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What shapes giant hogweed invasion? Answers from a spatio-temporal model integrating multiscale monitoring data

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Abstract. In this study we simulated the invasion of *Heracleum mantegazzianum* with a spatiotemporal model that combined a life-cycle matrix model with mechanistic local and corridor dispersal and a stochastic long-distance dispersal in a cellular automaton. The model was applied to the habitat configuration and invader distribution of eight 1 km² study areas. Comparing the simulations with monitoring data collected over 7 years (2002–2009) yielded a modelling efficiency of 0.94. We tested the significance of different mechanisms of invasion by omitting or modifying single model components one at a time. Thus we found that the extent of *H. mantegazzianum* invasion at landscape level depends on both landscape-scale processes and local processes which control recruitment success and population density. Limiting recruitment success (100 → 30 %) and successively decreasing the carrying capacity of habitats (max → 0) over 30 years significantly improved the projections of the invasion at the landscape level. Local dispersal

reached farther than 10 m, i.e. farther than previously assumed, but appeared to be unaffected by wind directions. Long-distance dispersal together with local dispersal dominated the invasion quantitatively. Dispersal through corridors accounted for less invasive spread. Its importance, with respect to invasion speed (number of colonised model grid cells) is probably limited over short periods of time (7 years). Only dispersal along rivers made a significant quantitative contribution to invasion of *H. mantegazzianum*. We suggest that biotic heterogeneity of suitable habitats is responsible for varying invasion success and that successively increasing competition leads to declining population densities of *H. mantegazzianum* over several decades slowing down the spread on the landscape scale.

Keywords. dispersal vector, *Heracleum mantegazzianum*, matrix model, patch-corridor-matrix mosaic, recruitment, succession.

Introduction

Biological invasions are complex phenomena involving demographical processes and dispersal which are main determinants of a species' invasiveness, and ecological interactions with resident communities of variable invasibility. These processes comprise multiple spatio-temporal scales from recruitment of seeds at microsites to long-distance dispersal among habitat patches in structured landscapes (e.g. Theoharides and Dukes 2007). All of them may have an influence on the velocity and extent of an invasion (Pauchard and Shea 2006), but we know little about the relative importance of different processes for large scale spread and the final impact of an invader (Mack et al. 2007).

For a better understanding and projection of invasion processes, it is necessary to integrate data collected at different spatial and temporal scales, such as demographical surveys, assessments of habitat preference, records of local population expansion, maps of habitat configuration and dispersal into spatially-explicit models (Andrew and Ustin 2010). Here, we use such an integrative approach to study invasion processes. We combine multitemporal monitoring data of an invasive plant's local demography and distribution on landscape scale and spatio-temporal modelling.

Our model system is the well studied invasion of *Heracleum mantegazzianum* Somm. et Lev. (giant hogweed) which has spread massively in Europe since around the middle of the twentieth century (Tilley et al. 1996; Pyšek et al. 2007). Its invasion has got implications for human health due to phototoxic furanocumarins in the plant's sap that can cause severe skin burns (Lagey et al. 1995). Further, *H. mantegazzianum* can form dominant stands that reduce native species richness (Thiele et al. 2010). Comprehensive understanding of this species' invasion process will help to take efficient management decisions, e.g. to focus on those processes that have the strongest influence on invasion extent.

Previous studies have collected a plethora of knowledge on biology and ecology of this species (see Pyšek et al. 2007).

Particularly, multi-year demographic data has been collected (Hüls et al. 2007; Pergl et al. 2007) and the distribution has been mapped twice (2002 and 2009) in 20 landscapes (1 km² each) where exact locations and abundances of all incidences of *H. mantegazzianum* were recorded with GPS.

Previous models already combined individual mechanisms of demography and dispersal of *H. mantegazzianum*. On the population level, both matrix models and individual based models (IBM) have been applied so far. Nehrbass et al. (2006) made use of monitoring data collected over 3 years in the Czech Republic for parameterization and mainly found net growth rates smaller than 1 which represents declining populations. Additionally, they combined an IBM with a virtual ecologist (Zurell et al. 2010) based on the same data set. In doing so, they found that temporal variation in growth rates can lead to monitoring a decline in populations which expand in principle. Hüls, Otte and Eckstein (2007) made use of monitoring data from Germany for parameterization of four matrices separating open and dense stands over two consecutive years that differed markedly in weather conditions. They analysed the contribution of both year (weather) and density to the individual characteristics of populations being generation times, size distribution and net growth rates. The specific matrices could be applied for modelling population dynamics under specific conditions. But conditions vary with time, especially population density. Hence, for transient simulation one single matrix merging all specific matrices into one continuously defined density dependence is required.

For an analysis of spatial effects, Nehrbass and Winkler (2007) introduced deterministic local spread of up to 10 m and random long-distance dispersal of 1 % of the seeds into their IBM for a virtual landscape. Qualitatively they found that the effect of local spread depends on distribution of suitable habitats and that long-distance dispersal is more important than local dispersal. Nehrbass et al. (2007) applied the same modelling approach to one Czech site of approximately 50 ha and compared model predictions with maps

of *H. mantegazzianum* derived from aerial images at four dates spanning 27 years (Müllerova et al. 2005). It is possible to detect flowering plants of *H. mantegazzianum* on aerial images which makes them an efficient tool for retrospective monitoring of established stands. However, this method misses young stands that do not flower and, thus, its capacity to detect migration by transient incidents is limited. Nehrbass et al. (2007) supposed that a local dispersal is 5 m at most and quantified the percentage of long-distance dispersal through data fitting. They found 2.5 % of the seeds participating in long-distance dispersal.

Furthermore, recent findings ask for more detail in certain aspects of the models. Invasion probability and population density differ substantially between habitat types in Germany (Thiele and Otte 2006). Generally, population densities of *H. mantegazzianum* are highest in young-successional habitats (e.g. abandoned grasslands, disturbed sites) and markedly lower in older successional habitats (e.g. long-abandoned sites, woodlands). Hence, landscapes comprise patches of varying habitat suitability embedded in an inhospitable matrix. Invasion probability also depends on the structure of the landscape, particularly on the connectivity of suitable habitats and on corridors (rivers, streets) for dispersal or migration (Thiele et al. 2008). Also temporal dynamics of habitat suitability, e.g. through succession, have not been included in previous models. Finally, seed shed of *H. mantegazzianum* is not isotropic, as implicitly assumed in previous models, but biased towards main wind directions (W. Mayrink, unpublished data).

Hence, recent modelling approaches to the invasion of *H. mantegazzianum* gave valuable insights, e.g. into the prominent role of long-distance dispersal (Nehrbass et al., 2007), but tests of the relative importance of different mechanisms of the invasion and quantitative prediction of invasion extent require a complete model set up making use of recently published knowledge and unpublished field data.

Objective

The objective of this study was to assess the relative importance of different mechanisms for the invasive spread of plants on local and landscape scales. For this purpose, we built a spatio-temporal model comprising a density dependent matrix model and a cellular automaton, set up with real-world landscape configurations of suitable habitats and corridors. Then, we compared the efficiency of the basic model with alternative models, changing one process at a time, in order to test (via a likelihood ratio test) its importance for invasive spread.

We hypothesized that the dynamics of the invasion process, in terms of colonization events (invaded cells in the model) per unit time, were influenced by a. recruitment success of seeds dispersed to previously uninvaded sites, b. succession-driven changes in habitat suitability, c. spatially independent long-distance dispersal, d. dispersal via corridors (rivers, streets, railways), e. wind directions, and f. wind speed.

Materials and methods

Model species

Heracleum mantegazzianum flowers only once during its life cycle and then dies off so that population survival depends on recruitment from the short-term persistent seed bank. Duration of the life cycle varies between approximately 3 years under low competition (intra- or inter-specific) and 5 years under high competition (Hüls 2005; Pergl et al. 2006).

Due to its implications for humans and the environment, *H. mantegazzianum* is increasingly being managed with herbicides or mechanical measures. In some of the monitoring areas, management was obvious and may have affected the invasion process.

Landscape monitoring: invader distribution and habitat suitability

We monitored the invasion of *H. mantegazzianum* in eight landscape sections of 100 ha (1×1 km²) located in Western and Southern Germany (details in Thiele and Otte 2008) conducting two field surveys of each study area at an interval of 7 years (2002–

2009), corresponding to two completed life cycles. In these surveys, we located all incidences of *H. mantegazzianum* with GPS (Fig. 1). At both survey dates, we estimated abundances of flowering and vegetative individuals (excluding seedlings) and classified the invaded habitat type for each incidence of *H. mantegazzianum*. We also recorded type and effectiveness of control measures, if visible in the field. Additionally, we conducted interviews with local actors where official management projects were conducted in order to acquire information about onset and extent of control measures.

We mapped land cover and linear landscape elements (rivers, streets, railway lines) of the

study areas from aerial images in a Geographic Information System (GIS; ArcGIS 9.3.1). Land-cover types were classified into 'suitable' and 'unsuitable' for *H. mantegazzianum* based on a survey of invaded plant communities and habitats (Thiele and Otte 2006). Further, we quantified the invasibility of suitable land-cover types using the electivity index $E = (r - p)/(r + p)$ (Ivlev 1961), where r is the proportion of cover of *H. mantegazzianum* falling on the given land-cover type and p is the proportion of that land-cover type of the whole landscape; for the calculations of electivity indices, we combined monitoring data of 20 study areas.

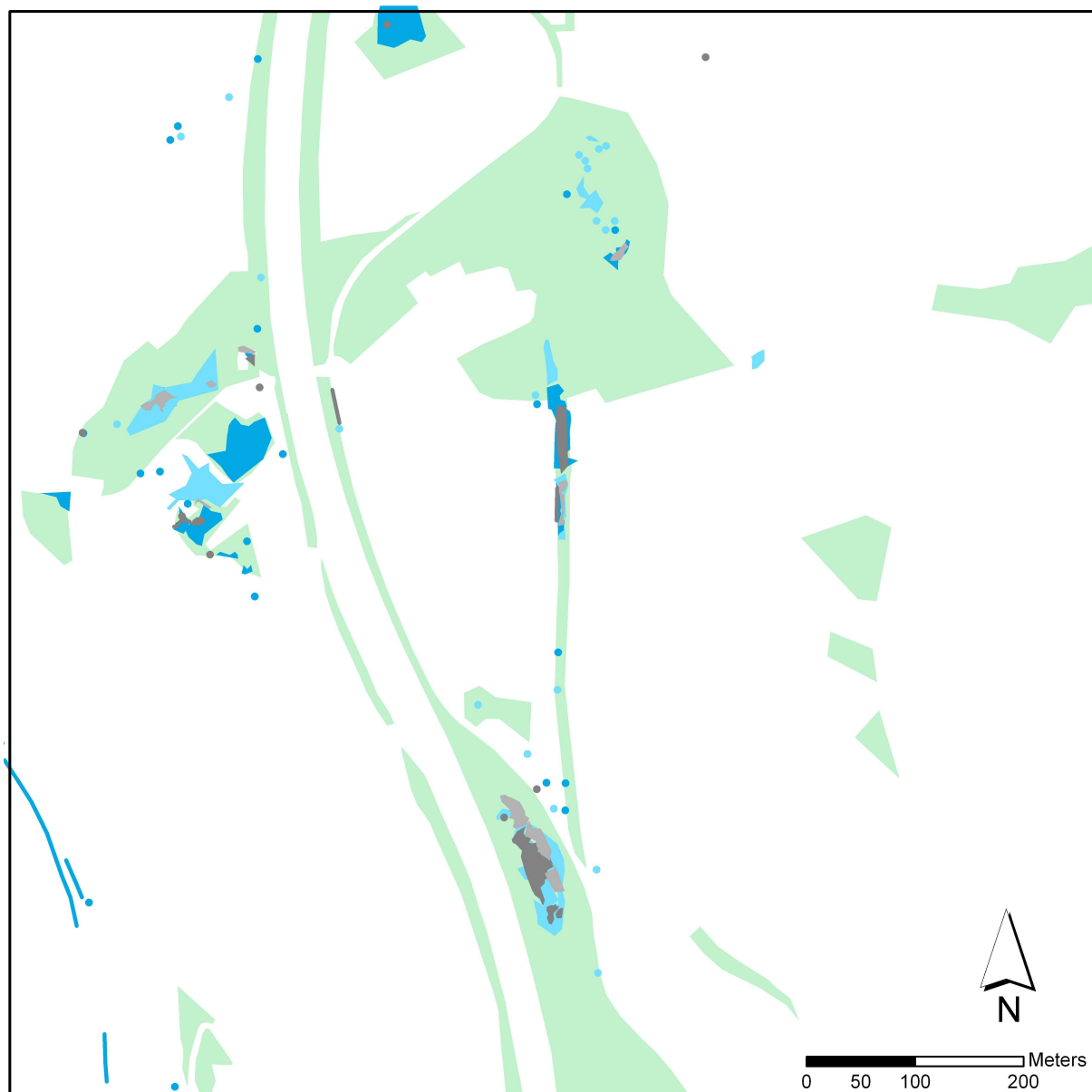


Fig. 1 Map of the study area Hagen-Waterhövel (HA-WAT; see Table 1) showing habitat patches (green) overlain with monitorings of *Heracleum mantegazzianum* (grey and blue). Grey colouring indicates *H. mantegazzianum* occurrences

in 2002; *blue* colouring is 2009. *Dark grey/blue* area signatures represent dominant stands of *H. mantegazzianum* (>50 % of area covered), lighter ones open stands (<50 % cover). *Small* or *narrow* stands are shown as *circles* or *lines*. The older survey is put on top of the younger, so that visible *blue colors* show the spread between 2002 and 2009, while *grey colors* show either persistent or, less often, abandoned stands. Note that narrow habitat strips along road and railway corridors are not shown, but were included in the spatiotemporal model.

Table 1 Study areas: locations, coordinates, altitude and basic climate parameters

No	County	ID	Coordinates		Altitude (m)	Precipitation mean annual (mm)	Temperature means (°C)		
			East	North			annual	January	July
1	Altenkirchen	AK-HEL	3410.500	5623.000	160	1041	8.5	0.3	16.7
2	Euskirchen	EU-OBE	2535.500	5589.000	590	938	7.3	-0.1	15.1
3	Freising	FS-PEL	4465.500	5362.500	490	838	7.5	-2.1	16.7
4	Garmisch-Partenkirchen	GA-ETT	4430.200	5270.000	865	1565	6.5	-3.0	15.8
5	Garmisch-Partenkirchen	GA-GLE	4443.500	5253.500	930	1437	6.7	-1.5	15.0
6	Hagen	HA-DAH	3396.700	5687.000	170	1157	9.5	2.0	17.4
7	Hagen	HA-WAT	3397.000	5689.800	275	1043	9.5	2.0	17.4
8	Waldeck-Frankenberg	WF-NIE	3488.300	5668.500	260	727	7.4	-0.9	15.8

Coordinates represent the south-western corner of study areas according to the German grid ('Gauss-Krüger'). Altitudes are the average between the highest and lowest stand of *Heracleum mantegazzianum* within the study area. Climate data refers to the nearest weather station and represents the years 1961–1990 (Deutscher Wetterdienst, www.dwd.de).

Model

Overview: state variables, scales and processes

Capacity-limited population dynamics comprising dispersal was modelled in heterogeneous environments. Hence, two spatially-explicit state variables were included: stage-structured population density and habitat suitability. With respect to the former we classified the life-cycle stages of *H. mantegazzianum* following the scheme of Hüls et al. (2007): small vegetative plants (y_1 , shorter than 50 cm), medium vegetative plants (y_2 , taller than 50 cm), large vegetative plants (y_3 , reaching canopy) and flowering plants (y_4). Simulation time covered 7 years with time intervals of 1 year. Analogous to the resolution of the land-cover maps, each of the study areas was tessellated into 200×200 cells of 5 m edge length.

In each time step, local population dynamics was modelled cell-wise in a combination of stochastic and probabilistic

approaches as follows in this section. We consecutively considered the demography of sessile plants via a matrix model (Caswell 2001) and dispersal of resulting mobile offspring via a cellular automaton (Adamatzky 1994), (Fig. 2).

In contrast, cell-wise habitat suitability was defined explicitly. It was supposed to decrease linearly over time from perfectly suitable to permanently unsuitable due to succession, i.e. competition. Spatial differences were supposed to be due to differences in developmental stage only. Additionally, we introduced a probability p_{HS} for cells which are not (yet) permanently unsuitable to be nevertheless unsuitable for recruitment considering stronger vulnerability of seeds. Finally, we introduced a probability p_{man} for cells to be subjected to pest management as preflowering cut of large plants affecting the third vegetative stage only; this probability was allowed to vary between years, and areas.

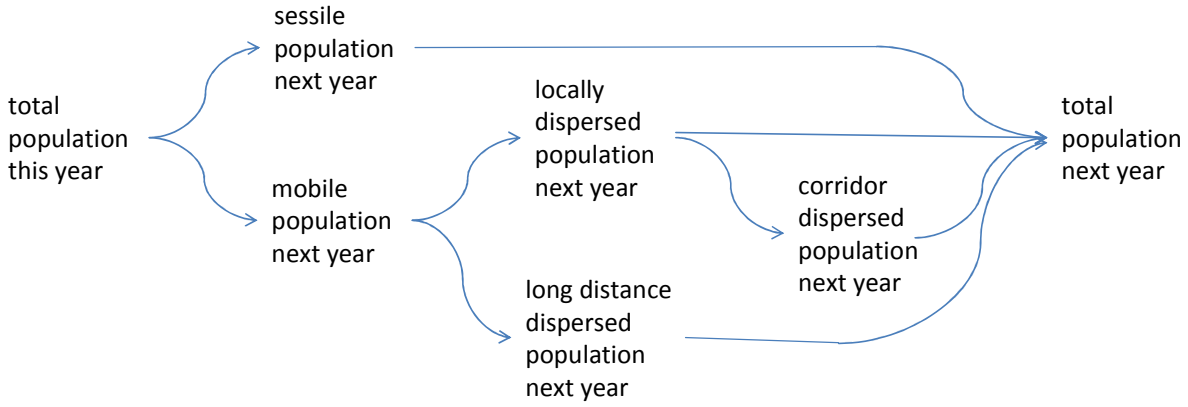


Fig. 2 Modelling concept: overview over processes and their scheduling within time steps of 1 year. Each process is modelled for each cell of the cellular automaton before proceeding to the next process

Demography of sessile plants

The matrix model reads

$$L = \begin{pmatrix} \sigma_1 \cdot (1 - \gamma_1) & 0 & 0 & 0 \\ \sigma_1 \cdot \gamma_{12} & \sigma_2 \cdot (1 - \gamma_2) & 0 & f_{42} \\ \sigma_1 \cdot \gamma_{13} & \sigma_2 \cdot \gamma_{23} & \sigma_3 \cdot (1 - \gamma_3) & 0 \\ 0 & \sigma_2 \cdot \gamma_{24} & \sigma_3 \cdot \gamma_{34} & 0 \end{pmatrix}$$

with survival rate σ_i of stage i and development rate γ_{ij} which is the portion of the surviving that transits from stage i to stage j . The total development rate of stage i is given as $\gamma_i = \sum \gamma_{ij}$.

Fecundity was considered to result in medium vegetative plants with rate f_{42} . The additionally assumed fecundity resulting in small plants with rate f_{41} represents the mobile offspring for dispersal, see next paragraph.

Capacity limitation was reported by Nehrbass et al. (2007) who integrated a ceiling capacity without density regulation below that threshold. Here, we integrated continuous density regulation smoothly decreasing both survival and development when capacity is approached. As water and nutrient supply was found to be of minor importance, the dominant density regulating environmental factor considered was light. Consequently, plants compete with equally large and larger conspecifics only. We therefore applied a Weibull function (Lindgren 1993) with stage specific thresholds $y_{\text{thres } i}$ and shape parameters δ_i , which modify zero competition rates of survival σ° and development γ° . In addition to density regulation through intraspecific competition, we integrated density regulation through interspecific competition accounting for all non-*H. mantegazzianum* competitors in *H. mantegazzianum*-equivalents x . We

supposed the latter to linearly increase with time due to succession as computed from habitat suitability such that

$$\sigma_i^*(x, y_i, y_{i+1}, y_{i+2}, \dots) = \sigma^\circ \exp \left(- \left(\frac{x + \sum_{j \geq i} y_j}{y_{\text{thres } i}} \right)^{\delta_i} \right)$$

and accordingly for the development rates γ^*_i . Finally, survival rates were altered by yearly pest management treatments yielding time dependent survival rates $\sigma_4 = p_{\text{man}} \sigma^*_4$.

Dispersal of mobile offspring

The number of mobile offspring was $f_{41} \cdot y_4$ and was subjected to dispersal. Three types of dispersal were taken into account: (1) local dispersal, (2) dispersal along corridors as rivers, streets and railways and (3) long-distance dispersal.

For long-distance dispersal, a portion p_{LD} of the mobile offspring of all cells were distributed randomly over the entire area. The remaining portion $(1 - p_{LD})$ of the mobile offspring was supposed to disperse locally over its neighbourhood with cell-specific probabilities s_j (Fig. 3).

Dispersal along corridors finally was modelled if cells which belong to corridors were reached by locally dispersing offspring. These cells were given a topological order (Streets and railways are bidirectional, while rivers are unidirectional as a matter of course). The affected offspring were distributed along the corridor's topology over a corridor-specific convection distance d_{con} . Shifts to non-corridor neighbour cells (Fig. 3) were afflicted with a random shift probability p_{shift} .

survival probabilities; In the final two, model assumptions on local dispersal were modified.

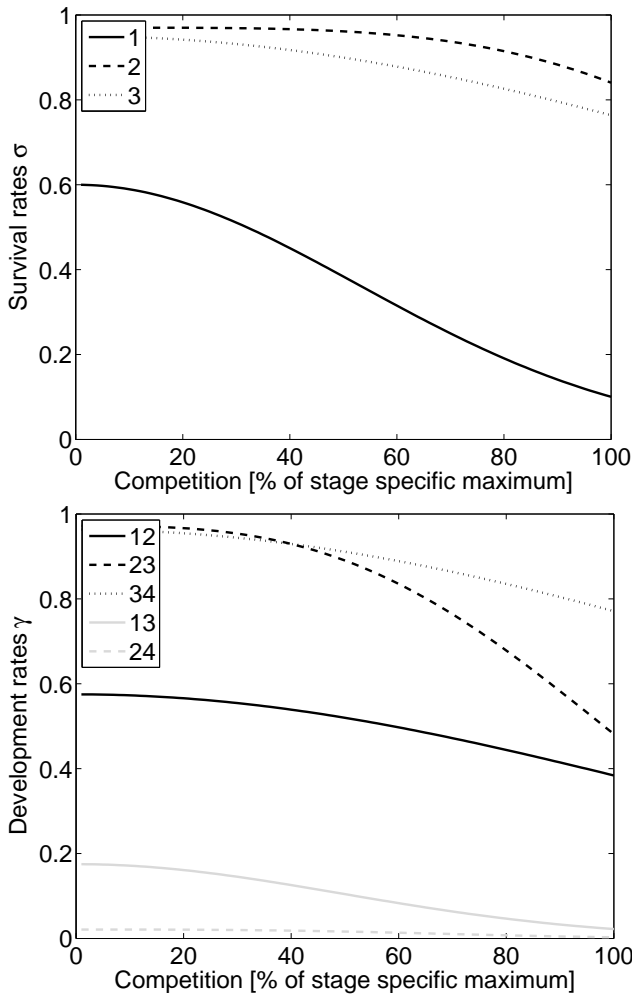


Fig. 4 Survival rates (*above*) and development rates (*below*) as dependent on competition. Survival rates are given for each stage indicated by the number, survival rate of stage 4 (generative stage) is zero. Development rates are given for each transition indicated by the pair of numbers, for instance 12 refers to a transition from stage 1 to stage 2. Stage specific maximum competition is the stage specific sum of competing incidences of *Heracleum mantegazzianum* at stable state if no other competitor is present

Here, we fitted the dependence of seed-rain density on the angle to the dominant wind direction, either limited to the same number of cells as the reference (hypothesis VIII with a neighbourhood W1) or allowing for dispersal extending over one additional cell leeward (hypothesis IX with a neighbourhood W2).

Each of the ten models (basic and nine hypotheses) was run for each of the eight areas. Quantities compared were (i) the number of cells occupied by the plant, (ii) the number of

cells occupied by vegetative stages of the plant, (iii) the number of cells occupied by the generative stage of the plant, (iv) the total number of cells newly colonised by the plant, (v) the number of cells colonised through local dispersal, (vi) the number of cells colonised through corridor dispersal via rivers, (vii) via streets, (viii) via railways and (ix) the number of cells colonised through longdistance dispersal. Dispersal type was judged from highest proximity of possible sources. Tracking of actual dispersal would have been possible for the modelling, but not for the monitoring data.

Table 2 Parameterization of the population matrix at steady state and of local dispersal probabilities (W0)

Parameter	Value
σ_1	0.20
σ_2	0.94
σ_3	0.90
σ_4	0.00
γ_{12}	0.450
γ_{13}	0.050
γ_{23}	0.772
γ_{24}	0.011
γ_{34}	0.913
f_{41}	7.1
f_{42}	0.4
S_0	0.584
S_1	0.072
S_2	0.027
S_3	0.005

Related parameters of density dependence and of additional local dispersal neighbourhoods (W1, W2) can be found in the supporting information

Comparison between the areas within one model run was based on relative deviation between modelled quantity m and monitored quantity o in area i

$$R_i = \frac{m_i - o_i}{o_i}$$

For a comparison between the models, modelling efficiency was used which reads with \bar{o} mean of monitored quantities over all n areas:

$$I = 1 - \frac{\sum_i (o_i - m_i)^2}{\sum_i (o_i - \bar{o})^2}$$

The likelihood ratio test, serving for making decisions between a complex (Comp) and a simpler model (Simp), was used for hypothesis testing. The test statistics Λ is χ^2 distributed with difference in number of parameters Δ_N degrees of freedom:

$$\Lambda = -2 \lg \left(\frac{\sum_i (o_i - m_{\text{Comp}i})^2}{\sum_i (o_i - m_{\text{Simp}i})^2} \right)^{n/2}$$

We applied a significance level of 0.05.

Sensitivity analysis

As the parameterization of corridor dispersal was based on approximations only, we conducted a sensitivity analysis (i) to estimate their influence and (ii) to eventually improve the approximations. For all types of corridor dispersal we accomplished model runs with altered maximum convection distance $d_{\text{con}} \in [0.5d_{\text{conref}}, 0.75d_{\text{conref}}, 1.5d_{\text{conref}}, 2d_{\text{conref}}]$ and for rivers also shifting probability $p_{\text{shift}} \in [0.1, 0.2, 0.3]$.

Results

General model

The basic model showed a high modelling efficiency of 0.94 both for all cells occupied (Table 3) and for vegetative stages only. Modelling efficiency for cells occupied with the generative stage was much smaller (0.32) and relative deviation from monitoring was high (Table A2). Also for the total number of cells newly colonised by the plant during the monitoring period, the basic model reached high modelling efficiency of 0.89 (Table 3). However, when considering the type of colonisation, modelling efficiency decreased from corridor dispersal via rivers (0.73), local dispersal (0.67), corridor dispersal via streets (0.21), corridor dispersal via railways (0.21) to very low efficiency for longdistance dispersal (-0.95).

Comparing the eight study areas (see table A2 in the supporting information for all R_i), model deviation of total number of cells occupied ranged from one incidence of comparably high overestimation by 43 % to an underestimation of -16 %. Nevertheless, the generally high modelling efficiency was

reached through a large number of areas with deviations smaller than 10 % for half of the areas. Model deviations of the number of cells occupied by vegetative plants were similar to the preceding, while those of the number of cells occupied by generative plants ranged from underestimations of -100 % to overestimation of more than 200 % (cf. Fig. 5).

Long-distance dispersal was underestimated for all areas; railway dispersal was underestimated in the three areas where it occurred. The remaining types of dispersal revealed a mixed picture with local dispersal tending to be overestimated and riverine dispersal tending to be underestimated (Figs. 6 and 7).

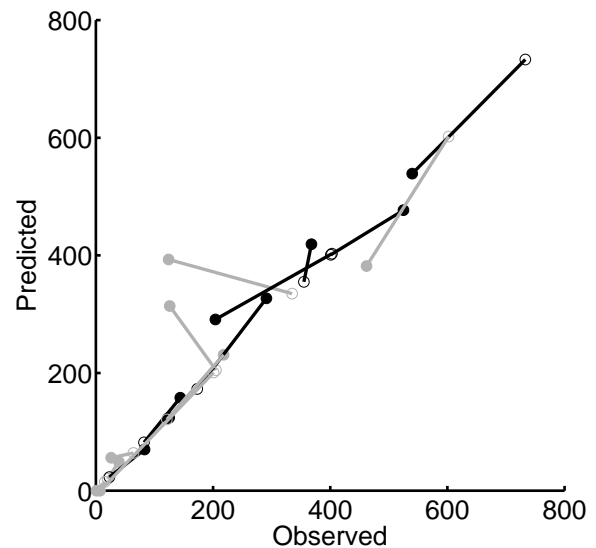


Fig. 5 Occupancy dynamics in terms of total numbers of cells occupied: observation versus prediction for vegetative (black) and generative (grey) plants respectively. For each study area, initial states are given in open dots and final states in full dots. Lines linking the two for clarity

Hypotheses testing

Limitation of recruitment after dispersal (I), decreasing habitat suitability with succession (II) and inclusion of long-distance dispersal (III) significantly improved the model (Table 3). In contrast, neither individual types of corridor dispersal nor their combined introduction (IV through VII) improved the model consistently, although dispersal via rivers and combined corridor dispersal was accepted with respect to the quantity number of cells invaded through riverine dispersal.

Table 3 Hypotheses testing

Hypothesis	Model modification	ΔN	Modelling efficiency		Test outcome: Complex model...	p
			Occupancy	Colonization		
I No recruitment limitation	$p_{HS} = 1$	-1	-1.86	3.58	Accepted	<0.001
II No succession	$\Delta_{Suc} = \infty$	-1	0.73	0.34	Accepted	<0.001
III No long distance dispersal	$p_{LD} = 0$	-1	0.88	0.82	Accepted	0.017
IV No street dispersal	$\sigma_{street} = 0$	-2	0.93	0.78	Rejected	0.637
V No riverine dispersal	$\sigma_{riv} = 0$	-3	0.94	0.87	Rejected	0.994
VI No railway dispersal	$\sigma_{rail} = 0$	-2	0.92	0.83	Rejected	0.287
VII No corridor dispersal	$\sigma_{street} = \sigma_{riv} = \sigma_{rail} = 0$	-5	0.95	0.86	Rejected	1.000
VIII Different wind direction	Neighbourhood W1	+5	0.90	0.87	Rejected	1.000
IX Different wind direction with leeward extension	Neighbourhood W2	+7	0.87	0.78	Rejected	1.000

Modifications applied to the basic model, the related difference in number of parameters as compared to basic model Δ_N , modelling efficiency of the modified model with respect to total number of occupied cells and to total number of colonized cells, the test outcome and related p value. For comparison: the model efficiency of the basic model was 0.94 with respect to occupancy and 0.89 with respect to colonization; the closer the modelling efficiency to its maximum of 1, the better. The test outcome is shown for a comparison of occupancy. The test outcome states whether the complex model is accepted or rejected; the modified model is more complex than the basic model if $\Delta_N > 0$ and vice versa

Finally, both modifications giving more detail to directed wind effects in local spread (hypotheses VIII and IX) did not improve the model.

Sensitivity analysis

Modelling efficiency did not increase by altering any of the parameters related to corridor dispersal in the way described above. Decreasing convection distances to 15 m for streets led to an importantly lower modelling efficiency of 81 % (i.e. -14 %), for all other distances the effect was minor (≥ -6 %). The shifting probability seemed to be of moderate importance (modelling efficiency of 84 % for $p_{shift} = 0.3$).

Discussion

General model performance

Modelling efficiency was low for the number of cells occupied by generative plants compared to vegetative plants. The monitoring revealed in several study areas, that generative plants occupied markedly fewer cells than vegetative plants did (see Fig. 5). This was probably due to weed control measures. The model yielded overestimation of generative plants by more than 200 % in a study area where the control measures taken remained too obscure to be taken into account. On the other hand, an underestimation of generative plants

by 100 % occurred for study areas where we modelled perfect success of these control measures, but still few remaining incidences were monitored. Thus, low modelling efficiency for generative plants seemed to be due to difficulties in simulation of weed control. However, as deviations were high where numbers were low the contribution of these deviations to modelling efficiency of total numbers was negligible.

Long-distance dispersal was always underestimated. Cells were defined to be colonized through long-distance dispersal, if no other source of dispersal was close enough to reach the respective cell through mechanisms defined by the model. However, some cells assigned to be invaded through long-distance dispersal in the monitoring were expanded occurrences in extension of previously existing stands (e.g. AK-HEL or HA-WAT). We conclude that regionally local dispersal reached farther than defined by our model, which is farther than 10 m. In the same vein, cells which were obviously colonized by long-distance dispersal in the model were assigned to other types of dispersal where respective sources were present (e.g. FS-PEL).

Hence, underestimation of long-distance dispersal was, at least in part, attributable to the classification scheme of dispersal types. As mentioned above, the classification scheme was adopted due to the

impossibility to track dispersal type in the monitoring. In an auxiliary classification for the modelling only, we judged dispersal type as the one carrying the highest percentage of offspring into a cell. As compared to this auxiliary classification, the adopted scheme resulted in an underestimation of local dispersal (5 % of total number of colonised cells), long distance dispersal (2 %) and railways (1 %) and an overestimation of streets and rivers (4 % each).

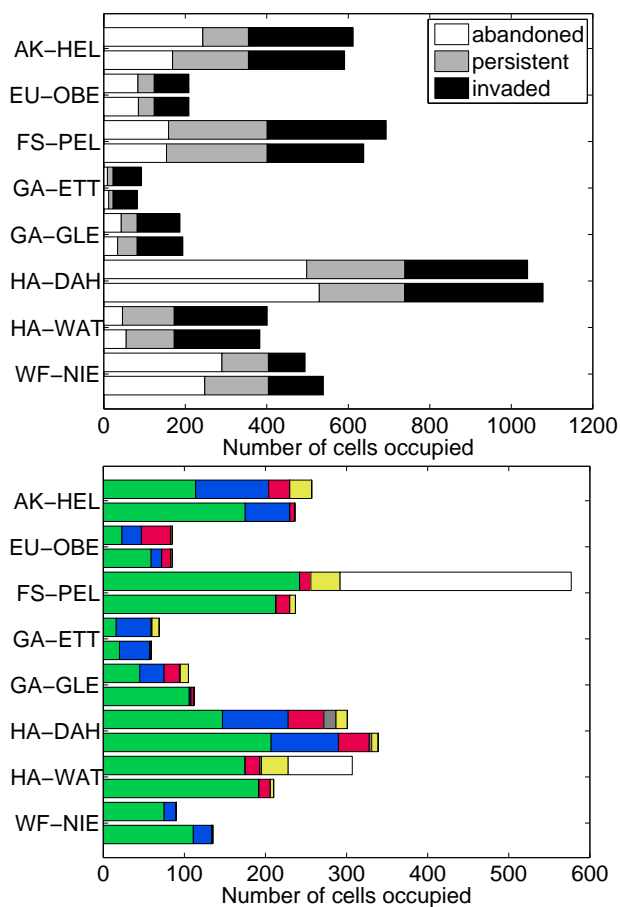


Fig. 6 Occupancy dynamics in terms of numbers of cells per history; observation (*upper bar*) and prediction (*lower bar*) for each area respectively. *Above*: General history, numbers of cells which were either (i) occupied only initially (abandoned thereafter), (ii) persistently occupied or (iii) colonized during the monitoring. *Below*: Colonization history, numbers of cells colonized through local dispersal (*green*), rivers (*blue*), streets (*red*), railway lines (*grey*) and long distance (*yellow*). *Open bars* represent additional anthropogenic disturbance not included in the model.

Modelling of corridor dispersal showed varying quality. We identified three possible reasons for deviations: (i) discretization, (ii) boundary effects and (iii) inappropriate

parameterization. Firstly, stands which are mapped at a large distance to corridor cells would not contribute to this dispersal mode in the model while the monitoring proves otherwise (e.g. GA-GLE). Secondly, corridors stretched over the boundaries of the area possibly introduced small plants into the study area (e.g. WF-NIE, EU-OBE). Finally, convection will differ not only between corridor types but also within, e.g. depending on local flow velocity of a river or intensity of use of a road. Specific parameterization could be necessary, but would be difficult to obtain. An alternative process model will be discussed below.

Recruitment

Seeds dispersed to suitable habitat often fail to establish new stands of *H. mantegazzianum*; this is suggested by the significant improvement of fit to the monitoring data, when the probability of dispersed plants in the model to colonize a new cell was decreased from 100 to 30 %. Thus, it appears that the recruitment phase of dispersed seeds represents a bottleneck of the invasion process.

Which environmental factors could constrain recruitment success of *H. mantegazzianum*? Germination percentages of the seeds are high in both laboratory and outdoor situations (Moravcová et al. 2005). Abiotic site conditions (nutrients and water supply) were not too heterogeneous among sites and were not correlated with abundance of *H. mantegazzianum* in the study areas (Thiele and Otte 2006).

Hence, we assume that heterogeneity of community composition may create the variable pattern of recruitment success of *H. mantegazzianum*. At some sites of generally suitable habitat, absence of constraining community components, such as competitors, herbivores or pathogens, might facilitate recruitment, whereas their presence would prevent it. This would be in line with the hypotheses of fluctuating resources (Davis et al. 2000) and niche opportunities (Shea and Chesson 2002) which suggest disturbances within habitats to facilitate invasion, whereas undisturbed sites within a habitat would be biotically resistant (Levine et al. 2004),

although species richness per se does not seem to convey resistance to *H. mantegazzianum* (Thiele et al. 2010). As effects of herbivores and pathogens on *H. mantegazzianum* usually appear to be moderate at least in its invaded range (Hattendorf et al. 2006; Seier and Evans 2007), competitive plants most likely constrain its invasion.

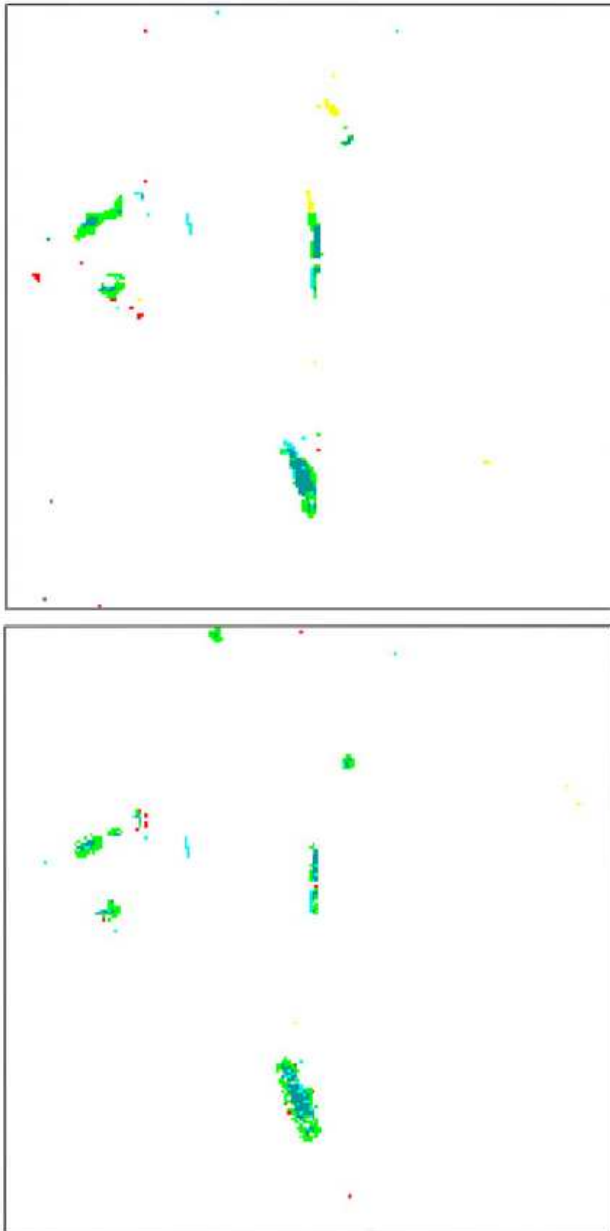


Fig. 7 Observed (*above*) and predicted (*below*) spatial distribution of *Heracleum mantegazzianum* in Hagen-Waterhövel (HAWAT, see Table 1) displaying persistent occupation (*dark grey*), abandonment (*turquoise*), and colonization through local dispersal (*green*), rivers (*dark blue*), streets (*red*), railway lines (*grey*) and long distance (*yellow*).

Succession

The suitability of habitats for *H. mantegazzianum* seems to decrease by time, since introducing succession of habitat suitability, from optimum suitability to zero, over 30 years, significantly improved modelling efficiency. Decreasing habitat suitability may affect the landscape distribution of an invasive species through declining population densities and reduced numbers of seeds shed to adjacent habitat cells or to dispersal corridors. Lower population densities of *H. mantegazzianum* in older successional habitats have been described before (Thiele and Otte 2006).

Abiotic site conditions, as said above, do not seem to be related to population density within suitable habitats. Thus, we would conclude that temporal dynamics of habitat suitability for *H. mantegazzianum* are shaped by biotic interactions, most likely plant–plant interactions. Older habitats increasingly feature woody plants which may shade out *H. mantegazzianum* and slow down population growth. But also competition between tall herbs may play a role (Thiele et al. 2010).

Long-distance and corridor dispersal

Long-distance dispersal significantly improved modelling efficiency, corroborating previous studies (Nehrbass et al. 2007). In contrast, dispersal along corridors (rivers, streets, railway lines) could be omitted from the model without a significant loss of modelling efficiency. The latter is surprising in the first instance because empirical studies indicate that corridors enhance invasive spread of *H. mantegazzianum* (Thiele et al. 2008) and other non-native plants (e.g. Pauchard and Alaback 2004; Rentch et al. 2005; von der Lippe and Kowarik 2007).

Dispersal through corridors is directly responsible for a small fraction of invaded area only because the amount of suitable habitat associated with corridors (e.g. road verges) is low compared to other habitat types. Hence, it is possible that omission of corridor dispersal was accepted because the fraction of cells invaded in this manner is of minor importance. This interpretation is supported by the fact that the omission of riverine corridor dispersal,

which represented the most important fraction of corridor dispersal in the eight areas (Fig. 6), was not fully accepted.

The importance of corridor dispersal may rather be rooted in increased colonisation probability of remote habitat patches that could not be reached by local dispersal, thus increasing the invasion speed on landscape and regional scales, while subsequent local expansive spread accounts for considerably larger proportions of invaded area. Corridor dispersal might become important over a longer period of time than the 7 years comprised in the monitoring at hand. Although it is possible from a life-cycle perspective that two generations (of 3–4 years each) are dispersed via corridors within this time horizon, their expansion range remains limited.

Yet another reason for minor significance could be that our mechanistic modelling approach was wrongly parameterized. Specific experiments on dispersal mechanisms of the respective corridors could be helpful. However, our model was not sensitive to increasing convection distances.

Combining the aforementioned two reasons, we could think of a simplified stochastic representation of corridor dispersal, similar to long-distance dispersal in general, but spatially constrained and directed according to corridor configuration, rather than a mechanistic dispersal process as assumed in our model. Rare far-dispersal events through rivers, streets or railway lines may have a strong influence on invasive spread, in addition to general long-distance dispersal.

Wind-directed dispersal

The introduction of asymmetric local dispersal by wind (hypotheses VIII and IX) did not improve the model, although seed rain was clearly wind-directed in a field experiment (W. Mayrink, unpublished data). However, we applied general wind directions; locally, wind may play an important role. Models fed with monitored wind fields would answer this question.

Conclusions

Demography, dispersal and variation of invasibility are important drivers for invasive spread. Stochastic long-distance dispersal is responsible for a significant proportion of newly invaded habitat. Dispersal through corridors probably increases invasion speed on larger temporal and spatial scales, but the proportion of newly invaded habitat at landscape scale is not significant as compared to local dispersal and stochastic long-distance dispersal.

Local-scale variation of invasibility in space and time (recruitment, succession of habitat suitability) also has a strong influence on landscape distribution of invasive plants. Our model shows that recruitment success of *H. mantegazzianum* seeds dispersed to suitable habitats is markedly lower than 100 %. We suggest that spatial or temporal heterogeneity of community composition, driven by disturbances and succession, may cause this pattern.

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SUPPORTING MATERIAL

What shapes giant hogweed invasion? Answers from a spatio-temporal model integrating multiscale monitoring data

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SP1 Parameterization of stable state

Survival rates were estimated from the stable state distribution and its comparison with dense field conditions. Hüls et al. (2007) reported that generation times in dense stands were longer than those in open stands. Shorter generation times are primarily reached through higher contributions of jumping transitions. We therefore supposed that at stable state jumping transitions are of minor importance: $g_{i\ i+2}=0$. From the same fact we suppose that stasis is not negligible at stable state which reads $\gamma_{i\ i+1}<1$. However, from $\gamma_{i\ i+1}=1$ lower limits of σ_i can be deduced. The stable state estimated from the monitoring data at hand was

$$y_{\text{stab}} = \begin{pmatrix} 200 \\ 35 \\ 30 \\ 25 \end{pmatrix}$$

As the plant is monocarpic, $\sigma_4=0$. Consequently, all 25 flowering plants were large vegetative plants in the previous year and with $\gamma_{34}=1$ the transition rate $g_{34} = 25/30$ equals the lower limit of $\sigma_3 > 25/30$. Analogously, a transition rate $g_{23} = 30/35$ results in $\sigma_2 = 30/35$ with $\gamma_{23}=1$. On the one hand, this can not be seen as a strict lower limit because stasis in large vegetative plants might allow $g_{23} < 30/35$. On the other hand, if stasis in medium and large vegetative plants is of similar order $\sigma_2 = 30/35$ is an acceptable approximation for a lower limit. No lower limit could be given for the survival rate of small vegetative plants, as additionally f_{42} was an unknown source.

Nehrbass and Winkler (2007) reported an empirical average survival probability to be 0.63 ± 0.05 excluding seeds and seedlings. In their individual-based model Nehrbass et al. (2006) assumed a survival probability between 0 and 1.0 depending on number of leaves and leaf length. Translation into our stage classification gives probabilities ranging between 0 and 0.5 for the first stage, and between 0.6 and 1.0 for the second and third stage. Combining all the information, we approximated the survival rate at steady state to be as given in Table 2 resulting in an average survival rate of 0.34.

Development rates γ and fertility rates f were estimated based on an introduction of the survival rates given above in the analytical steady state distribution. As this yields no more than four equations, that is four parameters, we chose to fix the smallest transitions and fertilities. As jumping transitions are scarce at steady state, we deliberately set them to $g_{ii+2} = 1\%$ each. Fertility f_{42} was approximated to be 0.4 (Hüls et al. 2007).

Analytically, the steady state distribution of the given matrix is

$$y_{\text{stab}} = \begin{pmatrix} \frac{f_{41}}{\lambda - p_1} \\ \frac{f_{41}g_{12} + f_{42}(\lambda - p_1)}{(\lambda - p_1)(\lambda - p_2)} \\ \frac{(\lambda(\lambda - p_2) - f_{42}g_{24})(\lambda - p_1) - f_{41}g_{12}g_{24}}{g_{34}(\lambda - p_1)(\lambda - p_2)} \\ 1 \end{pmatrix}$$

for the dominant eigenvalue $\lambda=1$. Together with $f_{41} = 7.1$ (Hüls et al. 2007) these assumptions force γ to be as given in Table 2.

In order to parameterize density dependence, that is σ_i^* , $y_{\text{thres } i}$ and δ_i , and according parameters for development we urged

$$\bullet \quad \sigma_i(y_{\text{stab } i}, y_{\text{stab } i+1}, y_{\text{stab } i+2}, \dots) = \sigma_i^* \cdot \exp\left(-\left(\frac{\sum_{j \geq i} y_{\text{stab } j}}{y_{\text{thres } i}}\right)^{\delta_i}\right) = \sigma_{\text{stab } i}$$

and analogously for development rates.

- Absence of oscillation which have never been reported
- Establishment of steady state population in less than 10 years' time (estimate from field observations during landscape monitoring).

Resulting parameters can be found in the table in appendix A2.

SP2 Parameterization of local dispersal taking wind into account

Dispersal probabilities differ in different directions if wind is taken into account. Indices n, s, w, e represent north, south, west and east respectively. In case of wind altered distribution of probabilities only we approximated:

1. $S_{1w} = 2/3 \cdot S_1$, $S_{1e} = 4/3 \cdot S_1$, $S_{1n} = S_{1s} = S_1$
2. $S_{2nw} = S_{2sw} = 2/3 \cdot S_2$, $S_{2ne} = S_{2se} = 4/3 \cdot S_2$
3. $S_{3w} = 2/3 \cdot S_3$, $S_{3e} = 4/3 \cdot S_3$, $S_{3n} = S_{3s} = S_3$
4. $S_{4ne} = S_{4nec} = S_{4see} = S_{4sse} = 0$
5. $S_{5e} = 0$

In case of wind altered distribution of probabilities including leeward extension by one cell we approximated:

1. $S_{1w} = 2/3 \cdot S_1$, $S_{1e} = 7/6 \cdot S_1$, $S_{1n} = S_{1s} = S_1$
2. $S_{2nw} = S_{2sw} = 2/3 \cdot S_2$, $S_{2ne} = S_{2se} = S_2$
3. $S_{3w} = 2/3 \cdot S_3$, $S_{3e} = S_3 + 1/6 \cdot S_1$, $S_{3n} = S_{3s} = S_3$
4. $S_{4ne} = S_{4nec} = S_{4see} = S_{4sse} = 1/6 \cdot S_2$
5. $S_{5e} = 1/3 \cdot S_3$

SP3 Tables

Table A1 Parameters of density dependence

Parameter	Value
σ_1^*	0.6
σ_2^*	0.97
σ_3^*	0.95
γ_{12}^*	0.5750
γ_{13}^*	0.1750
γ_{23}^*	0.9720
γ_{24}^*	0.0210
γ_{34}^*	0.9630
f^*	2
$y_{\text{thres}} - \sigma_1$	86
$y_{\text{thres}} - \sigma_2$	130
$y_{\text{thres}} - \sigma_3$	107
$y_{\text{thres}} - \gamma_{12}$	181
$y_{\text{thres}} - \gamma_{13}$	80
$y_{\text{thres}} - \gamma_{23}$	90
$y_{\text{thres}} - \gamma_{24}$	63
$y_{\text{thres}} - \gamma_{34}$	106
$\delta - \sigma_1$	2
$\delta - \sigma_2$	4
$\delta - \sigma_3$	2
$\delta - \gamma_1$	2
$\delta - \gamma_2$	3
$\delta - \gamma_3$	2

Table A2 Relative deviation R_i of the basic model from the landscape monitoring data of 2009 in terms of numbers of cells occupied by giant hogweed with respect to nine criteria (see section 2.5)

Criteria	AK-	EU-	FS-	GA-	GA-	HA-	HA-	WF-
	HEL	OBE	PEL	ETT	GLE	DAH	WAT	NIE
All plant stages	14	-1	-9	-16	11	1	-8	43
Vegetative plants	14	-1	-9	-16	10	0	-8	43
Flowering plants	149	26	217	-100	115	-17	6	-100
Cells invaded through								
... any dispersal type	-8	0	-19	-14	7	13	-8	50
... local dispersal	54	157	-12	25	136	41	10	48
... rivers	-39	-46	/	-14	-93	2	/	53
... streets	-77	-69	20	100	-79	-14	-2	/
... railways	/	/	/	/	-100	-80	-100	/
... long-distance dispersal	-100	0	-81	-100	-100	-43	-88	/