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Empirical and virtual investigation of the population dynamics of an alien plant under the constraints of local carrying capacity: *Heracleum mantegazzianum* in the Czech Republic

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Abstract

During the last decades, invasive alien species have become a global concern because of their ecological and economic impact. *Heracleum mantegazzianum* (Apiaceae), is a tall monocarpic perennial native to Caucasus and invasive in Europe since the 1950s. Within an interdisciplinary EU project aimed at assessing suitable management strategy, we analysed the demography and ecology of this species in its invasive range. The monitoring of population dynamics in the Czech Republic led to the result that in the observed sites the species showed decreasing populations. To find an explanation for this unexpected result, two types of models were parameterized, based on the empirical data: (1) a stage-based transition matrix model, which projected a continuous negative development, and (2) a spatially explicit individual-based model (IBM), including individual variation. This second model was able to create a population with steady individual numbers. Analyses of the simulation showed that in more than 54% of the simulated years ($n = 5000$) the growth rate was smaller than one. Still, population increase in the remaining years was sufficient to sustain a population. Nevertheless long-term observations document an invasive behaviour of the observed populations. Hence, we could assume temporal changes in the course of an invasion and thus wanted to evaluate the probability of sampling negative growth in dependence of time since first invasion. By using a method from 'Virtual Ecology', we approached the question: first we create an invasive population, based on the empirical data of *H. mantegazzianum* and second empirical sampling techniques were mimicked using the Virtual Ecologist approach. The results demonstrate how the probability of sampling negative growth increases with time since first invasion. Hence, we assume that the studied populations have already reached a maximum of their local invasive potential and thus stagnate in their size.

Keywords: Demography; IBM; Individual-based modelling; Invasion; Virtual Ecologist; Matrix model

Introduction

Biological invasions have been receiving increasing attention and become a global concern in the last decades (Davis, 2003; Weber, 2003). Of special ecological

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and economical interest are those species, which have been introduced by humans and rapidly spread in their new environment (see Richardson et al., 2000 for definitions of invasive species). Those alien invaders represent an appealing study subject because of their unprecedented dynamics (Pyšek and Hulme, 2005) and the high relevance of their demography for practical implications in controlling them. Some invasive species threaten biodiversity in natural habitats by displacement of native biota through competition, hybridization or predation (Cox, 2004) and the effects invasive species have are not only ecological but also economic (Zavaleta, 2000; Pimentel et al., 2005). One of the plant species posing such a threat to common goods in Europe is the Giant Hogweed (*Heracleum mantegazzianum* Sommier et Levier, Apiaceae; Tiley et al., 1996; Pyšek, 1991; Otte and Franke, 1998; Willis and Hulme, 2002). An interdisciplinary EU project ('Giant Alien') aimed at developing an integrated pest management for invasive plants, used *H. mantegazzianum* as a model species. To identify life history stages that make a species vulnerable in terms of the population dynamics and at which the control efforts could be targeted, a detailed knowledge of the plant's demography and ecology is necessary (Hobbs and Humphries, 1995). To obtain this information, empirical studies of local populations were conducted over a 3 years period in the Czech Republic. These data were analysed using stage-based transition matrix models (Caswell, 2001).

The empirical data and their analysis by matrix models led to surprising results: (1) instead of expected expansion the majority of populations showed decreasing individual numbers, and (2) the intrinsic growth rates λ of the matrix models also projected population decline. This contradicted conventional wisdom on the behaviour of *H. mantegazzianum* and the knowledge about the sites' history. From long-term observations in the study area a steady increase in the size of invading populations was documented for the last 40 years (Müllerová et al., 2005). Marked invasion dynamics were also reported for the geographical scale of the entire country: the number of reported localities of *H. mantegazzianum* has been increasing exponentially since the 1940s (Pyšek, 1991; Pyšek and Prach, 1993).

To resolve the contradiction between short-term empirical studies and matrix modelling on the one hand and long-term observations on the other hand a spatially explicit individual-based model (IBM) was built, based on the same data as the original matrix models. This individual-based approach allowed to incorporate rules that retained individual variation in growth behaviour. We also applied the 'Virtual Ecologist' (VEco) approach to analyse possible consequences of sampling on the empirically found results. The VEco tool mimics empirical sampling behaviour in a model environment (e.g. Berger et al., 1999; Tyre et al., 2001). It was applied in an altered model version, which was parameterized to show clearly invasive behaviour of a population.

To disentangle the puzzle of an invasive population apparently being declining we:

1. Compared results from a deterministic matrix model and an individual-based simulation model with each other, with data from short-term observations and with long-term knowledge.
2. Studied the effect of local population behaviour on the sampled growth rates with the method of Virtual Ecology.

Materials and methods

Study species

Heracleum mantegazzianum (Apiaceae) is the tallest forb in Europe, flowering individuals can reach up to 5 m of height. The plant is a monocarpic perennial and reproduces exclusively by seed. An average plant bears about 20,000 seeds (I. Perglová et al., unpubl. data), but individuals with over 100,000 seeds have been reported (Tiley et al., 1996). The species forms a short-term persistent seed bank (Krinke et al., 2005), with a small proportion of seed persisting dormant for at least 2 years (L. Moravcová et al., unpubl. data). Seeds germinate to high percentages (90% on average) once the morphophysiological dormancy is broken (Moravcová et al., 2005). The plant is capable of self-fertilization (I. Perglová et al., unpubl. data) which enables it to invade new habitats following a single long-distance dispersal event. *Heracleum mantegazzianum* is native to the W-Caucasus and the first record of its introduction is from Kew Botanic Gardens in Great Britain in 1817. Ever since, it has been popular as an ornamental plant in gardens throughout Europe. From such nascent foci the plant continuously spread into the wild. In the Czech Republic, there is a detailed knowledge of the history of invasion both at the national (Pyšek, 1991, Pyšek and Prach, 1993) and regional scales (Müllerová et al., 2005), the latter from the region of the first introduction to the country in 1862. Nowadays, there are 603 localities reported from the Czech Republic (P. Pyšek and K. Prach, unpubl. data) and the species is considered invasive in this country (Pyšek et al., 2002). Within its new range, *H. mantegazzianum* is a problem species due to its tendency to form monospecific stands and its phototoxic sap causing human injuries (Tiley et al., 1996).

Study sites and empirical methods

The study sites were situated around the earliest introduction known in the Czech Republic (Pyšek, 1991), in the Slavkovskỳ Les Protected Landscape Area, W-Bohemia. Within the study area there are extensive wetlands with a high diversity of flora and pastures where *H. mantegazzianum* occurs. In the years following the end of the 2nd World War, the change of land use with lack of appropriate management and abandoning of the area lead to the rapid spread of the Giant Hogweed and the consequent heavy infestation. To cover the range of various habitat conditions, 11 sites were chosen and in each one permanent plot ($1 \times 10\,\mathrm{m}^2$) with dominance of *H. mantegazzianum* was established in 2002. For these sites additional detailed studies were carried out on the biology and ecology of studied species (Krinke et al., 2005; Moravcová et al., 2005; Müllerová et al., 2005).

Within each of the plots position of all *H. mantegazzianum* plants with leaves larger than 7 cm was mapped and their size characteristics were recorded. Hence, the fate of each individual in the plot could be followed throughout the survey period of 3 years. To characterize size for each plant the following attributes were measured: number of leaves, length of the longest leaf, height of flowering stem and number of branches.

The first two were correlated with flowering and survival probability and thus were used (1) to categorize the plants for the matrix model, and (2) to characterize plants in the IBM. For the models data from the annual census in late summer was used. The data set is based on more than 1000 individuals.

Transition matrix model

Matrix models describe population dynamics by transition probabilities between categories (age or stage). In the presented study a stage-based approach was chosen and the plant's life cycle divided into: seedling, small plant, vegetative adult plant, and flowering plant (Fig. 1). During sampling plants in vegetative stage were sorted into three classes (seedling, juvenile, rosette) and later were reclassified according to their size (number and length of largest leaf) to make the stage classes comparable and filter out subjectivity. Thus we distinguished seedlings with 1–3 leaves and leaf length <70 cm, juveniles with <5 leaves and leaf length <140 cm and rosettes having $\geqslant 5$ leaves and leaf length $\geqslant 140$ cm). For *H. mantegazzianum* the observed transitions were growth (G), survival/longevity (L), retrogression (R), and sexual reproduction/fecundity (F). In cases where data were missing, data for matrix entries were pooled across years and populations.

The model uses discrete time-steps. Chosen model interval was one year from flowering to flowering. The equation

$$n(t+1) = A\,n(t) \tag{1}$$

projects the population at time $t+1$, where A is the transition matrix (cf. Fig. 1)

$$A = \begin{pmatrix} L_1 & R_1 & 0 & F_1 \\ G_1 & L_2 & 0 & F_2 \\ G_2 & G_3 & L_3 & 0 \\ 0 & G_4 & G_5 & 0 \end{pmatrix} \tag{2}$$

and n the vector describing the number of individuals in each category. The dominant eigenvector of the matrix (λ) represents the intrinsic growth rate of the population. Increase in population number results in a $\lambda > 1$, for $\lambda < 1$ the population is projected to go extinct and $\lambda = 1$ indicates a stable population size. The method by Cochran and Ellner (1992) was used to calculate the eigenvalues and to perform elasticity analyses.

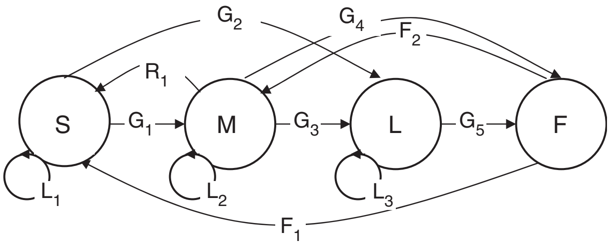

Fig. 1. Life-cycle diagram of the implemented plant species. Small (S), medium (M) and large (L) vegetative plants can grow or remain in the same category. Flowering individuals (F) die after flowering. The transitions mark survival (longevity L), growth (G), regression (R), and reproduction (fecundity F). The plant has no vegetative reproduction. A possible seed-bank is neglected in the model.

Individual-based model

Some programs (e.g. Ramas/Stage; Ferson, 1994) are able to handle matrix models with discrete individuals. Still, those individuals undergo distinct stages, and size parameters are not assigned continuously. Also, the spatial aspect of dispersal is not included in those approaches. Thus, we used a custom-tailored IBM (Fig. 2).

The model was designed to investigate the consequences of local spread and of continuous variability of individual behaviour of *H. mantegazzianum*. Model rules and parameters were derived from the same data as the matrix models. Elasticity analyses of the original matrix model served as an indicator which life-cycle stages were most relevant for changes in growth rate. Following, the parameters for growth and survival were modelled in detail, including the found variation in the transition behaviour of the individual. The model was constructed rule-based; in the description the parameterizations of the model follow each introduced rule.

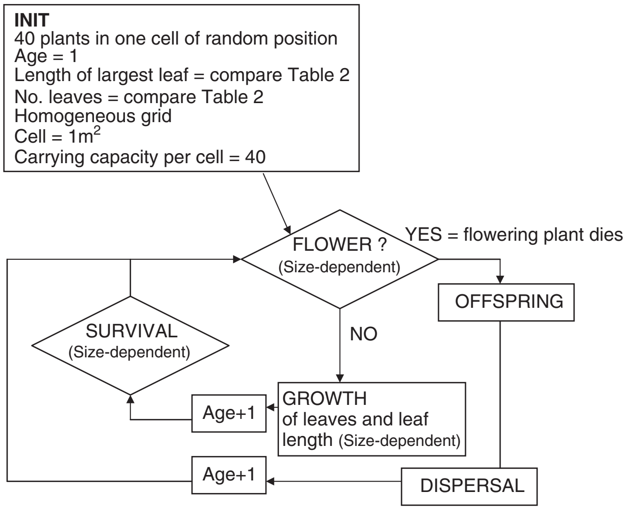

Fig. 2. Flow chart of the individual-based model. Each simulation is initialized and then carried out for 50 time-steps (years) in which the different modules of plant development are accessed for each individual on requirement.

Time

The model is discrete in time. One time step represents the year from one flowering period to the next, such as in the matrix model.

Space

The model was spatially explicit in a two dimensional grid, consisting of 2500 cells (50∗50). Each grid cell represented one square meter. The entire grid represented the area of habitat one population could locally invade. Single cells were characterized by a maximum carrying capacity, representing habitat suitability. Landscape was assumed to be homogeneous. Population dynamics were regulated locally in each cell, but cells were connected via dispersal. Carrying capacity for a cell was set to 40 individuals, as was found in empirical studies. It was implemented as ceiling capacity (no density regulation before the maximum number is reached).

Plants

Plants were treated as individuals. Each individual was characterized by a set of traits: age, number of leaves and length of largest leaf. The latter was implemented as a continuous variable. The fate of a plant was recorded as soon as it got established in a cell. In a complete life-cycle a plant grew over several years, flowered, produced offspring and died.

Reproduction, offspring and dispersal

As Giant Hogweed is monocarpic, only plants older than 2 years could flower. Flowering probability was determined by a combination of the two size attributes (number of leaves and length of the largest leaf, see Table 1). After flowering an individual died. If not flowering, vegetative growth continued a further year (see below).

The number of offspring produced by a plant could not be correlated with any trait of the maternal plant, and data to estimate the probability for individual flowering plants to have a certain number of offspring were not available. Hence, in the model all plants created the same mean number of offspring. Offspring production per plant was adapted to a fat-tailed probability distribution, resembling a Poisson distribution, but with a higher probability for low offspring production and allowance for rare events of high offspring productions (Fig. 3). Thus, this distribution comprised the different average values from the populations under study. The function had the same mean value as the empirical data ($M = 2.6$; weighted mean from all populations). New plants with the age of zero were assigned a randomly chosen number of leaves between one and four. Initial size (length of the longest

Table 1. Flowering probability for plants

Number of leaves	Length of largest leaf (cm)	Flowering probability
<3	—	0
3	⩽140	0
3	>140	0.51
4	⩽180	0.33
4	>180	0.77
5	—	1.0

The flowering probability is determined by a combination of leaf number and the size of the largest leaf. Individuals need to be at least 2 years old and have a leaf length of >140 cm to be able to flower.

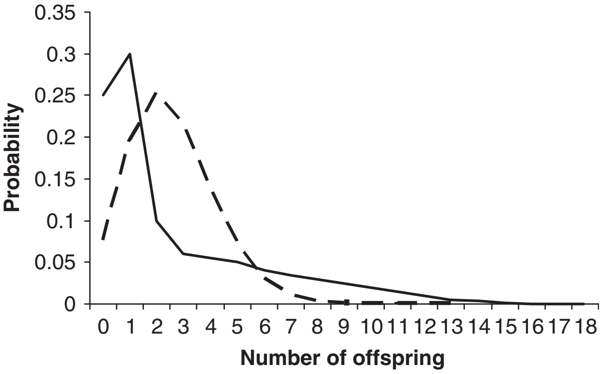

Fig. 3. Probability function for the number of offspring produced by a flowering individual (black line). The realized mean of the chosen function is the same as in the empirical data ($M = 2.6$). In comparison a Poisson distribution with $M = 2.6$ (broken line) is shown.

Table 2. Assignment for the initial size of a plant at establishment

Number of leaves	Probability	Length of longest leaf
1	0.40	52.2±30.6
2	0.38	53.4±39.1
3	0.15	94.8±67.7
4	0.07	105.7±59.5

The number of leaves is determined by chance, following empirically observed probabilities. Dependent on the number of leaves the length of the longest leave is calculated, again using empirical-based values.

Table 3. Dispersal probability for offspring

Distance from cell of origin	Offspring (%)
0 (mother cell)	46
1	29
2	14
3	4
4	5
Random dispersal	2
Total	100

Probability to disperse into a neighbouring cell is dependent on its distance from the cell of origin. All cells within one radius have the same likelihood to be occupied. Additionally 2% of the offspring are randomly dispersed across the grid.

Table 4. Transition probabilities for the annual decrease and increase in leaf number, based on empirical findings

Leaves in year ($t+1$)	Leaves in year (t)			
	1	2	3	4
1	0.36	0.18	0.04	0
2	0.35	0.28	0.15	0.09
3	0.24	0.30	0.41	0.18
4	0.04	0.19	0.33	0.09
5	0.01	0.05	0.07	0.45
6	0	0	0	0.18

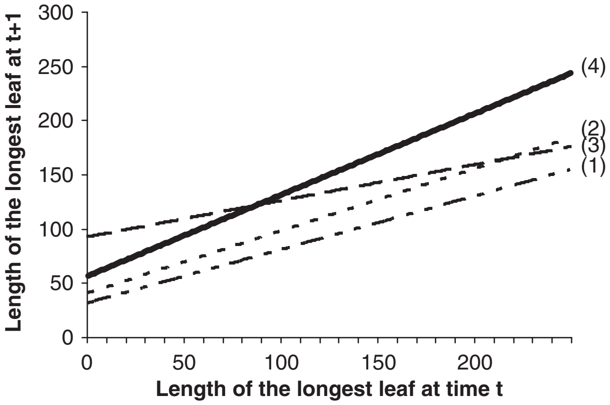

Fig. 4. Growth functions for the length of the largest leaf in dependence of the number of leaves, derived by logistic regression from empirical data. One leaf (1), two leaves (2), three leaves (3), and four leaves (4).

leaf) was determined depending on this number (Table 2). Plants could not die in the year that they were created; any mortality within the first year was already considered in the offspring values. New plants were placed in the cell of origin (parent plant), or in the neighbourhood. The number of offspring dispersing into neighbouring cells was decreasing with distance (Table 3). All cells within one radius around the cell of origin were considered equal in the probability of new plants established there. Additionally, we incorporated long-distance dispersal of 2% of the new plants at random over the whole grid.

Establishment of new plants could only take place in cells, where carrying capacity was not reached.

Vegetative growth

Growth of an individual from year t to year $t+1$ was dependent on its previous size, defined as length of largest leaf and leave number. The new number of leaves was calculated on the basis of probabilities from a transition matrix (Table 4).

The length of the longest leaf (l) was calculated using linear relationships between leaf-length values l in years t and $t+1$ (Eqs. (3a)–(3d) and Fig. 4) where each relationship depended on the number of leaves in year $t+1$:

$$\text{One leaf}: \; l_{t+1} = 31.8 + 0.44 * l_t \tag{3a}$$

$$\text{Two leaves}: \; l_t + 1 = 41.0 + 0.57 * l_t \tag{3b}$$

$$\text{Three leaves}: \; l_t + 1 = 92.7 + 0.33 * l_t \tag{3c}$$

$$\text{Four leaves}: \; l_t + 1 = 57.1 + 0.75 * l_t \tag{3d}$$

These functions were derived through regression of empirical values. Retrogression of leaf length was possible through a reduction in leaf number (see Table 4) and hence through a change in calculation basis.

Death

The probability of death before reproduction decreased with increasing size of a vegetative individual (Table 5). All plants died after reproduction.

Simulations

Each simulation started by placing 40 individuals with the age of one within one randomly chosen cell. Simulations were timed for 50 years, and 50 repetitions were calculated. Global growth rates R for the IBM

Table 5. Survival probability of vegetative plants below the maximum age

Number of leaves	Length of largest leaf (cm)	Survival probability
1	—	0.50
2	$\leqslant 140$	0.61
2	>140	1.00
3	—	0.85
4	$\leqslant 180$	0.60
4	>180	1.00

The probability is dependent on the number of leaves and the length of its largest leaf. Plants with no leaves will die. Individuals with more than five leaves reproduce and die in the following. Therefore, for both cases the survival probability is zero.

were calculated by:

$$R = N_{t+1}/N_t, \tag{4}$$

where N_t is the individual number from last year and N_{t+1} this year's individual number summarized over all cells.

Virtual Ecologist sampling

In the context of our study, the VEco approach was designed to address the question how sampling probabilities for $R<1$ change with time since invasion. Hence, we first had to create an invasion scenario from our original IBM. Therefore, we increased survival rates for individuals (i.e. we had death only for flowering, aged, and individuals with no leaves, but no size dependent mortality). Also, a smaller grid size (10×10 cells) was chosen so carrying capacity for the entire grid (area) was reached within a reasonable time span. The simulations were again initiated with ten plants in one randomly chosen cell, simulations repeated ten times. The VEco was parameterized to sample all occupied grid cells (representing permanent plots) for each time-step (year) and calculate the growth rates R_P from the individuals in the cell P. We categorized the results into growth rates $R_\mathrm{P}\geqslant 1$ and $R_\mathrm{P}<1$.

Results

Matrix model

Where data were available, the intrinsic growth rate (λ) and the elasticities for each plot (population) and transition between years were calculated. From the 11 study sites only two data sets were completely covering both transitions. For four study sites, only pooled matrix across 3 years were available. In two populations there were not enough individuals in the permanent plot to fill all matrix entries; three study sites were destroyed during the study. However, for a pooled matrix, transition data of individuals from all eight undamaged sites were used. Instead of an invasive behaviour the data indicating a decreasing trend in populations' individual number with only two exceptions, where a slight growth was projected (Table 6). The pooled matrix, using the data, of all populations had an intrinsic growth rate of $\lambda = 0.85$. From pooled set of populations, the calculated average age of flowering plants was 5.8 ± 3.2 years. The elasticity analysis of the pooled matrix revealed that the most important transitions were survival and growth (Table 7). Changes in those values would result in the largest changes in growth rate (λ). This result was taken into account for the implementation and parameterization of the IBM.

Table 6. Summary of growth rates based on matrices for available plots (populations)

Transition Plot/site	2002–2003	2003–2004	2002–2004
1	n.a.	n.a.	0.667
2	n.a.	n.a.	1.002
3	1.077	0.634	0.864
4	0.901	0.880	0.882
5	n.a.	n.a.	0.727
6	n.a.	n.a.	0.887
Pooled λ	0.779	0.823	0.792

Where possible, values for the intrinsic growth rate (λ) of each plot is shown.

Table 7. Elasticity matrix for a matrix pooled across plots and years

	Seedling	Juvenile	Rosette	Flowering
Seedling	0.0664	0.0368	0	0.0968
Juvenile	0.1016	0.1344	0.0378	0.0752
Rosette	0.0320	0.1300	0.1169	0
Flowering	0	0.0478	0.1242	0

Survival of the juvenile stage was the most decisive transition in the observed populations and years.

Individual-based model

The simulated populations, which were started with 100 individuals, showed a sustaining behaviour but little or no invasion with an average growth rate of $R = 1.003\pm0.33$ (Fig. 5). By comparing the long-term size structure calculated in the IBM with the empirically recorded values, we were able to make a statement about the ability of the model to reflect Giant Hogweed demography. Both measures for size of the plants: length of the longest leaf and number of leaves, were well approximated in the model (Fig. 6a and b). Mean

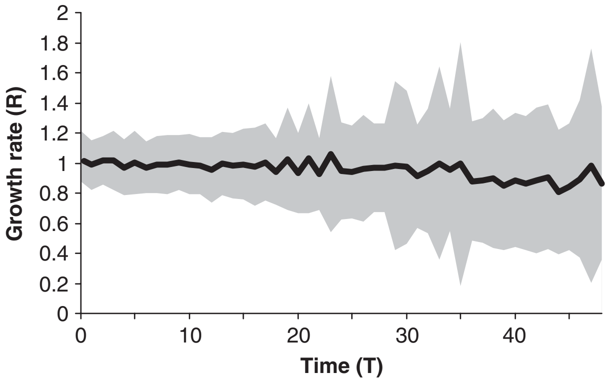

Fig. 5. Annual development of the mean growth rate in the simulated populations. Overall mean was $R = 1.003 \pm 0.33$ SD ($n = 5000$, 100 simulation runs each for 50 years). But 54.7% of the annual growth rates were $R < 1$. The mean annual growth rate decreased with time since invasion.

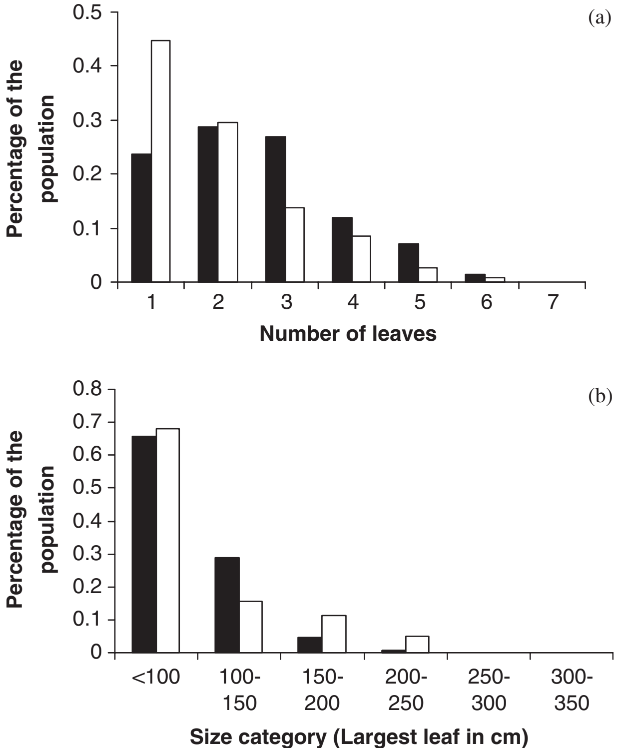

Fig. 6. Comparison of population structures from the model (black bars, $n = 65{,}535$) and from empirical observations (white bars, $n = 460$ and 777; a, number of leaves; b, length of the largest leaf).

age of flowering plant however was lower than in the matrix models ($M = 3.2 \pm 1.2$). But both model results do not significantly differ and the parameter cannot be validated by empirical data. Mean number of offspring produced was $M = 2.6 \pm 1.4$, thus with a slightly lower standard deviation than in the empirical data. The overall population growth rate, averaged over all simulation runs and simulation years, was slightly above one ($R = 1.003$; $n = 5000$). However, in a majority of years (54.7%) we found a growth rate below one. If growth rates in subsequent years are statistically independent the probability for an observer to witness 2 years with an annual growth rate below one is $p = 0.3$. This result of IBM-modelling may explain the discrepancy between the well-established long-term dynamics of *H. mantegazzianum* on the one hand and the observed short-term population decrease together with the matrix-model analysis on the other hand.

This consideration was reason to assess sampling probabilities for $R < 1$ with the VEco approach.

Virtual Ecologist sampling

In an ideal course of a local invasion the population develops from one introduced plant to a stand that has reached local carrying capacity, where population growth rate is approximating $R = 1$ and further invasion can only take place as long distance-dispersal events into other habitat. In the study case the observed growth rate of the population was $R \leqslant 1$ and thus we assume that the local carrying capacity had been reached. After calculating the probability to sample to independent years of growth rate $R < 1$ under current population dynamics, we further wanted to evaluate the probability to sample a growth rate R in the course of an invasion. By means of the VEco approach we explored the probability to sample growth rates in a plot (represented by one grid cell) with $R_P < 1$ in a growing population and the dependence of this probability on the time since the start of invasion. This model used as a basis for the evaluation had a mean growth rate $R = 1.12 \pm 0.18$. The number of offspring remained similar to the original simulations ($M = 2.3 \pm 1.09$), the slight decrease being caused by enhanced effects of carrying capacity and border losses, due to the smaller grid size.

The overall probability to sample a plot with growth rate of $R_P < 1$ was 11.4% and thus markedly lower than in the simulations using actual empirical findings for survival. But, when analysing the development over time, it becomes apparent that the probability increases with time since invasion (Fig. 7).

Discussion

Heracleum mantegazzianum is known to be invasive in Europe and its spread has been observed for the last 50 years in the Czech Republic (Pyšek, 1991; Pyšek and Prach, 1993; Tiley et al., 1996; Müllerová et al., 2005). This study was concerned with populations of the plant, situated in the vicinity of what is thought to be the

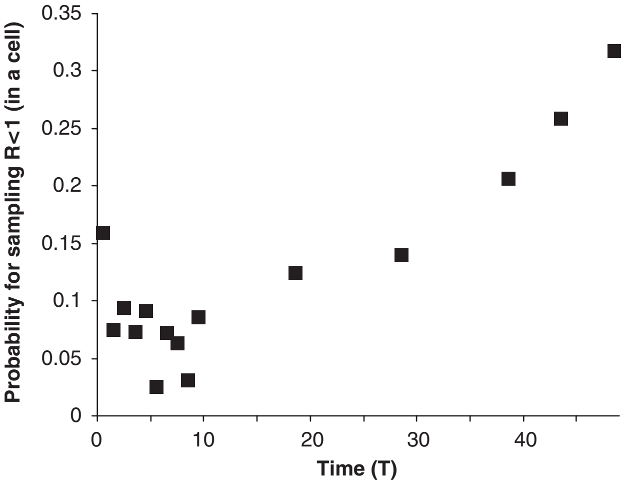

Fig. 7. Probability to sample a plot (represented by one grid cell) with a growth rate $R<1$ depending on the time elapsed since the start of population development. Evaluated in a simulation (10 repetitions) with the Virtual Ecologist approach. In the beginning of the invasion this probability strongly fluctuates due to low individual numbers. With progressing invasion of the populations the probability to sample plots which have reached local carrying capacity and thus have a growth rate fluctuating around $R = 1$ exponentially increases. At $t = 50$ the probability to sample a plot with $R<1$ is $p = 0.32$ ($n = 912$).

nascent focus of the invasion in the Czech Republic. Empirical observations during three consecutive years led to the unexpected result of decreasing individual numbers in a majority of the observed populations. Data was analysed with deterministic matrix models. Such models are often used in population ecology due to their relatively easy applicability. They provide insights into the importance of different life cycle stages or transitions between them (Heppell et al., 2000a). Yet, in their simple form they have some structural deficiencies when it comes to the incorporation of characteristics essential for invasions, such as dispersal events leading to spatial extension. Moreover, some important mechanisms, like density-dependent development and stochasticity are often neglected as they require some effort to be successfully incorporated (Fieberg and Ellner, 2001; Claessen, 2005; Ehrlen et al., 2005). The analysis of our data with deterministic matrix models showed that the intrinsic growth rate λ of the entire region (pooled data) was smaller than one and hence projected further decrease. Thus, the development of a management scenario seemed no longer required. Even more, the elasticity analyses on which such a management suggestion would be based was derived from a matrix model of decreasing populations. Thus it might be misleading, as for expanding populations the relative influences of transitions on growth rate might change. Some authors even argue that in any case realistic predictions of future development cannot be derived from λ, but that it allows to develop ideas about the current state of a population and the importance of individual transitions on the population dynamics (Silvertown et al., 1996; Caswell, 2000; Heppell et al., 2000b). As there was no repeated sampling within populations, statements about differences between populations could not be made. Empirical results suggest that populations within the region show similar dynamics and that for an evaluation of the population dynamics it is possible to pool the data from all censuses. Additionally the pooling of matrices is a common technique to account for missing data (e.g. Sinclair et al., 2005).

An IBM was parameterized with special consideration of the observed growth variations between individuals. The individual number did not increase markedly and mean growth rate R approximated one. So, in contrast to the deterministic matrix models the IBM simulations showed that under consideration of the observed individual variation the populations of *H. mantegazzianum* are rather stable but not decreasing, although their growth rate becomes negative at times. This is a dynamic behaviour, which can be observed for populations which have reached the carrying capacity of their habitat and encounter a ceiling capacity around which their individual numbers fluctuate. For practice this between-years variation in growth rate implies a high probability for the observation of a population to fall within such an unfavourable year. With the VEco approach it was demonstrated that this probability steadily increases with time since invasion and thus with the approximation of the local carrying capacity. Additional factors like global environmental stochasticity (e.g. climatic conditions), which might contribute to the fact that a negative growth is encountered in all observed populations simultaneously were not quantified by empirical studies and thus not included in the models. Nevertheless, we can hypothesize two likely causes for the populations not being locally invasive:

(1) Local carrying capacity: For this aspect we are aware that habitat heterogeneity might be a relevant factor, which has been neglected in the IBM. But, this factor is accounted for further studies (Müllerová et al., 2005; N. Nehrbass et al., unpubl. data). The populations studied are situated in a sparsely populated and extensively managed protected landscape area. *Heracleum mantegazzianum* is present there for more than 140 years but the invasion in the localities investigated only started approximately 40 years ago (Müllerová et al., 2005). Thus, we have to assume that growth rates of the observed populations have been $R > 1$ in past years, throughout the local invasion process and that within this time span the carrying capacity of the habitat was reached.

Yet, there is no indication that the species has lost its invasive potential. Hence, although for single populations the limits might be reached the invasion process is likely to proceed on different scales, enhanced by long distance dispersal events.

(2) In other studies annual variation in climatic conditions have been named as a potential cause for negative growth rates (Hüls, 2005). Hot and dry season of 2003 might have influenced the performance of populations in this year. Nevertheless, as populations did not perform any better in 2004, this factor seems to have only an additional influence.

In empirical studies of plant invasions, a detailed knowledge of variation of individual plants between years and for a number of populations is rarely available. Our analysis of the data obtained for *H. mantegazzianum* suggests that local saturation is responsible for observing growth rates $R \leqslant 1$. This is coupled with time since the beginning of invasion (Müllerová et al., 2005).

Let us assume that *H. mantegazzianum* would be a species, being introduced to a new region and no information on its invasive nature was available from elsewhere. When using data from short-term observations in already existing populations only decreasing and constant population growth rates were observed and deduced from models. Knowledge about the invasion history of an existing population might thus be an important factor, when considering invasive ability of a species. Else the false conclusion could be reached that the species does not pose the threat of invasion in the new area. The VEco approach could illustrate how the probability of such 'flawed' sampling increases with time since invasion at the original site.

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