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

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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 sub-patch level factors and landscape factors for the invasion of the megaforb *Heracleum mantegazzianum*. In particular, we tested which factors affect the presence in suitable habitat patches and the cover percentage within invaded patches. 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 cover percentage in invaded patches was independent from landscape factors, except for patch shape, and even unsatisfactorily explained by sub-patch level factors included in the analysis ($R^2 = 0.19$). In contrast, presence 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 corridors and habitat connectivity 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, *Heracleum mantegazzianum*, invasion, island-biogeographic model, logistic regression, spread, transport corridors.

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Introduction

The landscape distribution and abundance of plant species may depend on sub-patch level factors and on landscape factors (Freckleton and Watkinson 2002; Ehrlén and Eriksson 2003). Sub-patch level factors affecting the occurrence and abundance of plant species within a habitat patch include habitat structure, disturbances, 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). Additionally, 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). In a rather complementary fashion, landscape factors, such as the connectivity of habitat patches, their distance from dispersal corridors as well as their size and shape, 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, conversely, connectivity) of spatially structured habitats 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 invaded habitat patches should decrease with increasing isolation, whereas patch size should have a positive effect. Furthermore, corridors (e.g. roads, rivers, hedgerows 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 dispersal abilities which live in fragmented or 'patchy' habitats (de Blois et al. 2002). Such species may be hypothesised to perceive landscapes as patch-corridor-matrix mosaics.

To date, 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). On the other hand, however, 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 hypothesised that both invasive and 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 the 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; Stephenson et al. 2006). Thus, there is a need to empirically study effects of habitat configuration on the 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 the spread of plant species.

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 limited long-distance dispersal capacity and occurs in discrete habitat patches in its native and invasive 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 for correlation 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 with the presence of *H. mantegazzianum* in suitable habitat patches and with the cover percentage of this species in invaded patches.

Materials and methods

Study species

The study species *Heracleum mantegazzianum* Somm. et Lev. is a megaforb of the Apiaceae family native to the Western Greater Caucasus (Otte et al. 2007). It was introduced to European botanical gardens in the nineteenth century and showed a massive increase in several European countries in the twentieth century (e.g. Pyšek 1991; Tiley et al. 1996). Plant individuals produce around 20,000 seeds (Hüls 2005) which are dispersed by water (long-distance dispersal) and wind (short-distance dispersal). Between 60 and 90% of wind-dispersed seeds drop within 4 m from the parent plant (unpublished data). Further mechanisms are dispersal with soil material, garden refuse, and vehicles (Tiley et al. 1996; Otte and Franke 1998).

Habitats of *H. mantegazzianum* are predominantly 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). However, the species cannot properly develop and reproduce in regularly used agricultural land (arable land, managed meadows and pastures) or dense forests.

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 and forests. Therefore, *H. mantegazzianum* qualifies as a model species for testing the patch-corridor-matrix model (habitat isolation, patch size, distance from corridors).

Field inventories

We investigated 20 study areas (each 1 km²) that represented the landscapes most heavily invaded by *H. mantegazzianum* in Germany. As assessment of relationships between environmental factors and invasion pattern is difficult in the early stages of invasion owing to a lack of equilibrium with the new environment, 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. The selection of study areas was based on a Germany-wide questionnaire survey addressed to the nature conservation authorities of all 440 districts (*Landkreise*) in 2001 which we used to rank districts according to invasion intensity (rate of return 70.2%; Thiele and Otte, in press). In order to identify potential study areas, we conducted detailed interviews of the authorities in districts with high or medium invasion intensity. Potential study areas as indicated by the authorities were scrutinized on field excursions and, finally, we did field investigation in all areas meeting the criterion mentioned above. Within these 20 study areas (Table 1, see end of document), we mapped all stands of *H. mantegazzianum* with a GPS system (differential GPS, sub-meter accuracy). Additionally, we recorded habitat type and land use of invaded sites as attribute data, which served as '*a priori*' ground-truth data for subsequent mapping of invaded and uninvaded habitat patches from aerial photographs.

Mapping of habitat patches

We acquired multitemporal series of aerial photographs for all study areas for three dates: 1950s, 1970s and present day (approx. 2000). Patches of suitable habitats for *H. mantegazzianum* were identified by interpretation of present-day digital orthophotographs and mapped in ArcView GIS 3.2 (© Environmental Systems Research Institute, Inc.). 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 (Fig. 1). Digitised historical aerial photographs served to determine habitat age and history. If parts of a present-day 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 a uniform history over the time period covered by aerial photographs. These LCGs, hereinafter 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 (Fig. 2).

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 railway embankments
Ruderal areas
Cable routes
Woody habitats
(Partly-) Shaded riverbanks
(Partly-) Shaded roadsides
(Partly-) Shaded railway embankments
Tree fallow
Afforestations
Copses

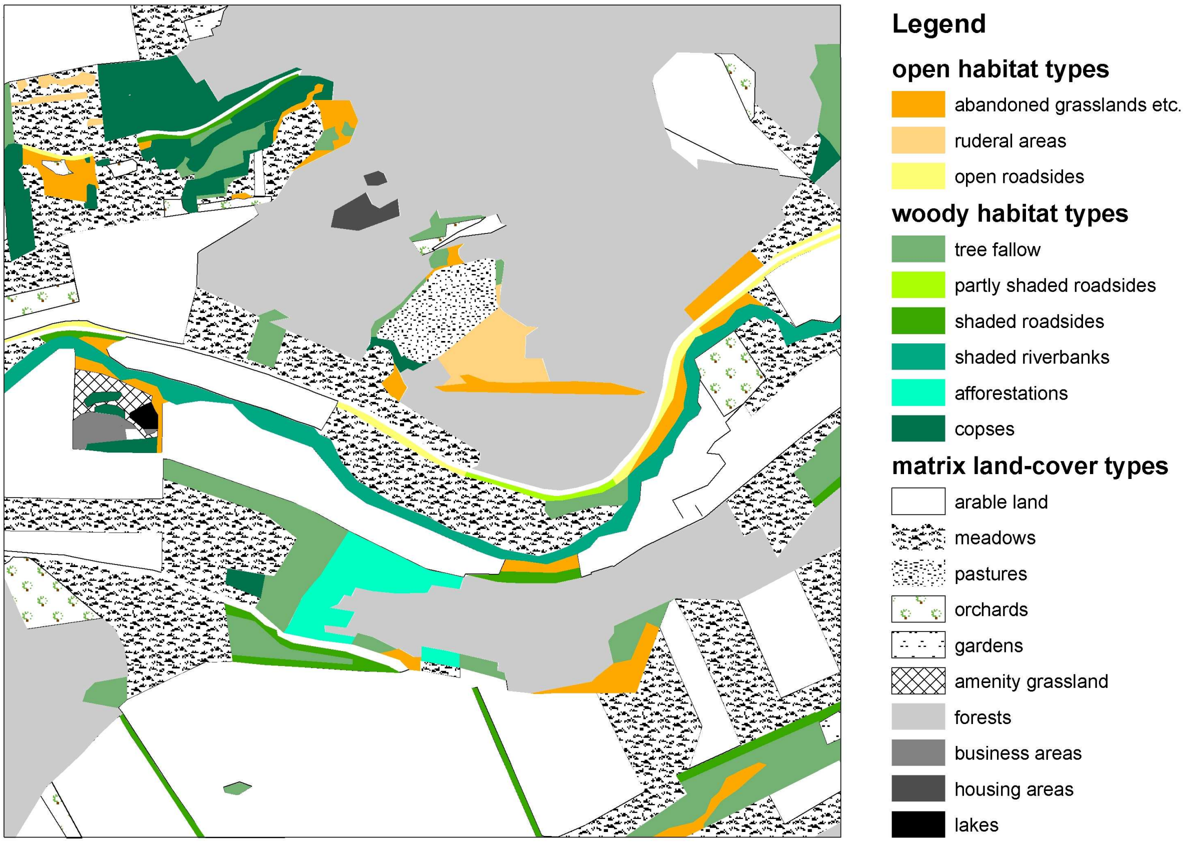

Fig. 1. Map of habitat types of *Heracleum mantegazzianum* and other land-cover types in an exemplary study area (Rhineland-Palatinate, Ahrweiler). Edges of the study area are 1 km.

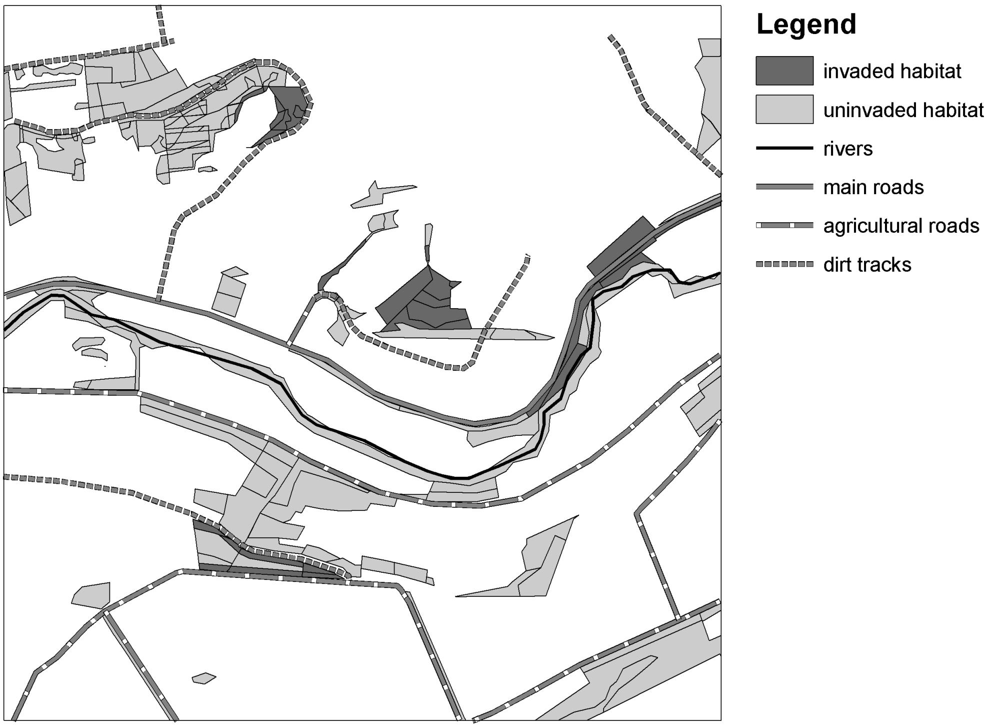

Fig. 2. Map of *Heracleum mantegazzianum* presence in habitat patches (least common geometries, LCG) and road and river corridors in an exemplary study area (Rhineland-Palatinate, Ahrweiler). Edges of the study area are 1 km.

Variables for statistical analyses

For analyses of the relationships between parameters of *H. mantegazzianum* landscape distribution and environmental properties of habitat patches, we compiled a set of two dependent variables and 12 potential predictor variables. Dependent variables were (i) presence of *H. mantegazzianum* in suitable habitat patches, and (ii) cover-percentage in invaded habitat patches. It is possible that the occurrence and cover percentage 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 (Fig. 2). Similarly, we mapped housing areas and garden lots which might have served as anthropogenic seed sources. Then, we calculated nearest-feature distances (edge to edge) of habitat patches from each 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 these (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 *patch sizes* in GIS and assessed the *patch shape* with the shape index in FRAGSTATS for ArcView 1.0.1 (McGarigal and Marks 1995) for each LCG habitat patch.

Obviously, suitability of habitat types for *H. mantegazzianum* differs depending on *habitat structure*, in particular the 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. Additionally, we classified current *land use* of habitat patches into either ‘Fallow’ or ‘Maintenance’. Moreover, we obtained data on soil productivity from the German soil rating survey (*Reichsbodenschätzung*). 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 assigned each habitat patch to a topographic unit (valley, slope, hilltop, plateau).

Statistical analyses

We conducted two separate analyses for the two dependent variables (i) presence ($n = 1555$) and (ii) cover percentage ($n = 333$) using appropriate regression models. Before calculating final models, we identified ‘best subsets’ of predictor variables based on Akaike’s Information Criterion (AIC). As presence was a binary variable, we tested for effects of ‘best subset’ predictor variables with a Logistic Regression Model (LRM) which we calculated in SAS 9.1 (© 2002-2003 SAS Institute Inc.). For cover percentage, which was a continuous variable, we calculated a General Regression Model (GRM) in STATISTICA 6.0 (© StatSoft, Inc.). Cover percentages were $\log_{10}$-transformed prior to the analysis in order to fulfil the assumption of normality. Collinearity of the predictor variables was tested for extensively by sets of multiple regressions of each predictor on all the others. The R² values of these regression models never exceeded 0.4. Thus, there was no considerable collinearity in the models.

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. Distance matrices were calculated for each study area separately as well as for random samples of all objects over all study areas. The Mantel tests revealed three out of the 20 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. Similarly, 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.

Results

Logistic Regression Model (LRM) of presence

Tests of the overall model (Score test, Wald test) were highly significant and the C statistic (86%) which measures association between observed and predicted presence, as well as McFadden's R² (0.29) indicated good model fit (Table 3). Habitat patches with predicted probabilities below 0.1 were invaded by *H. mantegazzianum* in 3.4% of cases, while for predictions >0.9 the percentage of presence was 87.9% (Fig. 3). 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 4). The overall percentage of correct predictions was 84.2%. The model performed especially well in correctly predicting the absence of *H. mantegazzianum* (specificity: 93.8%), whereas prediction of presence was rather moderate (sensitivity: 49.7%).

Significant positive effects on the presence of *H. mantegazzianum* were found for *H. mantegazzianum* cover in adjacent patches, habitat connectivity and patch size. In addition, 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 3).

With respect to 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 positive vicinity effect of agricultural roads was especially marked within 100 m from the road, and declined markedly beyond that range. Distances from agricultural roads were especially important in the topographic unit 'Hilltop' which showed a highly significant difference between uninvaded and invaded habitat patches (Mann-Whitney U-Test, $p < 0.001$), whereas in the 'Valley' unit 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 had positive effects on the occurrence probability up to approx. 300 m from the riverbed. 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 were other combinations of these two predictors. 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, presented in Table 5.

Table 3. Logistic regression analysis of presence 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

Explained variation: McFadden's $R^2 = 0.29$. 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.

Table 4. Classification table: the observed and the predicted frequencies for presence and absence of *Heracleum mantegazzianum* by logistic regression with a cutoff value 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%.

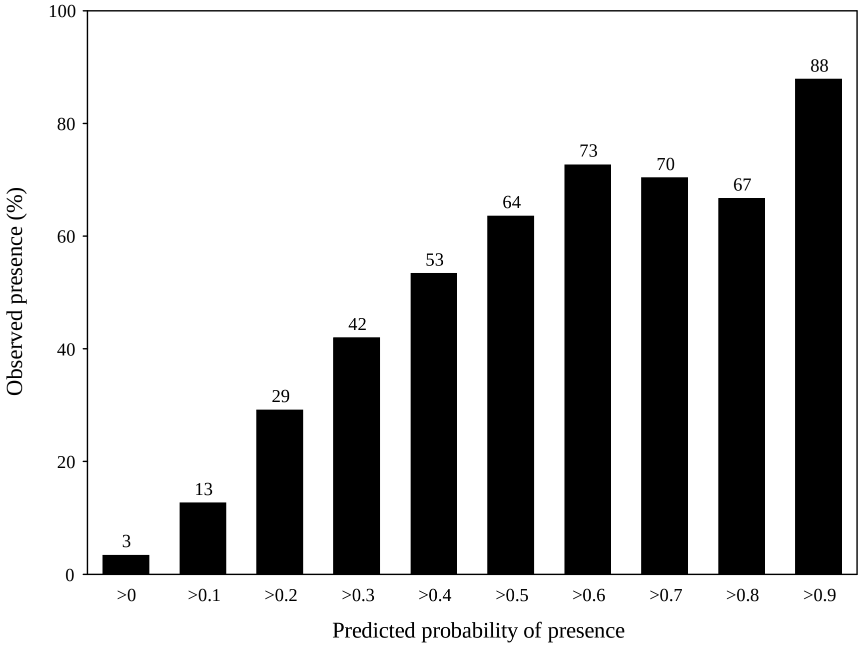

Fig. 3. Classified predicted probabilities by logistic regression of presence of *Heracleum mantegazzianum* in suitable habitat patches (abscissa) versus percentage of observed presence (ordinate). Predicted probabilities were classified into even intervals of 0.0-0.1, >0.1-0.2 etc.

Table 5. Profiles of suitable habitat patches with high (>.95) and low (<.05) predicted probabilities of *Heracleum mantegazzianum* presence by logistic regression. Profiles are given separately for open and woody habitat patches 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*.

General Regression Model (GRM) of cover percentage

The GRM of cover percentage was highly significant and explained approx. 20% of the variance (Table 6). 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 cover percentage. As expected, woody habitat structure had a negative effect on cover percentage. In contrast to the LRM of presence, the shape index was negatively related to cover percentage, which means that elongated or complex-shaped patches had lower *H. mantegazzianum* cover percentages than did 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 6).

Table 6. General linear regression analysis of cover percentage of *Heracleum mantegazzianum* in 333 invaded 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.

Discussion

Modifiable areal unit problem (MAUP)

With spatially aggregated data, it is possible to obtain different results from the same set of data depending on the areal units used for data representation (scale effect), e.g. differently sized grid cells or administrative boundaries, and on the aggregation of data categories within those areal units (aggregation or zoning effect). This phenomenon is known as the modifiable areal unit problem (MAUP; e.g. Jelinksi and Wu 1996). In our study, the areal units for statistical analyses were ecologically predetermined discrete spatial objects, i.e. habitat patches, and the categorical grouping level was biologically determined as the single plant species under consideration, i.e. *Heracleum mantegazzianum*. Hence, the MAUP does not directly concern our study. A similar effect could, theoretically, occur due to the varying size and shape of the habitat patches and the fact that sometimes only a part of a habitat patch has been invaded. Particularly, elongated patches lying perpendicular to transport corridors or other habitat patches could be a potential source of error in the correlational analysis of nearest neighbor distances and habitat connectivity, if the presence of *H. mantegazzianum* would be restricted to the averted ends of the patches. However, there were no such cases in out data set. With regard to data aggregation, we analysed different sub-categories of predictor variables separately to identify the ones that correlate with the dependend variables which we then included into the final models. Thus, we can exclude artifacts due to aggregation effects. In conclusion, our study does not suffer from MAU effects.

Presence

The LRM results confirm that both sub-patch level factors and landscape factors (distances from transport corridors, habitat connectivity, patch size and shape) influence presence of *H. mantegazzianum*. Sub-patch level 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, 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).

Effects of habitat configuration have predominantly 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* presence is remarkable, because this species is a fast-spreading, monocarpic plurennial with a 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, that the species has often 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 the presence 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 the spread of *H. mantegazzianum* along river corridors (e.g. Pyšek 1991). With respect to 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 greatly reduces growth height and seed production (Thiele and Otte 2006), and, hence, largely prevents spread into adjacent or nearby habitat patches. Nevertheless, the 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. 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; Godefroid and Koedam 2004; Pauchard and Alaback 2004; Rentch et al. 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 (Caffrey 1999). Furthermore, in a time series of aerial photographs, Müllerová et al. (2005) observed the spread of *H. mantegazzianum* from linear landscape elements (rivers, paths, roads) to adjacent extensive habitat patches within recent decades in the Czech Republic.

In addition 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 presence.

Müllerová et al. (2005) found an average rate of linear spread of 10.8 m year^{-1} for heavily invaded landscapes in the Czech Republic.

The classification table of the observed and predicted presence and absence of *H. mantegazzianum* showed a high percentage of correct classification (84.2%; Table 4). However, there was a great difference between the correct prediction of absence (93.8%) and the 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 the limitation of long-distance dispersal through the matrix, largely prevent invasion. On the other hand, the high rate of predicted absence in patches where the species was in fact present suggests that the pattern of presence is substantially influenced by factors not accounted for in the model, which help to overcome long-distance dispersal limitation. Most probably, these are human factors such as deliberate sowing into the wild as a bee plant and other human-related means of dispersal (e.g. translocation of dry umbels).

With respect to 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. Therefore, application of the model to construction of probability maps does not appear to be advisable for already invaded landscapes. Nevertheless, in currently uninvaded landscapes, the model might be appropriate to identify habitats that are most likely to be invaded in the first place after *H. mantegazzianum* arrival. A promising extension of static LRM models 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.

Cover percentage

In contrast to presence, cover percentage was not substantially influenced by habitat configuration (apart from patch shape, see below). Instead, habitat structure and the cover percentage of *H. mantegazzianum* in adjacent patches prevailed. These results suggest that cover percentage depends, firstly, on local habitat conditions governing the recruitment, growth and seed production, and, secondly, on propagule pressure from adjacent patches. The negative effect of woody habitat structure confirms that the cover percentage 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 cover percentages of *H. mantegazzianum*, which is plausible taking into account the fact that the species has quite a high demand for nutrients and moisture (Pyšek and Pyšek 1995; Tiley et al. 1996; Otte and Franke 1998; Thiele and Otte 2006).

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

Conclusions

Our study confirms that the presence of plant species may depend on both sub-patch level and landscape factors. In particular, 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 the invasive *Heracleum mantegazzianum* is strongly mediated by dispersal processes which depend on transport corridors (rivers, roads) and high 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 of presence for construction of probability-of-occurrence maps could provide a means for more efficient early detection and prevention in previously uninvaded landscapes. With respect to preventive measures, regular maintenance of roadside habitats could impede further spread of *H. mantegazzianum* outside river valleys.

In contrast to presence, cover percentage of *H. mantegazzianum* does not depend on landscape factors. We would suggest that sub-patch level factors, such as small-scale disturbances and biotic interactions, are more important determinants of cover percentage.

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Table 1. Study areas: state, district (*Landkreis*), date of field record, coordinates, altitude, basic climate parameters, and habitat patch statistics. 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: MA PREC = mean annual precipitation (mm). MA TEMP = mean annual temperature. JAN TEMP = mean January temperature. JUL TEMP = mean July temperature. Temperatures are given in °C. Climate data refer to the nearest climate station and represent the years 1961-1990 (Deutscher Wetterdienst, www.dwd.de).

			Coordinates			Climate						
State	District ('Landkreis')	Date of field record	East	North	Altitude (m a.s.l.)	MA PREC	MA TEMP	JAN TEMP	JUL TEMP	Habitat patches (LCG)	Invaded patches (LCG)	Aggr. patches
Rhineland-Palatinate	Altenkirchen	2002	3410.500	5623.000	160	1041	8.5	0.3	16.7	59	15	28
Rhineland-Palatinate	Ahrweiler	2003	2588.300	5594.500	155	703	9.1	1.1	17.4	182	24	29
North Rhine-Westph.	Ennepe-Ruhr-Kreis	2003	2593.800	5696.400	85	916	9.5	2.0	17.4	100	44	10
North Rhine-Westph.	Euskirchen	2002	2545.800	5595.000	480	769	7.3	-0.1	15.1	33	7	9
North Rhine-Westph.	Euskirchen	2002	2535.500	5589.000	590	937	7.3	-0.1	15.1	78	12	19
Bavaria	Freising	2002	4465.500	5362.500	490	837	7.5	-2.1	16.7	61	14	13
Bavaria	Garmisch-Partenkir.	2002	4430.200	5270.000	865	1565	6.5	-3.0	15.8	50	7	12
Bavaria	Garmisch-Partenkir.	2002	4443.500	5253.500	930	1437	6.7	-1.5	15.0	59	6	16
Lower Saxony	Göttingen	2003	3552.500	5710.500	235	768	8.7	0.3	17.1	21	7	5
North Rhine-Westph.	Hagen	2002	3396.700	5687.000	170	1157	9.5	2.0	17.4	132	43	25
North Rhine-Westph.	Hagen	2003	2600.100	5695.500	90	900	9.5	2.0	17.4	106	34	31
North Rhine-Westph.	Hagen	2002	3397.000	5689.800	275	1043	9.5	2.0	17.4	111	9	11
Hesse	Kassel	2003	3529.200	5684.000	290	811	8.1	-0.4	16.6	71	18	12
Hesse	Lahn-Dill-Kreis	2003	3467.000	5595.500	260	713	7.7	-1.0	16.3	81	6	17
North Rhine-Westph.	Olpe	2002	3421.500	5664.500	265	1185	8.1	0.3	16.0	81	9	24
Thuringia	Wartburgkreis	2003	3569.500	5620.500	340	697	8.7	-0.1	17.6	6	2	1
Hesse	Waldeck-Frankenb.	2003	3488.300	5668.500	260	727	7.4	-0.9	15.8	64	36	20
Hesse	Waldeck-Frankenb.	2002	3477.800	5655.500	335	876	7.4	-0.9	15.8	68	16	9
Hesse	Waldeck-Frankenb.	2002	3487.500	5661.200	285	735	7.4	-0.9	15.8	112	14	9
Saarland	St. Wendel	2003	2589.000	5482.100	380	809	9.1	0.6	18.1	84	17	35
									Σ	1559	340	335