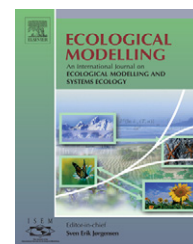


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## Is the Giant Hogweed still a threat? An individual-based modelling approach for local invasion dynamics of *Heracleum mantegazzianum*

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### ABSTRACT

The spread of invasive plant species is an increasing concern in many parts of the world. Negative effects on biodiversity, public health concerns, or economic damage are reported from the most vigorous of them. The monocarpic *Heracleum mantegazzianum* (Giant Hogweed, Apiaceae) is one of these species in Central Europe. The aim of the individual-based model (IBM) presented here was to assess the invasion status of *H. mantegazzianum*. This research was motivated by a recent study conducted by [Hüls, J., 2005. Populationsbiologische Untersuchung von *Heracleum mantegazzianum* Somm. & Lev. in Subpopulationen unterschiedlicher Individuendichte. Dissertation. Justus-Liebig-Universität Giessen, Germany (in German)], which predicted declines in a number of German Hogweed populations. This result contradicted many current, as well as past observations. In the presented study, we intend to resolve this controversy.

First, we show that the developed IBM is based on the same data set as the matrix model developed by [Hüls, J., 2005. Populationsbiologische Untersuchung von *Heracleum mantegazzianum* Somm. & Lev. in Subpopulationen unterschiedlicher Individuendichte. Dissertation. Justus-Liebig-Universität Giessen, Germany (in German)]. Yet, our results illustrate that the invasion status of *H. mantegazzianum* has not changed and that populations are still expanding in space.

Second, the reason for this opposite result is analyzed. Results from the IBM were compared with those of the transition matrix models and with a reduced version of the IBM. We identify individual variability as the main cause, which is accounted for in the original IBM but missing in the original matrix model and the reduced IBM.

Our studies also show that, although the long-term average of the population growth rate is larger than one and populations generally expand, there are years in which populations decline (actual growth rates  $R < 1$ ).

This highlights a need for longer-term monitoring of Giant Hogweed populations if matrix models are to be used to assess this species' invasion status. Results of IBMs, to the contrary, are insensitive to parameters estimated from "expansive" or "declining" years.

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## 1. Introduction

The number of introductions of non-native organisms has drastically increased during the last century. Among these neobiota (*sensu* Kowarik, 2003), some pose a threat to biodiversity in native ecosystems (Cox, 2004). One of the plant species falling under this category is the Giant Hogweed (*Heracleum mantegazzianum* Sommier et Levier, *Apiaceae*). The spread of this species in Central Europe was recognized as early as the 1960s (Ochsmann, 1992; Pysek, 1994). Since the 1990s there are numberless studies on the species ecology and its control, but most of them are rather qualitative than quantitative (Andersen and Calov, 1996; Lundström and Darby, 1994; Sampson, 1994; Tiley and Philp, 1994). Recent publications in unmanaged *H. mantegazzianum* stands predict declines in German and Czech Hogweed populations, derived from transition matrix models (Hüls, 2005; Pergl et al., *in press*). These results contradict many current, as well as past observations. In the presented study, we intend to resolve this controversy.

First, a model (HmIBM: *H. mantegazzianum* individual based model) was built to analyze dynamics of the Giant Hogweed. Method of choice was a spatially explicit, individual-based model (SEIB or IBM). Using discrete time and space, this approach is able to incorporate more complex types of heterogeneity and stochasticity within a species' performance than basic matrix models. Yet, matrix models are a popular tool in plant population ecology, as they can be easily applied through computer software (e.g. Ferson, 1988; Hood, 2003) and grant insight in the effect of life-cycle components on the dynamics of a species. Nevertheless, there are some constraints in their application, especially when populations are spatially expanding, inhomogeneous, or show annual variability in their dynamics; In such cases, sub-matrices and elaborate mathematical techniques become necessary, which take the simplicity from the approach (Fieberg and Ellner, 2001; Claessen, 2005; Münzbergova et al., 2005). Both IBM and matrix models are commonly used in population ecology, but there are few studies which actually compare two model types for the same data set and evaluate the advantages of one or the other (examples are Stephens et al., 2002; Nehrbass et al., 2006).

HmIBM was parameterized with demographic data collected in five populations over the 3 year period 2002–2004 (Hüls, 2005). We used the first transition for parameterization of our IBM and the second transition for model validation.

In the second step we compared the resulting population development with the outcome of the original evaluation. Hüls (2005) analyzed the data with statistical methods and stage-based transition matrix models (*sensu* Caswell, 2001a, b). Hüls (2005) used two unlinked sub-matrices per population, differentiating dense (100% *H. mantegazzianum* cover) and open (1–10% *H. mantegazzianum* cover) stands. For the first transition individual numbers and intrinsic growth rates from a majority of the matrices showed a decrease in the populations. Since long-term observations confirm *H. mantegazzianum* to be an invasive species (Pysek, 1991; Tiley et al., 1996), an explanation for those contradicting results was required. We asked ourselves whether the Giant Hogweed might no longer be a threat to Central Europe.

We intended to identify the processes leading to the divergence between expected and projected developments in the matrix models. In the IBM we evaluated the influence of internal (individual variability) and external factors (landscape structure) on the population's growth rates.

In the following:

- (1) We present how the IBM was developed and the fact that it is based on the same data set as the matrix model developed by Hüls (2005).
- (2) The results of the IBM show that the invasion status of *H. mantegazzianum* has not changed and that populations are still expanding in space.
- (3) Results from the IBM are compared with those of the transition matrix models and with a reduced version of the IBM to identify the reasons for those contradictory results.
- (4) Implications for the use of IBM and matrix models for the description of invasive plant species are discussed.

## 2. Material and methods

### 2.1. The species

In Germany and other European countries *H. mantegazzianum* is a prominent example of invasive plant species. It is a non-agricultural weed, indigenous to the Caucasus Mountains. The species was introduced to Central Europe in the late 19th century and has been recognized as an invasive species since the 1960s (Gutte, 1989; Pysek and Prach, 1993). *H. mantegazzianum* is a tall growing, monocarpic perennial, forming dense stands in riparian habitats, waste-grounds, on roadsides and other man-disturbed habitats (Ochsmann, 1992; Otte and Franke, 1998). A single flowering plant has been reported to produce more than 100,000 seeds (Tiley et al., 1996). Because of its size and tendency to form monospecific stands, it is considered a threat to biodiversity of the invaded communities (Pysek, 1994). Additionally, the phototoxic sap produced by the species causes public health concerns (Dodd et al., 1994; Tiley et al., 1996).

### 2.2. Empirical data

The data set consisted of morphological parameters for approximately 1000 individual plants collected by Hüls (2005). Information was collected in 76 permanent plots in five populations. Each permanent plot was 2.5 m<sup>2</sup> (1 m × 2.5 m). Census took place at the end of the flowering phase in autumn of the three consecutive years 2002, 2003, and 2004.

The author constructed a matrix model that divided the life cycle of the plants into four stages: small, medium, vegetative individuals and flowering plants. It intentionally neglected the dynamics of seedling recruitment (Hüls, 2005). Transition probabilities between stages for the matrix models were calculated from data collected in 2002 and 2003. The projection predicted a decrease in population size, with intrinsic growth rates around  $\lambda = 0.75$  for all populations (Hüls, 2005). Out of six parameters (plant height, number of leaves, length of longest leaf, stem diameter longest leaf, stalk diameter, umbel diameter) statistical analysis identified plant height and number

of leaves as relevant for time of reproduction (Hüls, 2005). This information was used in the parameterization of our individual-based model.

2.3. Individual-based model (IBM)

To describe population dynamics of *H. mantegazzianum* a stochastic, spatially explicit, individual-based model (IBM) was developed. The model was constructed rule-based. Life-history and dispersal rules were parameterized using empirical data.

2.3.1. Time

The model used discrete time-steps. One time-step represented a year corresponding to the censuses of the empirical study which took place each year during the flowering period.

For each time step growth of individuals, flowering, offspring dispersal and establishment, and death were computed.

2.3.2. Space

Landscape was represented by a two-dimensional grid, consisting of 2500 cells (50 × 50). Cell size was chosen according to the size of the permanent plots monitored in the field experiment (2.5 m<sup>2</sup>). Each cell could be parameterised with individual features, e.g. abiotic factors. According to the simulation scenarios (see below) we expressed habitat quality by different values of carrying capacity *K*, which was implemented as ceiling capacity (sensu Akcakaya et al., 1999; no density regulation before the maximum number of individuals in the grid cell was reached). Carrying capacity was estimated from empirical data on the number of adults.

2.3.3. Plants

Plants were represented as individuals. Demographic stochasticity was included in the model. Each plant was characterized by a set of traits: age, plant height and number of rosette leaves. Individual fate of a plant was recorded as soon as it was established as a seedling. Establishment meant the addition as an individual of age = 1 to the plant population (list) of a cell.

2.3.4. Growth

Initial height *h*<sub>0</sub> of new plants was assigned randomly to the individuals. Height *h*<sub>0</sub> obeyed a truncated normal distribution with *m* = 52 and *s* = 27. Subsequent height increase (in cm) per year followed a deterministic linear relationship (see Fig. 1)

$$h(t + 1) = 1.45 \times h(t) + 26.56 \tag{1a}$$

The maximum height a vegetative individual could reach in the model before it stopped growing was *h* = 220. Flowering plants followed a different size increase, characterising the extension of a flowering stalk *h*<sub>fs</sub> which was drawn as a random number with *m* = 175 and *s* = 43

$$h(t + 1) = h(t) + h_{fs} \tag{1b}$$

New plants started with a random number of leaves *l*<sub>0</sub> where *l*<sub>0</sub> obeyed a truncated normal distribution with *m* = 1.5 and

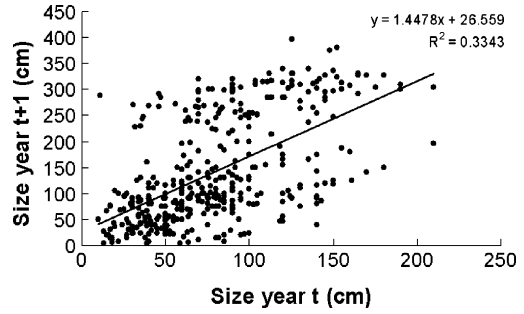


Fig. 1 – Linear growth function (Eqs. (1a)–(b)) derived from empirical data (*n* = 393, adjusted *R*<sup>2</sup> = 0.33, *p* < 0.005).

*s* = 0.65 which was rounded to the nearest integer. In each annual step vegetative plants increased or decreased their number of leaves randomly, with the increment Δ*l* obeying the same rule as initial number *l*<sub>0</sub>.

2.3.5. Flowering

Transition of an individual to reproductive state was determined at the beginning of each annual step (i.e. before growth). This transition depended on the number of leaves, plant height and age. A flowering plant has to match a minimum size (leaves ≥ 3, height > 95) and an age of at least 2 years. All plants matching these criteria underlay an additional global flowering probability, varying from year to year (*m* = 0.8 and *s* = 0.3). After flowering the plants died deterministically.

2.3.6. Seeds, seedlings and new plants

Each flowering plant produced a number of potentially viable seeds. Following the empirically found values, the number of offspring was normally distributed (*m* = 25 and *s* = 25), independent of the size of the mother plant. Seed dispersal was not modelled individually. New seedlings *S* were assigned to the cell of origin and in a radius around this home cell, following Eqs. (2a–e), where *S*<sub>rad</sub> equals the fraction of new seedlings assigned to a radius (rad) divided by the number of cells in the radius increment (with subsequent rounding of the numbers)

$$\text{home} : S_H = S \times 0.72; \text{minimum} = 1 \tag{2a}$$

$$\text{radius 1} : S_1 = S \times \frac{0.15}{8} \tag{2b}$$

$$\text{radius 2} : S_2 = S \times \frac{0.07}{16} \tag{2c}$$

$$\text{radius 3} : S_3 = S \times \frac{0.04}{24} \tag{2d}$$

$$\text{radius 4} : S_4 = S \times \frac{0.01}{32} \tag{2e}$$

One percent of the seedlings was randomly placed into cells over the whole grid, mimicking long-distance dispersal. All new plants established with certainty. Only when carrying capacity of the assigned cell had been reached no further establishment took place and the seedling was lost. We assumed that there is no permanent seed-bank.

### 2.3.7. Death

After seed production flowering individuals died. Plants exceeding the maximum age of six also died, even without reproduction. For all other plants there was a probability of  $p=0.5$  to die. Additionally, those plants died with no height (0 cm), due to a strong reduction in size after switching of individuals to flowering (Eq. (1b)).

### 2.4. Simulation scenarios

Each simulation was initiated with 10 new plants, which were placed in one randomly chosen cell. Simulations ran for 50 time steps (years) and each scenario was repeated 50 runs. Scenarios were differentiated according to individual variability and landscape structure.

### 2.5. Variation scenario

The “variation” scenario included individual variability in the starting conditions of growth and in leaf-number increase as given in the model rules.

### 2.6. No-variation scenario

The “no-variation” scenario excluded individual variability in the development of plant characteristics given by the random assignment of initial leaf number. All plants started with a fictive leaf number of  $l_0 = 1.5$  and a height of  $h_0 = 52$  cm. They had an annual increase of 1.5 leaves, and height increase followed Eqs. (1a)–(1b). Each flowering plant produced  $S=25$  offspring. Only those magnitudes that were assumed to be affected by environmental factors remained stochastic ones: death rate ( $p=0.5$ ) and global flowering probability ( $m=0.8$  and  $s=0.3$ ).

Landscape was described by either a homogeneous scenario where the carrying capacity  $K$  of all cells was set to  $K=20$  individuals or by a heterogeneous scenario. Here mean carrying capacity was also  $K=20$ , but equal proportions of suitable ( $K=40$ ) and unsuitable ( $K=0$ ) cells were distributed at random.

In model simulations population growth rate  $R$  was measured as the individual number  $N$  in year  $t+1$  divided by the individual number  $N$  from the previous year ( $t$ )

$$R = \frac{N_{t+1}}{N_t} \quad (3)$$

## 3. Results

### 3.1. Basic scenario: individual variation, homogeneous landscape (model verification)

In the homogeneous landscape the populations of the “variation” scenario exhibited an overall invasive behaviour. After surviving a lag phase, the individual number of the populations increased exponentially with a mean growth rate  $R=1.33$  until carrying capacity of the grid was reached. New nascent foci were placed by successful random long-distance dispersal. Local spread followed the pyramid-shaped dispersal kernel.

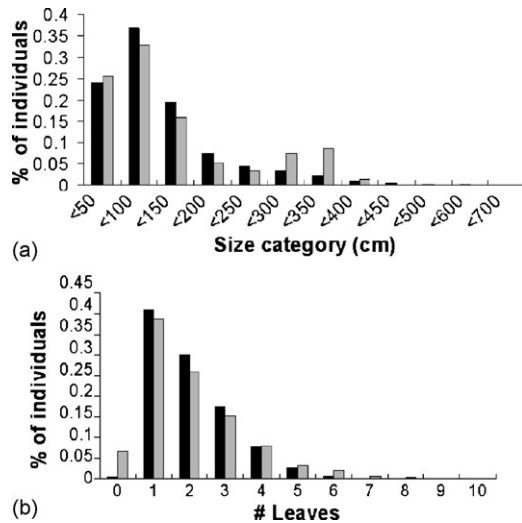
The stochastic simulation model was validated by comparing model results, obtained from simulations in a homogeneous landscape scenario, with known values for plant characteristics (Hüls, 2005) that were not used before for model parameterisation. Important reproductive values, such as the number of flowering plants per cell and fraction of flowering plants in a population were well approximated (Table 1). The number of new plants per flowering plant in the model lay slightly below the mean empirical value but had a higher variation (Table 1). The plant characteristics representing the vegetative state of the populations (height and number of leaves) were also matched (Fig. 2). We additionally compared results with a third census of the populations conducted by Hüls (2005) in 2004. This time the matrix models predicted a population growth rate of  $\lambda > 1.25$ . This value indicated a marked population increase and matched the long-term behaviour derived from our basic scenario.

In ecological reality every invasion can only take place once, and only these successful invasions are observed. It is possible

**Table 1 – Comparison of empirical findings (Hüls, 2005) with magnitudes derived from the simulation model**

Parameter	HmIBM (var)	HmIBM (non-var)	Empirical Data
Maximum age	6		?
Mean death rate	0.5		$0.37 \pm 0.05$ ( $n=2$ : one transition per habitat)
Fraction of flowering plants	0–0.5	$0.23 \pm 0.33$	$0.26 \pm 0.13$ ( $n=4$ : 2 years per habitat)
Mean # adult plants per cell	dependent on scenario		$6.44 \pm 4.63$ ( $n=4$ : 2 years per habitat)
Mean # flowering plants/cell	$1.70 \pm 1.01$	$2.03 \pm 0.54$	$1.83 \pm 0.99$ ( $n=4$ : 2 years per habitat)
Mean # new plants/flowering plant	$6.26 \pm 1.25$	$6.26 \pm 4.96$	$8.34 \pm 3.78$ (derived from matrices, $n=2$ )
Random dispersal rate	1% of new plants		?
Minimum height veg. plants (cm)	1		7
Maximum height veg. plants	220		228
Minimum height flowering plants	95		95
Maximum height flowering plants	548	201	364
Minimum # leaves	0		0
Maximum # leaves	9	4.5	12
Mean # leaves	$2.02 \pm 1.13$ ( $n=65,536$ )	–	$2.08 \pm 1.05$ ( $n=514$ )

Those magnitudes that were explicitly predefined by the model rules are indicated by shaded cells. Other values were used to test model suitability.

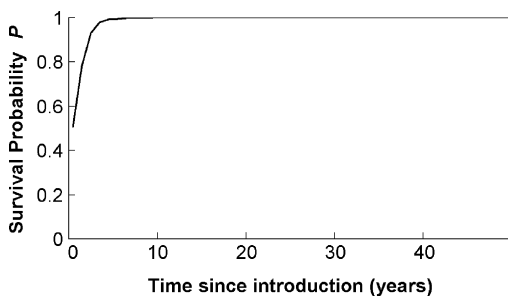


**Fig. 2 – Distribution of individuals on (a) size and (b) leaf-number categories. Grey bars give the empirical data set ( $n = 1313$ ), and black bars the HmIBM model results (scenario “variation”, homogeneous landscape;  $n > 50,000$ ).**

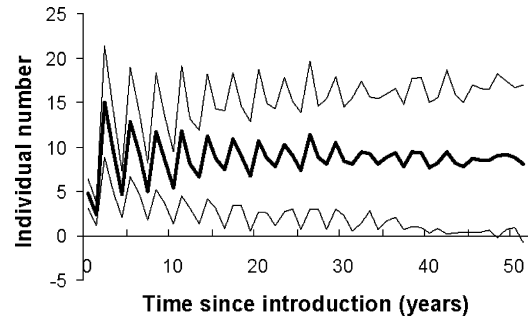
that many failed trials precede one successful invasion event (Heger, 2004). Repeated simulation runs allowed the evaluation of the probability of a successful invasion. Invasion failure after establishment of one individual is high in the first few years, but after having passed a threshold of approximately 5 years the population will spread almost deterministically (Fig. 3).

**3.2. Scenario: no individual variation, heterogeneous environment**

Contrasted to the “variation” scenario, we parameterized a model neglecting any individual variation and resembling the approach used in matrix models. As a result, the simulated populations showed no invasive behaviour. Although 60% of the populations became established, they persisted only with very low individual numbers ( $m = 8.93$  and  $s = 7.21$ ) (Fig. 4). Mean growth rate  $R$  was relatively high but underlay large annual variations ( $m = 1.99$  and  $s = 3.31$ ) (Fig. 5). When the global flowering probability, which causes divergence between the number of potential and actual number of flow-



**Fig. 3 – Incremental survival probability  $P$  for a simulated population of *H. mantegazzianum* (scenario “variation”) starting with a single individual in a homogeneous environment ( $n = 10,000$ ).**

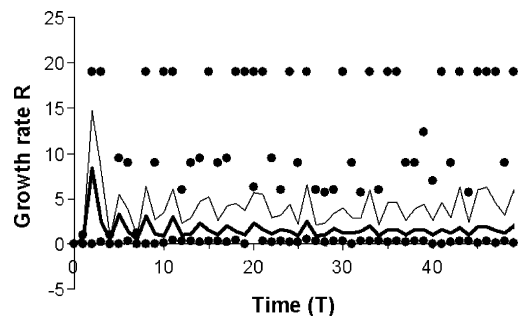


**Fig. 4 – Temporal development of individual numbers in the scenario “no-variation” ( $n = 50$ ). Mean values are represented by the thick line, S.D. indicated by the thin lines. Those populations persisting (approximately 60%) do so on a very low level, not exceeding 25 individuals.**

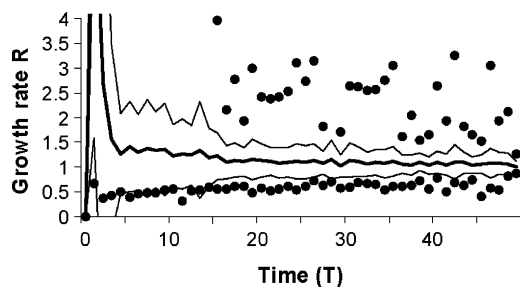
ering plants, was switched off, a pattern of cohort recruitment became apparent: the populations showed a reproductive cycle of flowering every 3 years (not shown). The populations without variation showed almost no spatial spread: the maximum number of occupied cells was  $C = 3$ .

**3.3. Scenario: individual variation, heterogeneous environment**

Taking the model parameterisation which resulted in invasive behaviour (variation scenario), we tested the influence of landscape on the spread rate. In the heterogeneous scenario, total carrying capacity of the landscape remained the same as in the homogeneous landscape, but the number of suitable cells was reduced by half and their distribution was random. The simulation again produced invasive population dynamics. Spatial extension of the populations in the heterogeneous landscape was mainly determined by long-distance dispersal success and not by local spread, the latter being determined by the chance of having a neighbourhood suitable for occupation. Mean growth rate was lower than in the homogeneous scenario with  $R = 1.25$ . The annual growth rate varied in this scenario, with 38% of the years showing growth rates  $R < 1$  (compared to 20% in the homogeneous scenario,  $n > 10,000$ ; Fig. 6).



**Fig. 5 – Annual growth rates  $R$  in the scenario “no-variation” ( $n = 50$ ). Mean values are represented by the thick line, S.D. indicated by the thin lines. Dots indicate maximum and minimum values and show the large variation caused by low individual numbers (compare Fig. 4).**



**Fig. 6** – Annual growth rates  $R$  in a heterogeneous landscape (scenario “variation”,  $n = 50$ ). Mean values are represented by the thick line, S.D. indicated by the thin lines. Although the values fluctuate (dots indicate maximum and minimum values for each time step), the mean value never drops below a growth rate of  $R = 1$ .

#### 4. Discussion

Matrix models have proven to be a supportive tool for ecological research for many years (for examples, see Caswell, 2001a, b); so have IBM models (for examples see Grimm, 1999). Both methods have their advantages and disadvantages. Yet, comparisons between both methods for one set of data are rare and contradictory in their conclusions (Stephens et al., 2002; Nehrbass et al., 2006).

In the presented study, we had the opportunity to present another case of such comparisons to the scientific public. Since the 1960s *H. mantegazzianum* is categorized as an invasive species requiring monitoring and control in Central Europe. However, data obtained by Hüls (2005) and his subsequent analysis by a matrix model led to the impression of declining, non-invasive populations of the species. To resolve this apparent contradiction we developed an additional IBM model, parameterized with the same data set and compared the model outcomes. In their comparison of modelling approaches Stephens et al. (2002) indicate that one should always opt for the most structured model, which can be reliably drawn from a given data set. Hence, an appropriate model has to include those features assumed to be responsible for a population's behaviour and it has to rely as much as possible on given empirical information. This empirical information is often limited due to resource constraints. Previous IBM studies of invasive plants, which were built to reconstruct and predict the spread of a species, tend to be information loaded and thus resource intense (Buckley et al., 2003; Kriticos et al., 2003). The high numbers of parameters included in those models have the disadvantage of making them error prone, as Doak and Mills (1994) and a number of recent publications (e.g. Reineking and Schröder, 2006) have noted. The presented study shows that the construction of an IBM for invasive plant species can be advantageous compared to a matrix model, even if only a limited data set is available and hence only few parameters are available.

In the following we want to accommodate possible requests concerning the performance and parameterization of our individual-based model. Then we will discuss the validation and divergence from empirical analysis before we draw

any conclusions on population behaviour from the IBM results. These conclusions will include comments regarding why, in our opinion, the Giant Hogweed is still an invasive plant in Central Europe and hence needs monitoring and control.

Our IBM corresponded to a census interval of one full year. Thus, it was not necessary to include any details of seedling dynamics: the outcome of seed dispersal, germination and seedling establishment after 1 year is decisive. Following our limited knowledge we did not include density-dependent regulation, except that of “ceiling control”. Important factors determining population growth, such as percentage of flowering plants and death rate are not dependent on habitat carrying capacity. Although there was some size-dependent mortality in the field data, we opted for a global death rate. This simplification was sufficient to give a size distribution as in the empirical results (Fig. 2). Number of offspring varied between years and plants. The model parameter “flowering rate” included effects of environmental stochasticity and compensated for lacking detailed knowledge of actual triggering factors. It has been observed that in even-aged stands, only the largest individuals flower (Tiley et al., 1996). Therefore, we assumed size to be a suitable trait to determine which of the vegetative individuals will be the one that flowers. In the empirical study, plants flowering in the next year had a higher mean number of leaves and taller average height. Minimum height for flowering was  $h = 95$  in the year of reproduction. A possible influence of age, apart from the fact that the plant had to be at least 2 years old was not identified and therefore not considered in the model. Empirical data were not able to show any correlation between seed-set and the size of the flowering plant. Thus, we have to assume that unknown factors determine this value. Seeds of *H. mantegazzianum* can be stored for a number of years and there is indication of a permanent seed-bank (Krinke et al., 2005). Due to a lack of quantitative data and considering the ongoing controversy on the topic (Tiley et al., 1996), we refrained from including such a seed bank.

As we did not consider any details for the establishment process, our model limited seedling establishment only in a lack of suitable habitat and attainment of the carrying capacity (ceiling model). Dispersal distances followed a rather conservative assumption given by observed maximum local dispersal distances of propagules ranging from 2 to 10 m (Neiland et al., 1987). We assumed a skewed distribution away from the mother plant, with a maximum local dispersal distance of approximately 6.5 meters. Additionally, randomly placed propagules might have an important influence on the invasion dynamics (Collingham et al., 1997). Assuming that such long-distance dispersal events are not predictable, they were incorporated as a random mechanism. Even if not directly backed by empirical data we considered such a long-distance dispersal as indispensable as invasion speed might depend more on dispersal distance than seed number (Cannas et al., 2003).

Our choice of seed dispersal kernel caused most new plants to be placed in the cell of origin. Hence, homogeneous grid had the advantage of more space available, while the heterogeneous grid had a higher capacity of some single cells. The difference in population growth rate and thus individual numbers in the two “variation” scenarios is due to the fact that in the homogeneous case all cells can be colonized,

thus all seedlings become established (until carrying capacity is reached), while in the heterogeneous scenario the neighbourhood of a cell might be uninhabitable and therefore new establishment fails.

To support reliability of our model we compared projections from the heterogeneous model scenario with data from a third empirical census in 2004 (Hüls, 2005). Matrix models now projected a marked increase in individual numbers, confirming the simulation results of the IBM. Yet, inclusion of the new data (from 2004) into model parameterization did not affect simulation results, as the parameter range for individual plants, which was implemented in the model, did not change significantly.

Despite the restricting assumptions, we were able to validate our IBM in two ways:

- (1) The predicted values for population structure and distribution of individual features could be confirmed by empirical values.
- (2) Empirical observations from the third census (second transition) showed population behaviour as predicted by the IBM.

This validation allows us to estimate the long-term development of the examined populations of *H. mantegazzianum* and to characterize invasive behaviour of the species. Short-term empirical observations recorded decreasing individual numbers for one transition and the deterministic matrix model approach conserved this state and projected it as future development. Conversely, the IBM provided the opportunity to incorporate variability into individual-behaviour as well as environmental stochasticity. In this study we demonstrated that the inclusion of individual variability (size increase) leads to populations, which show long-term invasive behaviour, despite annually fluctuating growth rates, even if deterministic matrix models do not always allow detection of this trend.

Landscape characteristics had a quantitative, but no qualitative effect on these results.

After analysis of the IBM, we had to face three diverging predictions about the future development of *H. mantegazzianum* in Germany:

- (1) Field observations over recent decades suggest that the Giant Hogweed has been an invasive species in many places, but scientific data on the temporal and spatial development of individual populations is rarely available in literature and mostly of a qualitative nature (Wade et al., 1997; Collingham et al., 2000; Wadsworth et al., 2000).
- (2) Matrix models derived from a single transition and empirical observations from a limited number of populations may project a marked decrease in individual numbers.
- (3) An IBM derived from the same empirical data set as the matrix model indicated the possibility of on-going invasion, despite occasional depression. For such depressions, despite intrinsic variability, there are a number of possible environmentally induced causes.

Hot and dry climate of 2003 was used as a possible explanation for the low performance of the populations (Hüls, 2005). This consideration is important in the context of poten-

tial climate changes in Europe (Baker et al., 2000). One may assume that seedling establishment fluctuates considerably from year to year and that this externally driven stochastic effect will enhance the effect of internal variability as included in this study. Unfortunately, no data were available to test this hypothesis. We must also give attention to a differentiation between dense and open stands (Hüls, 2005). Such a differentiation may be due to the spatial spread of populations (core and edge populations) or to habitat heterogeneity. But this differentiation could not be incorporated into the analysis of our IBM due to the small data set available, with the exception of an “all-or-nothing” assumption regarding cell capacity.

In conclusion, the Giant Hogweed is still an invasive species, but choice of sampling place and time might lead to large variations in what data suggests about invasive potential. Analysis of the model results showed that in more than one third of the cases invasive populations could have an annual growth rate below one. Hence, even in a good year local variation in growth rates might be encountered with a considerable likelihood, while the variation in individual parameters, as used in an IBM remain within the same range. This underlines a need for longer-term monitoring of *H. mantegazzianum* if matrix models should be used to assess current and future invasion status, as well as potential aims for control methods. Conversely, results of the developed IBMs, were insensitive to parameters estimated from “expansive” or “declining” years and hence they were more suitable to predict population behaviour using short term data sets.

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## REFERENCES

- Akcakaya, H.R., Burgman, M.A., Ginzburg, L.R., 1999. Applied Population Ecology. Sinauer Associates, Inc., Sunderland MA.
- Andersen, U.V., Calov, B., 1996. Long-term effects of sheep grazing on Giant Hogweed (*Heracleum mantegazzianum*). *Hydrobiologica* 340, 277–284.
- Baker, R.H.A., Sansford, C.E., Jarvis, C.H., Cannon, R.J.C., MacLeod, A., Walters, K.F.A., 2000. The role of climatic mapping in predicting the potential geographic distribution of non-indigenous pests under current and future climates. *Agricult. Ecosyst. Environ.* 82, 57–71.
- Buckley, Y.M., Briese, D.T., Rees, M., 2003. Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies. *J. Appl. Ecol.* 40, 494–507.
- Cannas, S.A., Marco, D.E., Paez, S.A., 2003. Modelling biological invasions: species traits, species interactions, and habitat heterogeneity. *Math. Biosci.* 183, 93–110.

- Caswell, H., 2001a. Matrix Population Models: Construction, Analysis and Interpretation. Sinauer.
- Caswell, H., 2001b. Matrix Population Models: Construction, Analysis and Interpretation. Sinauer.
- Claessen, D., 2005. Alternative life-history pathways and the elasticity of stochastic matrix models. *Am. Nat.* 165, 27–35.
- Collingham, Y.C., Huntley, B., Hulme, P.E.A., 1997. Spatially explicit model to simulate the spread of riparian weed. In: Cooper, A., Power, J. (Eds.), Proceedings of the Sixth Annual Conference of IALE (UK) on Species Dispersal and Land Use Processes, pp. 45–52.
- Collingham, Y.C., Wadsworth, R.A., Huntley, B., Hulme, P.E., 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. *J. Appl. Ecol.* 37, 13–27.
- Cox, G.W., 2004. Alien Species and Evolution. Island Press, Washington.
- Doak, D.F., Mills, L.S., 1994. A useful role for theory in conservation. *Ecology* 75, 615–626.
- Dodd, F.S., de Waal, L., Wade, M., Tiley, G.E.D., 1994. Control and management of *Heracleum mantegazzianum* (Giant Hogweed). In: de Waal, L., Child, L., Wade, M., Brock, J. (Eds.), Control and Management of Invasive Riverside Plants. John Wiley & Sons, Chichester, pp. 111–126.
- Münzbergova, Z., Mildén, M., Ehrln, J., Herben, T., 2005. Population viability and reintroduction strategies: a spatially explicit landscape-level approach. *Ecol. Appl.* 15, 1377–1386.
- Ferson, S. Ramas/Stage. 1988. Setauket, New York, Applied Biomathematics. Computer Program.
- Fieberg, J., Ellner, S.P., 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecol. Lett.* 4, 244–266.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future. *J. Ecol. Model.* 115, 129–148.
- Gutte, P., 1989. Die wildwachsenden und verwilderten Gefäßpflanzen der Stadt Leipzig. Naturkundemuseum Leipzig, Germany (in German).
- Heger, T., 2004. Zur Vorhersagbarkeit biologischer Invasionen. Entwicklung und Anwendung eines Modells zur Analyse der Invasion gebietsfremder Pflanzen. Dissertation. Neobiota Band 4 (in German).
- Hood, G., 2003. PopTools. Computer Program.
- Hüls, J., 2005. Populationsbiologische Untersuchung von *Heracleum mantegazzianum* Somm. & Lev. in Subpopulationen unterschiedlicher Individuendichte. Dissertation. Justus-Liebig-Universität Giessen, Germany (in German).
- Kowarik, I., 2003. Biologische Invasionen: Neophyten und Neozoen in Mitteleuropa, Stuttgart (in German).
- Krinke, L., Moravcová, L., Pyšek, P., Jarošík, V., Pergl, J., Perglová, I., 2005. Seed bank in an invasive alien *Heracleum mantegazzianum* and its seasonal dynamics. *Seed Sci. Res.* 15, 239–248.
- Kriticos, D.J., Brown, J.R., Maywald, G.F., Radford, I.D., Nicholas, D.M., Sutherst, R.W., Adkins, S.W., 2003. SPAnDX: a process-based population dynamics model to explore management and climate change impacts on an invasive alien plant *Acacia nilotica*. *Ecol. Model.* 163, 187–208.
- Lundström, H., Darby, E.J., 1994. The *Heracleum mantegazzianum* (Giant Hogweed) problem in Sweden: Suggestions for its Management and Control. In: de Waal, L., Child, L., Wade, M., Brock, J. (Eds.), Ecology and Management of Invasive Riverside Plants. John Wiley & Sons, Chichester, pp. 93–100.
- Nehrbass, N., Winkler, E., Pergl, J., Perglová, I., Pyšek, P., 2006. Predicting plant invasions: comparing results of a matrix model and an individual-based model. *Progr. Plant Ecol. Evol. Syst.* 7, 253–262.
- Neiland, M.R.M., Proctor, J., Sexton, R., 1987. Giant Hogweed (*Heracleum mantegazzianum* Somm. & Levier) on the River Allan and part of the River Forth. *Forth Natural History* 9, 51–56.
- Ochsmann, J., 1992. Riesen-Bärenklau (*Heracleum spec.*) in Deutschland, Morphologie, Ökologie, Verbreitung und systematische Einordnung. In: Dissertation. Georg-August-Universität Göttingen, Germany (in German).
- Otte, A., Franke, R., 1998. The ecology of the Caucasian herbaceous perennial *Heracleum mantegazzianum* Somm. et. Lev. (Giant Hogweed) in cultural ecosystems of Central Europe. *Phytocoenologia* 28, 205–232.
- Pergl, J., Hüls, J., Perglová, I., in press. Population dynamics of *Heracleum mantegazzianum*. In: Pyšek, P., Cock, M.J.W., Nentwig, W., Ravn, H.P. (Eds.), Ecology, Management of Giant Hogweed (*Heracleum mantegazzianum*), CAB, International, Wallingford.
- Pyšek, P., 1991. *Heracleum mantegazzianum* in the Czech Republic: the dynamics of spreading from the historical perspective. *Folia Geobot. Phytotaxon.* 26, 439–454.
- Pyšek, P., 1994. Ecological aspects of invasion by *Heracleum mantegazzianum* in the Czech Republic. In: de Waal, L., Child, L., Wade, M., Brock, J. (Eds.), Ecology and Management of Invasive Riverside Plants. John Wiley & Sons, Chichester, pp. 45–54.
- Pyšek, P., Prach, K., 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. *J. Biogeogr.* 20, 413–420.
- Reineking, B., Schröder, B., 2006. Constrain to perform: regularization of habitat models. *Ecol. Model.* 193, 675–690.
- Sampson, C., 1994. Cost and impact of current control methods used against *Heracleum mantegazzianum* (Giant Hogweed) and the case for instigating a biological control programme. In: de Waal, L., Child, L., Wade, M., Brock, J. (Eds.), Ecology and Management of Invasive Riverside Plants. John Wiley & Sons, Chichester, pp. 55–66.
- Stephens, P.A., Frey-Roos, F., Arnold, W., Sutherland, W.J., 2002. Model complexity and population predictions. The alpine marmot as a case study. *J. Anim. Ecol.* 71, 343–361.
- Tiley, G.E.D., Dodd, F.S., Wade, P.M., 1996. *Heracleum mantegazzianum* Sommier and Levier. *J. Ecol.* 84, 297–319.
- Tiley, G.E.D., Philp, B., 1994. *Heracleum mantegazzianum* (Giant Hogweed) and its control in Scotland. In: de Waal, L., Child, L., Wade, M., Brock, J. (Eds.), Ecology and Management of Invasive Riverside Plants. John Wiley & Sons, Chichester, pp. 101–110.
- Wade, M., Darby, E.J., Courtney, A.D., Caffrey, J.M., 1997. *Heracleum mantegazzianum*: a problem for river managers in the Republic of Ireland and the United Kingdom. In: Brock, J., Wade, M., Pyšek, P., Green, D. (Eds.), Plant Invasions: Studies from North America and Europe. Backhuys Publishers, Leiden, pp. 139–152.
- Wadsworth, R.A., Collingham, Y.C., Willis, S.G., Huntley, B., Hulme, P.E., 2000. Simulating the spread and management of alien riparian weeds: are they out of control? *J. Appl. Ecol.* 37, 28–38.