germany

The high percentage of returns (70.2%) of the survey indicated that nature conservation authorities in Germany are well aware of the invasion of *H. mantegazzianum*. Nearly all returned questionnaires (97%) stated that the species was present and half of them confirmed occurrences in nature reserves. These ratios, however, cannot be extrapolated to the whole of Germany, as missing returns mostly coincided with regions where the species is absent or exhibits only sparse records according to the national floristic map as of 2002 (German National Floristic Database, 'Datenbank Gefäßpflanzen'; www.floraweb.de). Apparently, districts in which the species is not present or too rare to be considered relevant refused to reply (except for 3% of returns), whereas returned questionnaires suggest that *H. mantegazzianum* is perceived as a potentially hazardous invader in the respective districts. If we start from this assumption, in approximately two-thirds of German districts *H. mantegazzianum* is perceived as an invader, in about one-third it reportedly occurs in nature reserves and in almost 30% it has allegedly invaded protected habitat types.

While keeping in mind the pitfalls of subjectivity, the index of invasion intensity based on the survey results appears suitable for comparing districts with regard to *H. mantegazzianum*'s invasion success and to identify districts likely to face implications. The field surveys confirm that districts

Table 3. Invasion percentages of different stand types of *Heracleum mantegazzianum* Somm. et Lev. and total habitat saturation aggregated over 20 study areas (landscape sections of 1 × 1 km²) in Germany

Habitat type	Habitat area available (m ²)	Open stands		Dominant stands		Point-like and linear stands		Habitat saturation	
		Area invaded (m ²)	Invasion percentage (%)	Area invaded (m ²)	Invasion percentage (%)	Area invaded (m ²)	Invasion percentage (%)	Area covered (m ²)	Habitat saturation (%)
Abandoned grasslands, grassland margins and tall-forb stands	427,804	50,720	11.9	27,398	6.4	958	0.2	37,214	8.7
Open railwaysides	19,647	808	4.1	786	4.0	320	1.6	830	4.2
Open riverbanks	65,747	7,077	10.8	1,537	2.3	428	0.7	1,855	2.8
Ruderal areas	79,259	1,806	2.3	2,707	3.4	56	0.1	2,189	2.8
Open roadsides	67,001	1,057	1.6	307	0.5	899	1.3	1,085	1.6
Shaded riverbanks	219,569	3,809	1.7	462	0.2	299	0.1	2,108	0.7
Woodlands	1,284,723	10,414	0.8	11,320	0.9	649	0.1	5,760	0.7
Shaded railwaysides	172,833	364	0.2	445	0.3	161	0.1	706	0.4
Shaded roadsides	212,431	1,126	0.5	48	0.0	520	0.2	339	0.2
Managed grasslands	3,871,259	37,897	1.0	593	0.0	12	0.0	2,498	0.06
Forest margins/fringes	1,115,017	1,777	0.2	251	0.0	168	0.0	393	0.04
Housing area	1,062,694	86	0.0	124	0.0	0	0.0	54	0.01

Invasion percentage is calculated here as the ratio between the area sum of *H. mantegazzianum* stands and the total available habitat area. Habitat saturation is calculated as the ratio of the area covered by individuals of *H. mantegazzianum* and total available habitat area.

classified into 'medium' or 'high' level of invasion intensity comprise 'hot spots' of invasion. However, experience from field studies shows that invasion intensity is rather over-estimated than under-estimated. This can be concluded from the fact that one-third of all potential study areas allegedly representing invasion 'hot spots' in districts classified into 'medium' or 'high' level of invasion intensity turned out to be only negligibly invaded by *H. mantegazzianum* (i.e. single stands with few individuals). Districts classified into 'low' invasion level prevalently reported *H. mantegazzianum* to be 'rare' or 'occasional', at the most, and seldom reported large stands. Given the tendency to over-estimate invasion severity, it can be assumed that in these districts occurrences of *H. mantegazzianum* are merely sporadic and small.

Thus, it seems reasonable to narrow down the number of districts with actual or imminent hazards of *H. mantegazzianum* to those with 'medium' and 'high' invasion intensity. If we rate all missing returns as either 'species absent' or 'low' invasion intensity, we can project 'medium' and 'high' levels to 13% and 2% of all districts, respectively. Altogether, this suggests that *H. mantegazzianum*, although present and perceived as an invader in the majority of districts, is an actual or short-term hazard in comparatively few districts. The map of invasion intensity in German districts (Figure 1)

shows that districts likely to face problems with *H. mantegazzianum* are prevalently found in the 'western low mountain ranges'. Projections of 'medium' and 'high' invasion intensities are about twice as high for districts overlapping with this region (23% and 5%, respectively) as for the whole of Germany.

Furthermore, the survey results suggest a secondary focus around the foothills of the Bavarian Alps. However, the national floristic map states only sparse records in this region and our own investigations gave the impression that only a few isolated centres of invasion exist (two study areas were investigated). Presumably, in these cases classification into 'medium' level of invasion intensity is an over-estimation which might be attributable to the greater awareness of nature conservation authorities in this region of areas of especially high conservation value.

Three different factors may play a role to explain the focus of *H. mantegazzianum* invasion on low mountain ranges of mid-western Germany: (i) the climate of this region (sub-atlantic and (sub)montane) closely resembles climatic conditions of the native range of the species as compared to other regions of Germany ('north-eastern lowlands', 'south-western low mountain ranges'); (ii) habitat availability might be higher, depending considerably on changes in land-use regimes, especially

abandonment of grasslands (Thiele & Otte, 2006); or (iii) the number of local introductions by humans (e.g. sowing in the wild by bee keepers, cultivation in gardens and parks) per unit area might have been higher. It seems quite possible that all three factors have an effect on the intensity of *H. mantegazzianum* invasion. However, confirming their significance is beyond the scope of this study.

Invasion pattern in study areas

Saturation of suitable habitats with stands of *H. mantegazzianum* best represents the invasion success (Pyšek & Pyšek, 1995). According to this measure (defined as the ratio between habitat area covered by *H. mantegazzianum* and total available habitat area), *H. mantegazzianum* is most successful in abandoned grasslands, grassland and field margins, and tall-forb stands at disused sites. An additional measure of the invasion success and the invasibility of habitats is dominance of the invader (Lundholm & Larson, 2004). The moderate percentage of dominant stands (36%) among large stands of *H. mantegazzianum* suggests that this species is not always dominant although stands are not necessarily in equilibrium with their environment and possibly could further increase in density. Comparing the percentages of dominant stands for the mentioned habitat types, *H. mantegazzianum* seems to be less successful in tall-forb stands (24% of large stands dominant) than in the former two habitats (both above 50% dominant stands). Thus, it can be stated that *H. mantegazzianum* is especially successful in abandoned grasslands and grassland-like fringe habitats in the open landscape and these habitats are most vulnerable to invasion.

H. mantegazzianum is similarly successful in open riverbanks with respect to invasion percentage but the percentage of dominant stands (25% of all large stands) is rather moderate in this habitat type resulting in moderate habitat saturation (Table 3). Hence, riverbanks are considerably less vulnerable to invasion of *H. mantegazzianum* than abandoned grasslands. Nevertheless, they certainly represent an important habitat for the species, particularly with regard to long-distance dispersal. The same applies to open roadsides which also play an important role in the spread of the species (Thiele & Otte, 2008).

In western Bohemia (Czech Republic) Pyšek and Pyšek (1995) found that 'water courses' and 'path margins' had a much higher habitat saturation and, conversely, unmanaged grasslands showed a considerably lower habitat saturation than in the present study. This opposite pattern might be

attributable to differing maintenance regimes of water courses and roads, and to unfavourable conditions of the unmanaged grasslands which were characterised by either drought or wetness in the Czech study.

Comparing the results of the Germany-wide questionnaire survey with the findings of our field studies, the most striking difference is in the ranking of abandoned grasslands and grassland margins. According to the questionnaire survey, these are among the least occupied habitats of *H. mantegazzianum* while they are among the commonest and most preferred habitats of the species in the most heavily invaded landscapes. There are two possible explanations for this conspicuous difference: (1) the survey estimates might be influenced by pre-existing studies about invaded habitats which often found roadsides, riverbanks, and waste places as common habitats (e.g. Neiland et al., 1987; Ochsmann, 1996; Pyšek, 1994; Pyšek & Pyšek, 1995; Wade et al., 1997) but rarely (abandoned) grasslands (e.g. Tiley et al., 1996); and, (2) the spectrum of invaded habitat types may differ between heavily and marginally invaded landscapes. This would imply that *H. mantegazzianum* has managed to spread from riversides and roadsides into the open landscape in its invasion 'hot spots', while it is still restricted to rather rare occurrences in habitat types outside these foci.

According to the Germany-wide survey, *H. mantegazzianum* has invaded nature reserves in approximately one-third of all districts and protected habitat types in almost as many. However, within the 20 selected study areas virtually no protected habitat types were found to be invaded. This might primarily be attributable to the fact that the study areas hardly contained habitats of interest for nature conservation. But an analysis of plant communities and preferred site conditions indicated that *H. mantegazzianum* is barely capable of invading sites offering suitable conditions (drought, wetness, poor nutrient status, shade, management) for protected plant communities (Thiele & Otte, 2006). These findings seem to contradict reports of occurrences in protected habitat types. An explanation may be found in the details of spatial arrangement of *H. mantegazzianum* stands and habitats of conservation concern. Possibly, in the questionnaire survey, stands of the species in close proximity to rare or endangered communities were interpreted as ongoing or impending invasion into those habitats. One example could be observed by comparing the questionnaire of one district with a case study of a nature reserve in the same region (Schepker, 1998).

The questionnaire stated that *H. mantegazzianum* occurred within the protected habitat types of the nature reserve (calcareous marsh, acidic marsh, salt meadows), whereas the case study showed that *H. mantegazzianum* was growing close to these habitats but not inside them. An alternative explanation might be that invasion of protected habitat types has occurred after deterioration of habitat quality (e.g. due to abandonment or eutrophication).

Assessment of impacts

H. mantegazzianum has managed to become a common feature in landscapes of the 'western low mountain ranges'. Hence, here the species is probably sufficiently abundant and widespread today to sustain pools of metapopulations, and, from a medium- or long-term perspective, it may disperse to landscapes of this region where it has not been present until now without further deliberate assistance by humans (i.e. sowing in gardens or in the wild). Thus, concerning the invasive range it can be stated that *H. mantegazzianum* fulfils the prerequisites to be a hazardous invader and to have negative impacts at the regional and landscape scales within the focal region 'western low mountain ranges'. However, at present, even in the most heavily invaded landscapes, the species occupies only moderate or low proportions of potentially suitable habitats, and thus current impacts are moderate at the landscape and regional scale.

Concerning the future development of the invasion of *H. mantegazzianum*, we presume that this species, just as competitive native species, will not be able to exhaust its potential growth sites in the future. Hence, the ability to displace native species and their communities seems to be limited at the landscape scale and regional endangering or extinction of natives by *H. mantegazzianum* appears to be unlikely unless the invasion pertains to rarities.

As *H. mantegazzianum* seems not a serious threat to nature conservation and regional biodiversity large-scale control programmes appear not to be mandatory. Nevertheless, the species bears other implications, e.g. for human health (Drever & Hunter, 1970; Jaspersen-Schip et al., 1996; Lagey et al., 1995), river management (Caffrey, 1994; Tiley & Philp, 1994; Williamson & Forbes, 1982), and public accessibility of sites, such as riverbanks, amenity areas, and trails (Lundström, 1984; Tiley & Philp, 1994). Hence, it is of concern to stakeholders and land managers. Where problems arising from

the species are imminent or extant, suitable measures of management should be taken. Instructions about how to manage *H. mantegazzianum* and a comprehensive list of references on this topic are provided in Nielsen et al. (2005).

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