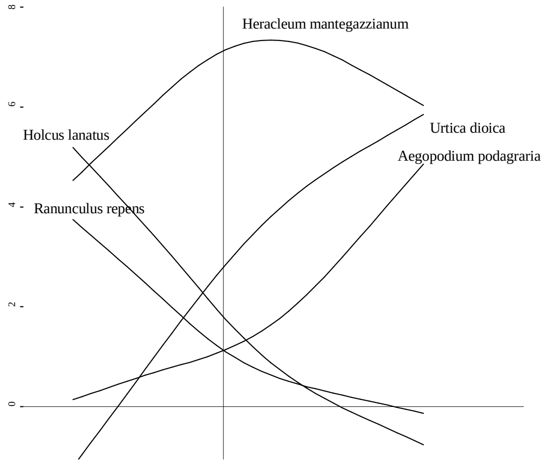
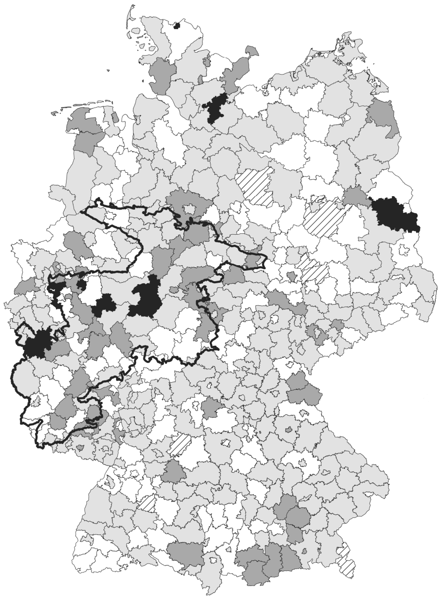
Patterns and processes of *Heracleum mantegazzianum* invasion into German cultural landscapes on the local, landscape and regional scale

Jan Thiele

2007





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This thesis is based on the following three publications:

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Publication I, II and III are regular research papers. In all publications, I performed the field work and was responsible for data analysis and writing. Annette Otte was involved in sketching out the research tasks and planning of the study designs. Furthermore, she gave helpful comments on drafts of the papers and made constructive contributions in discussing issues of *Heracleum mantegazzianum* and invasive species in general. In paper II, Ulrike Schuckert was partly responsible for interpretation and classification of aerial photographs.

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> Thiele, J., Otte, A. and Eckstein, L. (2007). Ecological needs, habitat preference and plant communities invaded by *Heracleum mantegazzianum*.
>
> Thiele, J., Otte, A., Eckstein, L. (2007). Impact of *Heracleum mantegazzianum* on invaded vegetation and human activities.
>
> Otte, A., Eckstein, L., Thiele, J. (2007). *Heracleum mantegazzianum* in its primary distribution range of the Western Greater Caucasus.

Table of Contents

1 General Introduction

1.1 Background

Biological invasions are, in principle, a natural phenomenon which has been recurring since the beginning of life on this planet. However, human activities, such as international trade and tourism, have increased the exchange of earth's biota between regions and continents by several orders of magnitude during recent centuries (di Castri 1989; Williamson 1996) making contemporary invasions a prevalently human-caused issue (Sala et al. 2000; Hulme 2003). Observed and presumed implications for biodiversity are the primary reason for concern about biological invasions which are, today, regarded as the second largest threat to biodiversity worldwide (Vitousek et al. 1997, Keane and Crawley 2002). Therefore, biological invasions have received increasing attention in recent decades from land managers and scientists and have become one of today's top research topics in ecology and biology. But despite considerable research efforts which have spawned an enormous amount of scientific literature, our knowledge and understanding of biological invasions and their potential impacts are still limited (Scherer-Lorenzen et al. 2000).

Concerning the invasion of vascular plant species, their chronology comprises different *phases* and *stages*. In general, the invasion itself can be separated into (i) introduction phase, (ii) establishment phase (of self-sustaining populations), and (iii) spread phase. At least in theory, an invasion will ultimately result in some kind of (iv) equilibrium distribution of an invader within its new range, which may or may not entail (v) implications for native species, ecosystems, and biodiversity on the whole (Williamson 1996; Puth and Post 2005). Despite this rather simple basic structure, each phase of a plant invasion involves a number of (sub-) *processes*. For example, the spread phase involves an iterative process consisting of *recruitment*, *growth*, *seed production*, and *dispersal* to new sites. Complex interactions of these processes with the new environment create invasion *patterns*. While it is often difficult to study the processes (e.g. dispersal) directly in the field (Pauchard and Shea 2006), especially on large spatial scales, we can readily analyse the resulting patterns found by field surveys, remote sensing, or other survey methods.

The components of plant invasions (processes, patterns) encompass virtually all spatial scales, from local to global. For a particular component, one or even all spatial scales can be relevant. Regarding invasion *processes*, introductions of non-indigenous species occur on supra-regional to global scales, while recruitment and growth occur locally, and dispersal occurs on local (patch expansion) to regional scales (range expansion). Equilibrium distributions will mostly be found on regional scales while implications may arise on local to regional scales.

Likewise, resulting invasion *patterns* can be observed on a variety of spatial scales. Common methods of recording abundances and distributions of invasive and native species comprise vegetation samples (plot scale), field inventories (landscape scale), grid mappings and mappings based on administrative boundaries (regional scale).

It follows from the varying scale dependency and specificity of the invasion components that different spatial scales will exhibit different patterns and processes and might lead to supplementary or even contrasting conclusions about drivers and implications of plant invasions. For example, distribution patterns might strongly depend on scale resolution (Hulme 2003). A county-wise map of an invasive plant species might suggest that the species is evenly distributed over a wide geographic range, whereas a higher-resolution grid map might exhibit a patchy distribution with only few invasion foci. Moreover, sampling plots might show variable patterns of local abundances within these foci. Therefore, it is mandatory to adopt multi-scale approaches in order to understand plant invasions and to assess possible impacts (Pauchard and Shea 2006).

Furthermore, the relative importance of particular processes and spatial scales may vary with species attributes, such as taxonomic affiliation or plant functional type, or it may even be entirely species-specific. Hence, it is necessary to consider particular species separately, if one wishes to assess the relative importance of different processes and scales for an invasion. Only few species-specific studies tackling multiple scales have been conducted hitherto. Therefore, endeavours to species-specific multi-scale approaches appear to be promising and fruitful.

As prediction of invasion success is still in its infancy, plant invasions are usually studied *post hoc*, i.e. after introduction, establishment, and a considerable spread of a non-indigenous species have already taken place (Müllerová et al. 2005). Likewise, this thesis deals with an on-going invasion of a plant species which has attained prominence due to a mass increase in recent decades. Hence, the investigations of this thesis are confined to the spread phase, apart from some hypothetical considerations of potential impacts at a future equilibrium. In order to detect as many relevant processes and patterns as possible, this thesis comprises studies on the local, landscape, and regional scale.

1.2 Objectives

The general aim of this study was to identify and assess the relative importance of environmental factors facilitating or constraining the invasion of the Caucasian megaforb *Heracleum mantegazzianum* Somm. et Lev. into Central European cultural landscapes. A further aim was to assess current and potential future impacts of *H. mantegazzianum* on native plant species and communities.

Important filters determining colonisation or invasion of sites by plant species are local environmental conditions and biotic interactions (Lortie et al. 2004). Thus, this study is at first based on the identification of preferred site conditions and communities of *H. mantegazzianum* in its invaded range in Central Europe.

Beyond habitat matching, plant invasions are mediated by dispersal processes which may depend on seed sources and transport vectors. The study species, *H. mantegazzianum*, is known to have been dispersed over long distances by humans and rivers whereas its basic dispersal modes, barochory and short-distance wind dispersal (anemochory), are strongly limited in spatial extent (usually few meters; Mayrink 2005). Hence, it may be hypothesized that the invasion success of *H. mantegazzianum* depends on the specific structure and configuration of the invaded cultural landscape. Therefore, I studied the relative importance of local habitat quality and landscape structure on the presence and abundance of *H. mantegazzianum*.

Finally, the severity of potential impacts of a plant invader will largely depend on invasion extent and habitat saturation. Therefore, I assessed regional extent and severity of *H. mantegazzianum* invasion at the national scale and investigated habitat-specific saturation patterns at the landscape scale in order to assess current impacts and future impact potential.

After a short introduction to the study species (chapter 2), study areas (chapter 3) and an overview of data collection and statistical analyses (chapter 4) the chapters 5-7 comprise detailed studies, the objectives of which are presented in the following:

Analysis of habitats and communities (chapter 5)

Questions: What are the characteristics of preferred sites of *H. mantegazzianum* in its invaded range in Germany? Which plant communities have been invaded? How are local abundances of *H. mantegazzianum* related to site conditions and community type? How does *H. mantegazzianum* affect invaded communities? Under which circumstances is *H. mantegazzianum* a problem for nature conservation?

In chapter 5, 202 sites invaded by *H. mantegazzianum* were analysed with respect to floristic composition, community type, soil nutrient status, water balance, light supply, land use, disturbance, and habitat history. Plant communities were classified according to the Central European syntaxonomical system and preferred site conditions were identified. Furthermore, cover-abundances of *H. mantegazzianum* were analysed with respect to major vegetation gradients and community type. Finally, the potential of *H. mantegazzianum* to threaten aims of nature conservation was evaluated based on the assessment of preferred site conditions, local cover-abundance patterns, and nature conservation value of invaded communities.

Cultural landscapes are patch-corridor-matrix mosaics (chapter 6)

Questions: Which local and landscape factors influence the habitat occupancy and patch saturation of *H. mantegazzianum*?

The study presented in chapter 6 sought to identify local and landscape factors that affect presence-absence (occupancy) and cover percentage (patch saturation) of *H. mantegazzianum* in suitable habitat patches. For this purpose, inventories of *H. mantegazzianum* were conducted in 1 km² study areas and *H. mantegazzianum* stands were mapped with a Global Positioning System (GPS). Suitable habitat patches were mapped from aerial photographs of study areas. Furthermore, a variety of parameters of habitat configuration (e.g. patch shape and area, habitat connectivity, distance from transport corridors) were calculated with a Geographical Information System (GIS). Additionally, local factors were derived from aerial photographs (vegetation structure, land use) and official geodata (soil productivity). The significance and relative importance of these factors for presence and cover percentage of *H. mantegazzianum* was analysed using (logistic) regression models.

Invasion patterns on the regional and landscape scale (chapter 7)

Questions: What is the intensity of the invasion of *H. mantegazzianum* in Germany on a district base? How high is the saturation of suitable habitats with stands of this species in most heavily invaded landscapes of Germany? How severe are current impacts of *H. mantegazzianum* on native plant populations? Does or will *H. mantegazzianum* threaten regional populations of native plant species or their communities?

Firstly, chapter 7 comprises a Germany-wide assessment of the extent and intensity of *H. mantegazzianum* invasion based on a questionnaire survey addressed to the nature conservation authorities of districts. The questionnaire enquired frequencies and extent of *H. mantegazzianum* stands in different habitat types. These data were used to calculate index values of invasion intensity in districts. Secondly, the saturation of different habitat types with *H. mantegazzianum* was calculated based on field inventories and habitat maps from aerial photographs. These data were used to assess current impact intensity of *H. mantegazzianum* on the landscape scale. Finally, I ventured a tentative prognosis regarding the future impact potential of this species.

The results of the above-described chapters are summarized and discussed in a general discussion (chapter 8).

2 Study species

The study species *Heracleum mantegazzianum* (Figure 1) is a tall herb of the Apiaceae family native to the Western Greater Caucasus where it occurs in meadows, clearings and at forest margins at altitudes between 800 and 2200 m a.s.l. (Grossheim 1948; Mandenova 1950; Otte et al. 2007).

The species has a ruderal-competitive strategy and a monocarpic-plurennial life cycle (Ochsmann 1996). Depending on stand density and disturbance regime, individuals flower after three (undisturbed open stands) to five years (dense or grazed stands; Hüls 2005; Pergl et al. 2006). The maximum observed time until flowering was twelve years (Pergl et al. 2005). Undisturbed plant individuals produce around 20 000 seeds (mericarps) with an average weight of 13 ± 3.7 mg (Hüls 2005; Moravcová et al. 2005; Perglová et al. 2006) which build up short-term persistent seed banks (Krinke et al. 2005). Around 1% of seeds can remain viable and dormant in the soil for at least three years (Moravcová et al. 2006). Seeds are dispersed by water (long-distance dispersal) and wind (short-distance dispersal) and, furthermore, dispersal by soil material, garden refuse, and vehicles has been reported (Clegg and Grace 1974; Tiley et al. 1996; Otte and Franke 1998). Wind dispersal distances do mostly not exceed a few meters and 60% to 90% of seeds are shed within 4 m from the parent plant (Mayrink 2005).

Figure 1. Flowering individual of *Heracleum mantegazzianum* Somm. et Lev.

Heracleum mantegazzianum was introduced to European Botanic Gardens in the 19th century and, subsequently, distributed widely as an ornamental plant in gardens and parks (Wyse Jackson 1989; Pyšek 1991). Since the 19th century, the species has repeatedly escaped from cultivation and become naturalised in Germany (Ochsmann 1996). Next to increasing popularity as an ornamental plant, *H. mantegazzianum* was also widely used as a bee plant in the 20th century (Zander 1930; Adolphi 1995). In the second half of the 20th century, the species became invasive and showed a mass increase in several European countries (e.g. Pyšek 1991; Ochsmann 1996; Tiley et al. 1996) and also in some parts of North America (Morton 1978; Dawe and White 1979). The current distribution of *H. mantegazzianum* in Europe and Germany is depicted in Figures 2 and 3, respectively.

Heracleum mantegazzianum has serious health implications for humans due to phyto-photodermatitis caused by furocoumarins (syn. furanocoumarins) contained in the sap of the plant (Drever and Hunter 1970; Lagey et al. 1995; Jaspersen-Schip et al. 1996). Further, it conflicts with recreational and economic interests, e.g. by obstruction of trails and riverbanks (Tiley and 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; Pyšek and Pyšek 1995; Manchester and Bullock 2000; Thiele and Otte 2006). Therefore, *H. mantegazzianum* is commonly regarded as a problem plant that provokes costly and tedious control actions.

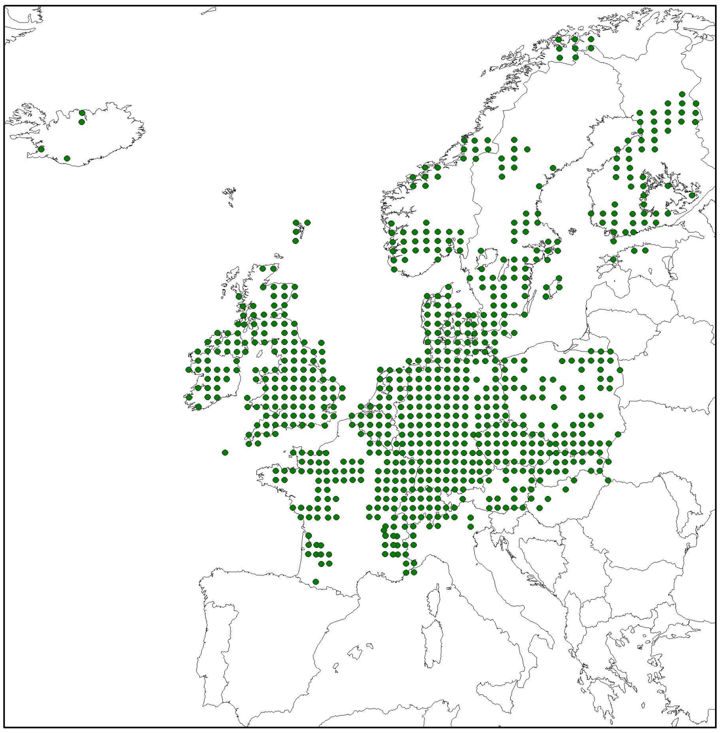

Figure 2. Current distribution of *Heracleum mantegazzianum* Somm. et Lev. in Europe. From Nielsen et al. (2005). Copyright Olaf Booy, Department of Environmental Sciences, University of Hertfordshire, Hatfield, Hertfordshire.

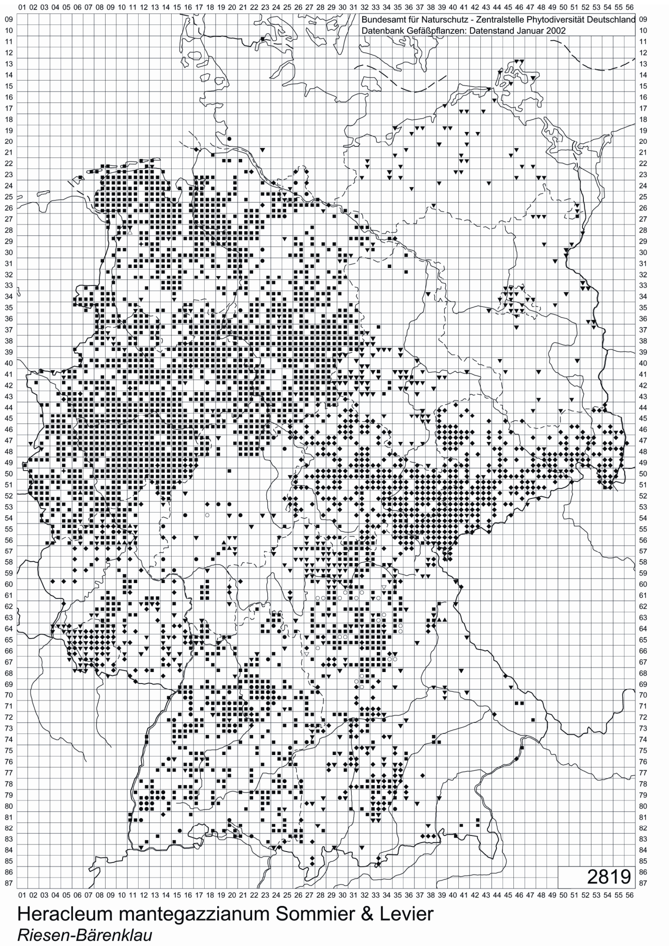

Figure 3. Current distribution of *Heracleum mantegazzianum* Somm. et Lev. in Germany. From the German national floristic database, 'Datenbank Gefäßpflanzen', www.floraweb.de. Sparse records of *H. mantegazzianum* in central parts of Germany (Hesse) are largely attributable to missing data for this region.

3 Study areas

For field investigations, study areas were defined as landscape quadrats of 1 km² which had to meet the criterion of containing at least three extensive stands (>25 m²) of *Heracleum mantegazzianum*. This criterion was set in order to (i) avoid marginally infested landscapes containing only isolated and maybe ‘accidental’ stands, (ii) to add objectivity to the sampling procedure (all encountered areas meeting the requirements were surveyed), and (iii) enable efficient data recording.

The selection of study areas was based on a Germany-wide questionnaire survey addressed to the nature conservation authorities of districts. According to survey statements about the frequency and areal extent of *H. mantegazzianum* stands, index values of invasion intensity were calculated and districts were ranked accordingly. The 35 most heavily invaded districts were chosen as potential study regions and their nature conservation authorities were requested 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 scrutinized 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 (North Rhine-Westphalia, Rhineland-Palatinate, Hesse, Bavaria, Lower Saxony, Thuringia, Saarland), were surveyed in the summer seasons of 2002 or 2003. Approximate locations of study areas are depicted in Figure 4. Exact coordinates and altitudes are presented in the respective tables in chapters 5, 6, and 7. The table of study areas in chapter 6, also contains some basic climate parameters.

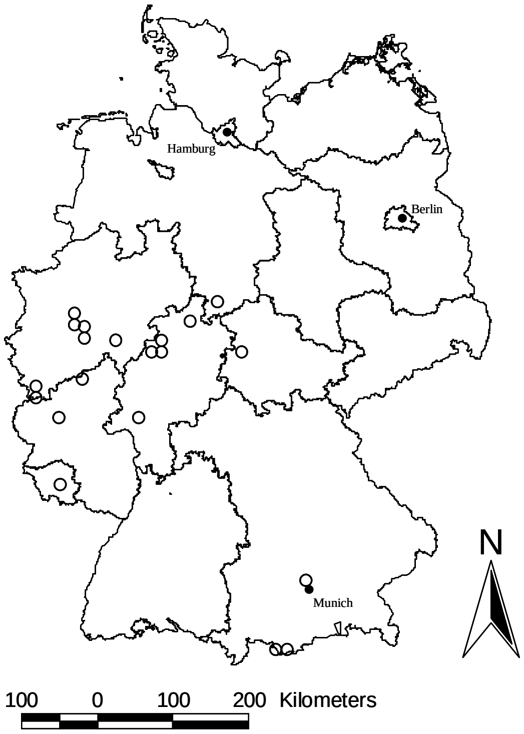

Figure 4. Approximate locations of study areas (circles) in Germany.

4 Data collection and statistical analyses

4.1 Overview

In this chapter, methods of data collection and statistical analyses applied in this thesis are summarized. At first, a Germany-wide questionnaire survey which has already been mentioned in the previous chapter was conducted. This survey helped to identify suitable study areas and, moreover, delivered data for the assessment of the Germany-wide invasion pattern of *Heracleum mantegazzianum*. Apart from this survey, data collection was confined to the study areas described in chapter 3, and comprised field studies and inventories, remote sensing (aerial photographs), and utilisation of pre-existing geodata sets. Statistical analyses were conducted on different objects representing different scales. These objects were (i) sampling plots (25 m²), (ii) habitat patches, and (iii) the entire study areas. For sampling plots and habitat patches a variety of exploratory methods of data analysis, such as ordination techniques and regression analyses, were used in preliminary and final analyses. For the entire study areas, area balances, simple statistics, and graphical methods were used to describe the landscape invasion pattern of *H. mantegazzianum*.

4.2 Data collection

4.2.1 Sampling of vegetation and site conditions

In each extensive stand of *H. mantegazzianum,* one 25 m² plot was established for the sampling of vegetation and site conditions (n = 202). Locations of plots were chosen to be representative of the stand as a whole and their position was recorded with GPS. If densities of *H. mantegazzianum* varied strongly within one stand two plots were established to account for high and low density areas.

Vegetation was sampled according to the method of Braun-Blanquet (1964) using the modified cover-abundance scale (Wilmanns 1989). All vascular plant species were recorded. Nomenclature followed Wisskirchen and Haeupler (1998). Additionally, height and cover percentage of vegetation layers (tree, shrub, field, moss layer), litter, and bare soil were measured or estimated, respectively. The field layer data were recorded separately for *H. mantegazzianum* and the remaining resident species. Environmental factors estimated or identified for each plot in the field included light availability (ordinal scale), land use (agriculture, maintenance, fallow) and disturbances (e.g. waste disposal, removal of shrubs).

In autumn, soil samples were taken from each plot and analysed for nutrient contents. Plant available phosphorus and potassium were determined using the CAL-method (Schüller 1969) while magnesium was extracted with $CaCl_2$ solution (Schachtschabel 1954). Total nitrogen and carbon content was measured using a CN-Analyser. In 2002, some additional soil parameters were recorded (n = 118). Drill cores of up to 1 m depth were taken to assess soil morphology, bulk density, and soil character beneath the a-horizon. Further, pH-values of topsoils were measured in H_2O with a laboratory pH meter.

4.2.2 Inventories of Heracleum mantegazzianum stands

Within each study area, all stands of *H. mantegazzianum* were mapped with a differential GPS system as either polygons (extensive stands >25 m²), points (small stands), or lines (narrow stands; Figure 5). Extensive stands were separated into open (*H. mantegazzianum* cover <50%) and dominant stands (>50%). For each stand, abundances of *H. mantegazzianum* and the percentage class of reproductive individuals among all individuals were estimated not taking into account seedlings and juveniles with only primary leaves. For extensive stands, cover percentages of *H. mantegazzianum* were estimated additionally. Supplementary attribute data recorded with *H. mantegazzianum* stands included habitat type, land use, and incidences of disturbances within the stands.

4.2.3 Mapping of habitat patches from aerial photographs

Complete inventories of suitable habitat patches for *H. mantegazzianum* in the study areas were conducted based on aerial photographs in GIS. For this purpose, multitemporal series of aerial photographs comprising present time (approx. 2000), 1970s, and 1950s were acquired for each study area. While present time aerial photographs were used to map current suitable habitat patches for *H. mantegazzianum*, historical photographs served to assess habitat age and history. Patches of suitable habitats were identified ‘by eye’ and mapped in GIS. Altogether, 15 different suitable habitat types of *H. mantegazzianum* could be discerned (Table 2 in chapter 6), apart from managed grasslands which present marginal habitats. Different types of habitats were mapped as separate polygons in GIS. If current habitat patches were not homogenous with respect to land-cover or habitat type in the 1970s, the patches were subdivided and treated as separate patches. This was repeated for the 1950s. Hence, this procedure resulted in habitat patches which were homogenous at all three time point (i.e. least common geometries, LCG). Several current habitat patches of different habitat types or histories could lie adjacent and form ‘aggregated habitat patches’ (Figure 6). The basic unit for later statistical analyses of habitat patches presented in chapter 6 was, however, the homogenous LCG habitat patch.

4.2.4 Parameters of landscape structure and habitat configuration

In order to account for landscape structure and configuration of habitat patches, maps of special landscape elements that might be important for *H. mantegazzianum* were created. On the one hand, these were potential transport or migration corridors for *H. mantegazzianum* which included flowing waters (rivers, brooks, ditches) and traffic routes (roads, railways). On the other hand, these were housing areas, business areas, and garden plots which might have served as anthropogenic seed sources. Based on the maps, nearest-neighbor distances from all categories of these landscape elements were calculated for each habitat patch. Furthermore, connectivity indices of aggregated habitat patches were calculated. For this purpose, the area-informed proximity index of McGarigal and Marks (1995) was chosen. Furthermore, shape indices and areas were calculated for all habitat patches (LCG). Finally, digital contour lines of study areas were used to delineate topographic units (Valley, Slope, Hilltop, Plateau) which were assigned to the habitat patches as attribute data.

Figure 5. GPS map of *Heracleum mantegazzianum* Somm. et Lev. stands from an exemplary study area. Stands were separated into extensive open (light polygons), extensive dominant (dark polygons), point-like (circles), and linear (lines) ones.

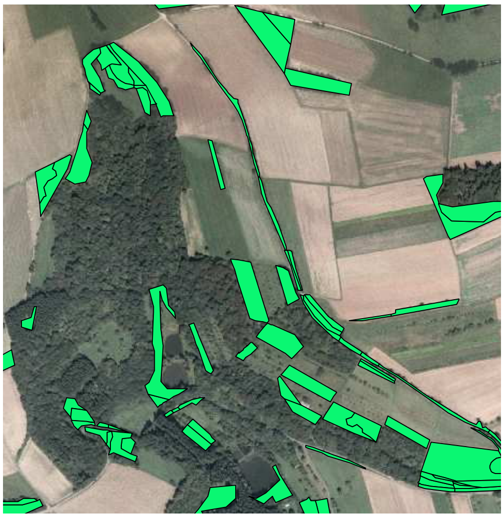

Figure 6. Map of suitable habitat patches for *Heracleum mantegazzianum* Somm. et Lev. Different habitat types and patches with different histories were mapped as separate polygons from digital aerial photographs in GIS.

4.3 Statistical analyses

4.3.1 Analyses of sampling plots

In chapter 5, classical plant sociological methods (e.g. Braun-Blanquet 1964, Dierschke 1994) were used to classify vegetation relevés according to the system of plant communities of Central Europe (e.g. Oberdorfer 1993, Pott 1995). The aim of this study was not to diagnose new plant communities but to assign vegetation relevés with *H. mantegazzianum* to plant communities known from the literature. Lists of character or differential species serving to discern plant communities were compiled from various relevant sources (Ellenberg et al. 1992, Oberdorfer 1993, Dengler 1997, Dierschke 1997, Dierschke 2004). Furthermore, the following explorative methods were used for the analysis of sampling plot data (chapter 5):

- Correspondence Analysis (CA) was used to explore major gradients in the floristic composition of vegetation samples;
- Detrended Correspondence Analysis (DCA) was used to measure the gradient length of the vegetation data set;
- General Additive Models (GAM) were used to calculate response curves of species abundances along the main vegetation gradient;
- Pearson and Spearman correlation coefficients were used to search for relationships between environmental factors, vegetation structure, and *H. mantegazzianum* parameters;
- Descriptive statistics (medians, percentiles etc.) of environmental data were used to characterize preferred site conditions of *H. mantegazzianum*.

4.3.2 Regression models of habitat patches

For the analyses of habitat patches mapped from aerial photographs (chapter 6), two dependent variables were set up: (i) habitat occupancy, i.e. presence or absence of *H. mantegazzianum* and (ii) patch saturation which was calculated as cover sum of *H. mantegazzianum* within a patch divided by patch area. In order to test for effects of a variety of patch-based environmental variables (see Table 3 in chapter 6) on the two dependent variables the following statistical methods were used:

- Correlation coefficients (Pearson, Spearman), simple (logistic) regression models, and Kruskal-Wallis ANOVA were used for pre-analyses searching for significant simple relationships between predictors and dependent variables;
- Best-subset model building with Akaike's Information Criterion (AIC) was used to identify a best subset of predictors for each dependent variable;

- Collinearity among best-subset predictors was tested for with multiple (logistic) regression models fitted on each predictor with all remaining predictors;
- To test for significant effects of the respective best-subset predictors on habitat occupancy a multiple Logistic Regression Model (LRM) was calculated;
- Similarly, a multiple General Regression Model (GRM) was fitted to patch saturation;
- Auto-correlation of regression residuals was tested for by Mantel-tests with residual and spatial distance matrices of habitat patches.

4.3.3 Calculation of invasion rate and habitat saturation for study areas

Invasion rate and habitat saturation were calculated for each habitat type with *H. mantegazzianum* in order to identify current invasion patterns and assess impacts on the landscape scale, i.e. within study areas (chapter 7). For this purpose, area sums of habitat types over all study areas were calculated in GIS. Likewise, cover and area sums of *H. mantegazzianum* stands were calculated for each habitat type. Then, the invasion percentage was calculated as area sum (outlines!) of *H. mantegazzianum* stands divided by the area sum of the respective habitat type. Analogously, habitat saturation was calculated as the cover sum of *H. mantegazzianum* stands divided by habitat area.

4.3.4 Software

The following computer programs were used for statistical data analyses in this thesis:

- STATISTICA 6.0 (StatSoft Inc. 2001);
- SAS for Windows 9.1 (© 2002-2003 by SAS Institute Inc., Cary, NC, USA);
- CANOCO (ter Braak and Šmilauer 1998);
- PC-Ord 4.14 (McCune and Mefford 1999);
- XLSTAT (© 1995-2006 Addinsoft);
- PopTools 2.6 (Hood 2005);
- ArcView GIS 3.2 (© Environmental Systems Research Institute, Inc.);
- ACCESS 2002 (© Microsoft Corporation 1992-2001).

More detailed information on the applied methods of data analysis will be found in the materials and methods sections of the chapters 5, 6, and 7.

5 Analysis of habitats and communities invaded by *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in Germany

Jan Thiele and Annette Otte

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5.1 Abstract

The aim of the present study was to analyse *Heracleum mantegazzianum*'s habitat preference and to identify recipient communities in its invaded range in Central Europe with regard to the species' effects on resident vegetation and potential implications for nature conservation. Field investigations were carried out in 20 study areas (each 1 x 1 km²) in Germany. In all encountered stands of *H. mantegazzianum* the vegetation composition and various site parameters were sampled. Additionally, time series of aerial photographs of study areas were analysed to reconstruct the history of invaded sites. *Heracleum mantegazzianum* occurs in a variety of different habitat types, such as grasslands, roadsides, riverbanks, woodland margins etc. Stand densities of the species vary widely from scattered individuals to dominant stands. Primary constraining factors for *H. mantegazzianum* densities are land use, shading and low-productive site conditions. Site conditions of preferred habitats are more or less uniform, and are characterised by high productivity in combination with lack of land use and recent or historic disturbances or habitat changes. *Heracleum mantegazzianum* is a successful invader and a potentially dominant species only if these particular habitat requirements are met. However, even then most stands of the species are not dominant. The majority of invaded sites have been subject to human caused habitat changes within the last 50 years which have enabled or facilitated invasion. The most important process here is land-use decline, especially abandonment of grasslands. The prevailing vegetation types with *H. mantegazzianum* are ruderal Arrhenatherion grasslands and Galio-Urticetea tall-forb stands which represent stages of secondary successions from grasslands to woodlands after abandonment of land use. Successional age seems to play a role with respect to stand densities of *H. mantegazzianum* as maximum densities occur prevalently at sites which represent young successional stages. The results of the present study suggest that high densities of *H. mantegazzianum* can decrease native diversity of invaded stands, especially in abandoned grasslands. However, a loss in diversity is a typical effect of the processes that facilitate the invasion of *H. mantegazzianum*, i.e. abandonment of grassland management and severe disturbances or even habitat destruction (e.g. due to mining), and can be brought about by native species, such as *Urtica dioica*, as well. From this point of view *H. mantegazzianum* can be seen rather as a symptom of diversity loss than the cause of it. Further, the results suggest that *H. mantegazzianum* does not seriously threaten to conflict with nature conservation as preferred habitats and plant communities are very common today and habitats which are of special conservation interest present no favourable conditions for this species.

Keywords: invasive alien species, tall forbs, succession, Galio-Urticetea, Arrhenatheretalia, land-use change, disturbance, dominance.

5.2 Introduction

5.2.1 Motivations and objectives

The study species, *Heracleum mantegazzianum* Somm. et Lev.(Giant Hogweed) is a monocarpic, plurennial mega forb of the Apiaceae family (Ochsmann 1996) native to the Northwestern Great Caucasus where it occurs in meadows, clearings and at forest margins at altitudes between 800 and 2200 m a.s.l. (Mandenova 1950). It was introduced to Europe as an ornamental plant in the 19th century and after repeated escapes from cultivation a massive spread was observed in several European countries (e.g. Great Britain, Czech Republic, Germany) during the second half of the 20th century (cf. Pyšek 1991; Pyšek 1994; Ochsmann 1996; Tiley et al. 1996; Wade et al. 1997).

Heracleum mantegazzianum is reported to reduce native biodiversity of invaded vegetation (Lundström 1984; Pyšek and Pyšek 1995). Moreover, a survey addressed to the nature conservation authorities of German districts in 2001 brought up reports of the species to occur in nature reserves and sometimes even in protected habitat types (Thiele and Otte, submitted). Yet hitherto invasion of habitats and plant communities of special conservation interest has never been scientifically confirmed. Also research on the species' habitat preferences and its effect on local native biodiversity has to date been restricted to rather few localities or single regions.

Therefore, the objectives of the present study were:

1. To analyse the species' habitat preference over a possibly wide geographical range in Germany,
2. to identify invaded plant communities,
3. to assess effects on recipient communities and, finally,
4. to evaluate risks imposed by the species on nature conservation.

5.2.2 Overview of previous knowledge

On national level, information on the distribution of vascular plant species is provided by the floristic mapping project of Germany ('Floristische Kartierung') based on the grid of the topographic map of Germany 1:25 000 (cell size ca. 11 x 11 km²). In 2002, *H. mantegazzianum* was reported for 57% of grid cells (considering all records observed or confirmed after 1980). But this is probably an underestimate as data from two German states (Schleswig-Holstein, Hesse) were virtually missing. The present distribution of *H. mantegazzianum* is biased towards western and north-western Germany and the southernmost parts of eastern Germany (Saxony, Thuringia) where the species is present in the vast majority of cells, whereas the remaining parts of eastern Germany exhibit only sparse records and southern Germany shows intermediate frequency (German national floristic database, 'Datenbank Gefäßpflanzen'; www.floraweb.de).

The extent of *H. mantegazzianum* stands in invaded landscapes was studied by Pyšek and Pyšek (1995) in the Czech Republic, as well as by Schepker (1998), and by Thiele and Otte (submitted) in Germany. Some basic information on invaded habitats has been provided recently by listings (e.g. Wade et al. 1997) or quantitative accounts of broad habitat categories (Pyšek 1994; Pyšek and Pyšek 1995; Ochsmann 1996). Characterisations of site conditions based on Ellenberg indicator values of Central European plant species (Ellenberg et al. 1992) were given by Pyšek and Pyšek (1995) from western Bohemia (50 sites) and Ochsmann (1996) from the Göttingen area in Germany (57 sites). Specific measurements of site parameters have to date been limited to small numbers of plots. Data on soil nutrients, pH values, and soil organic matter were presented by Neiland (1986) and Tiley et al. (1996) from a total of 20 sites in Scotland and by Otte and Franke (1998) from two sites in Germany. Clegg and Grace (1974) reported data on pH values and organic matter in the soil from the region of Edinburgh (18 sites). Finally, a preliminary overview of the invasion and ecology of *H. mantegazzianum* can be found in Kowarik (2003, pp. 207).

Previous descriptions of plant communities with *H. mantegazzianum* have been based on comparatively small numbers of relevés and restricted to single localities or regions. The first published vegetation relevés of *H. mantegazzianum* stands were reported from the Czech part of the Ore Mountains by Weber (1976). Dierschke (1984) described a similar stand from the eastern part of Lower Saxony (Germany) which he classified as Heracleum mantegazzianum – Galio-Urticenea-community, i.e. a rankless community of the (sub)class of nitrophilous herb communities of fresh to moist habitats (Galio-Urticenea (Passarge 1967) Th. Müller in Oberd. 1983, syn. Galio-Urticetea Passarge ex Kopecky 1969). On the basis of 18 relevés from Schleswig-Holstein (northern Germany) and Saarland (south-western Germany) Klauck (1988) introduced a new association, Urtico-Heracleetum mantegazzianii, which he categorised under the alliance Aegopodion Tx. 1967. The notion of a separate association of *H. mantegazzianum* was accepted by Kolbeck et al. (1994) who reported 40 relevés from Central Bohemia pointing out that this community occurs in a variety of mesophilous to hygrophilous habitats, such as forest fringes, field edges, ditches, moist grassy slopes and ruderalised areas. They also reported three relevés from forest vegetation which corresponded to human-influenced forms of Stellario-Alnetum Lohm. 1957 forests (sub-alliance of Alder-Ash-Forests, Alnenion glutinoso-incanae Oberd. 1953, within the alliance Alno-Ulmion Br.-Bl. et Tx. 1943). Next to predominant occurrences of *H. mantegazzianum* in Galio-Urticetea and Aegopodion communities, Ochsmann (1996) also found the species in grassland communities and, though only vegetatively, in beech forests of the Göttingen area (Lower Saxony, Germany). In accordance with Schwabe and Kratochwil (1991) he advocated the rejection of a separate association of *H. mantegazzianum* (Urtico-Heracleetum Klauck 1988). This view was supported by Otte and Franke (1998) who conducted eight relevés in Hesse (Germany) in derelict sites (grasslands and gardens) and in riverbank sites which they subsumed to the orders Glechometalia Tx. in Tx. et Brun-Hool 1975 and Calystegietalia (Convolvuletalia) Tx. 1950, respectively, and by Sauerwein (2004) who presented a study of *H. mantegazzianum* communities in northern Hesse.

5.3 Study areas

For field investigations, study areas were defined as landscape sections of 1 by 1 km² which had to meet the criterion of containing at least three stands of *H. mantegazzianum*. This criterion was set in order to (i) avoid marginally infested landscapes containing only isolated and ‘accidental’ stands, (ii) to objectify the sampling procedure (all encountered areas meeting the requirements were surveyed), and (iii) enable efficient data ascertainment.

In 2001, a survey on *H. mantegazzianum* was conducted by addressing questionnaires to the nature conservation authorities of all of 440 German districts (‘Landkreise’) including cities independent from a district administration (‘kreisfreie Städte’). The received data were used to create a ranking of districts by invasion intensity (Thiele and Otte, submitted) in order to identify districts most likely to contain suitable study areas.

The 35 most heavily invaded districts, according to the estimates based on the 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 by 33 districts and on examination 22 seemed to have suitable investigation areas. Altogether, 30 potential study areas were scrutinized on field excursions and, finally, 20 study areas proved to meet the requirements defined above. These study areas, distributed over 14 districts in seven German states (North Rhine-Westphalia, Rhineland-Palatinate, Hesse, Bavaria, Lower Saxony, Thuringia and Saarland), were surveyed in the summer seasons of 2002 or 2003. Grid coordinates and altitudes of study areas are given in Table 1.

Table 1. State, district, grid coordinates and altitudes of study areas. Coordinates represent the south-western corner of each study area (1x1 km²) according to the German geodetic system (‘Gauß-Krüger’). If the altitudinal range of plots in a study area was less than 20 m, average values are supplied, otherwise the lowest and highest value of investigated plots.

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

5.4 Materials and Methods

5.4.1 Establishment of plots

In all extensive stands except for some stands of which the vegetation cover had been completely destroyed recently, e.g. by ploughing or rotovating, plots of 25 m² were established in order to investigate site conditions and record plant communities. Locations of plots were chosen to be representative of the stand as a whole and their position was mapped with GPS. If two patches of conspicuously different densities of *H. mantegazzianum* were located inside one homogenous habitat, both patches were sampled separately. Altogether, 202 plots were studied in 2002 or 2003.

5.4.2 Reconstruction of site history

Time series of aerial photographs (1950s, 1970s, approx. 2000) were acquired for study areas and overlain with the coordinates of plots in ArcView GIS 3.2 (© Environmental Systems Research Institute, Inc.). Aerial photographs were interpreted by eye and plots were assigned to a particular habitat type for every point of the time series. On the whole, 11 different land-cover types, e.g. ‘arable land’, ‘grassland’, ‘shrub’ could be discerned. The different combinations of land-cover types along the time series were classified ‘by hand’ into groups of similar site histories.

5.4.3 Sampling of site conditions

Soil samples were collected in October of the respective year using a soil corer of 3 cm diameter. In each plot, five cores of 25 cm depth were taken at random locations after removing litter and dead plant material from the soil surface. Samples were air-dried, sieved (<2 mm) and extracted with both calcium-acetate-lactate for the determination of plant-available phosphorus and potassium (Schüller 1969), and $CaCl_2$ solution for the determination of magnesium (Schachtschabel 1954). Total nitrogen and total carbon content were analysed with a CN-Analyser.

In 2002, also the pH values of topsoil samples were measured in H_2O with a laboratory pH meter (WTW '325-A / Set 1 Electrode SenTix 97T') and additional drillings were conducted up to 1 m depth, if possible, to characterise soil morphology, especially with regard to water supply (n = 118). The drill cores were investigated for signs of soil wetness and, where applicable, soil wetness or impeded drainage was classified on an ordinal scale according to AG Boden (1982). Bulk density was estimated (low, medium, high) and soil material was taken from the drill core beneath the a-horizon to determine the soil character. Values of available field capacity were derived from soil character and bulk density with corrections for lateral inflow or outflow of water depending on topology (AG Boden 1982).

Light availability was estimated using an ordinal scale, which comprised five levels (dark shade, shade, semi-shade, light, full light). Land use of the study sites as identified in the field was assigned to three categories, 'none' (including fallow and derelict land), 'maintenance' (e.g. irregularly mown fringes or road verges), and 'grassland' (regularly used meadows and pastures). Where applicable, disturbances of sites were recorded, which in the context of this study include all externally caused changes to the structure of the vegetation apart from land-use practices, e.g. deposition of waste material or removal of shrubs and trees.

5.4.4 Sampling of vegetation

Vegetation sampling was done following the method of Braun-Blanquet (1964) using the modified cover-abundance scale as proposed by Wilmanns (1989). Height and cover of the different vegetation layers and cover percentages of litter and bare soil surface were estimated for each plot as parameters of vegetation structure. In addition to tree, shrub, herb and moss layers, the vegetation structure parameters were separately estimated for *H. mantegazzianum.* All vascular plant species within a plot were recorded. Nomenclature follows Wisskirchen and Haeupler (1998).

The assignment of species as character or differential species was adopted from Ellenberg et al. (1992), Oberdorfer (1993), Dengler (1997), Dierschke (1997), and Dierschke (2004). Nomenclature of plant communities below the (sub-) class level follows Oberdorfer (1993) if not otherwise indicated.

5.4.5 Parameters derived from the floristic composition of vegetation samples

Unweighted averages of the indicator values for light, moisture, soil reaction and nutrients given by Ellenberg et al. (1992) and calibrated C-S-R strategy types by Grime et al. (1988) were calculated for each sample to supplement the set of recorded site parameters. To avoid bias due to the selection of plots under the premise of *H. mantegazzianum* occurrence, this species was omitted in the calculations. The calibration of unbalanced C-S-R radii for species was performed in the manner demonstrated by Ejrnæs and Bruun (2000) and Ecke and Rydin (2000). Only species categorised by Grime et al. (1988) were included in this analysis. These comprised about 70% of the entire species pool of the data set and 98% of species with relative frequencies greater than10%. Furthermore, the cover sum of nanophanerophytes and woody chamaephytes pooled together was calculated by summing up mean values of cover-abundance classes of the modified Braun-Blanquet scale.

5.4.6 Data analysis

Major gradients in the vegetation data set were explored by correspondence analysis (CA, Hill 1973), a method of indirect gradient analysis (Lepš and Šmilauer 2003), using the program package CANOCO for Windows 4.5 (© Biometris). For gradient analysis the cover-abundance of species was transformed to the numeric values 1 to 9 representing the levels of the modified cover-abundance scale. A detrended correspondence analysis with detrending by segments revealed a gradient length on the first axis of 2.8 and thus indicated predominant linear response of species along the first ordination axis. Therefore, CA was setup with biplot scaling (ter Braak and Šmilauer 1998). Furthermore, scaling was chosen to focus on inter-sample distances and downweighting of rare species was selected. In addition, response curves of selected species along the first ordination axis were produced using Generalized Additive Models (GAM) in CANOCO.

Calculations of descriptive statistics and correlation coefficients were performed with Statistica 6.0 package (© StatSoft, Inc.). Medians and percentiles were calculated instead of means and standard deviations as distributions of soil nutrient concentrations and average indicator values for soil reaction deviated considerably from normal distribution. Classification of medians was done according to content classes of P, K and Mg for arable fields (Landesanstalt für Landwirtschaftliche Chemie 2002) or rather according to AG Boden (1994) for organic carbon, pH and available field capacity.

Sorting of vegetation samples and assignment to known syntaxa was done ‘by hand’ on the basis of characteristic and differential species.

5.5 Results

5.5.1 Habitat preference

5.5.1.1 Land use and disturbance

Heracleum mantegazzianum prevalently occurred at sites without a regular land use regime, like abandoned grasslands or other derelict land (71% of plots). 17% of sites were subject to rather irregular management (e. g. maintenance cut) and 12% were regularly mown or grazed. Notably, when regular management was applied *H. mantegazzianum* was constrained to low densities, while lack of land use or irregular maintenance allowed for high densities of the species.

Recent mechanical disturbances of the vegetation were found in 27% of plots altogether (Figure 1A) and were predominantly human caused. The encountered kinds of disturbances generally cause open patches in the vegetation. 34% of plots were situated inside the inundation area of rivers and, thus, were subject to episodic or periodic disturbance due to flooding (Figure 1B) which sometimes overlapped with anthropogenic disturbances. All disturbances combined accounted for 57% of plots.

5.5.1.2 Site history

During the period covered by the time series of aerial photographs (1950s to approx. 2000), the majority of sites with *H. mantegazzianum* showed changes which are attributable to land use decline (53.5%, Table 2). The most prominent process was abandonment of managed grasslands leading to herbaceous successional stages which accounted for 27.7% of all sites. Prevalently, the abandonment occurred between the 1950s and the 1970s (33 sites) and, secondarily, between the 1970s and today (23 sites). In another 14.9% of sites cessation of grassland management before the 1970s or, exceptionally, between the 1970s and today led to development into woodlands or forests. Furthermore, conversion of margins of managed grasslands and, subordinately, arable fields into disused but probably occasionally maintained herbaceous fringes occurred alongside boundary lines, like e.g. paths, tracks, ditches, and small rivers (7.9%) and, rather rarely, recent abandonment of arable fields was observed (3%).

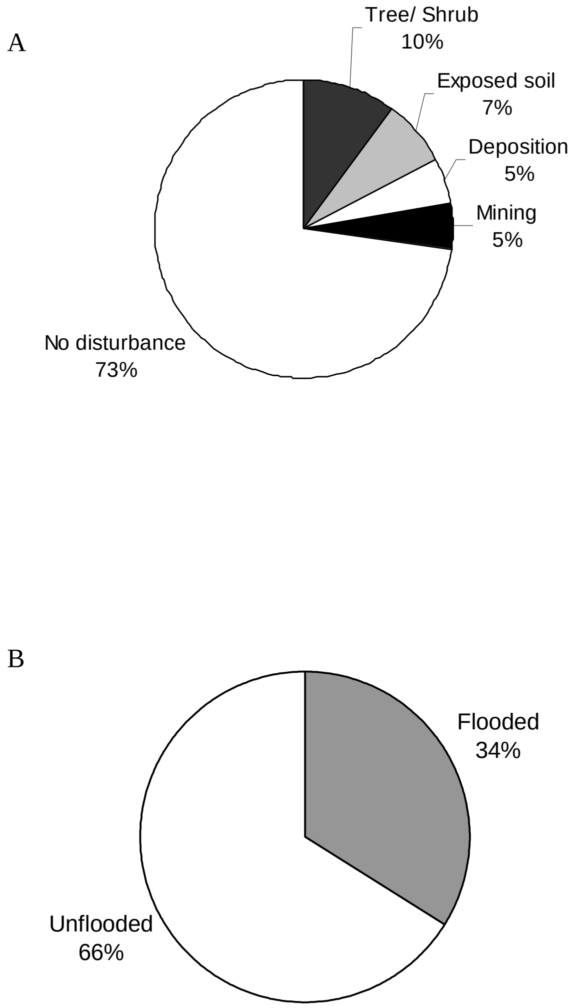

Figure 1. Relative frequencies of disturbances in investigated plots. (A) Mechanical disturbances (predominantly human caused) and (B) disturbance due to flooding. Short cuts for disturbance categories: (A) Tree/ Shrub = Removal of single trees or shrubs in the open landscape or along fringes, Exposed soil = mechanical disturbances of the sward leading to patches of exposed soil, Deposition = deposition of organic material, e.g. garden waste, Mining = recently abandoned open cast mining (former sand pit or rock quarry), No disturbance = no obvious signs of disturbance found in the field; (B) Flooded = site located inside the inundation area of a river and, thus, subject to periodic or episodic flooding, Unflooded = site located outside inundation areas.

Sites subject to continuous agricultural land use over the whole period were found with a frequency of 17.9%. Predominantly, these sites were persistently managed grasslands and, secondarily, former arable land which was converted to managed grasslands prior to approx. 2000. However, 25% of these sites showed signs of declining use or abandonment during the time span between the most recent aerial photograph (approx. 2000) and the field survey (2002, 2003). Other constant habitats were maintained grassland-like fringes which persisted since the 1950s at 4.5% of sites.

Table 2. Frequencies (absolute and relative) of categories of site history for investigated plots. Individual site histories were grouped on two levels: (i) broad groups of site history representing similar processes (given in bold) and (ii) subdivisions of the former comprising very similar or identical site histories.

Site history category	**Frequency** abs.	 rel. [%]
Abandonment of agricultural land use	**108**	**53.5**
Abandonment of grasslands	56	27.7
Natural or human assisted afforestation of former grasslands	30	14.9
Conversion of grassland margins to (irregularly maintained) fringes	16	7.9
Abandonment of arable land use	6	3.0
Persistent agricultural land use	**36**	**17.9**
Persistently managed grasslands	26	12.9
Rotation of land use (arable ↔ grassland)	10	5.0
Persistent maintenance	**9**	**4.5**
(Irregularly) maintained margins and fringes	9	4.5
Removal of forest, woodland, scrubland	**19**	**9.4**
Recent deforestation (natural (windfall) or anthropogenic)	14	6.9
Recent clearing of scrubland	5	2.5
Mining / habitat destruction	**17**	**8.4**
Succession after abandonment of sand pits or rock quarries	14	6.9
Succession after habitat destruction	3	1.5
Persistent disuse	**22**	**6.5**
Disused terrestrial herbaceous sites	6	3.0
Disused riverbanks	5	2.5
Forest (margins)	2	1.0

Processes putting afforested sites and scrubland back to herbaceous stages were found at 9.4% of sites. These included felling of forest trees on supply line routes, windbreak (during a 1990 hurricane), removal of extensive scrub by land machinery, and removal of single bushes or trees along field margins and railway embankments.

Habitat destruction by opencast mining (rock quarry, sand pit) or other (unknown) means inducing subsequent secondary successions on bare soil occurred at 8.4% of sites. Termination of mining had, throughout, taken place after the 1970s, while other kinds of habitat destruction were found before the 1970s, between the 1970s and today, or in both time spans.

Constant habitats which were never subject to any kind of land management within the surveyed time period were observed at 6.5% of sites in the form of forests, quasi-natural herbaceous riverbanks or disused terrestrial herbaceous vegetation.

To summarize, by far the majority of sites had undergone considerable habitat alterations due to change or abandonment of land use, or severe disturbances (71.3%). Constantly managed or maintained sites (22.4%) and, on the other hand, long-term disused sites (6.5%) accounted for much lesser proportions.

5.5.1.3 Soil texture and water balance

Concerning soil texture, loamy soils prevailed (63%), followed by silty or loamy sands (19%), silty or loamy clay (14%) and loamy silt (4%). Pure sand was found only once at a riverbank site and pure clay soils did not occur. Estimates of available field capacity showed a median of 168 mm and the 10-90 percentile range was 140 to 220 mm which can be classified (from an agricultural perspective) as medium capacity for soil moisture (Table 3). Some sites showed signs of impeded drainage which was classified as ‘very modest’ or ‘modest’ in 19% and ‘medium’ in 2.5% of sites. Periods of wetness did not extend into the summer. On the whole, soils offered favourable conditions, were generally well aerated, at least during the growing season, and provided for a good water supply.

Table 3. Chemical characteristics and available field capacity of the effective root zone (AFC) of soils sampled from investigated plots (median, minimum, 10 and 90 percentile, maximum and evaluation of the medians where applicable). Nutrient content classes B, C and D refer to suboptimal, optimal, and more than optimal supply of the respective nutrients in arable fields.

Parameter	n	median	min.	10 perc.	90 perc.	max.	evaluation of median
P_{CAL} [mg/ 100g]	202	1.7	0.0	0.2	8.1	31.4	content class B
K_{CAL} [mg/ 100g]	202	8.3	0.8	4.2	21.6	77.8	content class C
N_t [% SDM]	202	0.3	0.0	0.2	0.4	1.0	n/a
Mg_{CACl2} [mg/ 100g]	202	14.3	3.0	7.0	27.0	50.1	content class (C-)D
C_{org} [% SDM]	192	2.8	0.4	1.6	5.2	9.0	medium humic
C/N ratio	192	9.8	6.4	8.2	16.3	28.3	narrow
pH_{H2O}	118	5.6	4.0	4.9	6.4	7.3	medium acidic
$AFC_{root\ zone}$ [mm]	118	168	30	140	220	275	medium

5.5.1.4 Chemical soil conditions

Median values of phosphorus, potassium and magnesium (Table 3) could be classified as fair or rich, according to the classification of nutrient contents of arable soils (classes B, C, (C-)D, respectively). Also total nitrogen content suggested good supply of this resource. Notwithstanding wide-ranging variance and occasional low values, measured soil nutrient concentrations indicated a generally high trophic level of investigated plots.

Total carbon content was exceedingly high in 10 samples altogether, which was due to a noticeable lime content in 9 samples and high content of organic carbon in one sample from an anthropogenically disturbed soil. These samples were left out when calculating statistics for carbon given in Table 3. In the remaining 192 samples total carbon content was equivalent to organic carbon (humus). The median value was 2.8% which indicates medium humic soils.

C/N ratios were markedly narrow with a median of 9.8 and values only exceptionally exceeding 20. These values make a reference to fast nutrient cycling and underpin a good nutrient balance of sites.

PH values varied widely and the limiting values of the 10-90 percentile range (4.9 - 6.4) corresponded to strongly acidic and moderately acidic soil reaction while the median of 5.6 could be classified as medium acidic. This shows that the species is quasi indifferent to soil reaction and can colonise, with respect to pH values, all soils except for extremely calcareous or acidic ones.

5.5.1.5 Light supply

Heracleum mantegazzianum was prevalently found at open sites whose light supply was classified as ‘full light’ (46%) or ‘light’ (32%) while ‘semi-shade’ (15%) and, in particular, ‘shade’ (7%) made up only minor proportions. The median value was in the class ‘light’. Results show a clear preference of the species for sites with high light supply although growth of the plant is still fair in semi-shaded situations. No occurrences, however, were found in dark shade of a closed tree canopy.

5.5.1.6 Ellenberg indicator values

Ellenberg indicator values are presented here (Table 4) to supplement the results of site parameters measured or estimated in the field. Mean light supply numbers underpinned the preference for open sites with a tolerance for moderate shading. Also moisture values which indicated water supply in the range of fresh to moist conditions were in good agreement with the field records. Average nutrient values suggested moderate to pronounced nutrient richness which again fitted the field data well.

The median of average soil reaction numbers was 6.5 which corresponded to near neutral pH values and, for comparison, plants assigned to the value 7 are not able to colonise strongly acidic soils. Only very few outliers were in a range that is indicative of soil reaction intermediate between moderately acidic and acidic conditions. Thus, Ellenberg values for soil reaction seemed to indicate slightly higher pH values than actually measured in the soil samples. Altogether, Ellenberg values corresponded well to measured and estimated parameters of abiotic site conditions.

Table 4. Unweighted mean Ellenberg indicator values of vegetation relevés from investigated plots (median, minimum, 10 and 90 percentile, maximum and evaluation of median). Evaluations of medians follow the definitions of the indicator scales in Ellenberg et al. (1992).

Indicator scale	n	median	min.	10 perc.	90 perc.	max.	evaluation of median
Light	202	6.6	4.8	5.6	7.0	7.4	semi-light (- semi-shade)
Moisture	202	6.0	4.8	5.2	6.8	7.5	fresh – moist
Reaction	202	6.5	4.1	5.6	7.0	7.7	circum-neutral – lightly acidic
Nutrients	202	6.4	4.0	5.3	7.5	8.3	moderately rich - rich

5.5.2 Plant communities invaded by H. mantegazzianum (Table 5)

5.5.2.1 Overview

Heracleum mantegazzianum occurred primarily in two main vegetation classes: (1) semi-natural grasslands (Molinio-Arrhenatheretea) and (2) nitrophilous tall-forb communities (Galio-Urticetea). Some occurrences were also found in alluvial woodlands (Alnenion glutinoso-incanae, Salicion elaeagni), pioneer tree stands, plantations and former orchards. In such tree-dominated communities *H. mantegazzianum* was, however, restricted to margins and gaps. Singular occurrences of *H. mantegazzianum* could be observed in herbaceous pioneer vegetation at strongly disturbed sites such as former quarries and a brownfield.

5.5.2.2 Grasslands (Molinio-Arrhenatheretea)

Within the class Molinio-Arrhenatheretea *H. mantegazzianum* was confined to eutrophic grassland communities with mesic water balance, i.e. freely-draining soils with favourable water supply, namely the alliances Arrhenatherion and Cynosurion (Table 5, 1.1 and 1.2). Only twice *H. mantegazzianum* was found in wet-grassland communities of the alliance Calthion.

The stands belonging to the alliances Arrhenatherion and Cynosurion share frequent records for the full range of Molinio-Arrhenatheretea and Arrhenatheretalia species. Cynosurion stands additionally show preferential occurrences of species characteristic of pastures and meadows with high mowing frequency, namely *Lolium perenne, Phleum pratense, Trifolium repens* and *Plantago major*, while the Arrhenatherion stands are characterised by consistent records of *Arrhenatherum elatius* and generally slightly higher frequencies and abundances of other tall grasses, such as *Alopecurus pratensis* and *Trisetum flavescens*.

Table 5. Constancy table of vegetation types with *Heracleum mantegazzianum* found in study areas. All relevés that could be assigned to specific syntaxa or at least compiled to a group of similar vegetation stands (anthropogenic floodplain forests) were included into the constancy table (n = 179) while singular relevés not assignable to a specific syntaxon were omitted and are referred to in the text only (n = 23). The symbols representing constancy classes follow common convention (cf. e.g. Dierschke 1994, p. 192). If the number of relevés in a column is less than five, absolute frequencies are presented (columns 2.2, 3.1, 3.2, 4). Companion species that never exceeded frequency class 'I' in any column and had no more than a single occurrence in a column with less than five relevés are left out. Differential species of associations and higher syntaxa are marked with 'D' while differential species of sub-communities are marked with 'd'. Differential species of the class Galio-Urticetea differentiate against Artemisietea s.str. and vice versa. Differential species listed under Calystegion or Alliarion each differentiate against the other alliances within Galio-Urticetea (cf. Dengler 1997).

1 Arrhenatheretalia
1.1 Cynosurion
1.2 Arrhenatherion
1.2.1 Managed Arrhenatherion meadows
1.2.2 Managed Arrhenatherion meadows, wet sub-com.
1.2.3 Ruderal Arrhenatherion grasslands
1.2.4 Ruderal Arrhenatherion grasslands, wet sub-com.

2 Galio-Urticetea
2.1 Galio-Urticetea basal communitiy
2.2 Galio-Alliarion
2.3 Aegopodion
2.3.1 Aegopodion, typical sub-communities
2.3.2 Aegopodion, Calystegia sub-communities
2.4 Calystegion, Aegopodium sub-communities

3 Alno-Ulmion
3.1 Stellario-Alnetum
3.2 Alnetum incanae
4 Salicion elaeagni
5 Anthropogenic floodplain forests

	1					2					3		4	5
	1.1	1.2				2.1	2.2	2.3		2.4	3.1	3.2		
		1.2.1	1.2.2	1.2.3	1.2.4			2.3.1	2.3.2					
Number of relevés	7	24	5	43	10	21	3	10	13	31	3	2	2	5
Average height of layers [m]														
Tree layer				13 $^{0-20}$	10 $^{0-10}$	16 $^{0-30}$	14 $^{10-18}$	19 $^{0-20}$	12 $^{0-18}$	15 $^{0-20}$	19 $^{17-20}$	9 $^{8-10}$	14 $^{12-15}$	17 $^{12-20}$
Shrub layer				5 $^{0-5}$	3.3 $^{0-5}$	2 $^{0-2.3}$	2.8 $^{0-3}$	0.8 $^{0-0.8}$	7 $^{0-7}$	1.8 $^{0-2.2}$		1.5 $^{0-1.5}$	4.3 $^{2.6-6}$	2.5 $^{0-2.5}$
Field layer	0.2 $^{0.15-0.3}$	0.4 $^{0.2-0.8}$	0.5 $^{0.4-0.7}$	0.6 $^{0.1-1.2}$	0.6 $^{0.3-1}$	0.6 $^{0.1-1.4}$	0.4 $^{0.3-0.5}$	0.5 $^{0.2-1.1}$	0.7 $^{0.3-1.2}$	0.8 $^{0.3-1.7}$	0.4 $^{0.35-0.4}$	0.8 $^{0.8-0.8}$	0.8 $^{0.4-1.2}$	0.6 $^{0.3-1.1}$
Heracleum mantegazzianum	0.4 $^{0.25-0.6}$	0.6 $^{0.3-1}$	0.8 $^{0.6-1.1}$	0.9 $^{0.35-1.7}$	1.0 $^{0.8-1.7}$	1.4 $^{0.6-2.4}$	1.2 $^{1-1.3}$	1.2 $^{0.4-1.8}$	1.2 $^{0.8-1.8}$	1.0 $^{0.4-1.7}$	1.0 $^{0.8-1.1}$	1.1 $^{0.8-1.3}$	1.3 $^{1.3-1.3}$	0.9 $^{0.6-1.1}$
Average cover of layers [%]														
Total	93 $^{80-98}$	93 $^{60-100}$	97 $^{90-100}$	94 $^{80-100}$	89 $^{50-98}$	90 $^{45-95}$	90 $^{90-90}$	82 $^{15-100}$	89 $^{70-98}$	88 $^{45-98}$	87 $^{80-90}$	75 $^{60-90}$	75 $^{65-85}$	86 $^{80-90}$
Tree layer				42 $^{0-90}$	38 $^{0-50}$	33 $^{0-50}$	52 $^{30-65}$	20 $^{0-30}$	22 $^{0-45}$	33 $^{0-60}$	80 $^{70-85}$	28 $^{15-40}$	48 $^{30-65}$	73 $^{60-80}$
Shrub layer				5 $^{0-5}$	3 $^{0-5}$	5 $^{0-5}$	3.5 $^{0-5}$	2 $^{0-2}$	80 $^{0-80}$	1.5 $^{0-2}$		5 $^{0-5}$	5.5 $^{1-10}$	3 $^{0-3}$
Field layer	88 $^{80-95}$	88 $^{60-99}$	93 $^{85-95}$	72 $^{20-95}$	79 $^{30-95}$	35 $^{1-90}$	45 $^{20-65}$	38 $^{5-98}$	58 $^{20-80}$	66 $^{20-95}$	30 $^{25-40}$	48 $^{15-80}$	25 $^{25-25}$	44 $^{25-80}$
Heracleum mantegazzianum	15 $^{2-60}$	17 $^{1-70}$	15 $^{10-20}$	46 $^{5-90}$	35 $^{10-80}$	67 $^{5-95}$	57 $^{10-80}$	52 $^{5-95}$	47 $^{10-85}$	34 $^{5-90}$	13 $^{5-20}$	15 $^{10-20}$	40 $^{35-45}$	16 $^{5-30}$
Litter	5 $^{1-10}$	19 $^{0-60}$	15 $^{1-60}$	19 $^{0-70}$	11 $^{1-20}$	18 $^{5-60}$	9 $^{2-15}$	23 $^{5-60}$	24 $^{1-60}$	23 $^{5-60}$	52 $^{35-60}$	5 $^{5-5}$	23 $^{20-25}$	26 $^{1-60}$
Mosses	1 $^{0-2}$	2 $^{0-10}$	2 $^{0-5}$	12 $^{0-45}$	18 $^{0-75}$	15 $^{0-70}$	30 $^{5-50}$	14 $^{2-60}$	10 $^{0-60}$	8 $^{0-60}$	1 $^{1-2}$	3 $^{1-5}$	15 $^{5-25}$	12 $^{5-30}$
Soil	15 $^{2-60}$	12 $^{0-50}$	3 $^{0-10}$	18 $^{0-60}$	5 $^{0-20}$	47 $^{0-90}$	33 $^{20-50}$	42 $^{1-85}$	32 $^{0-70}$	41 $^{0-95}$	27 $^{20-30}$	50 $^{20-80}$	43 $^{25-60}$	28 $^{0-80}$
Average species number	32 $^{15-46}$	22 $^{8-35}$	27 $^{21-32}$	20 $^{6-47}$	29 $^{17-40}$	11 $^{4-23}$	22 $^{22-23}$	11 $^{6-17}$	19 $^{12-29}$	15 $^{4-26}$	14 $^{11-18}$	23 $^{16-30}$	19 $^{12-26}$	17 $^{11-22}$
Heracleum mantegazzianum	V $^{+-4}$	V $^{+-4}$	V $^{a-b}$	V $^{a-5}$	V $^{a-5}$	V $^{a-5}$	3 $^{a-5}$	V $^{a-5}$	V $^{a-5}$	V $^{a-5}$	3 $^{a-b}$	2 $^{a-b}$	2 ^{3}	V $^{a-3}$
Cynosurion														
Phleum pratense	**V** $^{1-a}$	IV $^{+-b}$	I ^{a}	II $^{1-b}$	I ^{1}	+ $^{1-a}$	.	.	+ ^{1}	.	.	1 ^{1}	.	.
Trifolium repens	**V** $^{1-a}$	II $^{1-a}$	.	I $^{+-m}$	+ ^{m}	.	.	.	.	.	.	.	.	.
Lolium perenne	**V** $^{1-b}$	II $^{1-b}$	.	r ^{1}	.	r ^{1}	.	.	.	.	.	.	.	.
D Plantago major major	**V** $^{+-1}$	.	.	r $^{+}$	.	.	.	.	.	.	.	.	.	.
Arrhenatherion														
Arrhenatherum elatius	.	**IV** $^{1-4}$	**III** ^{a}	**IV** $^{1-4}$	**IV** $^{1-a}$	I $^{1-a}$	.	II $^{1-m}$	II ^{1}	II $^{1-a}$	.	.	.	.
Galium mollugo agg.	III $^{+-1}$	**IV** $^{+-1}$	**IV** $^{1-m}$	**III** $^{+-a}$	**III** $^{+-a}$	.	.	I $^{1-a}$	I ^{1}	+ ^{1}	.	1 $^{+}$	.	.
d Angelica sylvestris	.	r $^{+}$	**V** $^{+-a}$	+ $^{r-+}$	**IV** $^{+-1}$	.	.	.	.	+ $^{r-+}$	.	.	.	.
d Cirsium palustre	.	r $^{+}$	**IV** $^{+-1}$	r $^{r-+}$	**V** $^{r-+}$	I $^{r-+}$	.	.	+ $^{+}$	.	.	.	.	.
d Lotus pedunculatus	I ^{1}	.	**III** $^{+-m}$	.	**III** $^{1-m}$	.	.	.	.	.	.	.	.	.
Arrhenatheretalia														
Dactylis glomerata	V $^{1-b}$	V $^{1-3}$	IV $^{+-b}$	V $^{1-3}$	IV $^{1-3}$	III $^{+-b}$	1 ^{1}	I ^{1}	IV $^{+-a}$	I $^{1-a}$	1 $^{+}$	.	1 ^{r}	IV $^{+-m}$
D Anthriscus sylvestris sylvestris	III $^{+-1}$	IV $^{+-1}$	.	III $^{r-a}$	+ ^{r}	r ^{a}	.	+ ^{1}	II $^{r-+}$	I $^{r-a}$	.	.	.	I ^{r}
D Veronica chamaedrys s.l.	.	II $^{+-m}$	I ^{a}	II $^{+-m}$	III $^{+-m}$	.	.	.	+ ^{m}	.	.	.	.	I ^{m}
D Heracleum sphondylium	I ^{1}	III $^{r-a}$	.	II $^{r-1}$	.	r ^{r}	.	+ ^{1}	+ ^{r}	.	.	.	.	.
Trisetum flavescens flavescens	.	II $^{1-a}$	.	I $^{+-m}$	+ ^{1}	r ^{1}	.	.	+ ^{1}	.	.	.	.	.
Leucanthemum vulgare	I ^{1}	I $^{1-m}$	.	+ $^{+-1}$	III $^{+-1}$	.	.	.	.	.	.	.	.	.
Crepis biennis	II $^{+}$	I $^{+}$	.	r $^{+}$	.	.	.	.	.	.	.	.	.	.
Mol.-Arrhenatheretea														
Holcus lanatus	IV $^{1-b}$	IV $^{1-4}$	V $^{1-b}$	IV $^{+-3}$	V $^{1-b}$	I $^{1-a}$	.	.	I $^{1-b}$	+ $^{+-a}$	.	.	.	.
Ranunculus repens	V $^{1-b}$	IV $^{+-a}$	IV ^{1}	III $^{r-a}$	IV $^{1-a}$	II $^{+-1}$	2 ^{1}	.	II $^{+-m}$	+ $^{+-1}$	1 $^{+}$	1 $^{+}$	.	I ^{1}
Alopecurus pratensis	IV $^{1-a}$	V $^{1-4}$	IV $^{a-3}$	III $^{1-3}$	II $^{a-4}$	r ^{a}	.	I $^{1-b}$	III $^{1-a}$	II $^{1-m}$	.	.	.	.
Festuca rubra agg.	I ^{a}	II $^{1-b}$	IV ^{m}	II $^{1-3}$	IV $^{1-a}$	r ^{m}	.	+ ^{1}	.	.	.	.	.	.
Rumex acetosa	I $^{+}$	III $^{+-m}$	II ^{1}	II $^{r-1}$	III $^{r-1}$	.	.	.	+ ^{r}	r ^{r}	.	.	.	.
Agrostis stolonifera	III $^{a-b}$	II $^{1-3}$	I ^{3}	I $^{1-a}$	II $^{1-3}$	r ^{a}	.	+ ^{m}	I ^{1}	+ ^{1}	.	2 $^{a-b}$	1 ^{1}	.
Lathyrus pratensis	III $^{+-1}$	II $^{+-1}$	II ^{1}	II $^{+-a}$	+ $^{+}$	r $^{+}$	.	+ $^{+}$	+ $^{+}$	+ $^{+-1}$	.	.	.	.
Achillea millefolium agg.	III $^{1-m}$	II $^{+-b}$	I ^{1}	I $^{+-1}$	I $^{+-m}$	r ^{1}	.	+ ^{r}	.	.	.	.	.	.
Poa pratensis s.str.	III $^{+-a}$	II $^{+-a}$	.	I $^{1-a}$	III ^{1}	r ^{1}	.	.	+ ^{1}	.	.	.	.	.
Bistorta officinalis	V $^{+-1}$	I $^{+-m}$	IV $^{1-a}$	r ^{1}	I ^{1}	.	.	+ ^{1}	.	+ $^{+}$	.	.	.	.
Festuca pratensis	III $^{1-b}$	III $^{+-b}$	II $^{1-m}$	r ^{1}	I $^{1-a}$	.	.	.	.	.	.	.	.	.
Cardamine pratensis pratensis	I ^{r}	II $^{+-1}$	III $^{+-1}$	r $^{+-1}$	I ^{1}	.	.	.	+ $^{+}$	+ $^{+}$	.	.	.	.
Vicia cracca	I ^{1}	+ $^{+-1}$	II $^{+-m}$	I $^{1-a}$	II $^{+-1}$	.	.	.	+ $^{+}$	r ^{1}	.	.	.	.
Plantago lanceolata	I ^{1}	III $^{+-m}$	.	+ $^{+}$	I $^{+}$	r ^{r}	.	.	.	.	.	.	.	.
Cerastium holosteoides	III $^{+-1}$	II $^{+-m}$	.	I $^{+-1}$	.	.	.	.	.	.	.	.	.	.
Ajuga reptans	.	r $^{+}$	I $^{+}$	r ^{1}	III $^{+-1}$	r ^{1}	.	.	.	r $^{+}$	.	.	.	.
Trifolium pratense	I ^{1}	II $^{+-a}$	I $^{+}$	+ $^{+-1}$	.	.	.	.	.	.	.	.	.	.
Prunella vulgaris	III $^{1-m}$	r $^{+}$	.	.	III $^{r-1}$	r ^{r}	.	.	.	.	.	.	.	.
Sanguisorba officinalis	II ^{1}	+ $^{+-1}$	III $^{+-1}$	.	+ ^{1}	.	.	.	.	.	.	.	.	.
Centaurea jacea	III $^{+-1}$	+ $^{+-1}$	II $^{1-m}$	r $^{r-+}$	.	.	.	.	.	.	.	.	.	.
Ranunculus acris agg.	III $^{+}$	+ $^{+-1}$	I ^{1}	r ^{1}	+ ^{1}	.	.	.	.	.	.	.	.	.
Bellis perennis	III $^{+-1}$	r $^{+}$	.	.	.	.	.	.	.	.	.	.	.	.
Colchicum autumnale	.	.	I $^{+}$	.	.	.	.	.	.	.	.	.	.	.

(Table 5 continued)

Galio-Urticetea															
D	Poa trivialis	V$^{1-3}$	IV^{1-b}	IV^{m-a}	IV^{+-4}	III^{1-b}	III$^{1-4}$	3^{+-1}	IV$^{1-4}$	IV$^{1-3}$	IV$^{1-3}$	3^{1}	2^{m}	1^{1}	III^{a-b}
	Urtica dioica dioica	III^{+-1}	II^{+-a}	.	**IV**$^{1-3}$	**II**^{1}	V^{+-5}	3^{m-b}	V^{+-3}	V$^{1-3}$	V$^{1-5}$	3^{1}	2^{+}	2^{1-b}	V^{1-a}
D	Galium aparine	.	I^{+}	.	**IV**$^{+-a}$	**II**$^{+-1}$	III^{+-a}	3^{1}	IV^{+-a}	IV^{+-a}	V^{+-a}	1^{+}	.	2^{+}	IV^{1}
D	Galeopsis tetrahit	.	r^{+}	.	**II**$^{r-1}$	**III**$^{+-1}$	I^{r-1}	.	II^{r-1}	.	II^{+-1}	.	.	2^{r-+}	I^{1}
	Glechoma hederacea	III^{+-1}	II^{+-m}	.	**II**$^{1-m}$	**+**$^{+}$	I^{1-m}	2$^{1-3}$	III^{1-b}	IV^{+-a}	II^{+-a}	.	.	1^{1}	IV^{1-a}
	Geum urbanum	II^{+}	.	.	**II**$^{+-m}$	**.**	I^{+-1}	2^{+-1}	I^{+-1}	III^{+-1}	+^{1}	.	.	1^{r}	IV^{+-a}
	Rumex obtusifolius	III^{+}	II^{r-1}	.	**I**$^{r-+}$	**+**$^{+}$	+$^{+}$	1^{1}	.	+$^{+}$	+$^{r-1}$	.	1^{r}	1^{r}	.
	Chelidonium majus	.	.	.	.	.	.	.	.	+$^{+}$	.	.	.	.	.
Artemisietea s. l.															
	Solidago gigantea	.	.	.	+$^{+-1}$	.	I^{+-1}	2^{+}	.	+$^{+}$	I$^{1-4}$	.	.	.	I^{1}
	Artemisia vulgaris	I^{1}	.	.	r^{+}	+$^{+}$	.	.	.	+^{r}	+$^{r-+}$	.	.	.	.
	Arctium minus	III^{+-a}	.	.	r^{+}	.	.	.	.	.	r^{+}	.	.	.	.
Artemisietea s.str.															
	Elymus repens	III^{1-a}	IV^{+-3}	III$^{1-3}$	III^{+-4}	I^{1-a}	I^{1-a}	.	.	II^{1-m}	I^{+-a}	.	.	.	.
	Tanacetum vulgare	II^{+}	r^{a}	.	I^{r-a}	.	.	.	+$^{+}$	.	+^{r}	.	.	.	.
D	Agrimonia eupatoria	.	.	I^{1}	I^{+}	+^{1}	r^{r}	.	.	.	.	.	.	.	I^{r}
D	Cirsium vulgare	.	.	.	.	I^{r-+}	.	.	.	.	+$^{+}$	.	.	.	.
D	Convolvulus arvensis	.	r^{1}	.	+$^{r-1}$	.	r^{r}	.	.	.	.	.	.	.	.
	Pastinaca sativa	.	r^{+}	.	r^{+}	.	.	.	.	.	.	.	.	.	.
	Linaria vulgaris	.	r^{r}	.	.	.	.	.	.	.	.	.	.	.	.
	Melilotus albus	.	.	.	r^{r}	.	.	.	.	.	.	.	.	.	.
	Melilotus officinalis	.	.	.	.	+$^{+}$	.	.	.	.	.	.	.	.	.
	Picris hieracioides s.l.	.	r^{+}	.	.	.	.	.	.	.	.	.	.	.	.
Alliarion															
	Alliaria petiolata	.	.	.	.	.	r^{1}	**3**$^{1-a}$	II^{+-1}	II^{+-1}	II^{r-m}	1^{1}	.	.	I^{1}
D	Stachys sylvatica	.	r^{+}	.	II^{+-1}	.	r^{+}	**2**$^{r-1}$	+^{1}	I^{+}	+$^{r-1}$	1^{+}	.	.	I^{+}
	Geranium robertianum	I^{r}	.	.	.	.	+$^{+-1}$	**2**$^{+-1}$	.	.	r^{1}	.	1^{+}	1^{1}	II^{+-1}
D	Moehringia trinervia	.	.	.	r^{+}	.	I^{+-1}	**1**^{1}	+^{1}	I^{+-1}	r^{1}	.	.	.	II^{1-m}
D	Poa nemoralis	.	.	.	+$^{+-1}$	.	+^{1}	**1**^{a}	.	+^{a}	I^{1-m}	1^{1}	.	1^{1}	III^{1-a}
D	Brachypodium sylvaticum	.	.	.	.	.	.	**1**^{1}	.	+^{1}	.	.	1^{1}	.	.
D	Scrophularia nodosa	.	.	.	.	.	.	**1**^{1}	.	.	r^{r}	.	.	.	.
D	Epilobium montanum	.	r^{+}	.	.	I^{+-1}	I^{+-1}	.	.	+^{1}	.	.	.	.	.
	Chaerophyllum temulum	.	r^{1}	.	+$^{+-1}$	.	.	.	+^{1}	+$^{+}$	.	.	.	.	.
D	Lapsana communis	.	r^{1}	.	r^{+-1}	.	r^{r}	.	.	.	r^{+}	.	.	.	.
D	Lamiastrum galeobdolon	.	.	.	.	.	r^{b}	.	.	.	+$^{+-1}$	.	.	.	.
Aegopodion															
	Aegopodium podagraria	III^{a}	II^{+-a}	II^{a}	II^{+-a}	.	.	1^{3}	**V**$^{+-3}$	**IV**$^{1-4}$	**IV**$^{+-b}$	3^{a-3}	.	1^{1}	III$^{1-3}$
	Petasites hybridus	II^{+-a}	+$^{+-1}$	.	+$^{+-a}$	.	.	.	**I**$^{+-5}$	**II**$^{1-3}$	**I**$^{+-a}$	.	.	.	.
	Lamium maculatum	.	.	.	r^{1}	.	.	.	**+**^{1}	**II**$^{+-1}$	**+**^{1}	.	.	.	.
	Silene dioica	.	.	.	.	.	.	.	.	**II**$^{+-1}$	**+**$^{+-1}$	1^{+}	.	.	.
	Lamium album	.	r^{1}	.	r^{+}	.	.	1^{1}	.	**I**$^{+}$	**I**$^{+-1}$	.	.	.	.
	Cruciata laevipes	.	r^{1}	.	.	.	.	.	.	**I**^{1}	.	.	.	.	.
	Chaerophyllum bulbosum	.	.	.	r^{+}	.	.	.	.	**+**^{r}	.	.	.	.	.
	Chaerophyllum aureum	.	I^{+-1}	.	r^{+}	.	.	.	.	**.**	.	.	.	.	.
Calystegion															
	Impatiens glandulifera	I^{+}	.	.	r^{r}	.	I^{1-b}	3^{+-1}	.	**II**$^{+-a}$	**IV**$^{r-3}$	2^{+-1}	1^{1}	2^{+-a}	I^{1}
D	Symphytum officinale	I^{1}	I^{r-+}	.	r^{3}	.	r^{a}	3^{+-a}	+$^{+}$	**III**$^{+-b}$	**III**$^{r-4}$	.	.	.	III^{1-a}
	Calystegia sepium	I^{1}	r^{+}	.	I^{+-1}	+^{1}	I^{+-1}	.	.	**II**$^{+-3}$	**III**$^{+-a}$	1^{+}	.	.	.
	Carduus crispus	.	.	.	r^{r-+}	.	.	1^{r}	+$^{+}$	**I**$^{r-1}$	**II**$^{+-1}$	.	.	.	.
	Humulus lupulus	.	.	.	r^{+}	.	.	1^{+}	.	**+**$^{+}$	**II**$^{+-a}$	.	.	.	.
D	Filipendula ulmaria	III^{1}	+$^{+-1}$	III^{+-1}	II^{+-1}	+$^{+}$	r^{a}	.	+$^{+}$	**II**$^{+-1}$	**I**$^{+-b}$	.	.	.	.
D	Phalaris arundinacea	.	.	I^{b}	I^{+-1}	.	.	.	.	**I**^{1}	**I**$^{+-a}$	2^{+-1}	2^{1-a}	.	I^{+}
D	Cirsium oleraceum	I^{+}	I^{r-+}	.	+$^{+-1}$	.	+$^{r-1}$	.	.	**I**$^{r-+}$	**I**$^{+-a}$	.	.	.	.
D	Stachys palustris	I^{1}	.	I^{1}	r^{1}	.	.	.	.	**II**$^{+-1}$	**r**^{1}	.	.	.	.
D	Lythrum salicaria	III^{+}	.	.	r^{r}	.	.	.	.	**.**	**+**$^{r-1}$	.	.	.	.
D	Eupatorium cannabinum	.	.	.	+$^{+-1}$	.	.	.	.	**.**	**+**$^{+-1}$	.	.	.	.
D	Poa palustris	.	.	.	r^{1}	.	.	.	.	**+**^{1}	**+**^{1}	1^{+}	.	.	.
	Cuscuta europaea	.	.	.	.	.	.	.	.	**.**	**+**$^{+-m}$	.	.	.	.
D	Rubus caesius	.	.	.	.	.	.	.	.	**+**$^{+}$	**r**$^{+}$	.	.	.	I^{+}
	Myosoton aquaticum	.	.	.	.	.	.	.	.	**.**	**r**^{1}	.	.	.	.
	Epilobium hirsutum	.	.	.	r^{r}	.	.	.	.	**.**	**.**	.	.	.	.
D	Mentha longifolia	.	.	.	+^{1}	.	.	.	.	**+**$^{+}$	**.**	.	1^{+}	.	.
Stellario-Alnetum															
D	Stellaria nemorum	II^{+-1}	.	.	r^{1}	.	.	.	I^{a}	IV^{1-a}	III^{+-3}	**3**$^{+-a}$	.	.	I^{a}
D	Alnus glutinosa	.	.	.	.	.	.	2$^{3-4}$	+^{3}	+^{3}	.	**3**$^{4-5}$	.	.	I^{4}
D	Salix fragilis	.	.	.	.	.	.	.	+^{a}	+^{a}	I^{a-4}	**1**^{a}	1^{a}	.	.
Alnetum incanae															
	Alnus incana	.	.	.	.	.	.	.	.	.	.	.	**2**^{a}	.	.
Alno-Ulmion - Fagetalia															
	Elymus caninus	.	.	.	r^{1-a}	.	.	.	.	I^{+-1}	I^{+-a}	**2**^{1}	.	.	.
	Festuca gigantea	II^{1}	.	.	.	.	.	.	.	I^{+}	I^{+-1}	**2**^{1}	1^{+}	.	.
	Stellaria holostea	.	.	I^{1}	I^{+-1}	+^{1}	+$^{1-m}$	.	.	I^{+-1}	r^{1}	**1**^{a}	.	.	II^{m}
	Circaea lutetiana	.	.	.	.	.	r^{1}	.	.	.	.	**1**^{1}	.	.	.
	Impatiens noli-tangere	.	.	.	.	.	.	.	.	+^{r}	.	**1**^{1}	.	.	.
	Arum maculatum	.	.	.	.	.	.	.	.	.	.	**1**$^{+}$	.	.	.
	Rumex sanguineus	I^{+}	.	.	r^{r-1}	+$^{+}$	r^{+}	.	+$^{+}$	+^{1}	.	**.**	1^{+}	.	.
Salicion elaeagni															
	Salix eleagnos	.	.	.	.	.	r^{b}	.	.	.	.	.	.	**2**$^{3-4}$	.
Anthropogenic floodplain forests															
	Fraxinus excelsior	.	+$^{+}$	.	+$^{+-a}$	.	I^{+}	1^{+}	+$^{+}$	.	+$^{r-+}$	.	.	1^{+}	III^{+-4}
	Acer pseudoplatanus	.	r^{r}	.	.	.	+$^{r-+}$	2^{1-a}	.	.	r^{a}	.	1^{+}	.	IV^{+-5}
	Populus nigra	.	.	.	.	.	.	.	.	.	.	.	.	.	II^{b-4}
	Salix alba	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{4}

(Table 5 continued)

Companions														
Cirsium arvense	V^{+-a}	IV^{r-1}	V^{+-1}	II^{+-a}	III^{+-b}	+$^{r-a}$	.	+^{1}	.	I^{+-a}	.	.	.	.
Taraxacum officinale agg.	V^{+-b}	IV^{+-a}	.	II^{+-1}	I^{+-1}	I^{r-+}	1^{+}	.	+$^{+}$	.	.	1^{+}	.	.
Rubus fruticosus agg.	.	.	.	II^{+-a}	+$^{+}$	II^{r-b}	2^{+-1}	.	II^{+}	+^{1}	1^{+}	1^{a}	.	I^{+}
Deschampsia cespitosa	I^{+}	+$^{+-1}$	III^{a-b}	+$^{+-1}$	III^{+-a}	+$^{+-1}$	1^{+}	I^{+-1}	+$^{+}$	r^{+}	.	2^{1-a}	1^{1}	II^{+-b}
Vicia sepium	III^{+}	r^{+}	I^{1}	II^{+-m}	I^{1}	r^{+}	.	.	+$^{+}$	r^{+}	.	.	.	.
Hypericum perforatum	.	II^{+-a}	I^{1}	II^{1}	III^{+-1}	.	.	+$^{+}$	.	r^{1}	.	.	.	.
Agrostis capillaris	III$^{1-3}$	II^{1-b}	I^{1}	r^{1-a}	I^{a-b}	I^{1-b}	.	+^{1}	+^{1}	r^{m}	.	.	.	.
Rubus idaeus	.	r^{1}	.	I^{+-a}	II^{+-a}	I^{+-b}	1^{+}	+^{1}	+^{r}	+$^{+-b}$	.	.	.	.
Epilobium sp.	.	r^{+}	.	+$^{r-1}$	III^{+-1}	+$^{r-+}$	.	+$^{+}$	+$^{+}$	r^{+}	.	1^{1}	1^{1}	.
Stellaria graminea	III^{+-m}	II^{+-m}	I^{+}	+$^{+-a}$	III^{+-1}	.	.	.	.	.	.	.	.	.
Bromus hordeaceus agg.	III^{+-m}	II^{+-1}	.	I^{+-1}	.	r^{1}	.	.	.	.	.	.	.	.
Myosotis nemorosa	II^{+}	r^{+}	IV^{+-1}	.	II^{+}	.	.	.	.	.	.	2^{1}	1^{1}	.
Alchemilla sp.	II^{+}	II^{+-1}	.	r^{+}	+$^{+}$	.	.	.	.	r^{+}	.	.	.	.
Senecio fuchsii	.	.	.	r^{r-+}	II^{+-1}	+^{1}	1^{+}	.	+$^{+}$	+$^{+-1}$	.	.	.	.
Holcus mollis	I^{a}	r^{b}	II^{1-b}	r^{b}	III^{1-b}	r^{1}	.	.	.	.	.	.	.	.
Vicia hirsuta	.	II^{+-1}	.	I^{+-1}	.	.	.	.	.	.	.	.	.	.
Sambucus nigra	.	.	.	.	.	r^{r}	3^{r-+}	.	+$^{+}$	+^{r}	.	.	2^{r-a}	.
Anthoxanthum odoratum	.	II^{1-a}	II^{+-1}	.	+^{1}	.	.	.	.	.	.	.	.	.
Cardamine flexuosa	.	.	.	.	.	r^{1}	1^{1}	.	II^{1-a}	.	.	1^{1}	1^{a}	I^{a}
Stellaria media agg.	III^{+-1}	.	.	r^{1}	.	.	.	.	+^{1}	+^{1}	.	.	.	.
Veronica hederifolia	.	.	.	r^{1}	.	.	1^{+}	.	.	I^{+-a}	.	.	.	II^{+-1}
Chaerophyllum hirsutum hirsutum	.	.	.	+$^{+-a}$	.	.	.	.	+^{a}	r^{1}	.	.	2^{r-+}	.
Geranium sylvaticum	.	r^{1}	IV^{1}	.	+$^{+}$	.	.	.	.	.	.	.	.	.
Valeriana officinalis agg.	.	.	II^{1}	+$^{r-+}$	.	.	.	.	.	.	.	.	.	I^{1}
Achillea ptarmica	II^{1}	.	II^{1-m}	.	.	.	.	.	.	.	.	.	.	.
Caltha palustris	.	.	III^{+-a}	.	.	.	.	.	.	r^{+}	.	.	.	.
Epilobium angustifolium	.	.	.	.	II^{r-a}	r^{+}	.	.	.	.	.	.	.	.
Epilobium palustre	.	.	II^{+-1}	.	+^{1}	.	.	.	+^{1}	.	.	.	.	.
Juncus inflexus	.	.	III^{1-m}	.	+^{1}	.	.	.	.	.	.	.	.	.
Mentha arvensis	II^{1}	.	I^{1}	.	+$^{+}$	.	.	.	.	.	.	.	.	.
Potentilla erecta	.	.	I^{1}	.	II^{1}	.	.	.	.	.	.	.	.	.
Trifolium medium	.	r^{1}	.	.	II^{1-m}	.	.	.	.	.	.	.	.	.
Senecio alpinus	.	.	.	.	.	r^{r}	.	.	.	.	.	2^{+-1}	.	.
Tussilago farfara	.	.	.	.	+^{r}	.	.	.	.	.	.	2^{+-a}	.	.
Veronica beccabunga	.	.	.	.	.	.	.	.	.	.	.	2^{1}	.	.

Cynosurion-grasslands colonised by *H. mantegazzianum* were found in horse paddocks and mown pastures representing the typical sub-community of the Cynosuro-Lolietum Br.-Bl. et De Leeuw 1936. Species typical of poor or dry subtypes (e.g. C.-L. luzuletosum, C.-L. ranunculetosum bulbosi; cf. Dierschke 1997), such as *Luzula campestris* agg., *Hieracium pilosella*, *Viola canina* or *Ranunculus bulbosus*, were completely absent whereas differential species of moist sub-communities (C.-L. lotetosum uliginosi), such as *Lotus pedunculatus* (syn. *Lotus uliginosus*), *Achillea ptarmica* and *Carex hirta* occurred at least in some of the relevés in moderate quantity. Notably, tall forbs characteristic of the alliance Filipendulion (*Filipendula ulmaria*, *Lythrum salicaria*) and of nitrophilous herb communities of the class Galio-Urticetea (*Urtica dioica*, *Aegopodium podagraria*), had fairly high constancies indicating low land-use intensity.

The observed Arrhenatherion communities comprised (managed) meadows (Table 5, 1.2.1 and 1.2.2) and ruderal grasslands (1.2.3 and 1.2.4). Meadows with *H. mantegazzianum* mostly belonged to the Arrhenatheretum elatioris Koch 1926 although some stands were missing the characteristic species *Arrhenatherum elatius* and *Galium mollugo* agg. Most of the stands were used for haymaking, however, some meadow-like stands without agricultural land use were included too. These were road verges and green areas apparently subject to regular maintenance mowing and also former agricultural meadows, which have been abandoned only recently prior to sampling. The meadows and meadow-like stands could predominantly be allocated to the typical sub-community group of the Arrhenatheretum elatioris (Table 5, 1.2.1) which is characterised by the lack of differential species (Dierschke 1997). Some relevés contained species indicating fairly moist conditions, such as *Angelica sylvestris*, *Cirsium palustre* and *Lotus pedunculatus*, and therefore belonged to the sub-community group of *Silene* (= *Lychnis*) *flos-cuculi* (Table 5, 1.2.2) which is transitional to Molinietalia wet grasslands. As with Cynosurion stands, species indicative of nutrient poor or dry subtypes (sub-community group of *Briza media*, cf. Dierschke 1997) could not be found.

The ruderal grasslands (Table 5, 1.2.3 and 1.2.4) comprised abandoned or neglected stands of agricultural origin and rather irregularly managed swards on road verges, field margins, embankments and ditches. They could be distinguished from the meadows by species characteristic of Artemisietea and, especially, Galio-Urticetea communities supplementing the stock of common grassland plants and sometimes reaching fairly high abundances. On the other hand, ruderal grasslands are, by definition, distinct from tall-forb communities in the preponderance of grassland monocots and herbs (Fischer 1985). The most constant and typical ruderal species of the ruderal grasslands with *H. mantegazzianum* were *Urtica dioica*, *Galium aparine* and *Galeopsis tetrahit*. Additional ruderal species of fresh to moist tall-forb communities (Alliarion, Aegopodion, Calystegion) as well as other species with low mowing and grazing compatibility, such as *Lupinus polyphyllos*, *Senecio fuchsii*, *Epilobium angustifolium*, *Rubus* sp., and *Rosa* sp.) had rather scattered and infrequent occurrences.

Due to constant occurrences of *Arrhenatherum elatius* and *Galium mollugo* agg. it was possible to integrate the ruderal grasslands colonised by *H. mantegazzianum* into the alliance Arrhenatherion, yet a more detailed assignment to associations or rankless communities known from literature was not feasible. Vegetation types described as, e.g., Artemisia-Arrhenatherum community (Bornkamm 1974; Dierschke 1997) or Tanaceto-Arrhenatheretum (Fischer 1985) typically contain species characteristic of Artemisietea communities, the most frequent being *Artemisia vulgaris* and *Tanacetum vulgare* among others. As Fischer (1985) points out, the Tanaceto-Arrhenatheretum (Artemisia-Arrhenatherum-community) is transitional between Arrhenatheretum and Tanaceto-Artemisietum Sissingh 1950 of the alliance Dauco-Melilotion, which belongs to the drought-resistant and thermophilic branch (Onopordetalia) of the Artemisietea s.l. In contrast, the ruderal grasslands colonised by *H. mantegazzianum* contained several species of the Galio-Urticetea but rarely Artemisietea species. Consequently they are transitional to Glechometalia or Calystegietalia, which represent tall-forb communities of permanently fresh or moist sites.

By analogy with the meadows, the ruderal grasslands colonised by *H. mantegazzianum* could be split up into fresh (Table 5, 1.2.3) and moist sub-communities (1.2.4).

In two relevés from abandoned grassland sites that could vaguely be connected with Calthion wet grassland communities *H. mantegazzianum* co-occurred with wetland species such as *Angelica sylvestris*, *Cirsium palustre*, *Lotus pedunculatus*, *Juncus effusus*, *Galium palustre, Juncus inflexus*, *Silene flos-cuculi* and *Juncus articulatus*. As these relevés did not exactly match Calthion communities but differed considerably from the Arrhenatheretalia communities they were grouped as ‘other’ vegetation types in the gradient analysis (ch. 4.3) and not included into the frequency table.

5.5.2.3 Nitrophilous tall-forb communities (Galio-Urticetea)

Relevés of tall-forb communities with *H. mantegazzianum* showed consistent records of species characteristic or typical of the class Galio-Urticetea of which the most constant and abundant were *Urtica dioica*, *Poa trivialis* and *Galium aparine* (Table 5, 2). On the basis of presence-absence and proportions of diagnostic species groups the stands could mostly be assigned to the alliances Aegopodion, Calystegion and, subordinately, Alliarion, but some stands almost completely lacking character species of syntaxa below the class level had to be classified as a basal community of the class. Altogether, five types of tall-forb communities with *H. mantegazzianum* were distinguished: (1) Galio-Urticetea basal community, (2) Alliarion, (3) Aegopodion, typical sub-communities, (4) Aegopodion, *Calystegia* sub-communities, and (5) Calystegion, *Aegopodium* sub-communities.

Galio-Urticetea basal community was quite ubiquitous in its range of habitats and found at a variety of man-made sites without regular management, such as roadsides, railway embankments, former horticultural land, abandoned meadows, an abandoned sand pit, and forest clearings. Apart from the typical species of Galio-Urticetea mentioned in the previous paragraph, *Dactylis glomerata* was the only constant (Table 5, 2.1). Various other grassland, tall-forb, and sometimes woodland species co-occurred but usually with low frequency and abundance, and the stands were generally species poor. *Heracleum mantegazzianum* was mostly the dominant species (i.e. cover >50%), sometimes with co-dominant *Urtica dioica* which occasionally was dominant as well.

Alliarion stands with *H. mantegazzianum* were rare exceptions (3 relevés) and occurred in more shaded situations along fringes or in gaps of tree rows. Characteristic species were *Alliaria petiolata* and *Geranium robertianum*, accompanied by some woodland species such as *Stachys sylvatica*, *Poa nemoralis* and *Brachypodium sylvaticum* among others (Table 5, 2.2).

Aegopodion and Calystegion communities made up the majority (70%) of tall-forb stands with *H. mantegazzianum* found in the present study. The two alliances are quite closely related not only by sharing a full set of class character species, but also Calystegion character species may spread to Aegopodion stands, and vice versa (Table 5, 2.3 and 2.4) with an increase of Calystegion species with flooding frequency.

Typical Aegopodion sub-communities are fully terrestrial and differentiated from the remaining by the lack of Calystegion species (Table 5, 2.3.1). The stands were characterised by constant co-occurrences of *Urtica dioica* and *Aegopodium podagraria*. The latter is, in fact, rather a characteristic species of the class (Dengler 1997) but also commonly regarded as an Aegopodion character species (Ellenberg 1992; Oberdorfer 1993). Further character species of the alliance Aegopodion were widely lacking in the given set of relevés except for few records of *Petasites hybridus* and *Lamium maculatum*. Basically, this community type corresponded to the Urtico-Aegopodietum podagrariae (R.Tx. 1963) Oberdorfer 1964 in Görs 1968 in its typical sub-association although floristically noticeably impoverished in character species of the alliance and typical companions. Habitats colonized by this community type were mostly abandoned grassland sites and sometimes disturbed forest margins and small clearings in (floodplain) forests.

Aegopodion sub-communities with *Calystegia sepium* differed floristically from Calystegion sub-communities with *Aegopodium* only in the number and cover-abundance sum of the character and differential species of the respective alliances and orders (Table 5, 2.3.2 and 2.4). The only constant Aegopodion species was again *Aegopodium podagraria*. Other species characteristic of Aegopodion (or the order Artemisietalia sensu Dengler 1997) were *Petasites hybridus*, *Lamium maculatum*, *Silene dioica*, *Lamium album*, *Cruciata laevipes* and *Chaerophyllum bulbosum* which, however, were limited in frequency to class II (max. 40%) or lower classes. Recorded character species of Calystegion (or Calystegietalia, respectively) were *Impatiens glandulifera*, *Calystegia sepium*, *Carduus crispus*, *Humulus lupulus* and, rarely, *Cuscuta europaea*, *Myosoton aquaticum* and *Epilobium hirsutum*. These were supplemented by a set of moisture-tolerant plants, most prominently *Symphytum officinale*, serving as differential species for the order Calystegietalia (cf. e.g. Dengler 1997).

Aegopodion sub-communities with *Calystegia* mostly corresponded to the Urtico-Aegopodietum convolvuletosum (cf. Oberdorfer 1993) except for two relevés which could best be affiliated with the Phalarido-Petasitetum hybridi Schwick 1933. Calystegion communities with *H. mantegazzianum* resembled most closely the Urtica-Convolvulus sepium-community Lohmeyer 1975, which is typical of the banks of small rivers in (sub-) montane regions (cf. Oberdorfer 1993).

These two vegetation types were found in a variety of different habitats, partly natural, like small clearings in alluvial Alder-Willow forests or riverbanks with tall-forb vegetation, but mostly in semi-natural or anthropogenic habitats like artificial river embankments, railway embankments, abandoned (alluvial) grasslands, understorey of planted tree rows along rivers, abandoned horticultural land, and at ruderalised forest fringes in river valleys.

5.5.2.4 Woodlands

Some relevés with *H. mantegazzianum* could be affiliated to specific woodland communities of the (sub-) alliances of Alder-Ash-gallery forests (Alnenion glutinoso-incanae, class: Querco-Fagetea) and Gray Willow scrub (Salicion elaeagni, class: Salicetea pupureae). Other woodland relevés that originated from afforestations of alluvial grasslands or man-made sites in river valleys could not be allotted to any specific syntaxa but were included into Table 5 as a group of substitutes of Alnenion communities (anthropogenic floodplain forests). Finally, *H. mantegazzianum* was singularly found in *Salix caprea* and *Populus tremula* pioneer stands, an Oak copse and beneath an Oak-Wild Cherry tree row. Altogether, occurrences of *H. mantegazzianum* in woodlands were rather scarce and restricted to gaps, sparse canopies or fringe areas where the species could benefit from increased light levels compared with closed forest stands. Noteworthy, all but two woodlands had developed from grasslands or similar vegetation after the 1950s (cf. chapter 4.1.2).

Within Alnenion glutinoso-incanae, *H. mantegazzianum* was found to occur in two associations of Alder-Ash-gallery forests that grow in the inundation area of small rivers in the (sub-)montane and colline zones. These are, by name, Stellario-Alnetum glutinosae and Alnetum incanae (Table 5, 3.1 and 3.2). The ecological distinction of these communities coincides with the preferences of the characteristic alder species - *Alnus glutinosa* on loamy soils of submontane and colline riversides and *Alnus incana* on calcareous sands and shingle banks of montane rivers. Both associations share common species of moist and rich woodlands such as, e.g., *Festuca gigantea* and *Circaea* sp. (cf. Oberdorfer 1993). Among the companions were some species typical of Galio-Urticetea tall-forb communities like *Urtica dioica*, *Galium aparine* and *Impatiens glandulifera*.
In Stellario-Alnetum stands also *Aegpodium podagraria* and *Stellaria nemorum* were consistent and conspicuous elements of the field layer and the relevés all belonged to the typical sub-community. Concerning eco-sociological subtypes of Alnetum incanae the relevés were more or less intermediate between typical and wetter sub-associations (A. i. typicum and A. i. phragmitetosum, respectively) and differential species of the summer-dry subtype (A. i. caricetosum albae) were lacking completely.

Salicion elaeagni comprises Gray Willow scrubs on base-rich shingles and sandbanks in the montane zone of alpine rivers. Stands with *H. mantegazzianum* were found in older, more consolidated stages of fresh variants of Salicion elaeagni communities which build up forest-like stands with a generally more or less closed canopy and an understorey of quite demanding plants (cf. Oberdorfer 1993), which are represented in the relevés by *Urtica dioica*, *Galium aparine, Galeopsis tetrahit* and *Impatiens glandulifera* among others (Table 5, 4). The investigated stands resembled quite closely a Salicetum elaeagni (Hag. 1916) Jenik 1955 phalaridetosum although differential and accompanying species did not perfectly match species lists known from literature. Oberdorfer (1993) points out that this sub-community type is transitional to Alnetum incanae.

Habitats of Salicion elaeagni and Alnenion glutinoso-incanae stands were more or less natural gallery forests that had developed from open riverbank habitats after the 1950s probably subsequent to abandonment of cattle grazing. Incidentally, seedlings of *H. mantegazzianum* were also found at open river sandbanks close to Salicion elaeagni stands but were not able to survive a summer flooding event.

As mentioned above *H. mantegazzianum* sometimes occurred in anthropogenic floodplain forests which did not match known syntaxa. These featured *Fraxinus excelsior, Acer pseudoplatanus, Populus nigra* and *Salix fragilis* among the dominant woody components and may be viewed as substitutes of the drier branch of Alnenion glutinoso-incanae forests. (Table 5, 5).

5.5.2.5 Other vegetation types with *H. mantegazzianum*

Next to the plant communities described above which accounted for the majority of relevés, *H. mantegazzianum* occurred in various other types of open vegetation which could not be affiliated with known syntaxa. These types stood out from the former primarily on account of severe disturbances of the sites and, in few cases, also due to comparatively unfavourable site conditions. To give an impression of the spectrum of these vegetation types some examples shall be briefly mentioned.

At a former military site and in former quarries some stands were found in young successional stages dominated by *Calamagrostis epigeios*. Companions were *Cirsium arvense*, *Urtica dioica*, *Rubus* sp., few other unspecific grassland species, and a variety of ruderal species of open habitats. Furthermore, singular occurrences of *H. mantegazzianum* were found on a recently abandoned arable field, in a former scrub which had been cleared by rotovating, and an abandoned orchard. Finally, two relevés were recorded from a windbreak site where *H. mantegazzianum* grew together with Molinietalia wet grassland species, like *Angelica sylvestris*, *Cirsium palustre*, *Molinia caerulea*, small sedges and rushes, interspersed with few tall forbs of the order Atropetalia, like *Senecio fuchsii* and *Epilobium angustifolium*.

5.5.2.6 Relative frequencies of vegetation types with *H. mantegazzianum*

Grasslands accounted for 45% of all relevés (Figure 2). Of these, the ruderal Arrhenatherion grasslands made up the largest proportion (27% of the total) followed by managed Arrhenatherion meadows (15%). Typical Arrhenatherion sub-communities prevailed by far over the moist subtypes. Tall-forb communities were slightly less frequent than the grasslands (39%) with more or less even shares of Aegopodion, Calystegion, and Galio-Urticetea basal communities while Alliarion communities were notably rare with only about 1% of all relevés. Alongside the gradient from typical Aegopodion sub-communities through *Calystegia* sub-communities of Aegopodion to Calystegion communities frequencies increased (5%, 6%, 15%, respectively). Woodlands (Alnenion glutinoso-incanae, Salicion elaeagni, anthropogenic floodplain forests) made up merely 6%, altogether. Other vegetation types contributed 11% of relevés.

5.5.2.7 Red list status of species and communities

According to national and regional red data lists for plant communities and vascular plant species in Germany (e.g. www.floraweb.de) the communities colonised by *H. mantegazzianum* are throughout listed as ‘not endangered’ and co-occurring indigenous plant species are also virtually absent from the red data lists. Single occurrences in man-made habitats of *Leonurus cardiaca* and *Orobanche flava*, both nationally and regionally listed as ‘endangered’, were the only exceptions.

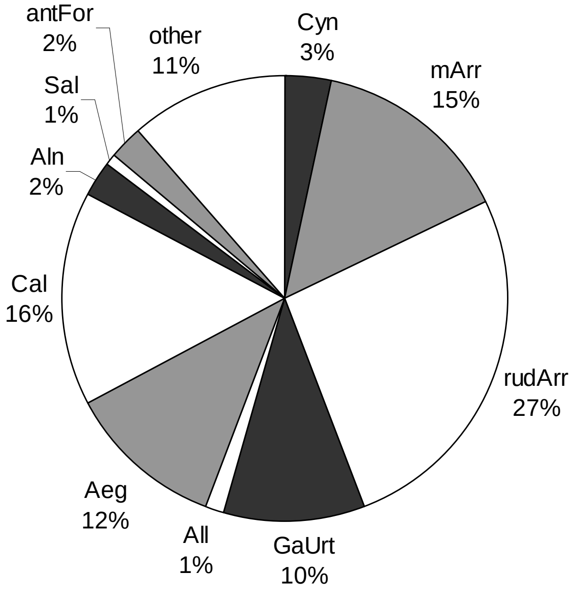

Figure 2. Relative frequencies of vegetation types with *Heracleum mantegazzianum* found in study areas. Percentages were rounded up or down to amount to 100%, exactly. Abbreviations of vegetation types: Cyn = Cynosurion; mArr = managed Arrhenatherion; rudArr = ruderal Arrhenatherion; GaUrt = Galio-Urticetea basal community; All = Alliarion; Aeg = Aegopodion; Cal = Calystegion; Aln = Alnenion glutinoso-incanae; Sal = Salicion elaeagni; antFor = anthropogenic floodplain forest; other = all remaining relevés not assigned to specific syntaxa.

5.5.3 Gradient analysis

The first axis of CA ordination of relevés mainly represented a gradient from managed grasslands – prevalently hay meadows and subordinately (mown) pastures – over young stages of abandoned or neglected grasslands (ruderal grasslands) to tall-forb stands with increasing proportions of woody components and, finally, woodlands (Figure 3). Environmental variables significantly correlated with the ordination axes are presented in Figure 4. Along the main gradient (axis 1) the intensity of land use declined from regular grassland management, via irregular maintenance to abandonment or disuse, and the time span since abandonment of sites increased. While light supply declined due to increasing cover of trees at the upper end of the gradient, the supply of moisture and soil nutrients, particularly phosphorus and potassium, increased. With regard to plant strategies, there was an increase in competition (C-strategy) while stress-tolerance (S-strategy) decreased.

The second axis separated (former) agricultural sites, i.e. managed grasslands or sites developed therefrom after abandonment, in the lower part of this axis from a smaller group of sites that never were subject to agricultural land use in the upper part (Figure 3). Most relevés of the latter group could neither be assigned to specific plant communities nor grouped in homogenous vegetation types and therefore were categorised as ‘Other’ in the ordination plot (see ch. 4.2.5).

Consequently, land use also declined along the second axis and likewise did the soil nutrient status, particularly nitrogen. In reverse, the proportion of disturbed sites increased and, especially, heavy disturbances, such as mining and windbreak, were found in the upper array of the second axis. With respect to vegetation texture, there was a marked increase in the pooled cover-abundance of nanophanerophytes and woody chamaephytes which was prevalently attributable to *Rubus* and *Salix* sp. Furthermore, an increase in stress-tolerance (S-strategy) could be observed along the second axis.

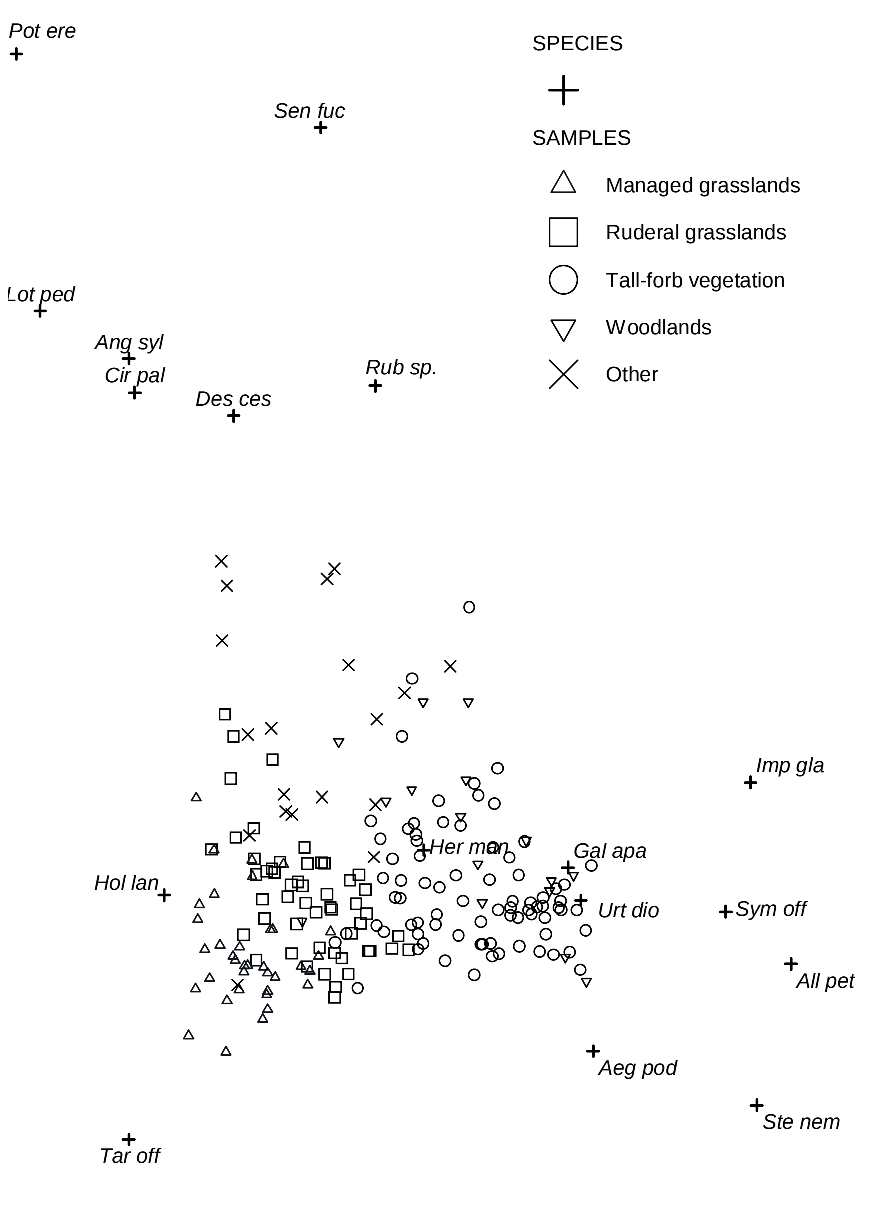

Figure 3. CA ordination biplot of sites and species. Axis 1 (x) and axis 2 (y) are presented. All of 202 investigated plots were included in the analysis and plotted in the diagram. The first CA axis mainly represented a successional series from grasslands to tall-forb stands and woodlands. Only species above a predefined cut-off value of fit on the first two axes were plotted. Abbreviations of species names: Aeg pod = *Aegopodium podagraria*, All pet = *Alliaria petiolata*, Ang syl = *Angelica sylvestris*, Cir pal = *Cirsium palustre*, Des ces = *Deschampsia cespitosa*, Gal apa = *Galium aparine* agg., Her man = *Heracleum mantegazzianum*, Hol lan = *Holcus lanatus*, Imp gla = *Impatiens glandulifera*, Lot ped = *Lotus pedunculatus* (syn. *uliginosus*), Pot ere = *Potentilla erecta*, Rub sp. = *Rubus fructicosus* agg. & *Rubus idaeus*, Sen fuc = *Senecio fuchsii*, Ste nem = *Stellaria nemorum*, Sym off = *Symphytum officinale*, Tar off = *Taraxacum officinale* agg., Urt dio = *Urtica dioica*. Classification of sites: 'Managed grasslands' comprise managed Arrhenatherion and Cynosurion communities, 'Ruderal grasslands' refers to abandoned or irregularly maintained Arrhenatherion grasslands, 'Tall-forb vegetation' includes all communities of the class Galio-Urticetea (basal community, Alliarion, Aegopodion, Calystegion), 'Woodlands' comprises all woodland relevés whether assigned to known syntaxa (Alnenion glutinoso-incanae, Salicion elaeagni,) or not, and 'Other' catches the remainder of relevés which could not be grouped or assigned to specific syntaxa.

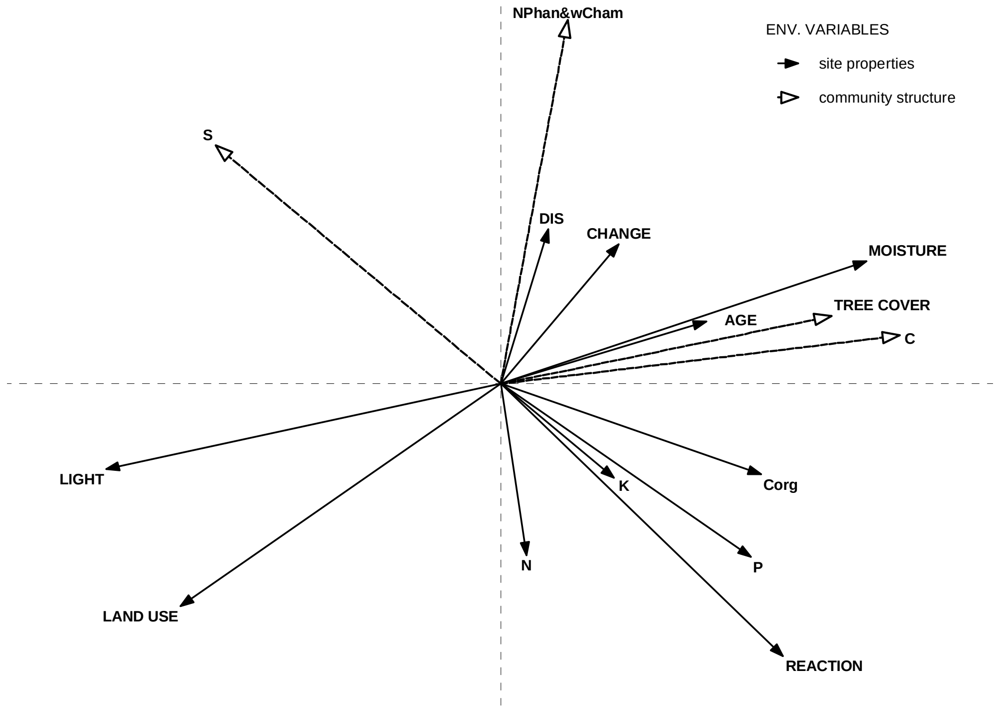

Figure 4. CA ordination diagram of environmental variables. Axis 1 (x) and axis 2 (y) are presented. The first CA axis mainly represented a successional series from grasslands to tall-forb stands and woodlands. Only environmental variables with a t-value of 1.96 or greater were plotted. Classification of environmental variables: ‘site properties’ include all variables actually measured or estimated in the field as well as average Ellenberg indicator values; ‘community structure’ comprises all parameters of the structure of the vegetation stands (strategy types, layers). Abbreviations of variable names: AGE = habitat change before the 1970s (yes, no), C = proportion of C-strategy (Grime et al. 1988), CHANGE = habitat change in the last fifty years (yes, no), Corg = organic carbon content of soils; DIS = disturbance (yes, no), K = plant-available potassium content of soils, LAND USE = regular management regime (yes, no), LIGHT = estimated light supply, MOISTURE = average Ellenberg indicator values for moisture supply, N = total nitrogen content of soils, NPhan&wCham = pooled cover-abundance of nanophanerophytes and woody chamaephytes, P = plant-available phosphorus content of soils, REACTION = average Ellenberg indicator values for soil reaction, S = proportion of S-strategy (Grime), TREE COVER = cover percentage of the tree layer (if present).

5.5.4 Cover-abundance of H. mantegazzianum in relation to recipient community, gradient analysis and species numbers

Cover values of *H. mantegazzianum* varied in a wide range between 1% and 95% and showed an uneven distribution with 47% of values in the class ‘1-20%’, 17% in the class ‘20-40%’ and 12% each in the higher classes (40-60%, 60-80%, 80-100%). The pattern of medians of cover values with regard to community type exhibited low values for managed grasslands (Cynosurion, Arrhenatherion meadows) and shady woodland habitats (Alnenion glutinoso-incanae, anthropogenic floodplain forests), while ruderal grasslands and tall-forb communities comprised the whole range of cover values (ruderal Arrhenatherion, Galio-Urticetea basal community, Alliarion, Aegopodion, Calystegion; Figure 5). Exceptional high cover percentages in managed grasslands were due to massive recruitment of *H. mantegazzianum* seedlings in disturbed swards but the specimens did not manage to grow to normal height due to mowing or grazing.

Dominant stands (cover of *H. mantegazzianum* >50%) made up the largest proportion in Galio-Urticetea basal community (85%) and Aegopodion (52%). Two out of three stands in Alliarion were dominant, but due to the small number of observations this ratio is vague. From these terrestrial tall-forb communities towards riparian ones (Calystegion) there was a conspicuous decrease in median cover values (Figure 5).

Regular mowing or grazing, and shading reduced the abundance of flowering individuals of *H. mantegazzianum* in managed grasslands (median / maximum: 1.5 / 26 generative individuals / 25 m^2) and woodlands (0 / 5) compared to ruderal grasslands (4.5 / 37) and tall-forb stands (7 / 54). Fruit set was strongly reduced by cutting or biting off of the primary stems in managed grasslands, while in the remaining vegetation types fruit set was generally abundant, even in woodlands where flowering individuals occurred.

As indicated by the gradient length of 2.8 measured by DCA most species showed linear response along the first ordination axis. Grassland species, such as *Holcus lanatus*, *Ranunculus repens*, *Taraxacum officinale* agg. and *Rumex acetosa* declined whereas tall-forbs and herbs typical of tall-forb vegetation, such as *Urtica dioica* and *Aegopodium podagraria*, increased (Figure 6). In contrast to the majority of species, *H. mantegazzianum* showed a unimodal response along the first ordination axis with a maximum predicted cover-abundance class of ‘3’ (cover percentage 25-50%) in the central part of axis 1 according to the fitted GAM. Also along the second axis the response of *H. mantegazzianum* was unimodal.

Cover values of *H. mantegazzianum* were negatively correlated with the number of vascular plant species of relevés. When all relevés were included into correlation analysis the Pearson correlation coefficient was r = -0.29 (p <0.001; Spearman’s R = -0.28, p <0.001). However, managed grasslands in which *H. mantegazzianum* cover values were low, had generally higher species numbers compared to the tall-forb communities. Leaving out managed grasslands, there was still a negative correlation but with a lower correlation coefficient of r = -0.24 (p = 0.002; Spearman’s R = -0.23, p = 0.003).

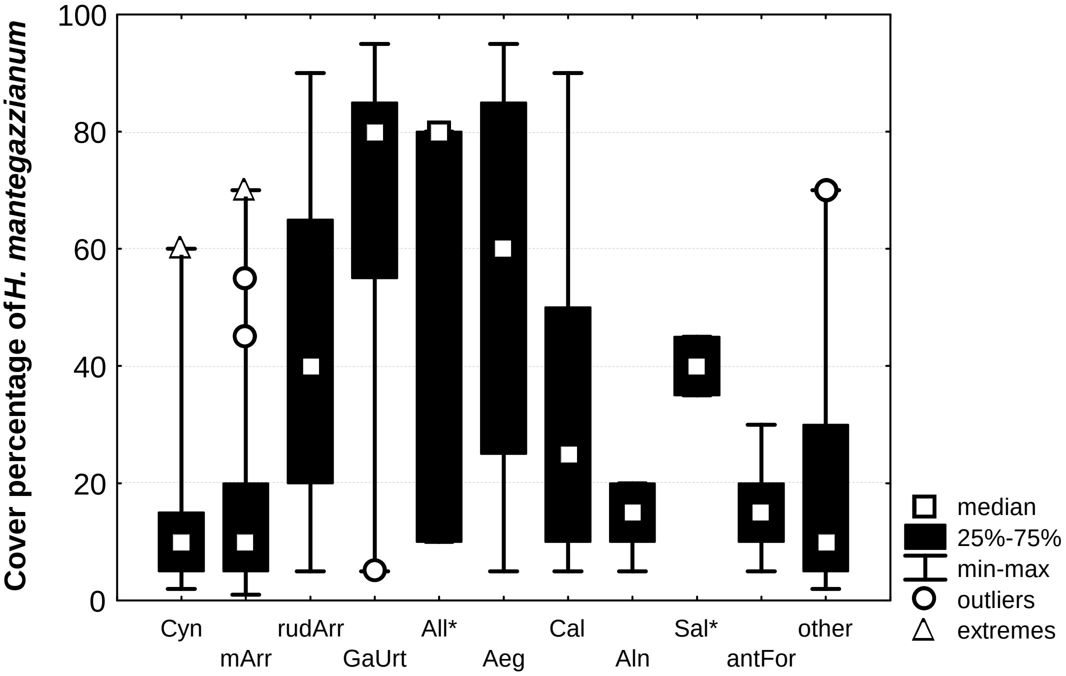

Figure 5. Cover percentages of *H. mantegazzianum* with respect to vegetation types (medians, quartiles and min-max ranges). Outliers are further from the upper box level than 1.5*inter-quartile-range. For extremes the coefficient is 3. Key to vegetation types: Cyn = Cynosurion; mArr = managed Arrhenatherion; rudArr = ruderal Arrhenatherion; GaUrt = Galio-Urticetea basal community; All = Alliarion; Aeg = Aegopodion; Cal = Calystegion; Aln = Alnenion glutinoso-incanae; Sal = Salicion elaeagni; antFor = anthropogenic floodplain forests; other = all relevés not assigned to specific syntaxa.* Few observations: All = 3, Sal = 2.

5.6 Discussion

5.6.1 Habitats

5.6.1.1 Spectrum of habitats and site conditions

From a broad perspective *H. mantegazzianum* colonises a variety of different habitats such as abandoned or neglected grasslands, roadsides, riverbanks, railway embankments, forest and scrubland fringes, ruderal areas and even managed grasslands or woodlands (Neiland 1987; Pyšek 1994; Pyšek and Pyšek 1995; Ochsmann 1996; Tiley et al. 1996; Thiele and Otte, submitted) which has lead to the assumption that the species is generally superior over indigenous ones and quality of the recipient habitat is rather unimportant (Pyšek 1991; Pyšek and Pyšek 1995).

However, closer examination of habitat characteristics reveals that the preferred habitats are more or less uniform. Abiotic sites conditions are generally characterised by high trophic level, fast nutrient cycling, favourable soil reaction and favourable water balance offering good water supply as well as good aeration of soils which altogether is in good agreement with other studies on chemical soil characteristics (e.g. Tiley et al. 1996; Otte and Franke 1998) or Ellenberg indicator values (Pyšek and Pyšek 1995; Ochsmann 1996) of *H. mantegazzianum* sites. Furthermore, preferred habitats have in common that they are disused or neglected and it seems that they are also regularly characterised by episodic disturbances providing particularly suitable conditions for recruitment.

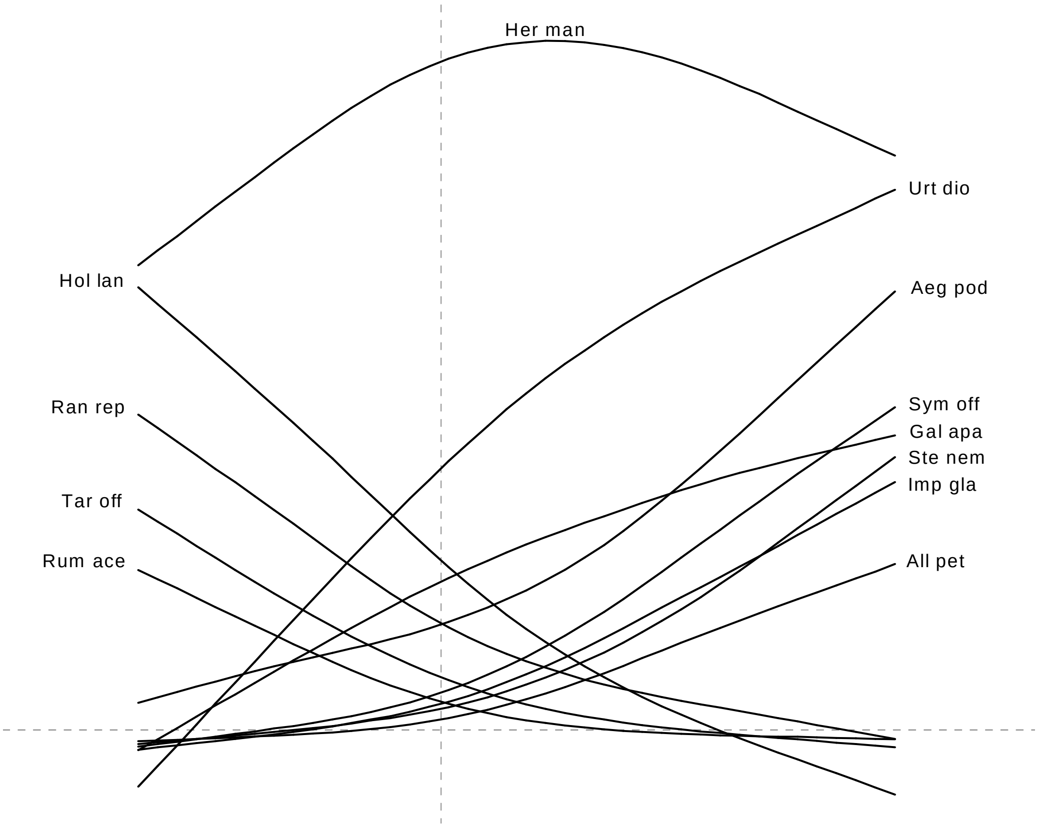

Figure 6. Response curves of selected species along the first axis of CA ordination. The first CA axis (x) mainly represented a successional series from grasslands to tall-forb stands and woodlands. The vertical dashed line indicates the zero point (i.e. center) of the first CA axis. The y-axis depicts predicted cover-abundances of the species. The horizontal dashed line indicates the zero point of predicted cover-abundances. The maximum predicted cover-abundance class of *Heracleum mantegazzianum* (Her man) was in class ‘3’ (i.e. 25-50% cover). Only species above a predefined cut-off value of fit on the first axis and *Heracleum mantegazzianum* were plotted. Curves were calculated by Generalized Additive Model in CANOCO using default settings.

Figure 6 (continued). Abbreviations of species names: Aeg pod = *Aegopodium podagraria*, All pet = *Alliaria petiolata,* Gal apa = *Galium aparine* agg., Her man = *Heracleum mantegazzianum*, Hol lan = *Holcus lanatus*, Imp gla = *Impatiens glandulifera*, Ran rep = *Ranunculus repens,* Rum ace = *Rumex acetosa,* Ste nem = *Stellaria nemorum*, Sym off = *Symphytum officinale,* Tar off = *Taraxacum officinale* agg., Urt dio = *Urtica dioica*.

The factors differing most conspicuously among different habitats and communities colonised by *H. mantegazzianum* are land use and light supply. These act as constraining factors on *H. mantegazzianum* at the lower or upper end of the major gradient in the vegetation data, respectively.

To further delimit the optimal range of abiotic site conditions it is interesting to consider *H. mantegazzianum* stands in more detail that grow under apparently pessimal conditions with regard to nutrient status and water balance. The sites in question are two abandoned wet grasslands (ch. 4.2.2) and a windbreak area colonised primarily by Molinietalia wet grassland species (ch. 4.2.5). All of these sites were open, disused and at least the latter was severely disturbed recently. Furthermore, *H. mantegazzianum* stands have been present in the immediate vicinity since about 10 years before the study which in combination should offer good possibilities for invasion of *H. mantegazzianum*. Nevertheless *H. mantegazzianum* abundances were low (cover values <10%) and the smaller than normal specimens rarely managed to flower. In contrast to the remaining sites, nutrient status was moderate to poor (P ~ 0.1 mg/ 100 g; N ~ 0.2 g/ 100 g) and drainage was noticeably impeded. Therefore, it seems likely that the species' abundance and growth is limited by poor and wet conditions. Obviously, *H. mantegazzianum* is also hampered by low water supply as it was never found in habitats characterised by dry soils.

Summarising, it can be concluded that the quality of recipient habitats is crucial for the invasion of *H. mantegazzianum*. Although its ecological niche is fairly wide the species is an invader, in the sense of attaining high densities and having great impact on the resident vegetation (cf. Davis and Thompson 2000) only if particular habitat requirements are met.

5.6.1.2 Creation of suitable habitats by changing land-use regimes

Generally, sites of *H. mantegazzianum* are well suited to agricultural land use. Analysis of site history revealed that more than 50% of sites had still been used agriculturally, predominantly as meadows or pastures, before the 1970s or even thereafter (Table 2) but have been abandoned or partly turned into rather irregularly maintained grasslands fringes or margins alongside rivers, roads, and forests. This shows that a major proportion of favourable sites has been newly created within the last 50 years in the course of declining grassland management in the invaded landscapes.

The timing of abandonment or de-intensification of invaded grasslands coincides, temporally, with the phase of exponential increase of *H. mantegazzianum* distribution from the 1960s onwards, which suggests that the massive spread and increase of the species was enhanced considerably by changes in land management.

5.6.2 Plant communities and vegetation dynamics

Correspondence analysis shows that the main gradient in the set of relevés is attributable to secondary successions on, primarily, abandoned grasslands and, secondarily, ruderal sites (Figure 3). Along this successional gradient *H. mantegazzianum* shows a unimodal response with the highest predicted stand densities in the array of recently abandoned or ruderalised sites. This suggests that successional age plays a role with respect to densities of *H. mantegazzianum* stands and possibly also to the invasion success of the species as hypothesized by Pyšek and Pyšek (1995).

At the older end of the successional gradient shading by woody components of the vegetation is an obvious constraining factor. But as only comparatively few plots featured a largely closed tree canopy and were consequently classified as woodlands, it appears that in older successional stages also competition by other herbaceous species, particularly tall forbs, restricts *H. mantegazzianum*.

Concerning the structure of the vegetation stands, it is striking that a shrub layer is either completely absent or very sparsely developed (max. 10% cover). Obviously, shrubs are, once successfully established, strong competitors to *H. mantegazzianum* and capable to suppress seedlings and adult plants with their shade.

Plant communities with *H. mantegazzianum* reflect site conditions and dynamics of the habitats which are characterised by high productivity and, in the majority, considerable historical or recent alterations in management regimes (cessation or de-intensification of land use) or severe disturbance events (e.g. mining, removal of tree or shrub layer, mechanical damaging of the sward). Floristically, this is expressed in high constancies of a set of more or less nutrient demanding and ruderal species regularly co-occurring with *H. mantegazzianum* in ruderal grasslands, tall-forb vegetation and woodlands. These are *Poa trivialis*, *Urtica dioica*, *Galium aparine* and *Glechoma hederacea* which act as baseline species of virtually all communities with *H. mantegazzianum* except for managed grasslands and indicate its preference for Galio-Urticetea communities. At the level of alliances *H. mantegazzianum* centers on Aegopodion which can be seen from its concordance with the characteristic or differential species of Aegopodion along the gradient from terrestrial to riparian communities of Calystegion. Notwithstanding, a considerable part of relevés belongs into the latter alliance. This centring on Aegopodion communities was also reported by other authors (e.g. Sauerwein 2004).

The findings of the present study support the view that it is not advisable to keep up a separate association of *H. mantegazzianum* (Urtico-Heracleetum Klauck 1988) within the alliance Aegopodion. Firstly, the Aegopodion communities with *H. mantegazzianum* are not ecologically different from other communities of this alliance (cf. Otte 1994, 1996) and consequently lack own character or differential species apart from *H. mantegazzianum* itself. Secondly, *H. mantegazzianum* would perform rather poorly as a character species as it frequently occurs in vegetation types belonging to different alliances or even different classes. While the spectrum of tall-forb communities found in the present study is in good agreement with findings of other authors, occurrences of *H. mantegazzianum* in managed grassland communities (Arrhenatherion, Cynosurion) and their early stages of succession after abandonment have been more or less neglected and never described in detail hitherto. However, the large proportion of ruderal grasslands found colonised by *H. mantegazzianum* in the present study emphasises the importance of abandoned or neglected grasslands for this species.

5.6.3 Assessment of impacts on the diversity of communities

Assessment of impacts of *H. mantegazzianum* on recipient communities should take into account the particular effects of the species but also its relationship to potential indigenous competitors and their effects on communities in comparable situations. Therefore, relevant questions concerning the role played by *H. mantegazzianum* are whether the species (i) affects community composition and α-diversity, (ii) is generally superior to competing indigenous species, and (iii) exerts different effects on resident communities as compared to indigenous species.

Heracleum mantegazzianum can attain high cover values of up to 95% of the stand's surface area. A possible effect of raised cover values of one species should be reduction in cover or even complete displacement of resident species. The negative correlation of *H. mantegazzianum* cover values with species-richness of relevés suggests that the species causes a decrease in α-diversity, which is consistent with assumptions of other authors (Lundström 1984; Pyšek and Pyšek 1995). Yet, it has to be considered that a higher species number at a given site before the species' invasion is hypothetical. It would also be conceivable that the species diversity was already low prior to the arrival of *H. mantegazzianum*, possibly due to disturbances or other historical factors which in turn could be a driving factor of *H. mantegazzianum* invasion (Woods 1997 in Meiners et al. 2001). Thus, a secure estimation of the species' effects on α-diversity could only be brought about by long-term observations starting prior to invasion.

Despite the difficulties to assess causal effects from the correlation between species numbers and cover values, it is quite plausible that light-demanding herbs will decrease and possibly disappear when a tall-forb builds up a closed canopy of leaves. Therefore, it is reasonable to assume that high densities of *H. mantegazzianum* cause a decrease in species numbers of swards consisting of light-demanding and rather low-growing species, which applies especially to abandoned grasslands.

Cover values of *H. mantegazzianum* were often rather low and only about a third of the surveyed stands had cover values greater than 40%. It has to be taken into account that populations of *H. mantegazzianum* and the abundances of the species are not necessarily in equilibrium with their environment. Populations with low abundances might be in an early stage of invasion and further increase but, on the other hand, dense stands might decrease under competition by other tall forbs, shrubs or trees. Nevertheless, the distribution of cover values suggests that the species does not always have the potential for becoming dominant. The most frequent native tall forb in relevés with *H. mantegazzianum* was *Urtica dioica* which is itself a strong and high-growing competitor (C-strategist according to Grime et al. 1988). Inferring from the observations of the present study it appears that neither species is generally competitively superior to the other one as they co-occur in virtually every possible mixing ratio.

Habitat changes as found for the majority of sites (abandonment of grasslands, severe disturbances) provoke secondary successions starting from herbaceous swards or bare soils and, thus, naturally involve colonisation by species formerly excluded or removed from the sites through land use, shading, or severe disturbances. Obviously, *H. mantegazzianum* can benefit from dynamics as described above in generally suitable habitats and under favourable site conditions. But this is also the case with some indigenous plant species. The most frequent and competitive is without doubt again *Urtica dioica*. With regard to the third question, it can be stated that *Urtica dioica* as well as *H. mantegazzianum* are occasionally able to build up dominant stands and decrease species numbers in the course of successions. In this respect, their impacts are comparable.

Concludingly, *H. mantegazzianum* is in fact a successful coloniser and sometimes invader (sensu Davis and Thompson 2000) but it is not generally superior to indigenous species and does not have more negative impacts on the vegetation than some natives or other non-natives do under the same circumstances. With regard to the processes forming the habitats of the species (abandonment, disturbance) which can often lead to a decrease in species numbers due to non-native as well as native colonisers (Schmidt 1981; Neuhäusl and Neuhäuslova-Novotna 1985; Meiners et al. 2001), it can be stated that *H. mantegazzianum* is rather a symptom of biodiversity loss than the cause of it.

5.6.4 Evaluation of risks for nature conservation

According to a survey, *H. mantegazzianum* has invaded nature reserves in approximately a third of all districts of Germany and it colonises protected habitat types in almost as many. Among the mentioned habitat types were, e.g., wet grasslands, alluvial (softwood) forests, alder swamp forest, lakeshores, calcareous and acidic marshes, terrestrial reed stands, and poor (chalk) grasslands (Thiele and Otte, submitted). This suggests that the species might be in conflict with aims of nature conservation.

However, within study areas virtually no habitat types or plant communities of interest for nature conservation were found to be invaded apart from exceptional open stands in slightly wet abandoned grasslands (Calthion-like stands) and some occurrences in alluvial (softwood) forests (Alnenion, Salicion). This might primarily be attributable to the habitat spectrum of the study areas that generally contained few habitats of interest for nature conservation. But site conditions supporting protected communities and rare species are often characterised by stress factors such as nutrient deficiency, drought, excessive wetness etc., and in the case of semi-natural habitats (e.g. grasslands) they also depend on suitable management. Starting from the observed habitat requirements of *H. mantegazzianum* it can be assumed that the species is not able to invade rare and endangered communities, as long as appropriate low productive site conditions and management are still prevailing. Only at the extreme margins of its ecological niche it could interfere with rare species and communities but there *H. mantegazzianum* is struggling itself and is constrained to low abundances. In conclusion, the assumption that *H. mantegazzianum* is in conflict with aims of nature conservation can be largely refuted by our findings.

5.7 Acknowledgements

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6 Cultural landscapes of Germany are patch-corridor-matrix mosaics for an invasive megaforb

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submitted to Landscape Ecology

6.1 Abstract

Predicting the vulnerability of landscapes to both the initial colonisation and the subsequent spread of invasive species remains a major challenge. The aim of this study was to assess the relative importance of local and landscape factors for the landscape distribution of the invasive megaforb *Heracleum mantegazzianum*. Particularly, we tested which factors affect the presence or absence in suitable habitat patches (occupancy) and the cover percentage within occupied patches (patch saturation). For this purpose, we used standard (logistic) regression modelling techniques. The regression analyses were based on inventories of suitable habitat patches in 20 study areas (each 1 km²) in cultural landscapes of Germany. The saturation of occupied patches was independent from landscape factors, except for patch shape, and even unsatisfactorily explained by local factors included in the analysis. In contrast, habitat occupancy of *H. mantegazzianum* was affected by both local and landscape factors. Woody habitat structure decreased the occurrence probability, whereas vicinity to transport corridors (rivers, roads), high habitat connectivity, patch size and perimeter-area ratio of habitat patches had positive effects. The significance of distances from corridors and habitat connectivity for habitat occupancy shows that dispersal of *H. mantegazzianum* through the landscape matrix is limited. We conclude that cultural landscapes of Germany function as patch-corridor-matrix mosaics for the spread of *H. mantegazzianum*. Our results highlight the importance of landscape structure and habitat configuration for invasive spread. Furthermore, this study shows that both local and landscape factors should be incorporated into spatially-explicit models to predict spatiotemporal dynamics and equilibrium stages of plant invasions.

Keywords: dispersal, habitat configuration, habitat occupancy, Heracleum mantegazzianum, invasion, island-biogeographic model, logistic regression, spread, transport corridors.

6.2 Introduction

The landscape distribution and abundance of plant species may depend on local (patch level) and landscape factors (Freckleton and Watkinson 2002; Ehrlén and Eriksson 2003). Local factors affecting the occurrence and abundance of plant species within a habitat patch include resource supply (nutrients, water, light etc.) and biotic interactions among plants and between trophic levels (e.g. competition, facilitation, herbivory; Lortie et al. 2004). They are key determinants of recruitment, growth, and production of seeds or other propagules (e.g. Schemske et al. 1994). Further, current occurrences of plant species can be generally influenced by habitat age or individual histories of habitat patches (Eriksson et al. 2002; Deil and Ludemann 2003; Ehrlén and Eriksson 2003). Rather complementary, landscape factors are primarily related to biogeographical processes concerning dispersal of propagules and species' abilities to reach patches of suitable habitat (Lortie et al. 2004).

Among contemporary biogeographical and landscape ecological concepts, patch size and isolation (or connectivity, conversely) of spatially structured habitats, especially discrete habitat patches in an inhospitable matrix, play a major role in explaining dispersal success and landscape abundance of plant (and animal) species (e.g. Eriksson and Ehrlén 2001). In theory, dispersal success and the rate of occupied habitat patches should decrease with increasing isolation, whereas patch size should have a positive effect. Furthermore, corridors (e.g. roads, rivers, hedge rows etc.) may enhance dispersal success by enabling movement of species and their propagules between otherwise isolated habitat patches (Tewksbury et al. 2002; Kirchner et al. 2003). These concepts apply especially to species with limited or imperfect dispersal abilities which live in fragmented or 'patchy' habitats (de Blois et al. 2002). Such species may be hypothesized to perceive landscapes as patch-corridor-matrix mosaics.

Recent studies confirming effects of patch size, isolation (or connectivity), and habitat age on plant populations have considered native species in fragmented natural habitats, such as serpentine seeps (Harrison et al. 2000), rosemary scrub (Quintana-Ascencio and Menges 1996), and forest fragments (Dupré and Ehrlén 2002; Jacquemyn et al. 2003; Kolb and Diekmann 2004; Petit et al. 2004). Concerning corridors, some recent empirical studies have brought evidence of their importance for animals whereas for plants empirical studies are still widely lacking (de Blois et al. 2002; Kirchner et al. 2003).

Hitherto, corridors have primarily played a role in conservation biology for improvement of dispersal success and gene flow and, thus, persistence of declining native species in fragmented habitats (Murphy and Lovett-Doust 2004; Horskins et al. 2006). But on the other hand, corridors might also have negative effects by facilitating the spread of diseases or species of concern, such as invasive non-indigenous species (Wiens 2002). In fact, studies investigating occurrences of non-indigenous plant species along road or river corridors have confirmed that corridors may enable or enhance migration of plant species into new regions (Parendes and Jones 2000; Gelbard and Belnap 2003; Pauchard and Alaback 2004; Hansen and Clevenger 2005). Altogether, it can be hypothesized that invasive as well as native plant species in discrete habitat patches may be affected by habitat configuration with respect to patch size, isolation (or connectivity) and corridors.

Factors affecting invasion processes and landscape distributions of invading species are of fundamental scientific and practical interest for invasion biology and the management of invasive species. Yet, despite presumable influences on plant invasion processes, only little research has explicitly investigated effects of landscape structure (With 2004). Apart from theoretical or modelling studies of dispersal of (invasive) plant species in fragmented landscapes (e.g. Collingham and Huntley 2000; King and With 2002), especially empirical studies of the effects of landscape structure on plant invasions are hitherto rare (but see Deckers et al. 2005; Bartuszevige et al. 2006). Thus, there is a need to empirically study effects of habitat configuration on spread and distribution of invasive plant species. In particular, landscapes with ongoing plant invasions provide a unique possibility to investigate relationships between landscape structure and plant species spread.

As relationships between regional plant populations and landscape structure may depend on life-history traits (e.g. dispersal mechanisms, life span, seed production; Dupré and Ehrlén 2002; Kolb and Diekmann 2005), it is advisable to adopt a species-specific approach. For our own empirical study, we chose *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) as a model species. This species invasive to central Europe appeared to be particularly suitable because it presumably has imperfect long-distance dispersal capacity and occurs in discrete habitat patches in its native and invaded range.

The aim of this study was to test the relevance of the patch-corridor-matrix model (Forman 1995) as well as local factors for the landscape distribution pattern of *H. mantegazzianum*. Specifically, we tested the relative effects of (1) transport corridors, (2) habitat connectivity (complementary to isolation), (3) patch size and shape, (4) habitat structure (herbaceous vs. woody habitats), (5) habitat age, (6) land use, (7) soil productivity, and (8) topography on the occupancy of suitable habitat patches by *H. mantegazzianum* and on the saturation of occupied patches by this species.

6.3 Materials and methods

6.3.1 Study species

The study species *Heracleum mantegazzianum* Somm. et Lev. is a megaforb of the Apiaceae family native to the Western Greater Caucasus. The species has a ruderal-competitive strategy and a monocarpic-plurennial life cycle (Ochsmann 1996). *Heracleum mantegazzianum* was introduced to European botanical gardens in the 19th century, and subsequently distributed widely as an ornamental plant in gardens and parks (Pyšek 1991). In the 20th century, the species became invasive and showed a mass increase in several European countries (e.g. Pyšek 1991; Ochsmann 1996; Tiley et al. 1996) and also in some parts of North America. Plant individuals produce around 20,000 seeds (mericarps) with an average weight of 13.1 mg (Hüls 2005; Moravcová et al. 2005), which build up short-term persistent seed banks (Krinke et al. 2005). Seeds are dispersed by water (long-distance dispersal) and wind (short-distance dispersal). Furthermore, dispersal by soil material, garden refuse, and vehicles has been reported (Tiley et al. 1996; Otte and Franke 1998).

Habitats of *H. mantegazzianum* are prevalently fresh to moist, nutrient rich abandoned grasslands, tall-herb stands, ruderal sites, road verges, and riverbanks. Although light demanding, the species can grow fairly well beneath tree rows, or in copses and woodlands with sparse canopies (Thiele and Otte 2006). In preferred habitats, the species can attain dominance and outcompete resident species (Pyšek and Pyšek 1995; Thiele and Otte 2006). However, the species cannot properly develop and reproduce in regularly used agricultural land (arable land, managed meadows and pastures) and closed forests. In the study region, the species is usually absent from housing areas apart from cultivation in gardens which has become rather uncommon in recent years (although *H. mantegazzianum* is fairly common in settlements in a heavily invaded region of the Czech Republic; Pyšek and Pyšek 1995).

Thus habitats of the species in European cultural landscapes form discrete patches or narrow strips along transport corridors (rivers, roads) situated in a virtually inhospitable matrix of agricultural land, forests, and housing areas. Therefore, *H. mantegazzianum* qualifies as a model species to test the patch-corridor-matrix model (habitat isolation, patch size, distance from corridors). Moreover, being the largest forb in Central Europe, the species is easily detectable in the field and, thus, conducive to field inventories.

6.3.2 Study areas

The selection of study areas which we defined as 1 km² landscape sections was based on a Germany-wide questionnaire survey addressed to the nature conservation authorities of all 440 German districts in 2001 (rate of return: 70.2%). As assessment of relationships between environmental factors and invasion pattern is difficult in early stages of invasion due to lack of equilibrium with the new environment (Hulme 2003), we set the criterion that each study area should contain at least three extensive stands (i.e. stands >25 m²) of *H. mantegazzianum*. Thus, the study areas could be considered to be in an advanced stage of invasion.

We investigated 20 study areas in Germany which were predominantly situated in the most heavily invaded natural geographic region ‘Western low mountain ranges’. Subordinately, study areas were situated in the natural geographic region ‘Foothills of the Alps’ (three study areas) which appears to be a secondary invasion focus of *H. mantegazzianum* in Germany (Thiele and Otte, submitted). Locations, coordinates, altitudes and basic climate parameters of study areas are presented in Table 1.

Table 1. Study areas: state, district, coordinates, altitude and basic climate parameters. Coordinates represent the south-western corner of study areas according to the German geodetic system (‘Gauß-Krüger’). Altitudes are the average between the highest and lowest stand of *Heracleum mantegazzianum* within the respective study area. Climate parameters: MAPREC = mean annual precipitation (mm). MATEMP = mean annual temperature. JATEMP = mean January temperature. JUTEMP = mean July temperature. Temperatures are given in °C. Climate data refer to the closest climate station and represent the years 1961-1990 (Deutscher Wetterdienst, www.dwd.de).

		Coordinates			Climate			
State	District ('Landkreis')	East	North	Altitude (m a.s.l.)	MA PREC	MA TEMP	JA TEMP	JU TEMP
Rhineland-Palatinate	Altenkirchen	3410.500	5623.000	160	1041	8.5	0.3	16.7
Rhineland-Palatinate	Ahrweiler	2588.300	5594.500	155	703	9.1	1.1	17.4
North Rhine-Westph.	Ennepe-Ruhr-Kreis	2593.800	5696.400	85	916	9.5	2.0	17.4
North Rhine-Westph.	Euskirchen	2545.800	5595.000	480	769	7.3	-0.1	15.1
North Rhine-Westph.	Euskirchen	2535.500	5589.000	590	937	7.3	-0.1	15.1
Bavaria	Freising	4465.500	5362.500	490	837	7.5	-2.1	16.7
Bavaria	Garmisch-Partenkirchen	4430.200	5270.000	865	1565	6.5	-3.0	15.8
Bavaria	Garmisch-Partenkirchen	4443.500	5253.500	930	1437	6.7	-1.5	15.0
Lower Saxony	Göttingen	3552.500	5710.500	235	768	8.7	0.3	17.1
North Rhine-Westph.	Hagen	3396.700	5687.000	170	1157	9.5	2.0	17.4
North Rhine-Westph.	Hagen	2600.100	5695.500	90	900	9.5	2.0	17.4
North Rhine-Westph.	Hagen	3397.000	5689.800	275	1043	9.5	2.0	17.4
Hesse	Kassel	3529.200	5684.000	290	811	8.1	-0.4	16.6
Hesse	Lahn-Dill-Kreis	3467.000	5595.500	260	713	7.7	-1.0	16.3
North Rhine-Westph.	Olpe	3421.500	5664.500	265	1185	8.1	0.3	16.0
Thuringia	Wartburgkreis	3569.500	5620.500	340	697	8.7	-0.1	17.6
Hesse	Waldeck-Frankenberg	3488.300	5668.500	260	727	7.4	-0.9	15.8
Hesse	Waldeck-Frankenberg	3477.800	5655.500	335	876	7.4	-0.9	15.8
Hesse	Waldeck-Frankenberg	3487.500	5661.200	285	735	7.4	-0.9	15.8
Saarland	St. Wendel	2589.000	5482.100	380	809	9.1	0.6	18.1

6.3.3 Field inventories

Within study areas, we conducted complete inventories of *H. mantegazzianum* in 2002 or 2003. We mapped all stands of the species with a GPS system (differential GPS, sub-meter accuracy). Extensive stands, i.e. stands larger than 25 m² and wider than about one meter, were mapped as polygons while smaller and narrower stands were mapped as points or lines, respectively. Attribute data recorded with *H. mantegazzianum* stands included (i) cover percentage (in cases of extensive stands), (ii) the abundance of individuals (not taking into account seedlings and juveniles with only primary leaves), and (iii) the proportion of reproductive individuals within the stand (six classes: none, -10%, -25%, -50%, -75%, >75%).

Furthermore, we recorded habitat type and land use of the sites as supplementary attribute data, which served as ‘a priori field controls’ for subsequent mapping of occupied and unoccupied habitat patches from aerial photographs.

6.3.4 Mapping of habitat patches

We acquired a multitemporal series of aerial photographs for all study areas for three dates: 1950s, 1970s, and present time (approx. 2000). Patches of suitable habitats for *H. mantegazzianum* were identified by interpretation of present time digital orthophotos and mapped in ArcView GIS 3.2 (© Environmental Systems Research Institute, Inc.; Figure 1). Suitable habitats were all habitat types recorded during field inventories except for managed grasslands which are marginal habitats of *H. mantegazzianum* but do not play a role for the invasion (Thiele and Otte 2006). Different habitat types (Table 2) were mapped as separate polygons. Digitalized historical aerial photographs served to determine habitat age and history. If parts of a present time habitat were different at an earlier date (i.e. different habitat type or non-habitat land-cover type) we subdivided the habitat accordingly. We repeated this procedure for both historical dates (1970s and 1950s) which led to habitat patches based on least common geometries (LCG) with uniform history over the time period covered by aerial photographs. These LCGs, hereafter referred to as ‘habitat patches’, were used as objects for later statistical analyses. Two or several of these habitat patches could lie adjacent forming altogether one contiguous ‘aggregated habitat patch’ consisting of different habitat types or histories (Figure 2).

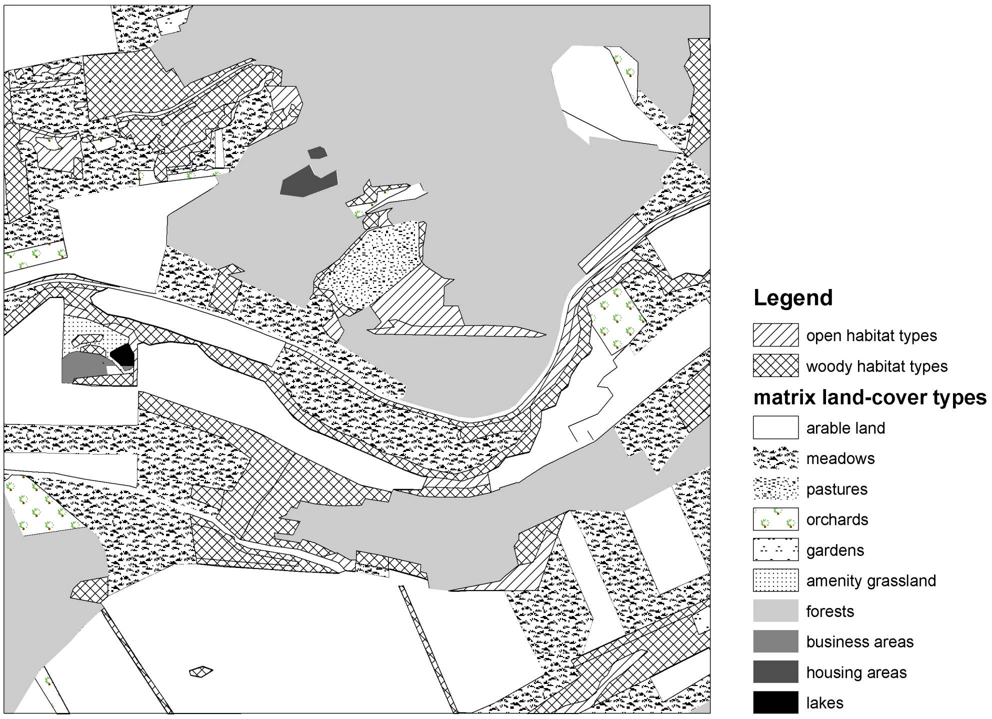

Figure 1. Map of habitat patches of *Heracleum mantegazzianum* and other land-cover types in an exemplary study area (Rhineland-Palatinate, Ahrweiler). Edges of the study area are 1 km.

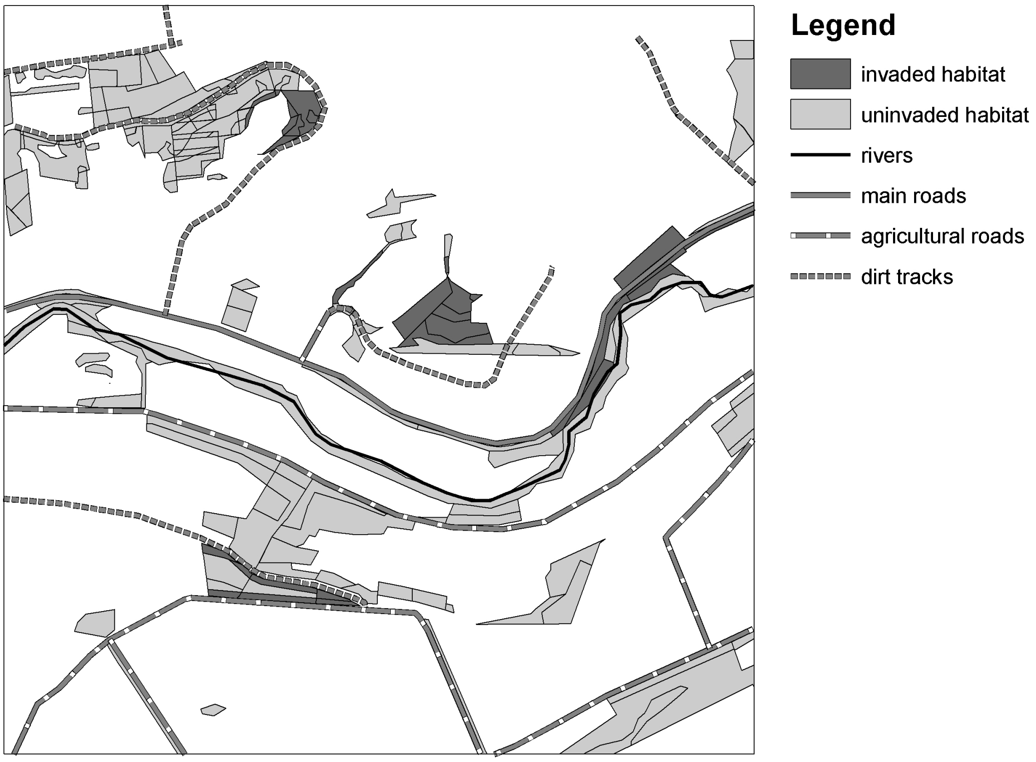

Figure 2. Map of *Heracleum mantegazzianum* presence in habitat patches (least common geometries, LCG) and road and river corridors in an exemplary study area (Rhineland-Palatinate, Ahrweiler). Edges of the study area are 1 km.

Table 2. Habitat types of *Heracleum mantegazzianum* which could be discerned in the mapping of habitat patches from aerial photographs in 20 study areas in Germany. Habitat types were classified based on habitat structure into open and woody ones (>10% tree or shrub cover).

Open habitats
Abandoned grasslands, neglected grassland and field margins, and tall-herb stands
Open riverbanks
Open roadsides
Open railwaysides
Ruderal areas
Cable routes
Woody habitats
(Partly-) Shaded riverbanks
(Partly-) Shaded roadsides
(Partly-) Shaded railwaysides
Tree fallow
Afforestations
Copses

6.3.5 *Variables for statistical analyses*

For analyses of relationships between parameters of *H. mantegazzianum* landscape distribution and environmental properties of habitat patches, we compiled a set of two dependent and 12 potential predictor variables (Table 3).

Dependent variables were (i) habitat occupancy (i.e. presence or absence of *H. mantegazzianum* in all suitable habitat patches), and (ii) saturation of occupied habitat patches (percentage of patch area covered by *H. mantegazzianum*). We calculated the latter as the cover sum of all *H. mantegazzianum* stands within a habitat patch divided by the area of that habitat patch. For this purpose, the cover of point-like and linear stands was calculated from abundance estimates and proportions of reproductive individuals while assuming that the area covered by each individual alone is on average 1 m² for reproductive individuals and 0.1 m² for vegetative individuals.

Table 3. Variables for regression analyses of habitat occupancy and patch saturation of *Heracleum mantegazzianum*.

Variable	Type	Description
Dependent variables		
Habitat occupancy by HM (n = 1555)	binary	Presence or absence of HM in suitable habitat patches
Patch saturation by HM (n = 333)	continuous	HM cover sum within patch / patch area (%)
Independent variables		
HM cover in adjacent patches	continuous	HM cover sum / area sum for all adjacent patches (%)
Distance from flowing waters	continuous	Edge-to-edge distance (m)
Distance from traffic routes	continuous	Edge-to-edge distance (m)
Distance from housing areas etc.	continuous	Edge-to-edge distance (m)
Habitat connectivity	continuous	Proximity index of McGarigal and Marks (1995)
Patch size	continuous	Area (m²)
Patch shape	continuous	Shape index of McGarigal and Marks (1995)
Habitat structure	binary	Open, woody
Habitat age	ordinal	Young (since recently), medium (70ies), old (50ies)
Land use	binary	Fallow, maintenance
Soil productivity	continuous	Official rating of agricultural soils (>0-100)
Topographic unit	categorical	Valley, slope, hilltop, plateau

Note. HM = *Heracleum mantegazzianum*.

Possibly, the occurrence and patch saturation of *H. mantegazzianum* in a particular habitat patch might be influenced by occurrences in the vicinity (auto-correlation). Therefore, we calculated the average cover percentage of *H. mantegazzianum* in adjacent habitat patches for every habitat patch as a potential predictor variable.

In order to take transport *corridors* into account, we mapped flowing waters and traffic routes which can serve as transport vectors and narrow habitat strips for *H. mantegazzianum* from aerial photographs (Figure 2). Likewise, we mapped housing areas and garden lots which might have served as anthropogenic seed sources for *H. mantegazzianum*. Then, we calculated nearest-feature distances (edge to edge) of habitat patches from all of these landscape elements. Distances were calculated separately for the different landscape element classes (traffic routes, flowing waters, housing areas etc.) and different sub-categories of them (e.g. major roads, agricultural roads). For assessment of the *connectivity* of habitat patches, we calculated the area-informed proximity index of McGarigal and Marks (1995) with a search radius of 100 m using the ‘Proximity Analysis’ extension in ArcView (S. Lang, Salzburg, AT). Prior to calculations of the proximity indices, we dissolved adjacent habitat patches to form aggregated patches of contiguous habitat. As the calculation of nearest-feature distances and proximity indices may be flawed by boundary effects (McGarigal and Marks 1995) habitat patches and landscape elements up to 500 m outside of study areas were taken into account. Moreover, we calculated the habitat *patch sizes* in GIS and assessed the *patch shape* with the shape index in FRAGSTATS for ArcView 1.0.1 (McGarigal and Marks 1995).

Obviously, suitability of habitat types for *H. mantegazzianum* differs depending on *habitat structure*, especially, presence or absence of woody components (Thiele and Otte 2006). Therefore, we classified habitat types into completely open and woody ones (tree or shrub cover >10%; Table 2). We derived *habitat age* on an ordinal scale for each current habitat patch from the multitemporal series of aerial photographs. For this purpose, we counted consecutive instances of a patch being a habitat (regardless of the particular habitat type) going back in time from present via ‘1970s’ to ‘1950s’. Furthermore, we classified current *land use* of habitat patches into either ‘Fallow’ or ‘Maintenance’ according to habitat type. ‘Maintenance’ referred to regular or occasional mowing or, at least, removal of shrubs and young trees and was ascribed to open roadsides and railwaysides while all other habitat types were assigned ‘Fallow’. Moreover, we obtained data from the German soil rating survey (‘Reichsbodenschätzung’). On the basis of digitalized cadastral maps, we used these data to create GIS layers of *soil productivity* which we intersected with the habitat mapping. Then, we attributed area-weighted means of soil productivity to the habitat patches. Data of the soil rating survey are not available for the whole landscape but for agricultural land parcels only (arable fields, grasslands). For this reason, soil data were available for only 52% of all habitat patches, while for the remainder average values calculated over all rated patches were used as substitutes. Finally, we subdivided study areas into four topographic units, valley, slope, hilltop, and plateau, which we delineated on the basis of digitalized contour lines in GIS. We assigned each habitat patch to one topographic unit. Habitat patches overlapping with two topographic units were assigned to the unit which took the largest part of them.

6.3.6 Statistical analyses

We conducted two separate analyses for the two dependent variables (i) habitat occupancy (n = 1555) and (ii) patch saturation (n = 333) using appropriate regression models. In a first step, we carried out pre-analyses to downsize the full set of 12 potential predictor variables for each dependent variable separately. Pre-analyses resulted in sets of predictor variables showing significant simple relationships with the respective dependent variable. These sets were used for ‘best subset’ model building in STATISTICA 6.0 (© StatSoft, Inc.) with Akaike’s Information Criterion (AIC) as measure for model selection. After identifying the best subset for each dependent variable, we calculated final regression models.

As habitat occupancy was a binary variable, we tested for effects of predictor variables with a Logistic Regression Model (LRM) which we calculated in SAS 9.1 (© 2002-2003 SAS Institute Inc.). The significance of single effects and interactions was assessed by Type III Likelihood-ratio tests. As a measure of explained variation we calculated McFadden’s R^2 (Shtatland et al. 2002).

For patch saturation, which was a continuous variable, we calculated a General Regression Model (GRM) in STATISTICA. Patch saturation was $\log_{10}$-transformed prior to the analysis in order to fulfil the assumption of normality. Coefficients of partial determination (partial r^2) were calculated according to the method described in Quinn and Keough (2002, p. 123).

The cover of *H. mantegazzianum* in adjacent habitat patches was in the best subsets for both dependent variables. Therefore, the final models were auto-regressive (Legendre and Legendre 1998). We tested residuals of both models for spatial auto-correlation by Mantel tests of spatial and residual distance matrices using XLSTAT (© 1995-2006 Addinsoft). Distance matrices were calculated in PopTools (Hood 2005) for each study area separately as well as for random samples of all objects over all study areas. Mantel tests with spatial and residual distance matrices revealed three study areas with significant spatial correlation of residuals for either model (LRM, GRM). However, except for one instance, these correlations were only marginally significant and would not have been significant after Bonferroni correction. For all other study areas, residuals were spatially uncorrelated. Likewise, random samples of patches over all study areas showed no significant spatial correlation of residuals for either model. Altogether, these tests showed that there was generally no significant spatial auto-correlation of residuals. Therefore, the autoregressive models appeared to be valid.

6.4 Results

6.4.1 Logistic Regression Model (LRM) of habitat occupancy

Tests of the overall model (Score test, Wald test) were highly significant (Table 4) which means the model significantly improved the prediction of *Heracleum mantegazzianum* presence (or absence) compared to a null model containing only an intercept. Although the goodness-of-fit tests suggested some lack-of-fit, the C statistic (86%) which measures association between observed and predicted presence, and McFadden's R² (0.29) indicated good model fit.

Table 4. Logistic regression analysis of habitat occupancy of *Heracleum mantegazzianum* in 1555 suitable habitat patches.

Predictor	Factor level	Estimate	SE Est.	χ^2	df	p	odds ratio (e^{β})	odds ratio units
Intercept[1]		-1.9698	0.3029	134.0195	1533	< 0.0001	*NA*	*NA*
HM cover in adjacent patches		0.8799	0.0790	271.7886	1	< 0.0001	2.4106	1
Habitat connectivity		0.0001	0.0001	12.3969	1	0.0004	1.1606	1000
Distance from rivers		-0.0013	0.0002	37.9279	1	< 0.0001	0.8776	100
Distance from agricultural roads		-0.0051	0.0014	14.9017	1	0.0001	0.6029	100
Patch size		0.0001	0.0001	8.4215	1	0.0037	1.0598	1000
Shape index		0.4116	0.0941	18.7687	1	< 0.0001	1.5093	1
Habitat structure	woody	-0.3779	0.1226	9.6589	1	0.0019	0.4697	*NA*
Land use	none	0.1064	0.1289	0.6944	1	0.4047	1.2373	*NA*
Topography		*NA*	*NA*	2.8582	3	0.4140	*NA*	*NA*
Land use*Topography	none*valley	0.5140	0.1791	8.6717	3	0.0340	*NA*	*NA*
Test				χ^2	df	p		
Overall model evaluation								
Score test				402.5020	21	< 0.0001		
Wald test				235.5080	21	< 0.0001		
Goodness-of-fit test								
Hosmer & Lemeshow				20.1861	8	0.0097		

Explained variation: McFadden's R² = 0.29. Measure of association: C statistic = 86.0%.

Note. All main effects but only significant interactions were included into this table. HM = *Heracleum mantegazzianum*. *NA* = not applicable.

[1] Significance tested by the Wald test.

The relationship between predicted probabilities of *H. mantegazzianum* presence and the percentage of observed presence is graphically represented in Figure 3. Habitat patches with predicted probabilities below 0.1 were occupied by *H. mantegazzianum* in 3.4% of cases, while for predictions >0.9 the percentage of presence was 87.9%. The turning point from less than 50% observed presence to more than 50% observed presence was between predictions of 0.3 and 0.4. Therefore, we calculated the classification table (observations vs. predictions) with a cut-off value of 0.4 (Table 5). The overall percentage of correct predictions was 84.2%. The model performed especially well in correctly predicting absence of *H. mantegazzianum* (specificity: 93.8%), whereas prediction of presence was rather moderate (sensitivity: 49.7%).

Significant positive effects on presence of *H. mantegazzianum* were found for *H. mantegazzianum* cover in adjacent patches, habitat connectivity, and patch size. Further, the significant positive regression coefficient of the shape index implied that elongated or complex polygon shapes favoured *H. mantegazzianum* presence. Conversely, increasing distances from transport corridors (rivers, agricultural roads) and woody habitat structure had negative effects. Furthermore, there was a marginally significant interaction between land use and topography (Table 4).

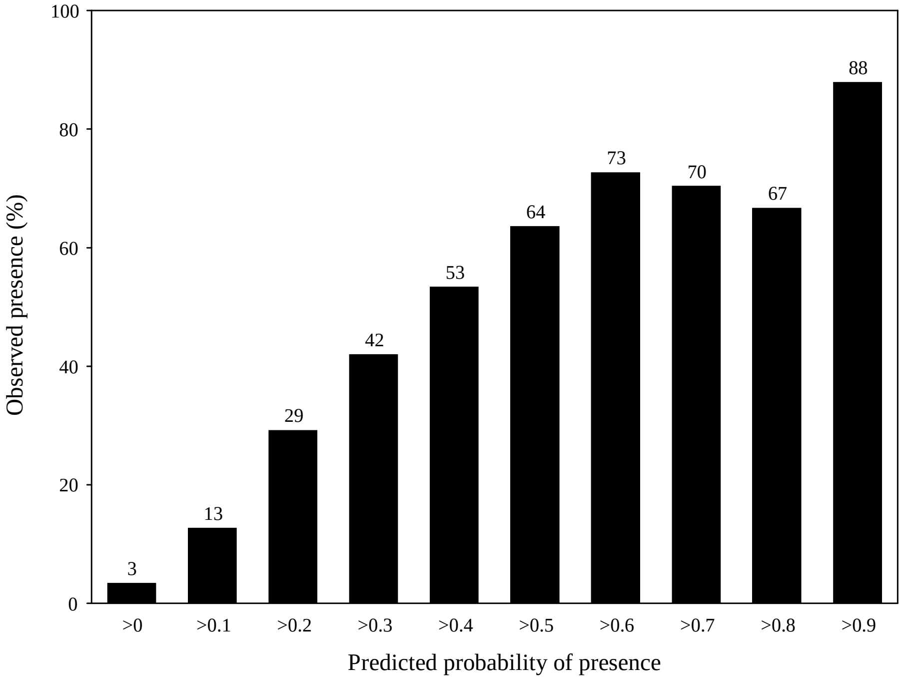

Figure 3. Classified predicted probabilities by logistic regression of presence of *Heracleum mantegazzianum* in suitable habitat patches (abscissa) versus percentage of observed presence (ordinate).

Table 5. Classification table: the observed and the predicted frequencies for presence and absence of *Heracleum mantegazzianum* by logistic regression with the cutoff of 0.4.

Observed	Predicted		% Correct
	Presence	Absence	
Presence	169	171	49.71
Absence	75	1140	93.83
Overall % correct			84.18

Note. Sensitivity = 169/(169+171)% = 49.71%. Specificity = 1140/(75+1140)% = 93.83%. False positive = 75/(75+169)% = 30.74%. False negative = 171/(171+1140)% = 13.04%.

Concerning traffic routes, the negative distance effect or, respectively, positive vicinity effect was significant only for agricultural roads but not for major roads and railways (railways occurred in only 7 out of 20 study areas). The distance effect of agricultural roads was especially marked within 100 m from the road and strongly declined beyond that range (Figure 4). Distances from agricultural roads were especially important in the topographic unit ‘Hilltop’ which showed a highly significant difference between unoccupied and occupied habitat patches (Mann-Whitney U-Test, p <0.001), whereas in the unit ‘Valley’ there was no difference at all, and ‘Slope’ as well as ‘Plateau’ showed intermediate but non-significant results. However, including an interaction between distance from agricultural roads and topographic unit did not significantly improve the model. Rivers affected the occurrence probability up to approx. 300 m from the riverbed (Figure 5). Beyond this threshold, predicted probabilities of presence dropped below 0.2.

The interaction between land use and topographic unit indicated that fallow sites situated in valleys were more prone to invasion by *H. mantegazzianum* than other combinations of these two predictors.

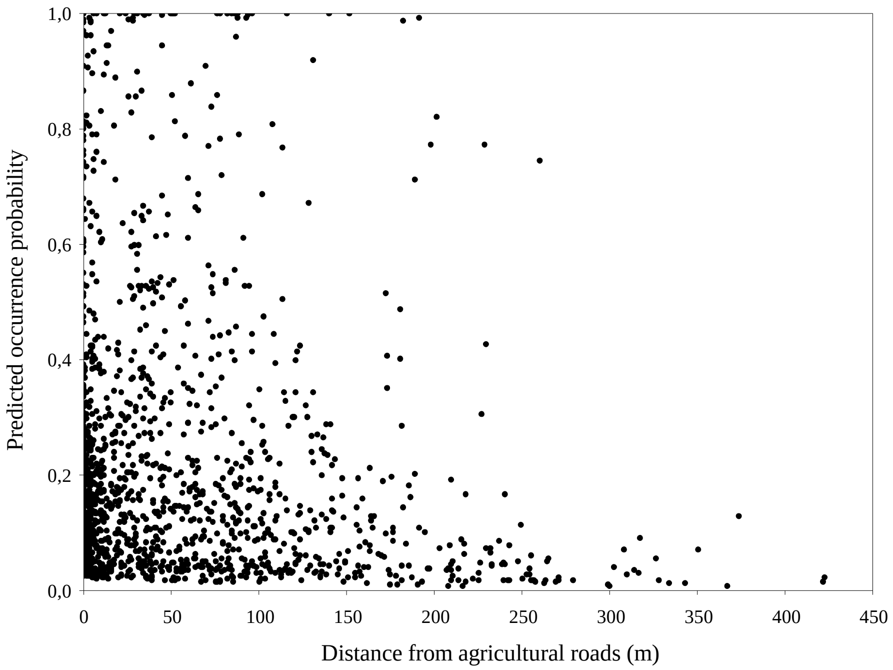

Figure 4. Predicted occurrence probabilities by logistic regression of *Heracleum mantegazzianum* in suitable habitat patches versus distances from agricultural roads.

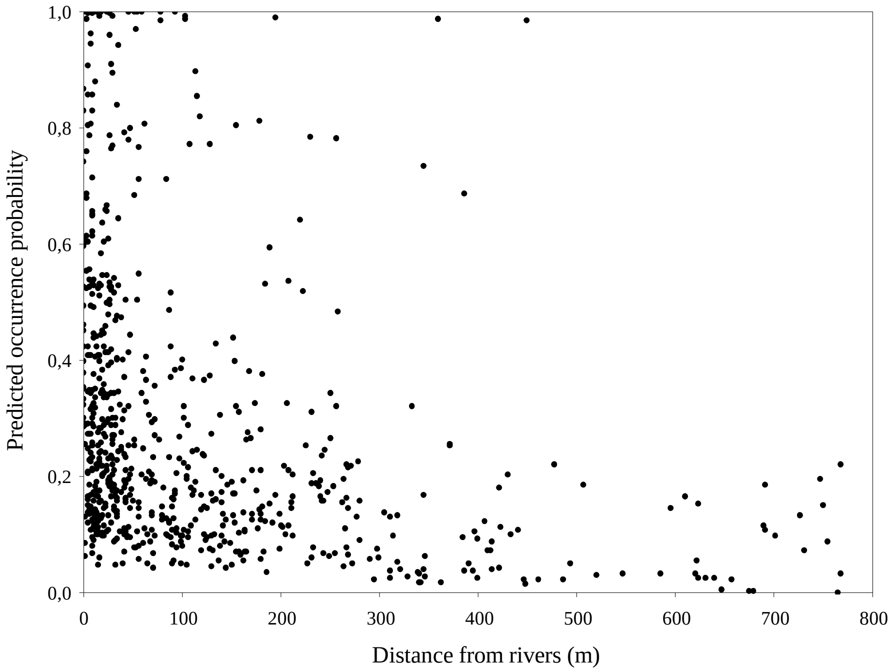

Figure 5. Predicted occurrence probabilities by logistic regression of *Heracleum mantegazzianum* in suitable habitat patches versus distances from rivers.

Measures of effect sizes are given by the odds ratios which represent the change in the odds of *H. mantegazzianum* presence given a unit change in the respective predictor. The odds are the probability of presence divided by the probability of absence. Therefore, odds ratios greater than one indicate an increase of the odds and also an increase in probability of *H. mantegazzianum* presence. However, it is noteworthy that odds ratios, odds and probabilities are different concepts which are positively related but not in a linear fashion (Peng et al. 2002). The odds ratio of *H. mantegazzianum* cover in adjacent patches was 2.41 which means that an increase in average cover of the surrounding from, e.g., 1% to 2% led to a 2.41-fold increase of the odds of *H. mantegazzianum* presence. In contrast, distance from rivers had an odds ratio of 0.88 which was calculated for a distance increase of 100 m. Thus, with every 100 m further from a river the odds of *H. mantegazzianum* presence decreased by the factor 0.88. In order to further illustrate the relationships between predictor variables and predictions, we compiled profiles of habitat patches with high (>0.95) and low (<0.05) predicted probabilities of *H. mantegazzianum* presence which are presented in Table 6.

6.4.2 General Regression Model (GRM) of patch saturation

The GRM of patch saturations was highly significant and explained approx. 20% of the variance (Table 7). Significant predictors were *H. mantegazzianum* cover in adjacent patches, habitat structure, and shape index. Moreover, there was an effect of soil productivity which, however, was only marginally significant.

Again high cover percentages of *H. mantegazzianum* in adjacent patches had a positive effect and, furthermore, high soil productivity tended to favour high patch saturation. As expected, woody habitat structure had a negative effect on patch saturation. In contrast to the LRM of habitat occupancy, the shape index was negatively related to patch saturation which means that elongated or complex-shaped patches had lower *H. mantegazzianum* saturation than isodiametric simple-shaped patches. Most of the explained variance was attributable to habitat structure and *H. mantegazzianum* cover in adjacent patches, whereas shape index and, especially, soil productivity had only minor contributions (see partial r^2 in Table 7).

Table 6. Profiles of suitable habitat patches with high (>.95) and low (<.05) predicted probabilities of *Heracleum mantegazzianum* presence by logistic regression. Profiles are given for open and woody habitat patches separately in each probability class. Values of continuous predictors and predicted probabilities are averages over all cases in the respective profile. For categorical predictors the most frequent category is presented. Number of cases in profiles: Open >.95 = 17. Woody >.95 = 31. Open <.05 = 21. Woody <.05 = 311.

Habitat structure	HM cover in adjacent patches	Distance from		Habitat connectivity	Shape index	Patch size	Land use	Topo-graphy	Predicted occurrence probability	Observed presence [%]
		Rivers	Agricultural roads							
Open	10.69	420.6	50.5	1018.9	1.8	3553.5	Fallow	Valley	0.994	100
Woody	11.93	382.1	51.8	787.5	1.9	1300.9	Fallow	Valley	0.993	87.1
Open	0.02	854.7	223.5	306.1	1.6	720.0	Maint.	Hilltop	0.029	1.3
Woody	0.03	923.4	83.1	886.0	1.5	1299.1	Fallow	Slope	0.032	0

Note. HM = *Heracleum mantegazzianum*.

Table 7. General linear regression analysis of patch saturation of *Heracleum mantegazzianum* in 333 occupied habitat patches.

Predictor	Factor level	Partial r^2	Estimate	β	SE β	F-ratio	p
Intercept		*NA*	0.7022	*NA*	*NA*	73.0236	< 0.0001
HM cover in adjacent patches		0.0750	0.0284	0.2572	0.0499	26.6053	< 0.0001
Habitat structure	woody	0.0995	-0.1442	-0.2977	0.0494	36.2559	< 0.0001
Shape index		0.0361	-0.0995	-0.1763	0.0503	12.2858	0.0005
Soil productivity		0.0152	0.0033	0.1121	0.0498	5.0608	0.0251
Test		Multiple R^2	Corr. R^2	df	MQ	F-ratio	p
Overall model evaluation							
Regression		0.2039	0.1942	4	3.8757	21.0058	< 0.0001
Residual				328	0.1845		

Note. HM = *Heracleum mantegazzianum*. *NA* = not applicable.

6.5 Discussion

6.5.1 Habitat occupancy

The LRM results confirm that both local (habitat structure) and landscape factors (distances from transport corridors, habitat connectivity, patch size and shape) influence habitat occupancy of *H. mantegazzianum*. Local factors are essentially related to recruitment and growth of *H. mantegazzianum*, while landscape factors are related to dispersal processes.

The effect of habitat structure might be directly attributable to trees or shrubs in woody habitats (>10% tree or shrub cover) which constrain by shading the effective patch area suitable for recruitment and growth and, thus, reduce the probability of *H. mantegazzianum* seeds to reach 'safe sites'. In addition to that, it would also be conceivable that lack of disturbance and old successional age of woody habitats exert indirect effects on *H. mantegazzianum* presence through increased competition by (native) tall-herbs under such conditions (Thiele and Otte 2006). Taking into account that recruitment and growth of *H. mantegazzianum* depend considerably on productive site conditions, the insignificance of soil productivity might be surprising. However, the differences of soil productivity between habitat patches were rather moderate and low-productive soils scarcely occurred in the study areas. In the face of these facts, it can be assumed that soil quality would affect occurrence probability of *H. mantegazzianum* in landscapes which feature low productive sites.

Effects of habitat configuration have prevalently been found for perennial species that produce rather low numbers of seeds and have rather poor capacities for long-distance dispersal (Dupré and Ehrlén 2002; Kolb and Diekmann 2005). In this light, the high significance of all parameters of habitat configuration for *H. mantegazzianum* habitat occupancy is remarkable, as *H. mantegazzianum* is a fast spreading, monocarpic plurennial with huge seed production.

Significant effects of distances from transport corridors (rivers, agricultural roads) indicate, on the one hand, that *H. mantegazzianum* successfully spreads through long-distance dispersal and migration along such corridors but, on the other hand, that the species often has failed to reach habitat patches distant from them. Thus, limited long-distance dispersal capability through the landscape matrix seems to be one of the key determinants of the landscape distribution pattern of *H. mantegazzianum,* at least up to the current stage of invasion in the study areas.

The positive effect of rivers on habitat occupancy of *H. mantegazzianum* extended approx. 300 m from the riverbed. This threshold coincided roughly with the largest extent of inundation areas of the rivers in the study areas suggesting that seeds might be dispersed outside riverbeds during floods. The significance of rivers for *H. mantegazzianum* distribution is in agreement with observational studies reporting spread of *H. mantegazzianum* along river corridors (e.g. Pyšek 1991; Tiley and Philp 1994).

Concerning traffic routes, only the distance from agricultural roads (including dirt tracks) had a significant effect while distances from major roads and highways were not significant. This might be due to higher maintenance efforts in the latter categories of traffic routes where roadside mowing is usually conducted on a regular basis (e.g. twice a year) which strongly reduces growth height and seed production (Thiele and Otte 2006) and, hence, spread into adjacent or nearby habitat patches. Nevertheless, migration of *H. mantegazzianum* along major roads has been observed in the Ruhr Area, Germany (Keil and Loos, pers. comm.), and it can be assumed that it also occurs elsewhere even though regular roadside maintenance decreases the opportunities for migration and spread. Lack of regular maintenance of road verges seems to favour the spread of *H. mantegazzianum* by allowing for high seed production in road habitats and, thus, colonisation of nearby habitat patches in the open landscape distant from rivers or human seed sources. In general, road corridors enhance the spread of many invasive and native plant species regardless of the intensity of use (e.g. Parendes and Jones 2000; Watkins et al. 2003; Godefroid and Koedam 2004; Pauchard and Alaback 2004; Rentch et al. 2005).

Railways showed no significant effect in the present study which might be attributable to the fact that they were present in 7 out of 20 study areas only. Nevertheless, railwaysides often present suitable habitats and they featured several occurrences of *H. mantegazzianum* in the respective study areas. Therefore, migration along railways cannot be fundamentally rejected. Generally, railways can support spread of invasive plant species (Hansen and Clevenger 2005).

The findings concerning transport corridors corroborate previous interpretations of *H. mantegazzianum* records which suggested that the species, apart from river corridors, has also spread along traffic routes (Pyšek and Prach 1993; Caffrey 1999). Furthermore, Müllerová et al. (2005) could observe spread of *H. mantegazzianum* from linear landscape elements (rivers, paths, roads) to adjacent extensive habitat patches within recent decades in the Czech Republic in time series of aerial photographs.

The chance of seeds dispersed along corridors to reach a new habitat patch is related to the area and shape of that particular habitat patch as indicated by the highly significant effects of these parameters on habitat occupancy. Generally, the chance of propagule input increases with area and perimeter (per area unit).

Next to long-distance dispersal along transport corridors which substantially influences the landscape distribution, short-distance dispersal affects the local distribution pattern (sub-landscape level) as indicated by the significant effect of *H. mantegazzianum* cover in adjacent patches. After arrival at a new site the species can successfully spread through contiguous aggregates of habitat patches regardless of habitat type, structure, or history. Moreover, the species can ‘jump’ to connected habitat patches in the vicinity (100 m buffer distance for proximity indices) by wind or other means. In such conducive situations of habitat connectivity *H. mantegazzianum* can attain high rates of local habitat occupancy. Rates of local spread have been determined by Müllerová et al. (2005) for 60 ha landscape sections in a heavily invaded region in the Czech Republic. Average rates of spread were 1261 m^2 $year^{-1}$ (areal) and 10.8 m $year^{-1}$ (linear), respectively.

The classification table of observed and predicted frequencies of presence and absence of *H. mantegazzianum* showed a high percentage of correct classification (84.2%; Table 5). However, there was a great difference between correct prediction of absence (93.8%) and correct prediction of presence (49.7%). These results suggest that there are factors included in the model which strongly impede *H. mantegazzianum* occurrence in a number of generally suitable habitat patches. These impeding factors are obviously large distances from transport corridors and disconnectedness of habitat patches which, given *H. mantegazzianum*’s limitation of long-distance dispersal through the matrix, largely prevent invasion of *H. mantegazzianum*. On the other hand, the high rate of predicted absence in patches where the species was in fact present suggests that the pattern of habitat occupancy is substantially influenced by factors not accounted for in the model which help to overcome long-distance dispersal limitation. Most likely, these are human factors such as deliberate sowing into the wild as a bee plant and other human related means of dispersal that were not accounted for by the model (e.g. translocation of dry umbels).

Concerning management, probability-of-occurrence maps (Rew et al. 2005) of invasive species within invaded regions would be a desirable tool to make early detection and application of preventive measures more efficient by narrowing down the area to be surveyed or treated, respectively. However, the low sensitivity (correct prediction of presence) with the cutoff of 0.4 would lead to unreliable probability maps. On the other hand, lowering the cutoff until acceptable sensitivity is reached would hardly diminish the number of patches to be surveyed. Therefore, application of the model to construction of probability maps appears not to be advisable for already invaded landscapes. Nevertheless, in currently uninvaded landscapes the model might be appropriate to identify habitats most likely to be invaded in the first place after *H. mantegazzianum* arrival. A promising extension of the static LRM model would be to incorporate parameters of landscape features together with more detailed local data into spatially-explicit dynamic models in order to assess invasion dynamics and predict equilibrium stages of invasive plant species.

6.5.2 Patch saturation

In contrast to habitat occupancy, patch saturation was not substantially influenced by habitat configuration (apart form patch shape, see below). Instead local factors prevailed and, additionally, spatial auto-correlation was found. These results suggest that patch saturation does not depend on seed input from long-distance dispersal. It rather depends on local habitat conditions governing recruitment, growth and seed production and, secondly, on propagule pressure from the immediate vicinity (adjacent patches). The negative effect of woody habitat structure confirms that patch saturation of *H. mantegazzianum* is constrained by woody components of the vegetation and, presumably, by increased competition from other tall-herbs under low disturbance and old successional age which characterize woody habitats. Conversely, high soil productivity seems to facilitate high patch saturation of *H. mantegazzianum* which would be plausible taking into account that the species has a quite high demand for nutrients and moisture (Pyšek and Pyšek 1995; Tiley et al. 1996; Otte and Franke 1998; Thiele and Otte 2006). Yet it has to be borne in mind that values of soil productivity were available for 52% of habitat patches only and the effect was only marginally significant. Although, we would expect the significance of soil productivity to rather increase given that all patches were rated, the diagnosis of a facilitating effect of soil productivity within the rather short productivity gradient of the habitat patches in our study areas appears to be vague.

Altogether, the sum of variance explained by local factors included in the model (habitat structure, soil productivity) was rather low suggesting that other local factors have additional influence or are even more important for patch saturation of *H. mantegazzianum*. At this point, small-scale disturbances facilitating recruitment of *H. mantegazzianum* (Thiele, Otte, Scholz-vom Hofe, unpublished data) and biotic interactions, particularly presence or absence of competitive species (Thiele and Otte 2006), come into consideration. However, in this study it was not possible to account for these factors. Moreover, it would be possible that *H. mantegazzianum* cover within habitat patches is not yet in tune with environmental conditions.

Concerning habitat configuration, patch shape was the only significant predictor and had a negative effect on patch saturation, which was diametrically opposed to its effects on habitat occupancy. The negative effect implied that elongated and complex shapes featured lower patch saturation of *H. mantegazzianum* which might be attributable to elongated habitat patches along major roads facing comparatively intense maintenance management which reduces *H. mantegazzianum* cover and abundance. Pyšek and Pyšek (1995) found that adjacency to roads and flowing waters was a significant factor for patch saturation of *H. mantegazzianum*. This pattern, however, was not found in the present study.

6.5.3 Insignificant factors

Against expectations, land use and patch age had no significant effects in both models. Concerning land use, other observations have shown that regular (agricultural) land use constrains *H. mantegazzianum* to low abundances, and reduces growth height and fruit set (Thiele and Otte 2006). However, suitable habitat types are either disused or maintained at rather low intensities compared to agricultural use. Apparently, there is no significant difference between disuse and low-intensity maintenance for habitat occupancy and patch saturation of *H. mantegazzianum*.

Regarding patch age we had assumed that younger successional stages after abandonment or disturbance should be more easily invasible by *H. mantegazzianum* and facilitate high patch saturation. However, this could not be confirmed by the models presented here. The reason for lack of significance might be the temporal and spatial scale at which patch age was measured. The temporal resolution was approx. 25 years which probably is too long to separate ‘young’ and ‘old’ habitats for *H. mantegazzianum*. Further, the grain of this study was patches which did not allow for recording possible small-scale disturbances facilitating recruitment.

6.6 Conclusions

The present study confirms that habitat occupancy of plant species may depend on both local and landscape factors. Particularly, the results emphasize the importance of habitat configuration for the landscape distribution of plant species and for the spread of invasive species.

The landscape distribution pattern of *Heracleum mantegazzianum* is strongly mediated by dispersal processes which depend on transport corridors (rivers, roads) and connectivity of habitat patches whereas dispersal through the landscape matrix is limited. Therefore, cultural landscapes of Central Europe function as patch-corridor-matrix mosaics for the spread of *H. mantegazzianum*.

Application of the LRM for construction of probability-of-occurrence maps could provide a means for more efficient early detection and prevention in previously uninvaded landscapes. Concerning preventive measures, regular maintenance of roadside habitats could impede further spread of *H. mantegazzianum* outside river valleys.

In contrast to habitat occupancy, patch saturation of *H. mantegazzianum* does not depend on landscape factors. Not even local factors included in this study (habitat structure, soil productivity) could satisfactorily explain patch saturation. Therefore, we would suggest that sub-patch level factors, such as small-scale disturbances and biotic interactions, are more important determinants of the saturation of habitat patches.

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

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7.1 Abstract

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 scale 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 *Heracleum 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 *Heracleum 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 *Heracleum mantegazzianum* was 8.7%. The invasion percentage (% area invaded) was 18.5%. In conclusion, our results suggest that today *Heracleum mantegazzianum* has only moderate impacts on the regional and landscape scale even in most heavily invaded regions of Germany.

Keywords*:* abandoned grassland, dominance, habitat saturation, impact assessment, invasion success, invasive alien species.

7.2 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 range in the Western Greater Caucasus to botanic and private gardens in several European countries in the 19th century (e.g. Wyse Jackson 1989; Ochsmann 1996; Kowarik 2003). During the 20th century the species became a popular ornamental plant (Kobylka 1977, in Pyšek 1991; Sheldon 1982; Lundström 1984) and was also propagated as a bee plant (Zander 1930; Adolphi 1995). Hence, the species has been widely dispersed by humans (gardeners and bee keepers) which substantially enhanced its spread (Pyšek 1991). *Heracleum 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 and 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).

Heracleum 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 and Hunter 1970; Lagey et al. 1995; Jaspersen-Schip et al. 1996). Further, it conflicts with recreational and economic interests, e.g. by obstruction of trails and riverbanks (Tiley and 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; Pyšek and Pyšek 1995; Manchester and Bullock 2000; Thiele and 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 mio. € (Reinhardt et al. 2003).

As monetary resources are always limiting, 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 nonindigenous species have rarely been conducted (Parker et al. 1999; Byers et al. 2002).

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 and 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 *Heracleum mantegazzianum* on native habitats at the regional and landscape scale. Our objectives were:

(1) to assess the large scale pattern of *H. mantegazzianum* invasion throughout Germany and to identify regions where the species is ‘invasive’,

(2) to record the distribution and abundance of the species in the most heavily invaded landscapes with regard to different habitat types,

(3) to 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) to assess present impacts and to make a prognosis for the species' potential to threaten regional biodiversity.

7.3 Methods

7.3.1 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 to 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.

7.3.2 Locating and mapping of study areas

For our own field research, study areas were defined as landscape sections of 1 by 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) to add objectivity to the sampling procedure (all encountered areas meeting the requirements 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 scrutinized 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 (submeter 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 (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.

Table 1. State, district, grid coordinates and altitudes of study areas. Coordinates represent the south-western corner of study areas (each 1 by1 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.

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

7.3.3 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 and 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 in interpretation of aerial images are listed and described in Table 2.

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.

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
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	Copses, 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

7.4 Results

7.4.1 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: $p < 0.001$). *Heracleum 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 mentioned 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 large extent (>1000 m²) 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.

7.4.2 Field investigations

The study areas were prevalently 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. The stands occupied an area of 16.4 ha (0.8% of the total study area) altogether. Open stands (11.8 ha) generally prevailed over dominant ones (4.6 ha). With both stand types, sizes of single stands between 100 to 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 to 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 whether 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 railway embankments. In contrast to the questionnaire survey, abandoned grasslands were among the commonest habitat types of *H. mantegazzianum* and the species was even found in managed grasslands quite regularly. Further the species occurred with intermediate frequencies in woodlands (copses, 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 lacking 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 and Otte 2006).

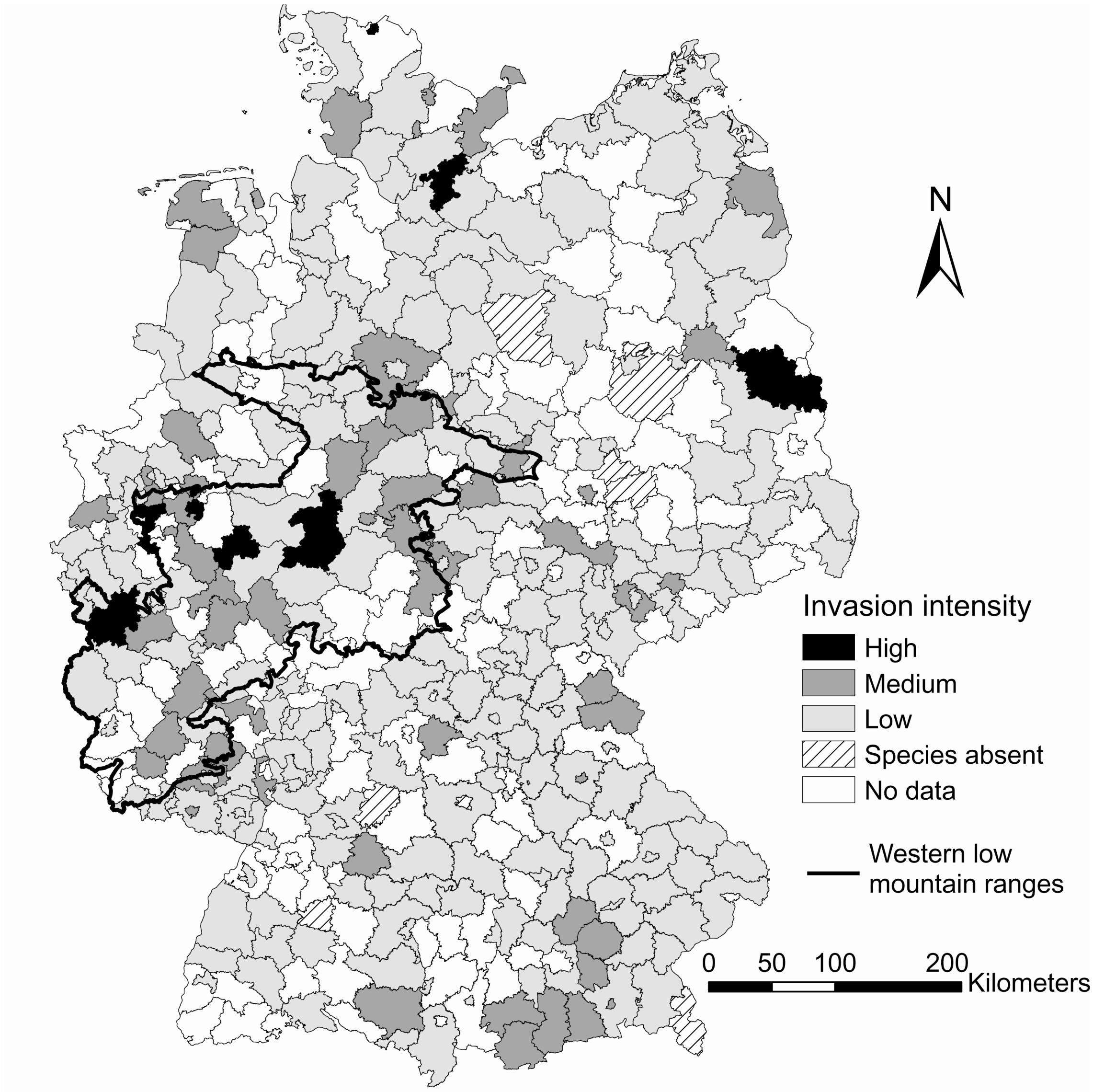

Figure 1. District-wise map of *Heracleum mantegazzianum* Somm. et Lev. invasion intensity in Germany. Classification of invasion intensity was based on a Germany-wide survey addressed to 440 district conservation authorities in 2001. The line signature delineates the natural geographic region ‘western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

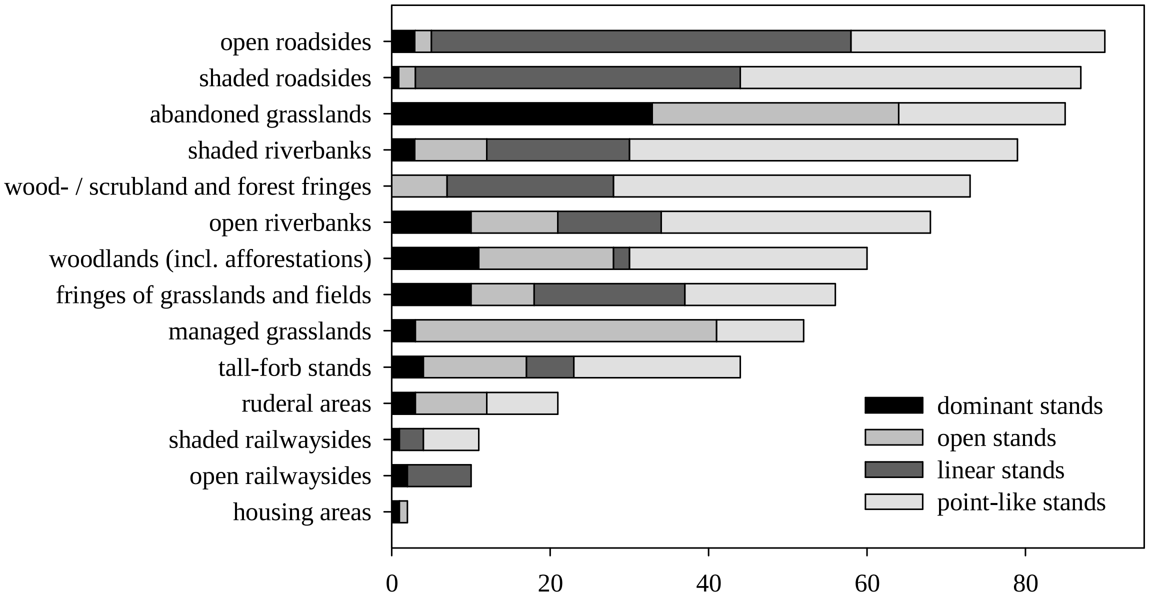

Figure 2. Absolute frequencies of *Heracleum mantegazzianum* Somm. et Lev. incidences found during field surveys of 2002 and 2003 in different habitat types. Signatures separate different stand types of *H. mantegazzianum* (point-like stands, linear stands, extensive open stands, extensive dominant stands).

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.

7.5 Discussion

7.5.1 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 third 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 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 overestimated than underestimated. 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 overestimate invasion severity, it can be assumed that in these districts *H. mantegazzianum* really has mere sporadic and small occurrences.

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 by 1 km^2) in Germany. 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.

Habitat type	Habitat area available (m^2)	Open stands		Dominant stands		Point-like & linear stands		Habitat saturation	
		Area invaded (m^2)	Invasion rate (%)	Area invaded (m^2)	Invasion rate (%)	Area invaded (m^2)	Invasion rate (%)	Area covered (m^2)	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	1855	2.8
Ruderal areas	79 259	1 806	2.3	2 707	3.4	56	0.1	2189	2.8
Open roadsides	67 001	1 057	1.6	307	0.5	899	1.3	1085	1.6
Shaded riverbanks	219 569	3 809	1.7	462	0.2	299	0.1	2108	0.7
Woodlands	1 284 723	10 414	0.8	11 320	0.9	649	0.1	5760	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	2498	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

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 few isolated centres of invasion do exist (two study areas were investigated). Presumably, in these cases classification into ‘medium’ level of invasion intensity is rather an overestimation which might be attributable to higher awareness of nature conservation authorities in this region 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) closer 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 and 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.

7.5.2 Invasion pattern in study areas

Saturation of suitable habitats with stands of *H. mantegazzianum* best represents the invasion success (Pyšek and 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 and 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, in the reverse, 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.

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 characterized 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: Firstly, 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 1987; Pyšek 1994; Pyšek and Pyšek 1995; Ochsmann 1996; Wade et al. 1997) but rarely (abandoned) grasslands (e.g. Tiley et al. 1996). Secondly, 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 these habitat types outside these foci.

According to the Germany-wide survey, *H. mantegazzianum* has invaded nature reserves in approximately a 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 and 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).

7.5.3 Assessment of impacts

Heracleum 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, in 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 scale within the focal region ‘western low mountain ranges’. However, even in most heavily invaded landscapes, today the species occupies only moderate or low proportions of potentially suitable habitats, and thus, at present, the 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 programs appear not to be mandatory. Nevertheless, the species bears other implications, e.g. for human health (Drever and Hunter 1970; Lagey et al. 1995; Jaspersen-Schip 1996), river management (Williamson and Forbes 1982; Caffrey 1994; Tiley and Philp 1994), and public accessibility of sites, such as riverbanks, amenity areas, and trails (Lundström 1984; Tiley and 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).

7.6 Acknowledgements

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8 General discussion

8.1 Factors facilitating or constraining the invasion of *Heracleum mantegazzianum*

8.1.1 Local scale

The results of the studies presented in this thesis show that habitat occupancy (i.e. presence or absence in suitable habitat patches) and cover-abundances of *H. mantegazzianum* depend on several factors acting on different scales and controlling different phases of the plant's life cycle. The first step in the colonisation of new habitat patches is recruitment (germination and establishment) of juvenile individuals. High proportions of disturbed sites among preferred habitats (chapter 5) in accord with the plant's competitive-ruderal strategy suggest that recruitment success of *H. mantegazzianum* depends on disturbed microsites (gaps). This was corroborated by a recruitment experiment in closed grassland swards where recruitment of *H. mantegazzianum* could only be observed in disturbed subplots (0.1 m²) where the sward had been removed completely, whereas in undisturbed or only slightly hoed subplots recruitment was zero (Thiele, Otte, Scholz-vom Hofe, unpublished data). Although large-seeded species, such as *H. mantegazzianum*, usually respond less to gaps than small-seeded ones (Gross and Werner 1982; Donath et al. 2006), recruitment in dense swards appears to rely more or less completely on gaps where competition with resident species has been reduced by small-scale disturbances. These findings are in accordance with the general theory of plant invasions which predicts that soil disturbances usually increase invasion success (e.g. Burke and Grime 1996; Prieur-Richard and Lavorel 2000). Such disturbances can be anthropogenic or natural, e.g. deposition of garden cuttings, wounding of the sward by land machinery, or digging by animals. In habitats where vegetation cover is strongly reduced due to larger-scale disturbances (e.g. open-cast mining) there is, of course, no need for further small-scale disturbances and gap creation.

Growth and seed production depend on local factors related to habitat patches. These local factors can be grouped into abiotic resources, land use, competition and large-scale disturbances. Good supply of abiotic resources (nutrients, water, light, soil aeration) facilitates growth and seed production and, subsequently, local spread, high cover-abundances and high patch saturation of *H. mantegazzianum*. In contrast, regular land use and competition are constraining factors and large-scale disturbances can have varying effects depending on timing and frequency.

Apart from shading which is a major constraining factor (Ochsmann 1996; chapter 5.5.1.5), statistical evidence for relationships between abiotic resources and growth or seed production of *H. mantegazzianum* (measured as height of the leaf canopy and proportion of flowering individuals, respectively) is rather weak in the studies of this thesis. This is probably attributable to the shortness of the gradient of nutrient and water availability at investigated sites which mostly offered favourable conditions (chapter 5.5; Table 3, 4). Nevertheless, it can be plausibly inferred from the analysis of vegetation and site data that growth depends on resource supply meeting comparatively high minimum requirements (chapter 5.6.1).

It appears, that regular land management at appropriate intensities, e.g. mowing twice a year, is the primary constraining factor, besides deep shade, of *H. mantegazzianum* presence and abundance in German cultural landscapes. In appropriately managed grasslands, *H. mantegazzianum* is usually confined to marginal zones, whereas the invasion of the interior of managed grasslands parcels could hardly be observed. This pattern indicates source-sink dynamics depending on seed input from vital stands in adjacent fringes. Thus, under regular grassland management *H. mantegazzianum* appears to be rather a transient species. Although this species has a high phenotypical plasticity and good resprouting capability, regular mowing or grazing prevent high abundances (chapter 5.5.4; Figure 5) and reduce fruit set (Otte and Franke 1998). Unlike co-occuring native Apiaceae species, such as *Anthriscus sylvestris* L. and *Heracleum sphondylium* L. which are also competitive ruderals but with a polycarpic-perennial life cycle (Grime et al. 1988), it seems that *H. mantegazzianum* is not capable to adapt to regular grassland management regimes. Explanations for the failure to establish self-maintaining populations in regularly managed grasslands are high mortality rates of juveniles after establishment in grasslands swards (Thiele, Otte, Scholz-vom Hofe, unpublished data), extension of the time until flowering up to 12 years (Hüls 2005; Pergl et al. 2005), flowering phenology not in tune with usual mowing regimes (cf. Perglová et al. 2006) and lack of clonal growth. However, transient stands can have founder effects (Grime 2001) and build up vital stands when land use is abandoned or relaxed below appropriate levels.

Effects of competition by other plant species on growth and seed production cannot be directly measured in empirical field studies as presented in this thesis. However, analysis of vegetation data (chapter 5) suggests that competition is an important mechanism constraining cover-abundances of *H. mantegazzianum*. Along the main vegetation gradient which reflected secondary successions following mainly abandonment of grasslands or large-scale disturbances, the proportion of C-strategy among resident species increased (chapter 5.5.3, Figure 3). This is attributable to the arrival and increases in cover-abundance of competitive species in the course of succession. The general increase of competitors is accompanied by a decrease of *H. mantegazzianum* cover-abundance (chapter 5.5.4, Figure 6). As the data were single records from different sites in different successional stages the exact mechanisms behind this pattern remain unclear. On the one hand, this pattern could be caused by less successful invasion into old successional stages or, on the other hand, by establishment of high cover-abundances in young successional stages and subsequent decline due to increasing competition. As the supply of nutrients and water was mostly high at investigated sites it can be assumed that *H. mantegazzianum* and native tall herbs prevalently compete for light. Adult individuals of *H. mantegazzianum* should not face problems to receive sufficient light because they are at least as tall as native competitors. But during the recruitment phase and the early growth phase competition with juveniles and adults of other species might increase mortality rates. On the whole, these considerations suggest that dominant stands might develop into mixed tall-herb stands over time due to arrival and increase of other competitive species. Outstanding examples of species rich mixed stands can be found in the native range in the Western Greater Caucasus (Otte et al. 2007).

While small-scale disturbances primarily facilitate recruitment in dense swards, large-scale disturbances can also have indirect facilitating effects on the growth phase of *H. mantegazzianum.* Initially after large-scale disturbance or abandonment of land use, competitive tall herbs are often lacking which opens ‘windows of opportunity’ for potential colonisers. *Heracleum mantegazzianum*, as well as native tall herbs, can make use of such opportunities, and the dominance by competitive-ruderal species, such as *H. mantegazzianum*, in young successional stages is often the outcome of a ‘race between seedlings’ (Grime 2001) and the sequence of colonisation (‘priority effects’; Ward and Thornton 2000; Seabloom et al. 2003). Thus, timing of disturbance (or abandonment) and arrival of tall-herb species might explain a large part of the high variability of *H. mantegazzianum* cover-abundances in tall-herb communities of successional seres.

Depending on life cycle characteristics and competitive abilities, plants have a preference for particular disturbance regimes. In general, frequent disturbances favour short-lived ruderals while relaxation of land management and other disturbances brings about a decline of competitive-ruderal strategies and a simultaneous increase of competitors (Grime 2001). Regarding *H. mantegazzianum*, the average time until flowering is three to five years in open and dominant stands, respectively (Hüls 2005). On the one hand, annual disturbances, such as mowing or cutting hamper the growth of *H. mantegazzianum* and, on the other hand, habitats which have not faced large-scale disturbance for more than 20 years show reduced cover-abundances. Therefore, it can be assumed that disturbances recurring every five to 20 years present especially suitable conditions for the long-time survival of *H. mantegazzianum* in a particular habitat patch. Such disturbance frequencies are reflected in the preferred plant community types of *H. mantegazzianum* (Aegopodion) which emerge after disturbance events in the course of several years of undisturbed development. Communities such as managed grasslands (Arrhenatherion, Cynosurion) or biennial tall-herb communities (Alliarion), are rather marginal vegetation types because here disturbances are too frequent to allow for optimal development of *H. mantegazzianum*.

8.1.2 Landscape scale

In the study areas, which represented the most heavily invaded landscapes of Germany, *H. mantegazzianum* occupied 21% of all suitable habitat patches (least common geometries; chapter 6) and 31% of optimal habitat patches (i.e. tree and shrubless habitat types). Thus, hitherto the species has not been able to utilise a large part of suitable habitat area in the most heavily invaded landscapes. Possibly, the species might reach higher rates of habitat occupancy in the future. However, at least at the current stage of invasion, dispersal limitation at the landscape scale is a key factor for the landscape distribution pattern and moderate rates of habitat saturation of *H. mantegazzianum* (maximum 8.7%; chapter 7, Table 3). Evidence for dispersal limitation is given indirectly by the significant facilitating effects on habitat occupancy of short distances from transport corridors (rivers, roads) and high habitat connectivity, which both help to overcome dispersal limitation (chapter 6).

The analysis of habitat occupancy showed that *H. mantegazzianum* occurs quite frequently in habitat patches which should be unoccupied according to the predictions of the LRM (chapter 6). It seems likely that colonisation of such ‘remote patches’ has been largely facilitated by human activities, such as sowing the species in the wild as a bee plant.

Habitats of *H. mantegazzianum* are mostly highly dynamic, and land-use changes, particularly abandonment of regular grassland management, are the main drivers of these dynamics in cultural landscapes of Germany (chapter 5; Table 2). At the landscape scale, the study areas showed a strong decline of agricultural land (arable land, grasslands) during the last 50 years and a simultaneous increase of suitable habitat area for *H. mantegazzianum* (Thiele and Otte, 2007a). This increase of available habitat area has, presumably, lead to increased connectivity of habitat patches. Possibly, there might be a more or less definite threshold level of habitat required for invasive spread at the landscape scale (With 2004).

8.1.3 Regional scale

The grid map from the national floristic database (chapter 2, Figure 3) shows a wide current distribution of *H. mantegazzianum* throughout Germany which is the outcome of the exponential increase of locations during the last 50 years with 75% of current incidences first recorded after 1980 (German national floristic database, www.floraweb.de). In general, long-distance dispersal events govern the invasion speed even when they are rare (With 2002). Therefore, long-distance dispersal by rivers may largely explain the fast spread of *H. mantegazzianum*. However, during recent decades there has obviously been a fast increase of invaded sites outside river corridors. Taking into account an observed average linear spread through habitat patches of 10.8 m year^{-1} (Müllerová et al. 2005) it is clear that the fast spread throughout regions cannot be fully explained by long-distance dispersal by rivers and subsequent dispersal and migration along road corridors outside rivers valleys. Apparently, the massive increase during recent decades has been mediated by hierarchic diffusion (Hengeveld 1989 in Weber 1998) based on a number of nascent foci outside river corridors. Obviously, the establishment of these foci is prevalently attributable to human factors such as cultivation in gardens and parks and sowing into the wild as a bee plant. Therefore, it appears that the invasion speed of *H. mantegazzianum* has been increased by massive human ‘assistance’ which helped to overcome dispersal limitation.

The estimates of invasion intensities on a district base (chapter 7, Figure 2) showed that there is a high degree of variation between districts and there are only comparatively few invasion ‘hot spots’. These are prevalently found in districts for which Bethe and Bolsius (1995) have recognized that agriculture is likely or very likely to be reduced. Therefore, it appears that land use dynamics are primarily responsible for the heterogeneous pattern of invasion intensities in districts. Large-scale abandonment of land use leads to a high habitat availability and connectivity and, thus, facilitates spread at the landscape scale. Moreover, low-intensity maintenance of road verges (especially of agricultural roads) facilitates migration of *H. mantegazzianum* into landscape sections outside river valleys or distant from anthropogenic invasion foci. In this way, the species has been able to make use of increased habitat availability. Altogether, these factors facilitate comparatively high invasion intensities in districts characterized by declining land use. On the other hand, intensive management of agricultural land and road verges which is typical of high-intensity land use regions largely prevents spread of *H. mantegazzianum*. On the whole, the regional pattern of *H. mantegazzianum* invasion supports the view of Radosevich (2003) who stated that “the existence of small nascent populations aided by long-distance dispersal agents and human perturbations may account for the marked population increase and expansion of exotic invading species.”

8.2 Impacts on native flora and vegetation

8.2.1 General comments

Following programs and conventions in the 1980s and 1990s, such as the Global Invasive Species Programme (http://www.gisp.org/) and the Rio-Convention on Biological Diversity (CBD; http://www.biodiv.org/convention/default.shtml), the awareness of the ‘invasive species problem’ has strongly increased. Research and reports on invasive species have understandably targeted such species which appeared to be especially harmful. In the light of worst cases and ‘horror stories’, differentiating views of invasive species may have been somewhat neglected in recent decades. Wholesale judgements, such as “Biological invasions are believed to be the second largest cause of current biodiversity loss” (Vitousek et al. 1997; Keane and Crawley 2002) lack differentiation between taxonomic groups (animals, plants, pathogens etc.), geographic situations (continents, oceanic islands), and spatial scales, and are of little help for policy makers and practitioners. It may be possible that scientists, nature conservationists, land managers and other people concerned may sometimes have tended to direct their perception especially at vital and dominant stands of invasive plants, while passing over subordinate stands rather cursorily or considering them as nascent foci.

Heracleum mantegazzianum has commonly been perceived as an especially harmful plant invader which is generally superior over indigenous species and dramatically suppresses native biodiversity (e.g. Lundström 1984; Pyšek and Pyšek 1995). Moreover, it has been considered to seriously invade and threaten protected plant communities and habitats (chapter 7). Without doubt *H. mantegazzianum* is a highly successful invader in Central European cultural landscapes which can be seen from its fast spread during the second half of the 20th century, its wide distribution, and its ability to form dominant stands. However, the studies of this thesis indicate some discrepancies between the perceived harmfulness and the reality of *H. mantegazzianum* in its invaded range in Germany and support a more differentiated view on this species.

8.2.2 Patch scale

In cases where *H. mantegazzianum* attains high cover percentages, these certainly lead to far-reaching alterations of resident plant communities. These alterations concern the abundance of resident species, vegetation structure, floristic composition, and eventually ecological function. In fact, there was an overall negative correlation between the number of vascular plant species and cover percentage of *H. mantegazzianum* (chapter 5), suggesting a suppressing effect on species diversity. However, a thorough assessment of impacts on species diversity requires to distinguish different plant community types and to consider presumable mechanisms. A more detailed analysis of sampling plots showed that within particular community types there are practically no significant relationships between cover percentage of *H. mantegazzianum* and species numbers but community type is the overruling factor (Thiele and Otte 2007).

Generally, tall-herb communities had lower species numbers per sampling plot (25 m²) than managed or ruderal grasslands. The main mechanism by which *H. mantegazzianum* can outcompete other plant species is outshading of lower-growing species. It is obvious that high cover percentages of *H. mantegazzianum* can exclude light-demanding species of grasslands or pioneer vegetation in the course of secondary successions towards tall-herb communities, resulting in reduced species numbers per unit area. However, *H. mantegazzianum* does not reduce species numbers below the average level of tall-herb communities. This suggests that effects of *H. mantegazzianum* do not differ from those of native tall-herbs and supplements evidence that invaders do not fundamentally differ from natives (e.g. Daehler 2003; Hulme 2003; Bruno et al. 2004). Generally, species numbers per unit area decrease in the course of succession from low-growing and light-demanding vegetation types towards tall-herb stands and, finally, woodlands (Schmidt 1981; Neuhäusl and Neuhäuslova-Novotna 1985; Meiners et al. 2001; Kahmen 2004). Thus, loss of plant species diversity in such cases is a general symptom of successional changes rather than a particular effect of invasive species.

Plot-level analyses (chapter 5) indicated that stands of *H. mantegazzianum* can have varying cover percentages between one and almost 100%. The current rate of dominant stands of *H. mantegazzianum* was 36% of all extensive stands (chapter 7). This cannot be treated as a fixed figure as cover percentages in sampled plots are not necessarily in equilibrium with their environment. However, response curves of *H. mantegazzianum* and native species along the successional gradient (chapter 5.5.4, Figure 6) suggest that there will be no uniform increase of cover-abundances but rather both increases and decreases depending on successional stage. Altogether, these results lead to the conclusion that *H. mantegazzianum* is not generally a dominant species as often feared but mostly a co-dominant and sometimes subordinate species.

8.2.3 Landscape and regional scale

At the current stage of invasion in the most heavily invaded German landscapes, which were studied here, the constraints and limitations of *H. mantegazzianum* are reflected in rather moderate rates of habitat saturation. Thus, up to the present stage of invasion, there appears to be no severe impact on regional populations of native plant species. Of course, the invasion pattern of *H. mantegazzianum* recorded in the study areas is merely a snapshot which does not provide means for predicting the future development. Nevertheless, some issues related to the invasion process and impact potential of *H. mantegazzianum* shall be discussed here.

The currently rather low rates of habitat occupancy and saturation suggest that there is a high potential for further spread and it could be assumed that *H. mantegazzianum* will further increase. In a heavily invaded region of the Czech Republic, Müllerová et al. (2005) observed a strong and steady increase of invaded area in landscape sections (60 ha). Rates of *H. mantegazzianum* spread were on average 1261 m² year^{-1} (areal) and 10.8 m year^{-1} (linear). However, these rates refer to spread through more or less contiguous habitats and do not apply to mosaics of cultural landscapes with regular land-use regimes. Taking into account the limited capacity for long-distance dispersal between habitat patches, it can be assumed that it would take *H. mantegazzianum* some more decades to occupy all suitable habitats within the study areas. At this point**,** dynamics of suitable habitats have to be considered. Most of the habitats of *H. mantegazzianum* are created by disturbance or abandonment of land use (chapter 5; Thiele and Otte 2007a) and, thereafter, gradually become more and more resistant or unsuitable for *H. mantegazzianum* due to secondary successions towards woodlands or forests. The time span to the establishment of closed tree or shrub canopies which exclude light-demanding tall herbs is variable but usually in the order of few decades (approx. 25-40 years; Harmer et al. 2001). Therefore, dynamics of habitats might prevent full habitat occupancy of *H. mantegazzianum*. Likewise, even common and abundant native species usually do not occupy all suitable patches of dynamic habitats. Altogether, I would assume that *H. mantegazzianum*, like comparable native species, will not occupy all suitable habitats and will attain dominance in only few stands. Thus, it appears rather unlikely that *H. mantegazzianum* will endanger populations of common native plant species at landscape to regional scales. In a general perspective, I support Scherer-Lorenzen et al. (2000) who suggested that plant invasion in Germany are "not an important threat to biodiversity at a national or regional scale, but could be problematic at a local scale".

8.3 Invasion hypotheses and the case of *Heracleum mantegazzianum*

In recent decades many studies tried to identify traits of invasive plant species which distinguish them from native species. The rationale behind these studies is the 'unlike invader' hypothesis which is based on the notion first mentioned by Darwin (1859) that "being unlike native species confers invasiveness". Although recent studies showed that traits of invasive plant species generally do not differ from natives ones (e.g. Daehler 2003; Bruno et al. 2004), the 'unlike invader' hypothesis may hold for regions which have not been saturated with plant functional types by immigration or evolution. This is obviously the case with many oceanic islands, such as Hawaii, Galapagos etc. It could be hypothesized, that there is also a lack of saturation with plant functional types in the temperate zone of Europe which has been impoverished in species due to shifting climate during the ice age. In the database of Grime (1988, 'Functional Plant Ecology') there is no plant species that has the same traits as *H. mantegazzianum* regarding the established strategy, life history, canopy height, lateral spread, and regenerative strategy. This suggests that the 'unlike invader' hypothesis might apply to this species and raises the question in which traits *H. mantegazzianum* differs from native species of its preferred plant communities (Aegopodion). Species of the alliance Aegopodion are usually competitive (e.g. *Urtica dioica* L.) or ruderal-competitive (e.g. *Aegopodium podagraria* L.) perennials with more or less pronounced clonal growth. But most species of this alliance either produce comparatively few seeds or small seeds. In contrast, *H. mantegazzianum* is a monocarpic-plurennial lacking clonal growth and it produces numerous large seeds (Hüls 2005; Moravcová et al. 2005; Perglová et al. 2006). After initial colonisation and seed production, it is conceivable that local 'swamping' (Williamson 1996) with seeds, and high germination percentages are the main traits of *H. mantegazzianum* that confer local invasiveness (Moravcová et al. 2005; Perglová et al. 2006). In particular, these traits might be very effective in young successional stages where clonal perennials have not yet reached high cover-abundances. Thus, in this respect, the 'unlike invader' hypothesis might be applicable to *H. mantegazzianum*.

Among recent hypothesis on plant invasions, the 'enemy release' and 'EICA' (Evolution of Increased Competitive Ability) hypotheses stand out because they are exclusive to the field of invasion biology, whereas other invasion hypotheses also apply to colonisations by native species and the fields of succession science and community assembly. 'Enemy release' and 'EICA' require that a plant species is constrained by substantial specialist herbivory or pathogen attack in its native range, whereas the species suffers less from such enemies in the invaded range (Crawley 1987; Blossey and Nötzold 1995; Keane and Crawley 2002). This appears to apply to some invasive plant species, e.g. *Silene latifolia* in North America (Wolfe 2002) or *Ambrosia artemisiifolia* in Europe (Genton et al. 2005). However, field surveys conducted in Central Europe and in the Caucasus have yielded no clear signs of herbivore or pathogen species having more severe impact on *H. mantegazzianum* in its native range (Seier et al. 2004; Hattendorf et al. 2006). Thus, although the proportions of oligo- and monophagous herbivores on *H. mantegazzianum* are higher in the Caucasus than in the invaded range of Europe (Hansen et al. 2006), it appears that ‘enemy release’ and ‘EICA’ are rather not relevant for this species.

Another concept based on leaving behind constraining opponents is ‘competitive release’ (Mitchell et al. 2006). When effects of competitors on potential invaders are low, e.g. due to lack of competitive species in young habitats, this provides an opportunity for invasion. In the reverse, older successional stages are less invasible by *H. mantegazzianum* which matches with the concepts of ‘maturity’ (Shea and Chesson 2002), successional age (Bastl et al. 1997), and biotic resistance (Darwin 1859; Elton 1958). Transferred to *H. mantegazzianum*, these concepts could mean that competitive plant species are fewer or less frequent in the habitats of the invaded range compared to the Caucasus. In fact, plant communities of *H. mantegazzianum* in the montane and subalpine zones of the Western Greater Caucasus contain many competitive tall-herb species, such as *Telekia speciosa*, *Inula helenium*, and *Cephalaria gigantea* to name but a few (Otte et al. 2007). In contrast, the relevés of invaded plant communities in Europe contain much fewer tall-herb species (chapter 5). Hence, there might be some degree of ‘competitive release’ of *H. mantegazzianum* facilitating dominant stands in the invaded range and, on the other hand, some degree of ‘biotic resistance’ due to numerous competitors in plant communities of the native range.

Next to traits of invasive species and biotic interactions, recent invasion hypotheses have been based on characteristics of the recipient environment. A general and mechanistic one among these is the ‘fluctuating resources’ hypotheses proposed by Davis et al. (2000). This hypothesis predicts that susceptibility of a community to invasion is controlled by the amount of unused resources which may vary in space and time. A temporary surplus in resources can be caused by an increase of the total amount of resources in the system or by a decrease of biomass and, thus, resource consumption. The latter case is consistent with the theory of ‘community disturbance’ facilitating invasion. Regarding *H. mantegazzianum*, the ‘fluctuating resources’ hypothesis seems to apply to the recruitment phase. This is suggested by the fact that recruitment in dense sward is only possible in gaps where biomass has been destroyed and, consequently, the amount of unused resources (light, water, nutrients) has temporally increased. ‘Fluctuating resources’ and ‘competitive release’ are both integrated into the general hypothesis of ‘niche opportunities’ (Shea and Chesson 2002).

The significance of human alterations of disturbance regimes and land-use changes for plant invasions has long been recognized and is common consensus today (Elton 1958; Crawley 1987; Vitousek 1997; Arroyo et al. 2000; Mooney and Hobbs 2000). Although they are no genuine issues of invasion biology but rather of the fields of succession science, vegetation ecology and conservation biology, it is clear that they have facilitated a large number of invasions worldwide. *Heracleum mantegazzianum* is just another example of invasion facilitated by anthropogenic disturbance and land-use changes.

Last but not least, an overriding factor of plant invasions is habitat matching. It is trivial that a plant species can only grow in a habitat which matches the requirements of the species physiology and life cycle. It is reasonable to expect that a species will establish and grow in a matching habitat given sufficient propagule input. Thus, on the whole, propagule pressure and habitat matching might explain a large part of plant invasions in general, and also the invasion of *H. mantegazzianum*.

9 Main conclusions

- *Heracleum mantegazzianum* Somm. et Lev. is an example of a plant invasion which has massively been facilitated by anthropogenic dispersal and land-use changes in cultural landscapes.
- *H. mantegazzianum* is not a generally superior species as often feared but has some limitations. These are:
  - dispersal limitation through the landscape matrix, and
  - competition by native tall herbs, especially in comparatively old successional stages of tall-herb vegetation.
- *H. mantegazzianum* can lead to far reaching local alterations of the structure and floristic composition of vegetation stands in the course of secondary successions; however effects of *H. mantegazzianum* do not differ significantly from those of native tall herbs.
- The studies of this thesis confirm that multiscale and species-specific approaches are mandatory for a thorough assessment of plant invasions and their impacts.

10 Summary

The present thesis on the invasion of *Heracleum mantegazzianum* Somm. et Lev. (Giant Hogweed) in Germany sought to answer the following questions:

i. Which habitats and plant communities have been invaded (chapter 5)?
ii. Which anthropogenic and environmental factors facilitate or constrain the invasion (chapters 5 and 6)?
iii. How is the abundance of *H. mantegazzianum* related to site conditions and plant communities (chapter 5)?
iv. How does *H. mantegazzianum* affect the local diversity of plant communities (chapter 5)?
v. In which regions of Germany is *H. mantegazzianum* invasive in the sense that it has shown mass increases (chapter 7)?
vi. Does the invasion of *H. mantegazzianum* threaten native plant species (chapter 7)?

Heracleum mantegazzianum is an invasive plant species in Germany which was introduced from its native range in the Western Greater Caucasus to European botanical gardens in the 19th century. Afterwards it has frequently been cultivated as an ornamental plant and has also been sown in the countryside as a bee plant. In the second half of the 20th century, the species showed a massive spread and today *H. mantegazzianum* is generally widespread throughout Germany. *Heracleum mantegazzianum* belongs to the Apiaceae family and has a monocarpic-plurennial life cylce with a competitive-ruderal strategy (CR strategy sensu Grime). This species is a conspicuous and remarkable plant due to its enormous growth height which regularly is between 2 and 3 m, its cart wheel sized flower umbels, and the formation of dominant stands. It is commonly regarded as a problem plant because of its massive spread and its ability to form dominant stands.

A questionnaire survey addressed to the nature conservation authorities of districts was conducted to assess the invasion intensity of *H. mantegazzianum* in Germany in 2001. Field studies were conducted in 2002 and 2003 in a total of 20 study areas (each 1 km²), which were distributed among Western and Southern parts of Germany with a focus on the natural geographic region ‘western low mountain ranges’. Study areas were chosen to represent the landscapes most heavily invaded by *H. mantegazzianum* in Germany.

In the study areas, all large enough stands of *H. mantegazzianum* were documented by vegetation relevés according to the method of Braun-Blanquet based on 25 m² plots. Plot data were completed by records of habitat characteristics (light supply, land use, incidents of disturbance within the stands), top soil nutrient analyses and soil morphological characterization of the water balance. Furthermore, all stands of *H. mantegazzianum* were mapped with GPS in the study areas. Field data were supplemented by multitemporal series of digitalized aerial photographs. These were used to map all patches of suitable habitat of *H. mantegazzianum* (unoccupied and occupied) for GIS analyses and to reconstruct individual histories of habitat patches for the last 50 years.

Heracleum mantegazzianum has invaded a number of different habitat types in Germany. The predominant ones are abandoned grasslands, riversides, and roadsides. From a plant sociological perspective, occurrences of *H. mantegazzianum* are more or less restricted to the vegetation class of agricultural grasslands (Molinio-Arrhenatheretea) where the species invades abandoned and ruderal variants and the class of nitrophilous tall-herb communities (Galio-Urticetea). In the latter class, *H. mantegazzianum* prevalently occurs in plant communities of the order Glechometalia and its sociological centre is the alliance Aegopodion. Plant communities of *H. mantegazzianum* represent different stages of successional seres, which mostly started from grasslands after abandonment of management or, secondarily, from disturbed grounds, such as sand pits, in the study areas. Along these

seres, *H. mantegazzianum* attains its highest cover-abundances in comparatively young successional stages whereas it shows lesser cover-abundances in old tall-herb stands and woodlands.

Preferred sites of *H. mantegazzianum* are generally highly productive and are consequently characterized by high nutrient availability, favourable water balances and good soil aeration during the growing season. The species prefers full light but it can fairly well grow and set fruit in semi-shade conditions as well. Relationships between site characteristics and stand structure of *H. mantegazzianum* (growth height, cover-abundance, proportion of flowering individuals) could hardly be detected in the studies presented in this thesis. Primarily, this is attributable to the short environmental gradient of investigated sites which mostly offered very favourable conditions. However, in a few less favourable sites, characterized by modest nutrient status or unfavourable water balance (periods of drought or wetness during the growing season), *H. mantegazzianum* showed markedly reduced vitality and low cover-abundances.

The studies of this thesis brought up several factors facilitating or constraining the invasion of *H. mantegazzianum* on the local, landscape, or regional scale. Among the most important facilitating factors is abandonment of land use of productive sites. A reconstruction of histories of invaded sites from multitemporal series of aerial photographs detected that a large part (53.5%) of the current extensive stands of *H. mantegazzianum* can be found in habitats which have been affected by abandonment or relaxation of land management. In the study areas, the primary land-use changes were abandonment of grassland management and secondary ones were abandonment of arable fields. Furthermore, low-intensity land use or maintenance, such as unregular mowing, enables invasion of *H. mantegazzianum*. Moreover, there are indirect effects of abandonment because former land-use regimes have excluded or strongly reduced tall herbs locally which opens ‘window of opportunity’ for native and non-native tall herbs to colonise after abandonment. Hence, early colonisers have an advantage over species which arrive later (‘priority effects’). These principles hold for secondary successions after large-scale disturbances, such as open-cast mining or deforestation, too. Probably, the chronology of abandonment or disturbance and propagule input of colonisers explains a large part of the high variability of cover-abundances of *H. mantegazzianum* and native tall herbs, and ‘priority effects’ are the main facilitating factor for dominant stands. Depending on the particular situation, abandonment or disturbance can favour *H. mantegazzianum* or native tall herbs, such as *Urtica dioica* L.

When competitive tall herbs co-occur with *H. mantegazzianum*, interspecific competition plays an important role for cover-abundances. This can be seen from the fact that cover-abundances of *H. mantegazzianum* are reduced in older successional stages while native tall herbs show increased values. It appears that dominant stands of *H. mantegazzianum* which have formed in young successional stages might develop into mixed tall-herb stands due to colonisation by native species and increasing interspecific competition.

Next to interspecific competition on the local scale, dispersal limitation on the landscape scale is a major constraining factor for the invasion. A lack of long-distance dispersal capabilities makes it difficult for *H. mantegazzianum* to reach patches of suitable habitat ‘by own means’ if these patches are isolated by a non-habitat landscape matrix (agricultural land, forests). However, the dispersal limitation can partly be overcome by dispersal of seeds along transport corridors – rivers and roads – or by gradual migration through corridor habitats, such as river embankments or road verges.

Furthermore, land-use changes also have effects on the invasion at the landscape scale. Multitemporal area balances of habitats and other land-cover types showed a massive increase of suitable habitat area during the last 50 years and a simultaneous decrease of agricultural land in the study areas. In addition to the increase of habitat area itself, this lead to an increase of habitat connectivity which presumably has facilitated spread on the landscape scale.

At the national scale, the district-based invasion intensities show a heterogeneous pattern and hitherto there are only few invasion ‘hot spots’ in Germany where a massive increase of *H. mantegazzianum* has occurred in some landscape sections. These are prevalently situated in low mountain ranges where agricultural land use has been declining. On the other hand, there has rarely been a massive increase in regions characterized by intensive agriculture. Obviously, *H. mantegazzianum* benefits from increased habitat availability and connectivity due to abandonment of land use in peripheral landscapes.

Heracleum mantegazzianum is generally considered to have severe impacts on native flora and vegetation. Specifically, it is often regarded to be a per se dominant species which locally suppresses native species. However, the field studies have shown a high variability of cover-abundances and only about a third of surveyed stands were dominant with cover-abundances exceeding 50%. The observed limitations of *H. mantegazzianum* – reduced cover-abundances in old tall-herbs stands and dispersal limitation at the landscape scale – suggest that only a part of stands will be dominant in the future, namely those which represent early invasions of habitats created by disturbance or land-use changes. On the whole, it can be stated that *H. mantegazzianum* is a highly successful species but not per se dominant.

Where *H. mantegazzianum* attains dominance, it has strong local effects on the structure, floristic composition and ecological function of invaded vegetation. High cover-abundances of the species bring about local suppression or exclusion of low-growing and light-demanding species which results in reduced numbers of vascular plant species per unit area (25 m² plots). However, a detailed analysis of relationships between species numbers, cover-abundances and vegetation type has shown a general decline of species numbers in the course of secondary successions from grasslands or ruderal pioneer vegetation towards tall-herb communities, regardless of the particular cover-abundances of *H. mantegazzianum*. The reason for this is that native tall herbs bring about similar changes of vegetation structure and composition. Thus, it can be concluded that local reduction of phytodiversity is not a specific problem of *H. mantegazzianum*.

The questionnaire survey of nature conservation authorities yielded comparatively frequent statements of *H. mantegazzianum* to have invaded protected habitat types, such as chalk grasslands or fens, and showed that the species is generally considered to be a problem for nature conservation. However, the analysis of preferred habitats and site conditions suggested that *H. mantegazzianum* cannot invade sites characterized by suitable conditions (drought, wetness, poor nutrient status, pasturing, mowing) for protected habitat types in cultural landscapes of Germany or if so it is constrained to low cover-abundances. Therefore, this species appears not to endanger protected habitat types. However, it is possible that the species invades protected habitat types after site conditions have deteriorated, e.g. due to eutrophication, artificial drainage or abandonment of land management. In such cases, *H. mantegazzianum* as well as native tall herbs can replace protected vegetation types. However, the underlying problem is not the invasive species by itself but rather the altered site conditions or management regimes. In this perspective, *H. mantegazzianum* is an indicator of landscape changes and habitat deterioration but not the genuine cause of them.

At the landscape scale, the limitations of *H. mantegazzianum* result in mostly moderate values of habitat saturation. The maximum value of habitat area covered by the species was 8.7% in abandoned grasslands, grassland margins, and tall-herb communities. The current values of habitat saturation suggest that quantitative impacts of *H. mantegazzianum* on native biodiversity have been rather moderate hitherto even in most heavily invaded German landscapes . Altogether, an endangering of native plant species and communities at the landscape or regional scale appears to be rather unlikely in the future.

11 Zusammenfassung

Der vorliegenden Arbeit zur Invasion des Riesen-Bärenklaus (*Heracleum mantegazzianum* Somm. et Lev.) in Deutschland liegen folgende Fragestellungen zugrunde:

i. Welche Habitate und Pflanzengesellschaften sind von der Invasion betroffen (Kapitel 5)?
ii. Welche anthropogenen und Umweltfaktoren begünstigen oder hemmen die Invasion (Kapitel 5 und 6)?
iii. In welchem Zusammenhang stehen die Abundanzen des Riesen-Bärenklaus mit Standortfaktoren und Pflanzengesellschaften (Kapitel 5)?
iv. In welchen Teilregionen Deutschlands ist der Riesen-Bärenklau invasiv in Sinne einer massenhaften Ausbreitung (Kapitel 7)?
v. Wie wirkt sich der Riesen-Bärenklau auf die lokale Diversität der invadierten Pflanzengesellschaften aus (Kapitel 5)?
vi. Gefährdet die Invasion des Riesen-Bärenklaus einheimische Arten (Kapitel 7)?

Der Riesen-Bärenklau ist in Deutschland eine invasive Art, die im 19. Jahrhundert aus seinem Ursprungsgebiet in Westlichen Großen Kaukasus in europäische botanische Gärten eingebracht wurde. In der Folgezeit wurde er häufig als Zierpflanze kultiviert und auch als Bienenweide in der freien Landschaft ausgesät. In der zweiten Hälfte des 20. Jahrhunderts ließ sich eine rasante Ausbreitung in weiten Teilen Mitteleuropas feststellen und heute ist der Riesen-Bärenklau in Deutschland allgemein weit verbreitet. Der Riesen-Bärenklau gehört zur Pflanzenfamilie der Apiaceen und hat einen monokarp-pluriennen Lebenszyklus mit einer kompetitiv-ruderalen Strategie (CR-Stratege sensu Grime). Er fällt durch seine enorme Wuchshöhe, die regelmäßig zwischen 2 und 3 m beträgt, seine wagenradgroßen Blütendolden und die Bildung von Dominanzbeständen auf. Aufgrund der massiven Ausbreitung in den letzten Jahrzehnten und der Fähigkeit zur Dominanz wird der Riesen-Bärenklau allgemein als Problempflanze angesehen.

Für die Abschätzung der Invasivität des Riesen-Bärenklaus in Deutschland wurde im Jahre 2001 eine Fragebogenkampagne durchgeführt, die sich an die Unteren Naturschutzbehörden der Kreise und kreisfreien Städte wandte. Geländeerhebungen wurden 2002 und 2003 in insgesamt 20 Untersuchungsgebieten (je 1 km² groß) durchgeführt, die über West- und Süddeutschland verteilt waren mit einem Schwerpunkt in der Naturräumlichen Großeinheit ‚Westliche Mittelgebirge'. Die Untersuchungsgebiete wurden so ausgewählt, dass sie die am stärksten invadierten Landschaften in Deutschland repräsentieren.

In den Untersuchungsgebieten wurden alle hinreichend großen Bestände des Riesen-Bärenklaus durch Vegetationsaufnahmen (25 m²) nach Braun-Blanquet belegt. Die Erhebungen der Aufnahmeflächen wurden durch Daten zu Habitateigenschaften (Lichtgenuss, Landnutzung, Störungen), Nährstoffanalysen des Oberbodens und bodenmorphologische Charakterisierungen des Bodenwasserhaushaltes komplettiert. Darüber hinaus wurden alle Bestände des Riesen-Bärenklaus in den Untersuchungsgebieten mit einem GPS-System kartiert. Die Geländeerhebungen wurden durch multitemporale Luftbildreihen ergänzt. Anhand der Luftbilder wurden alle geeigneten Habitat-Patches (besetzt und unbesetzt) im GIS kartiert und die individuellen Historien der Patches rekonstruiert.

Der Riesen-Bärenklau hat in Deutschland eine Reihe verschiedener Habitate invadiert, vor allem Grünlandbrachen, Fließgewässerböschungen und Straßen- und Wegseitenstreifen. Aus pflanzensoziologischer Sicht beschränken sich die Vorkommen des Riesen-Bärenklau weitestgehend auf die Vegetationsklassen Wirtschaftsgrünland (Molinio-Arrhenatheretea), wo er in junge Brachestadien und ruderalisierte Bestände, wie z.B. Wegränder, eindringt sowie nitrophytische Staudenfluren der Klasse Galio-Urticetea. Innerhalb der letzteren Klasse kommt der Riesen-Bärenklau vor allem in

Pflanzengesellschaften der Ordnung Glechometalia vor mit einem deutlichen soziologischen Schwerpunkt im Verband Aegopodion. Die Vegetationstypen mit Riesen-Bärenklau bilden Sekundär-Sukzessionsreihen ab, die in den Untersuchungsgebieten meist von Wirtschaftsgrünland ausgingen und untergeordnet von stark gestörten Flächen, wie z.B. Sandgruben. Innerhalb dieser Sukzessionsreihen hat der Riesen-Bärenklau seine höchsten Artmächtigkeiten in jungen Stadien wohingegen ältere Hochstaudenfluren und Gehölze geringere Artmächtigkeiten aufweisen.

Die bevorzugten Standorte des Riesen-Bärenklaus sind generell sehr produktiv mit entsprechend hohen Boden-Nährstoffgehalten, guter bis sehr guter Wasserversorgung und vollständiger Durchlüftung des Oberbodens während der Vegetationsperiode. Volle Belichtung wird bevorzugt, jedoch wächst und fruktifiziert der Riesen-Bärenklau auch in halbschattigen Lagen noch gut. Zusammenhänge zwischen Standortparametern und der Bestandesstruktur des Riesen-Bärenklaus (Wuchshöhe, Artmächtigkeit, Anteil blühender Individuen) waren in den hier vorgestellten Studien nur in Ansätzen zu erkennen. Dies ist vor allem der geringen standörtlichen Amplitude der untersuchten Flächen geschuldet, die fast ausschließlich ausgesprochen produktive Bedingungen zeigten. Anhand der wenigen relativ ungünstigen Standorte, die in den Untersuchungsgebieten invadiert wurden, lässt sich jedoch erkennen, dass mäßige Nährstoffverhältnisse und vor allem ungünstige Bodenwasserverhältnisse (Trockenphasen, Vernässung während der Vegetationsperiode) nur geringe Artmächtigkeiten des Riesen-Bärenklaus erlauben.

In den Studien dieser Arbeit ließen sich eine Reihe von Faktoren erkennen, welche die Invasion des Riesen-Bärenklaus auf der lokalen, landschaftlichen oder regionalen Ebene begünstigen bzw. hemmen. Zu den wichtigsten begünstigenden Faktoren zählt Landnutzungsaufgabe auf produktiven Standorten. Aus multi-temporalen Luftbildreihen abgeleitete Habitat-Historien ergaben, dass ein Großteil (53,5%) der aktuellen flächigen Bestände des Riesen-Bärenklaus in Habitaten zu finden ist, die durch Landnutzungsaufgabe oder –extensivierung entstanden sind. In den Untersuchungsgebieten handelte es sich dabei hauptsächlich um die Aufgabe von Grünlandwirtschaft und untergeordnet um Ackerbrache. Des Weiteren ermöglichen auch zu geringe Nutzungs- und Pflegeintensitäten, wie z.B. unregelmäßige Mahd, die Invasion des Riesen-Bärenklaus. Darüber hinaus ergibt sich ein indirekter begünstigender Effekt dadurch, dass vorangegangene landwirtschaftliche Nutzung konkurrierende Hochstauden lokal weitgehend ausgeschlossene hat. Die Nutzungsaufgabe oder Extensivierung bietet daher ein ‚window of opportunity' für einheimische wie neophytische Hochstauden wobei erstbesiedelnde Arten im Vorteil sind (‚priority effects'). Diese Prinzipien gelten ebenso für Sukzessionen nach großflächigen Störungen, wie z.B. Abgrabung oder Abholzung. Es ist wahrscheinlich, dass der zeitliche Verlauf des Diasporeneintrags nach Nutzungsaufgabe bzw. Störung einen großen Teil der hohen Variabilität der Artmächtigkeiten des Riesen-Bärenklaus und einheimischer Hochstauden erklärt und dass ‚priority effects' der Hauptfaktor für die Ausbildung von Dominanzen in den Vegetationsbeständen mit Riesen-Bärenklau sind. Je nachdem können dadurch Neophyten, wie der Riesen-Bärenklau, oder auch einheimische Hochstaudenarten, wie z.B. die Große Brennessel (*Urtica dioica* L.) begünstigt werden.

Kommen konkurrenzstarke Hochstauden zusammen mit dem Riesebärenklau vor so spielt interspezifische Konkurrenz eine wesentliche Rolle hinsichtlich der Artmächtigkeiten. Dies ist daran ersichtlich, dass mit zunehmendem Sukzessionsalter die Artmächtigkeiten des Riesen-Bärenklaus ab und im Gegenzug diejenigen der einheimischen Hochstauden zunehmen. Es ist zu vermuten, dass sich Dominanzbestände des Riesen-Bärenklaus, die sich in jungen Sukzessionsstadien gebildet haben, durch die Ansiedlung weiterer Hochstauden und dadurch zunehmende interspezifische Konkurrenz zu Hochstauden-Mischbeständen weiter entwickeln.

Neben interspezifischer Konkurrenz auf der lokalen bzw. Bestandesebene ist Ausbreitungslimitierung auf der Landschaftsebene ein wesentlicher invasionshemmender Faktor. Mangelnde Mechanismen für Fernausbreitung erschweren es dem Riesen-Bärenklau ‚aus eigener Kraft' Patches geeigneter Habitate zu erreichen, wenn diese durch eine unbesiedelbare Landschaftsmatrix (landwirtschaftliche Nutzfläche, Wald) voneinander getrennt sind. Die Ausbreitungslimitierung des Riesen-Bärenklaus auf der Landschaftsebene kann teilweise dadurch überwunden werden, dass seine Samen entlang von Ausbreitungskorridoren, namentlich Fließgewässern und Verkehrswegen, verdriftet werden oder dass eine allmähliche Migration in Korridorhabitaten, wie z.B. Uferböschungen und Seitenstreifen von Verkehrswegen, stattfindet.

Weiterhin wirken sich auf der Landschaftsebene auch Landnutzungsveränderungen auf die Invasion aus. Multitemporale Flächenbilanzen von geeigneten Habitaten und anderen Flächentypen in den Untersuchungsgebieten zeigten eine massive Zunahme der geeigneten Habitatfläche in den letzten 50 Jahren während landwirtschaftlich genutzte Fläche stark abnahm. Neben der Erhöhung des Habitatangebotes führt dies auch zu einer erhöhten Konnektivität der Habitat-Patches, wodurch Ausbreitung auf der Landschaftsebene in den Untersuchungsgebieten vermutlich begünstigt wurde.

Auf der nationalen Ebene lässt sich erkennen, dass die Invasionsintensität in den Landkreisen sehr variabel ist und bisher relativ wenige Invasions-‚Hot Spots' vorhanden sind, in denen eine massive Ausbreitung des Riesen-Bärenklau in einigen Landschaftsteilräumen stattgefunden hat. Diese finden sich vor allem in Mittelgebirgsregionen, in denen landwirtschaftliche Nutzung rückläufig ist. Dagegen lässt sich eine stärkere Ausbreitung in intensiven Agrarregionen kaum feststellen. Offensichtlich profitiert der Riesen-Bärenklau in peripheren Landschaften von erhöhtem Habitatangebot durch Landnutzungsaufgabe.

Der Riesen-Bärenklau wird im Allgemeinen als eine Gefahr für die einheimische Flora und Vegetation angesehen. Dabei wird häufig davon ausgegangen, dass der Riesen-Bärenklau per se dominant ist und einheimische Arten lokal unterdrückt. Die Geländeerhebungen zeigten jedoch eine hohe Variabilität der Artmächtigkeiten und nur rund ein Drittel der beobachteten flächigen Bestände waren dominant mit Deckungswerten über 50%. Die festgestellten Limitierungen des Riesen-Bärenklaus – geringere Artmächtigkeiten in älteren Hochstaudenfluren und Ausbreitungslimitierung auf der Landschaftsebene – lassen vermuten, dass auch in Zukunft nur ein Teil der Bestände des Riesen-Bärenklau dominant sein werden, nämlich solche die frühzeitige Besiedlung von neu entstandenen Habitaten darstellen. Insgesamt lässt sich feststellen, dass der Riesen-Bärenklau zwar eine erfolgreiche jedoch keine per se dominante Art ist.

Dort wo der Riesen-Bärenklau dominant wird führt er weitreichende lokale Veränderungen der Struktur, floristischen Zusammensetzung und ökologischen Funktion der Vegetation herbei. Bei hohen Deckungswerten des Riesen-Bärenklaus werden lichtliebende niedrigwüchsige Arten ausgeschattet und lokal verdrängt. Dies führt zu einem Rückgang der Pflanzenartenzahl pro Aufnahmefläche (25 m²). Eine detaillierte Analyse der Zusammenhänge zwischen Artenzahl, Deckungswerten und Vegetationstypen zeigte allerdings einen generellen Artenrückgang in Zuge der Sukzession von Grünland oder Pionier-Ruderalfluren zu Hochstaudenfluren, unabhängig von den Deckungswerten des Riesen-Bärenklaus. Dies liegt daran, dass auch einheimische Hochstauden entsprechende Veränderungen der Vegetationsstruktur und –zusammensetzung herbeiführen. Somit lässt sich feststellen, dass die lokalen Auswirkungen des Riesen-Bärenklaus auf die Phytodiversität kein spezielles Problem darstellen.

Aus der Befragung der Unteren Naturschutzbehörden in Deutschland ging hervor, dass der Riesen-Bärenklau in vielen Fällen schützenswerte Lebensräume, wie z.B. Kalk- und Silikatmagerrasen oder Niedermoore, invadiert haben soll und generell als Problem für den Naturschutz angesehen wird. Die Befunde der vorliegenden Arbeit legen jedoch nahe, dass der Riesen-Bärenklau geeignete Standorte (Trockniss, Nässe, Nährstoffarmut, Beweidung, Mahd) für schützenswerte Biotope der Kulturlandschaften Deutschlands nicht invadieren kann oder nur mit mäßigem Erfolg. Daher scheint eine originäre Gefährdung schützenswerter Biotope durch den Riesen-Bärenklau nicht gegeben zu sein. Allerdings besteht die Möglichkeit, dass schützenswerte Biotope dann invadiert werden, wenn sich die Standortbedingungen verschlechtert haben, z.B. durch Eutrophierung, Drainage oder Aufgabe von Landnutzung und Pflege. In solchen Fällen können der Riesen-Bärenklau wie auch einheimische Arten schützenwerte Vegetationstypen auflösen. Das zugrunde liegende Problem ist dabei nicht die neophytische Art sondern die ungünstigen Veränderungen der Standortbedingungen oder Bewirtschaftung. In diesem Sinne ist der Riesen-Bärenklau ein Indikator für landschaftliche Veränderungen und Verschlechterung schützenswerter Biotope aber nicht die Ursache derselben.

Auf der Landschaftsebene resultieren die Limitierungen des Riesen-Bärenklaus in meist moderaten Habitatsättigungswerten. Der höchste Wert wurde mit 8,7% gedeckter Habitatfläche für Grünlandbrachen und –raine festgestellt. Dieser Befund legt nahe, dass negative Auswirkungen des Riesen-Bärenklaus auf den Naturhaushalt und die Biodiversität bisher auch in den am stärksten invadierten Landschaften Deutschlands quantitativ nicht allzu gravierend sind. Insgesamt erscheint eine Gefährdung einheimischer Pflanzenarten und –gesellschaften auf der landschaftlichen bis regionalen Ebene auch in Zukunft eher unwahrscheinlich.

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