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The role of long-distance seed dispersal in the local population dynamics of an invasive plant species

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ABSTRACT

Aim Long-distance dispersal is important for plant population dynamics at larger spatial scales, but our understanding of this phenomenon is mostly based on computer modelling rather than field data. This paper, by combining field data and a simulation model, quantifies the fraction of the seed of the alien species *Heracleum mantegazzianum* that needs to disperse over a long distance for successful invasion.

Location Central Europe, Czech Republic.

Methods To assess the role of random dispersal in long-term population dynamics of the studied species, we combined longitudinal data covering 50 years of the invasion of this plant from its very start, inferred from a series of aerial photographs of 60-ha plots, with data on population dynamics at a fine scale of 10-m^2 plots.

Results A simulation model based on field data indicates that the fraction of seed that is dispersed from source plants not described by the short-distance dispersal kernel ranges from 0.1 to 7.5% of the total seed set. The fraction of long-distance dispersed seed that provides the best prediction of the observed spread was significantly negatively correlated with the percentage of habitats suitable for invasion.

Main conclusions Our results indicate that the fraction of seeds that needed to be dispersed over long distances to account for the observed invasion dynamics decreased with increasing proportion of invasible habitats, indicating that the spatial pattern of propagule pressure differs in landscapes prone to invasion. Long-distance dispersal is an important component of the population dynamics of an invasive species even at relatively small scales.

Keywords

Aerial photographs, biological invasions, *Heracleum mantegazzianum*, invasive plants, land-use change, long-distance dispersal, matrix models.

INTRODUCTION

Seed production and dispersal are crucial determinants of the colonization processes in sessile plant species and their populations (Crawley, 1997). However, despite recent progress in understanding the important role of seed dispersal in species' population dynamics at larger scales, the frequency of rare long-distance dispersal events is because of the difficulty of measurement and quantification still poorly documented (Cain *et al.*, 2000; Nathan *et al.*, 2003, 2008; Nathan, 2006). The majority of seeds are dispersed over short distances, and the probability of seeds being dispersed over long distances is assumed to be very low. Still, it has been suggested that long-distance dispersal is the key process that determines the extent and spatial dynamics of plant distributions (Cain *et al.*, 1998, 2000; Clark, 1998; Higgins & Richardson, 1999; Bullock & Clarke, 2000; Wilson *et al.*, 2009), but the evidence for this is still scanty. To date, the importance of long-distance dispersal has been confirmed by simulation studies exploring its role in population dynamics, migration and range shaping (e.g.

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Higgins *et al.*, 1996; Clark, 1998; Higgins & Richardson, 1999) rather than quantified by using field data (but see Rouget & Richardson, 2003). These studies indicate that in terms of population spread, occasional long-distance jumps are more effective than numerous small-distance dispersal events (Clark, 1998; Higgins & Richardson, 1999; Pyšek & Hulme, 2005; see Nathan, 2005 for a review). Rapid development of molecular tools enabled some progress in the detection of dispersal events, but the rarity and enormous stochasticity associated with long-distance dispersal make it extremely difficult to measure and quantify its role in plant species' population dynamics. This lack of quantitative data limits our understanding of mechanisms, causes and consequences of long-distance dispersal. This is particularly relevant when considering the spread of invasive alien species (Cain *et al.*, 2003; Nathan, 2005).

However, the difficulties associated with identifying the exact role of long-distance dispersal are not only because of the lack of data but also because of the fact that the scale, at which long-distance dispersal may be addressed, ranges across many orders of magnitude, from inter-continental distances to those between patches of habitats. To account for differences between the scales, the long-distance dispersal is therefore usually defined as seed travelling beyond some absolute distance threshold or as a certain small fraction of seed that travel the farthest distance from the maternal plant (Bullock & Clarke, 2000; Nathan *et al.*, 2003; Soons & Ozinga, 2005; Wilson *et al.*, 2009). For the purposes of this study, we define long-distance dispersal as uniform random dispersal independent of distance from maternal plant.

The major difficulty in assessing the role of long-distance dispersal results from its elusive nature, which defies quantification. For short-distance dispersal, reliable estimates can be based on density functions (seed dispersal kernels) and dispersal distance (Bullock *et al.*, 2006), inferred using various observational, experimental or inverse modelling methods (Jones & Muller-Landau, 2008; Jongejans *et al.*, 2008; Schurr *et al.*, 2008; Soons & Bullock, 2008; Hardy, 2009; Kamm *et al.*, 2009). A number of estimates of maximal dispersal distance hence exist, and the effects of long-distance dispersal on shaping species distributions, metapopulation dynamics or genetic structure of populations are documented (Davies *et al.*, 2004; Bohrer *et al.*, 2005; Bialozyt *et al.*, 2006; He *et al.*, 2009) as well as how the dispersal vectors affect the dispersal kernels (Kuparinen, 2006; Westcott *et al.*, 2008; Heinken & Winkler, 2009). Development of complex spatio-temporal dispersal simulation models is thus a promising tool for obtaining a better understanding of the processes underlying population dynamics that act in concert with environmental conditions (Malanson & Armstrong, 1996; Levey *et al.*, 2008; Franklin, 2010). Such models can include a variety of environmental parameters, but their use is often limited by inadequate field and observational data to parameterize the models (Neilson *et al.*, 2005; Gallien *et al.*, 2010). Therefore, empirical studies that assess the importance of long-distance dispersal at a reasonably large scale are needed, namely studies that link long-term observations of species distribution with species traits rather than by inferring long-distance dispersal from static data.

Identifying the role of long-distance dispersal is extremely difficult because of the long presence of species in current landscapes. Consequently, it may be more appropriate to study such dynamic dispersal processes in newly established populations, which is the case of ongoing invasions by alien species. Therefore, introduction of species into new ranges represents natural experiments ideally suited for studying the spread of the species and dynamics of their ranges (Sax *et al.*, 2005; Cadotte *et al.*, 2006; Xu *et al.*, 2010), including long-distance dispersal (Nehrbass *et al.*, 2007). However, few invasions are recognized and described early enough to capture the complete temporal dynamics of the process (but see Robinson, 1965; Richardson & Brown, 1986; Londsdale, 1993; Müllerová *et al.*, 2005). Therefore, our incomplete understanding of the role of long-distance dispersal in species' population dynamics results from the lack of reliable long-term data on how the distribution of a species changes over time. A well-documented pattern of spread at a finer scale, from local to regional, and over a sufficiently long period of time therefore would provide a unique opportunity to study the role of dispersal in shaping a species distribution and (meta-) population dynamics. Unfortunately, such data are rarely available for individual species.

One exception is *Heracleum mantegazzianum* (giant hogweed), a serious plant invader in many European countries and North America (Nielsen *et al.*, 2005; Pyšek *et al.*, 2007; DAISIE, 2009). Owing to its large and conspicuous flower heads and strong negative impacts, it has been the subject of many studies that yielded data on its distribution on different scales. By using aerial photographs, it was possible to analyse 50 years of its invasion dynamics at the landscape scale (Müllerová *et al.*, 2005), and floristic records were used to analyse the invasion by this species at the country and continental scales (Jahodová *et al.*, 2007; Nielsen *et al.*, 2008; Pyšek *et al.*, 2008). The existing detailed knowledge of various aspects of this species' population biology (Moravcová *et al.*, 2006; Pergl *et al.*, 2006; Perglová *et al.*, 2006) acquired during the recently accomplished EU FP project Giant Alien (http://www.giant-alien.dk; Pyšek *et al.*, 2007) allowed to properly understand the life cycle of the species and thus develop appropriate models.

The aims of the study were, using the model species *H. mantegazzianum*, to (i) identify the fraction of seeds dispersed at long distance that provides the best fit to the prediction of actually observed spread at a landscape scale and (ii) provide an insight into how these seeds contribute to the invasion dynamics over several decades, since the initial introduction of the species to the region. This was made possible by combining detailed data on the long-term invasion dynamics of *H. mantegazzianum* at a large scale (from a longitudinal series of aerial photographs) with detailed knowledge of its local fine-scale population dynamics. The estimate of the fraction of long-distance dispersed seeds was obtained by fitting a set of scenarios of stage-based matrix model linked to a spatial landscape dispersal model, and the outputs from these models were compared with the real *H. mantegazzianum* longitudinal data. Furthermore, we asked whether there is a relationship between the availability of habitats suitable for invasion and fraction of seed entering the long-distance dispersal.

METHODS

Study species

Heracleum mantegazzianum (giant hogweed, Apiaceae) is native to the western Greater Caucasus (Jahodová *et al.*, 2007; Otte *et al.*, 2007) where it grows on wet and nutrient-rich soils on mountain slopes in forests. In central Europe, *H. mantegazzianum* invades mainly semi-natural grassland communities, nutrient-rich sites, forest edges and anthropogenic habitats (Pyšek & Pyšek, 1995; Thiele *et al.*, 2007). It is able to develop large populations harbouring thousands of individuals, although more often populations consist of small groups of a few individuals scattered along linear landscape structures such as roadsides, water streams or in abandoned gardens and parks and unmanaged meadows. *Heracleum mantegazzianum* is the tallest herbaceous species in Europe; it reaches 200–500 cm in height, with leaves up to 300 cm long and a flowering stem that may reach up to 15 cm in diameter. The species is monocarpic, i.e. it can persist as a vegetative rosette for several years, then flowers and dies in the same year. Plants of *H. mantegazzianum* usually live 3 to 5 years, but a 12-year-old individual is recorded (Pergl *et al.*, 2006). *Heracleum mantegazzianum* reproduces entirely by seed and can produce enormous numbers of fruits; on average 10,000–20,000 seeds with maxima occasionally reaching up to 50,000 (Perglová *et al.*, 2006, 2007). The seeds start to germinate early in the season, and the species has a short-term persistent seed bank with the majority of the seed (92%) germinating in the first year (Moravcová *et al.*, 2005, 2006). Inflorescences of *H. mantegazzianum* are large compound umbels (up to 80 cm in diameter) (Perglová *et al.*, 2006), which makes it easy to identify flowering or early fruiting patches of plants or even individuals on aerial photographs taken during the flowering or early fruiting period (Müllerová *et al.*, 2005).

Under natural conditions, timing of flowering and mortality are dependent on the amount of accumulated resources, but do not seem to be significantly affected by local density (Pergl *et al.*, 2007), although in artificial conditions in an experimental garden with two distinct regimes of density, competition is important (Pergl *et al.*, unpublished). Only a very small proportion of the emerged seedlings (700–1700 seedling per m^2) survive to the flowering stage (0.5–1.0 plants per m^2) (Pergl *et al.*, 2007). Most of this population self-thinning occurs during the first season when the mortality is very high – maximum densities of plants older than 1 year vary between 20 and 31 per m^2 in the Czech Republic and Germany (Pergl *et al.*, 2007).

Study region

The study region is located in the western part of the Czech Republic, near the place where *H. mantegazzianum* was first introduced into the country in 1862 (Appendix S1 in Supporting Information). However, the spread of the species in this area, inferred from aerial photographs, started only after 1947 (Pyšek, 1991; Müllerová *et al.*, 2005). This region is now very heavily infested with *H. mantegazzianum* because of a radical change in land use that occurred 50 years ago; after the World War II, the inhabitants were displaced and a significant part of the region became a military area with restricted access. In 1974, 617 km^2 of this area was declared a landscape-protected area, Slavkovský les. It is sparsely inhabited, with remnants of natural vegetation consisting of beech and spruce forests, peat bogs and pine forests on serpentine (Neuhäuslová & Moravec, 1997). However, natural vegetation was replaced over much of its original extent by extensive wet grasslands with high species diversity, pastures and spruce plantations that cover 53% of the area (Kos & Maršáková, 1997).

Small-scale analysis: demographic data

To obtain the information about the species' small-scale demography, two field studies were carried out: (i) demographic data sampling in permanent plots that were used to construct the matrix models and (ii) analysis of transect data to describe the short-distance dispersal.

Eight permanent plots (1 × 10 m) were monitored in the study region to determine environmental heterogeneity and range of *H. mantegazzianum* populations in terms of size and density; at each site, the invasive population occupied at least an area of 30 × 30 m (see Pergl *et al.*, 2007 for details). The plots were located at sites for which demographic data are collated and the ecology of the species studied (Krinke *et al.*, 2005; Perglová *et al.*, 2006, 2007). Population dynamics of *H. mantegazzianum* were followed from 2002 to 2006 twice a year, in late spring (May/June) and summer (July/August). For the purpose of this study, only the late-summer censuses are used, in particular the 4 year-to-year transitions at each study plot.

All plants within the plots with leaves larger than 8 cm were mapped and their (i) height, (ii) number of leaves, (iii) length of the longest leaf blade and (iv) stalk length recorded. These plants were classified directly in the field according to their size as: (i) a seedling, (ii) juvenile, (iii) vegetative rosette or (iv) a flowering plant. The position of the plants within the plot was mapped using a Laser/Angle encoder (Laser technology, Inc.) and software Field map (ver. 8.1.203; http://www.fieldmap.cz), which enabled their identification at subsequent visits. At each visit, new seedlings were recorded and included in the study.

Based on the detailed knowledge of its biology (e.g. seed bank dynamics, emergence and mortality) and data on the growth, survival and emergence, matrix population models were constructed for each plot and between-year transition. The matrices used were four-stage matrices without persistence of seed in a seed bank. At sites where the information for all diagonal and subdiagonal cells in a given year was not available, the demographic data were pooled for the following years within that site.

Data on successful short-distance dispersal was collected along eight transects 40 cm wide and at least 10 m long. These transects were located in the study region and established in summer 2005 at sites where solitary *H. mantegazzianum* had flowered in 2004. The number of seedlings per 10 cm length of each transect that emerged in 2005 was recorded. The phenomenological dispersal model was chosen to accommodate the two aspects of the dispersal curve: density functions at a very short distance from the mother plant (exponential) and the tail of the dispersal kernel (hyperbolic) (Bullock & Clarke, 2000). Mechanistic dispersal models were not considered owing to data limitations (Bullock *et al.*, 2006).

Large-scale analysis: aerial photographs

Five *H. mantegazzianum*-dominated sites (subset of sites for demographic monitoring) were chosen for determining the role of long-distance dispersal. The sites were selected to minimize possible human-mediated directional seed dispersal along roads or pathways and natural dispersal along water courses from surrounding landscapes. Aerial photographs from 1947 to 2000 recorded the invasion since the first occurrences of individual *H. mantegazzianum* plants (for details see Müllerová *et al.*, 2005). At Žitná I study site, the first occurrence of *H. mantegazzianum* was documented in 1957, giving the longest period of 39 years; however, most sites were first invaded between 1962 and 1973, with the invasion history spanning 13–31 years (Table 1).

For the present analysis, each study site of 60 ha (750 × 800 m) was divided into 2.5 × 2.5 m grid cells. Using the aerial photographs (for details on the interpretation of the photographs, see Müllerová *et al.*, 2005), each cell was assigned presence/absence of *H. mantegazzianum* and suitability for invasion (see model description for details) based on the type of land use detectable from the photographs: individual trees in the neighbourhood, vicinity of roads or railways (5-m buffer along the corridor), tree plantations, open or young forest, forest clearings, surrounding of buildings and other disturbed areas, and edges of pastures were considered as suitable habitats; pastures and arable fields as partly suitable; and forest, buildings and water bodies as unsuitable. The suitability of land-use categories was classified based on long-term field observations in the study area by the authors and monitoring of other study plots invaded by *H. mantegazzianum* (Pergl *et al.*, unpublished data). This yielded two sets of grids for each site and year recorded in the aerial photographs: (i) grid of habitat suitability and (ii) grid of *H. mantegazzianum* distribution.

The sites studied markedly differed in the proportion of suitable, partly suitable and unsuitable habitats, with area suitable for invasion ranging from 10.4 to 53.4% of the total area of a site. The availability of suitable habitats decreased over time at the Arnoltov site (from 11.2 to 5.3%), increased at Žitná I (32.6–55.4%) and remained the same at the three other sites (Table 1).

The model

The purpose of the model was to create sets of scenarios of the population dynamics differing in the level of long-distance dispersal. Based on the knowledge of the species biology, a

Table 1 Geographical location (centroid) of the five 60-ha study sites and percentage of suitable, partly suitable and unsuitable habitats.

Site	Suitability	1957	1962	1973	1987	1991	1996	2000
Arnoltov	Suitable	–	–	11.2 (1.1)	12.1 (13.5)	10.8 (3.1)	13.1 (5.9)	5.3 (6.6)
N 50°6.801′,	Partly suitable	–	–	59.7 (0.1)	56.1 (0.8)	57.7 (2.3)	58.0 (6.4)	59.7 (11.8)
E 12°36.147′	Unsuitable	–	–	29.2 (0.0)	31.8 (0.6)	31.5 (0.7)	29.0 (0.1)	35.0 (1.2)
Dvorečky	Suitable	–	–	16.3 (0.0)	n.a.	22.4 (11.4)	18.6 (18.1)	–
N 50°5.982′,	Partly suitable	–	–	38.6 (0.5)	n.a.	29.7 (0.6)	29.8 (2.5)	–
E 12°34.137′	Unsuitable	–	–	45.1 (0.0)	n.a.	47.9 (0.6)	51.6 (0.0)	–
Krásná Lípa	Suitable	–	–	–	40.7 (1.9)	40.4 (1.3)	36.5 (3.2)	40.7 (3.1)
N 50°6.306′,	Partly suitable	–	–	–	52.9 (0.2)	52.4 (0.0)	56.1 (0.7)	52.1 (0.1)
E 12°38.393′	Unsuitable	–	–	–	6.4 (0.0)	7.2 (0.0)	7.3 (0.0)	7.2 (0.0)
Žitná I	Suitable	32.6 (3.0)	30.5 (7.1)	42.7 (10.8)	45.4 (30.0)	57.5 (32.0)	55.4 (21.4)	–
N 50°3.754′,	Partly suitable	45.5 (0.0)	48.3 (1.1)	36.0 (1.0)	37.8 (10.3)	35.1 (1.7)	38.0 (15.2)	–
E 12°37.569′	Unsuitable	22.0 (0.0)	21.3 (0.0)	21.3 (0.0)	16.8 (1.2)	7.4 (0.2)	6.6 (0.0)	–
Žitná II	Suitable	–	39.7 (4.6)	43.3 (10.7)	50.6 (25.0)	69.6 (29.3)	63.9 (16.4)	–
N 50°3.837′,	Partly suitable	–	36.0 (1.3)	33.0 (4.7)	31.8 (6.9)	20.7 (1.0)	32.1 (4.3)	–
E 12°37.304′	Unsuitable	–	24.4 (0.0)	23.8 (0.0)	17.6 (0.7)	9.7 (0.3)	4.0 (0.0)	–

Values in brackets show the percentage of the total area invaded by *Heracleum mantegazzianum*. See Methods for details of the classification of the suitability of habitats. –, the lack of distributional data before the start of the invasion; n.a., distributional data for the given period not available simple simulation model was developed that takes into account land-use structure and suitability for *H. mantegazzianum*, species traits included in a stochastic matrix model and short- and long-distance dispersal at a large scale. This model was based on stage-classified matrix models, which were extended using dispersal functions that allowed the spatial development of a population to be simulated. The local population dynamics was simulated at the level of patches. The dynamics at each patch were modelled using density-dependent (logistic growth), stage-specific transitions with a 1-year transition interval (see Münzbergová *et al.*, 2005 for details of the model used). At each step, each element in the predicted population vector was replaced by a Poisson-distributed deviate with the mean given by that element. The temporal stochasticity was simulated by randomly drawing one matrix from a pool of transition matrices at each step. The probability of drawing each matrix from the pool was the same.

Size and land use type of the patches (which determines their suitability for *Heracleum mantegazzianum*) were obtained by analysing the aerial photographs. The patches were represented as sets of neighbouring cells with the same land use and maximum size of 30 × 30 m. Three habitat quality categories were used in the model based on classification of aerial photographs: (i) habitats with no regular management were assumed to be suitable for establishment, growth and reproduction, i.e. full matrices with both growth and reproduction were used in the model; (ii) habitats with regular management like pastures or meadows were classified as partly suitable for *H. mantegazzianum*; instead of full matrices, matrices with reproduction set to zero were used, and (iii) in unsuitable habitats (forest, buildings, water bodies), no growth and reproduction was allowed.

The simulations were run on a simulation plane that was modified with respect to dates for which historical data inferred from the aerial photographs was available. Changes in landscape characteristics were implemented starting in the year when they were first recorded, resulting in discrete changes in landscape suitability. The rules of plant growth and reproduction at patches followed the changes in suitability; e.g. if plants occurred in patches that changed from suitable to unsuitable, all plants were deleted, or if it changed to partly suitable, their reproduction output was set to zero.

The dispersal in the model had two forms: (i) independent of distance (henceforth referred to as long-distance dispersal) and (ii) combined exponential and hyperbolic (short-distance dispersal). To minimize the potential bias in wrong parameterization of the model owing to stochasticity in seedling emergence and survival, instead of seeds the dispersed stage in the model was seedlings that survived to late summer (but henceforth referred to as seed dispersal). Short-distance dispersal in the model was performed numerically in a cell grid put over a plane with absorbing boundaries (see Münzbergová *et al.*, 2005; Herben *et al.*, 2006 for details). Absorbing boundaries were used because the plots were selected so that seed input from outside could be assumed to be minimal; this was confirmed by a previous analysis of the long-term dynamics at study sites (Müllerová *et al.*, 2005), which indicates that the spread is from foci within sites and not the surroundings.

Number of seeds arriving at cell i by short-distance dispersal was defined as

$$n_i = \frac{1}{T}\sum_k \sum_j I_{jk} \frac{x_{0k}}{A_k}\left[a_1 \exp(-\alpha_1(d_{ij}+c_1)) + \frac{a_3}{[\alpha_3(d_{ij}+c_3)]^{\vartheta}}\right] \tag{1}$$

where x_{0k} is the number of seeds produced in patch k, A_k is the area (number of cells) of the k-th patch, α_1, α_3 and θ are dispersal shape parameters, a_1 and a_3 are weights of these dispersal shapes, c_1 and c_3 are additive constants of these dispersal shapes, d_{ij} is the distance between cells i and j, I_{jk} is 1 if cell j lies in the habitat k, and 0 otherwise, and T is a constant to normalize the sum of dispersal function values $(\sum_j [a \exp(-\alpha_1(d_{ij}+c_1)) + \frac{a_3}{[\alpha_3(d_{ij}+c_3)]^{\vartheta}}])$ to unity; j means indexing over all cells in the grid, and k summation over all patches.

Number of seeds arriving by long-distance dispersal was assumed to be independent of distance to potential seed sources. This distance independence was modelled by removing a fraction of seeds at each step from each patch and redistributing them randomly over the whole simulation plane. The number of seeds arriving at the l-th patch by distance-independent dispersal is thus proportional to the area of that patch as follows:

$$N_{\mathrm{di}l} = p_{\mathrm{f}} \frac{A_l}{A} \sum_k x_{0k} \tag{2}$$

where p_{f} is the proportion of seeds dispersing long distance, x_{0k} is the number of seeds produced at the patch k, A_l is the area (number of cells) of the l-th patch and A is the total area of the simulation plane. The seeds dispersed into unfavourable patches within the study site were considered as not contributing to the population dynamics.

Model parameterization and initialization of simulations

For the majority of sites, the number of individuals within a plot or for some transitions between stages was insufficient for developing robust transition matrices for each year. Thus, only 14 transition matrices were available for the stochastic simulations. Three matrices pooled across years 2002–2006 and eleven year-to-year transitions were developed for the model. The values for the population growth rate (finite rate of population increase – lambda) varied within the range of 0.684–1.301. The estimate of the mean population growth rate of *H. mantegazzianum* based on 9999 random simulations (Caswell, 2001) was 1.081.

Maximum distance of seedlings from the maternal plant in these transects was 5.3 m, with the highest density of seedlings within the range 0.0–0.5 m, where ca 40% of the seedlings occurred, and with 89.2% of the seedlings within 2.5 m. Dispersal parameters for short-distance dispersal were estimated by fitting the combined exponential and hyperbolic model (Equation 1) to the data obtained from transects (Fig. 1). The model used for parameterization explained 78.1% of the variance in the data, and the adequacy of the fitted model was checked by plotting standardized residuals against fitted values, and by a normal probability plot.

The simulations for each study site started with an initial population corresponding in size to the distribution when *H. mantegazzianum* was first observed in photographs, and with the mean plant density and proportion between stages based on data from permanent plots.

Apart from local population dynamics, the following parameters were also estimated from field data. Density of *H. mantegazzianum* stands ranged from 0.2 to 23.4, with a mean of 6.7 individuals m^{-2} (eight permanent plots; SD 7.4). The mean density value was used for initialization of occupied cells in the initial occupancy layer, and maximum density was used for the carrying capacity (K). Initial occupancy layer was based on the observed species distribution obtained from aerial photographs with the proportion in the four stages (seedlings, juveniles, rosettes, flowering) based on a stable stage distribution as obtained from the fourteen matrices, namely 0.31:0.30:0.26:0.13.

Simulation experiment and sensitivity analysis

To identify the contribution of long-distance seed dispersal to overall landscape population dynamics not described by the short-distance kernel, sets of simulations with different fractions of randomly distributed seeds (p_f; from 0 to 10%, henceforth referred to as scenarios) were run for each site. To keep the number of seeds dispersed by short-distance kernel constant at simulations differing by the fraction of randomly dispersed seeds, we changed the number of produced seed in matrix accordingly. The simulations were run for an additional 10 years from the date of the last aerial photograph, and for each scenario, 20 simulations were run. Twenty simulations were used as the variability between the individual runs within the scenarios was relatively low. To compare whether the scenarios conform with the observed trends in occupancy of patches and reduce the bias owing to possible overlooked individuals in managed habitats, only data for patches in suitable habitats were used. As rosettes cannot be clearly detected from aerial photographs, only habitats that hosted at least one flowering plant were considered as occupied. The selection of the best scenario was based on visual inspection and on the comparison of the sum of squares between the average patch occupancy and the real number of occupied patches taken from aerial photographs.

The additional analysis of sensitivity for the whole model was performed for two parameters that are known to significantly affect the extrapolation of short-term data to long-term dynamics: density dependence expressed through the carrying capacity and average population growth rate (Mildén *et al.*, 2006). Five alterations in both parameters were used, giving 25 parameter combinations. The effect of changing the carrying capacity was tested by using 20% smaller, 10% smaller, unchanged, 10% bigger and 20% values of the carrying capacity. For population growth, five pools of matrices were used: lowest population growth (removing from the pool of available matrices the two matrices with the highest lambda, $\lambda = 1.01$); low population growth (removing one matrix with the highest lambda, $\lambda = 1.06$), unchanged pool of matrices (1.08), faster population growth (removed matrix with the smallest population growth, 1.11); and the fastest population growth (removing two slowest matrices, 1.15). The sensitivity analysis was carried out for the following fractions of long-distance dispersed seeds: 0, 0.2, 0.5, 1 and 5%. Owing to the computer-demanding simulations, this sensitivity test was performed only for one locality (Žitná I). Sensitivity was assessed by visual inspection and by using the sum of squares between individual scenarios and the real number of occupied patches taken from aerial photographs.

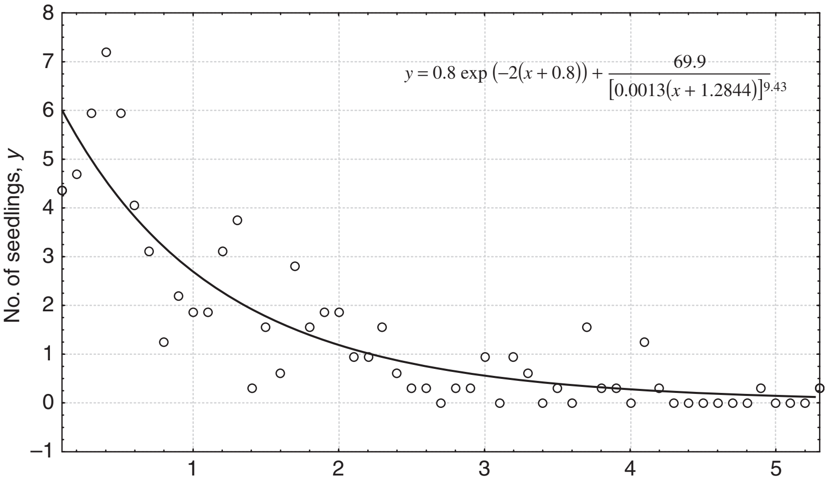

Figure 1 The pattern of short-distance dispersal showing data from the transects and estimated parameters for the dispersal curve (combined exponential and hyperbolic model), Equation 1.

RESULTS

Fraction of long-distance seed dispersal

The simulation scenarios in which the fraction of long-distant dispersed seed was manipulated showed that at all the sites studied this fraction must have been larger than zero. The scenarios in which this fraction was zero clearly showed that the predicted increase in the occupancy rate of patches within the simulation plane was much slower than that actually observed in aerial photographs. This indicates that the short-distance dispersal alone cannot account for the observed invasion dynamics (Fig. 2, Appendix S2 in Supporting Information). At the five study sites, the scenarios providing the best correspondence with aerial photograph data indicated fraction of long-distance dispersed seed to be in the range between 0.1 and 7.5% (Table 2). At two sites, it was higher or equal to 1%, and in the remaining three between 0.1 and 0.4%. In the scenario with the highest fraction of long-distance dispersed seed in the model (10%), *H. mantegazzianum* occupied the majority of suitable habitats at all study sites at a rate that was approximately double that observed. The relationship between the fraction of long-distance dispersed seed and sum of squares is clearly U-shaped for all the studied sites (Fig. 2, Appendix S2 in Supporting Information).

Sensitivity analysis

The sensitivity analysis assessing the effects of uncertainty of the estimates of carrying capacity and population growth rate (lambda) was performed for the locality Žitná I where the monitored period of invasion was longest and the estimated fraction of long-distance dispersed seeds was intermediate. The simulations for each combination of parameters and changed fraction of long-distance dispersed seeds revealed that the model was very robust to varying values of the carrying

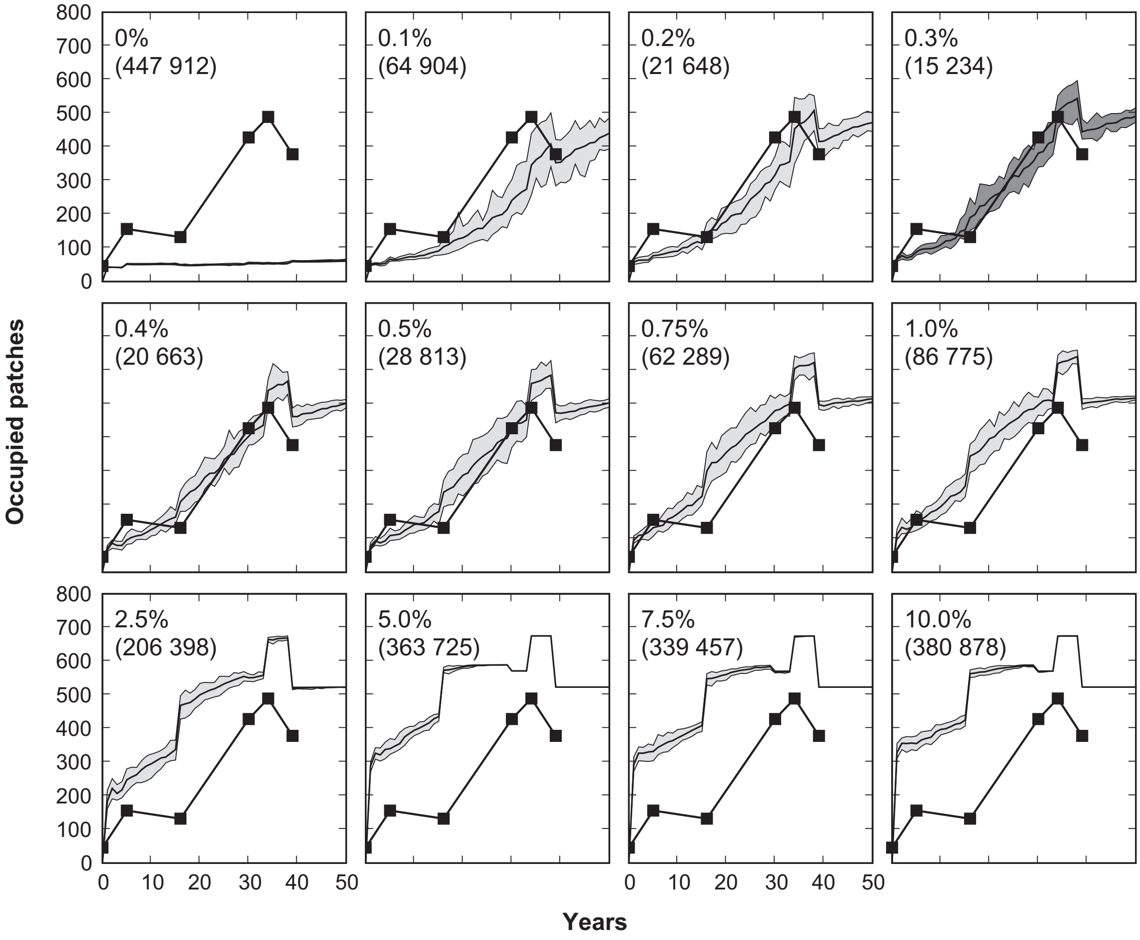

Figure 2 Simulations with different fractions of seeds dispersed over long distances (study site Žitná I). The solid line with squares shows observed number of occupied patches; the squares indicate the years for which aerial photographs were available. Black line shows the average patch occupancy predicted by simulations for each scenario, and grey lines show the 90% confidence interval. Numbers in graphs indicate fraction of seeds dispersed over long distances. The values in brackets show the sum of squares between the average patch occupancy and real number of occupied patches taken from aerial photographs. Graphs with dark grey indicate the scenarios that best fit to the observed data based on the minimal sum of squares. The sharp decrease in the number of occupied patches in the last year was because of an occasional management action.

capacity (Fig. 3, Appendix S3 in Supporting Information), but sensitive to changes in the estimates of population growth (average for CV over-carrying capacities was 0.096, while the CV for lambdas was 0.842). In case of the 0.3% fraction of long-distance dispersed seed, the 2% change in population growth resulted in 50–100% change in sum of squares (Table 3). Nevertheless, the sensitivity analysis of the model indicates that even in case of highly over- or underestimated population growth parameters with *c.* 7% change of lambda (1.01 or 1.15), the minimal sum of squares and therefore the best fit to the real data from aerial photographs with the estimates of fraction of long-distance dispersed seeds within a site does move between 0.2 and 1% fraction of the long-distance dispersed seed (Table 3, Fig. 3).

Correlation between long-distance dispersal and suitable habitats

The percentage of the area of habitats that were invaded ranged from 2.4% (site Krásná Lípa; first record of invasion in 1987) to over 17% at Žitná I and Žitná II (invaded between 1957 and 1962) and reflected the differences in the time that has elapsed since these sites were invaded (averages over the years) (Table 2). There was no clear correlation between the fraction of long-distance dispersed seeds and invaded area, or its percentage of the total site area (averages over the available years), but the fraction of long-distance dispersed seeds providing the best fit to the prediction of the observed spread in a given site was significantly negatively correlated with the percentage of suitable habitats at that site (both variables log-transformed, $r = -0.916$, d.f. = 3, $P < 0.05$) (Table 2).

DISCUSSION

In this study, the combination of long-term observational data at two different scales, based on monitoring the invasion from the beginning, allowed for the first quantitative insight into the importance of long-distance dispersal in the invasion of an alien plant species. The results illustrate how an analysis of a well-documented invasion of an alien species can contribute to a better understanding of general ecological phenomena, including species dispersal and spread (Kinlan & Hastings, 2005; Lewis *et al.*, 2006), and support the theories on how availability and spatial pattern of habitats shape the rate and population dynamics of species (Hill *et al.*, 2001; With, 2002; Soons & Ozinga, 2005; Murrell, 2006).

The proportion of seed that is randomly dispersed beyond the prevailing distance predicted by a density function, i.e. over relatively long distances from the source plants of

Table 2 Estimated fractions of seeds dispersed over long distances at each study site, average values of the percentage of suitable habitats at each study site and invaded area (averages over years with available data).

Locality	Fraction of seeds dispersed over long distances (%)	Suitable habitats (%)	Invaded habitats (%)	Invaded area (max. area invaded; m^2)	Mean rate of spread (areal; m^2 year^{-1})	Mean rate of spread (linear; m year^{-1})
Arnoltov	5.0–7.5	10.4	6.0	47,000	1241	12.8
Dvorečky	1.0	19.0	9.9	23,817	730	17.4
Krásná Lípa	0.1	39.6	2.4	9,000	350	3.8
Žitná I	0.3	44.0	17.4	113,000	2831	8.0
Žitná II	0.1	53.0	17.2	111,000	3275	8.2

Maximum area invaded and mean rates of areal and linear spread are taken from Müllerová *et al.* (2005).

Table 3 Sensitivity analysis based on sum of squares for the correspondence of the simulations of patch occupancy compared to real data from the locality Žitná I.

Population growth scenario	Sum of squares					
Fraction of long-distance dispersed seeds (%)	0.2	0.3	0.5	1.0	5.0	Average lambda (change in %)
Lowest λ	183,422	121,729	59,561	20,475	351,693	1.01 (93.5)
Low λ	51,228	22,507	16,773	54,107	361,130	1.06 (98.1)
Average λ	19,922	**15,679**	32,920	86,008	364,270	1.08 (100.0)
High λ	19,805	32,557	62,751	124,376	377,765	1.11 (102.8)
Highest λ	43,339	68,346	102,407	161,767	381,490	1.15 (106.5)

See Methods for details on modelling the sensitivity. The table shows averages of sum of squares for individual scenarios with varying fraction of long-distance dispersed seed and different population growth models differing by average lambda. Fraction of 0.3% was identified as fitting the best to the real data. Bold value indicates the scenario with the smallest sum of squares.

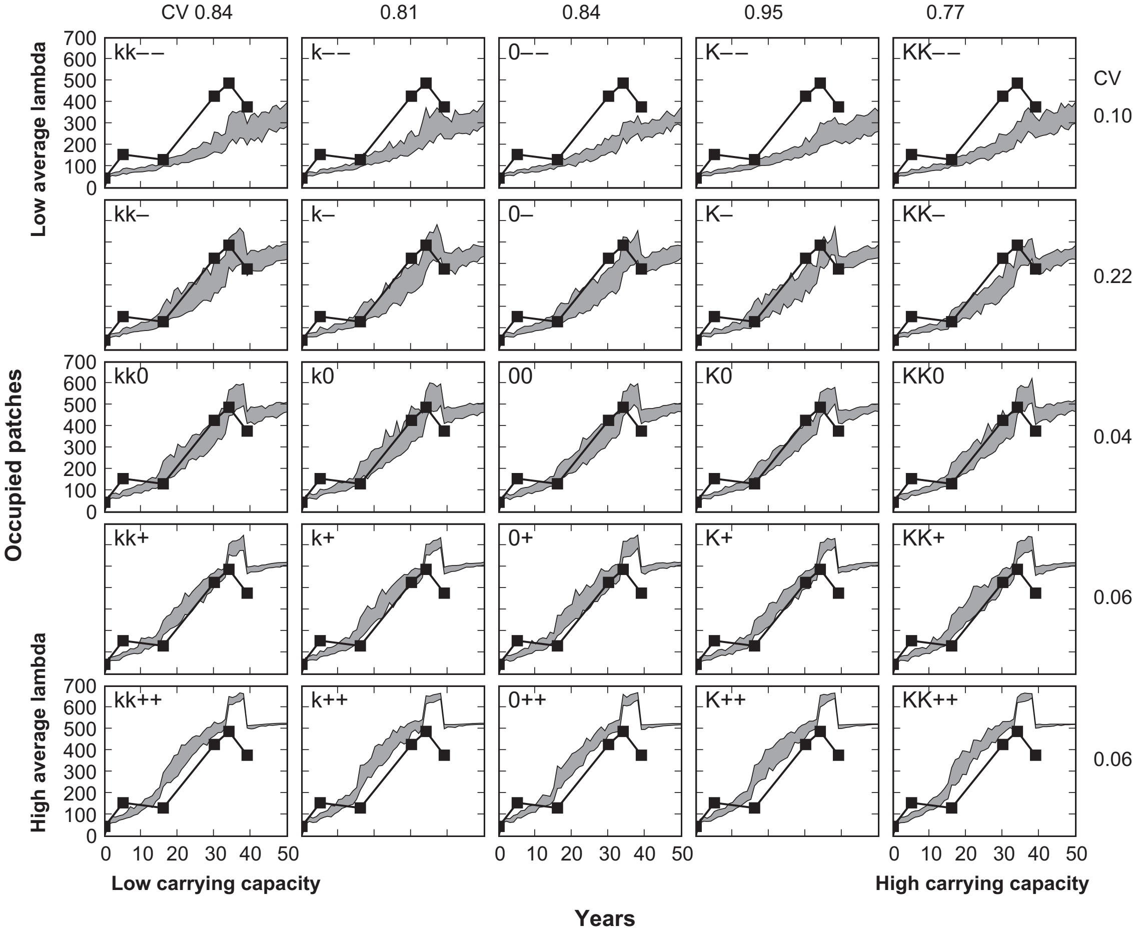

Figure 3 Results of sensitivity analysis for locality Žitná I and 0.3% fraction of long-distance dispersed seeds. The solid line with squares shows observed number of occupied patches. The squares indicate the years for which aerial photographs were available. Grey lines show the 90% confidence interval of patch occupancy predicted by simulations for each scenario. kk – indicates lowest, k – low, K – high and KK highest population growth (lambda); – indicates lowest, – low, +high and ++ highest carrying capacity used in the model. 00 indicates the standard values used in the simulations. See Methods for details. Above each column (carrying capacity constant) and on the left of each row (lambda constant), the values of coefficient of variation (CV) of sum of squares are shown.

H. mantegazzianum, ranged from 0.1 to 7.5% of the total seed set. Previous studies on long-distance dispersal indicated up to *c.* 5% of the seed travelled relatively far from mother plants, with a long and fat tail to the dispersal curve (see e.g. Higgins *et al.*, 2003 and examples therein; but see only 0.02% of *Rhododendron ponticum* seed estimated to travel further than 50 m; Stephenson *et al.*, 2007).

Although the existing estimates of long-distance dispersal (e.g. in Higgins *et al.*, 2003) seem to be directly comparable with ours, available data are mostly for tree species where distances over which seeds are dispersed are larger because of seeds being released from higher up and many species have specialized structures that support passive dispersal by wind. As seeds of *H. mantegazzianum* have no specific adaptation to dispersal vectors and the only indication of wind dispersal is flat and thin seed margins, water dispersal was suggested as a more important mode of its distribution (Walker *et al.*, 2003). Compared to other alien species in the Czech Republic, *H. mantegazzianum* exhibits an average capacity for dispersal by water and wind (Moravcová *et al.*, 2010). This indicates that, compared to species possessing special adaptation for dispersal such as wind-dispersed trees or animal-species species, its long-distance dispersal is rather random, depending on landscape structures, especially water streams, and human activities.

It may be argued that the size of the study sites in relation to the overall seed production in these sites and the shape of the long-distance dispersal kernel may significantly affect the output of our study. The scale of the study generally affects the interpretation of the colonization patterns found in ecological studies because the same size of initial population will play a different role at a small study site or if it covers only a small proportion of a large area. As we were aware of these constraints, we attempted to take into account all possible aspects of landscape dynamics in our study: individual study sites were of the size that allowed to capture the dispersal at landscape level and chosen so as to be comparable in terms of the initial proportion of invaded area that ranged from 0.5 to

5% of the suitable area (Table 1). We believe that by taking these issues into account, we achieved a sound basis for analysing the long-distance dispersal at the used level.

Furthermore, it may be argued that long-distance dispersal can follow similar rules, in terms of density dependence on distance, as short-distance dispersal, and dispersal models combining both short- and long-distance dispersal should be used. However, such models are more suitable for larger distances and suffer by the need of precise estimate of dispersal parameters (Jongejans *et al.*, 2008; Münzbergová *et al.*, 2010). Therefore, we preferred, for our relatively small study sites, a general model with completely random dispersal being constant throughout the simulation plane instead of using a more accurately parameterized dispersal model for long-distance dispersal with higher uncertainty of the parameters. The distance function is therefore integrated only in the short-distance dispersal kernel.

Monitoring by using aerial photographs provides excellent information on spatio-temporal dynamics, despite lack of information on links between mother plants and offspring, which means that the inferred rates of spread are conservative estimates (Müllerová *et al.*, 2005). However, it needs to be noted that individual plants can be overlooked on aerial photographs, especially in the close neighbourhood of shrubs or in the forest understorey. This might be a source of two types of potential bias in the simulation models: underrepresented distribution in the initialization of the simulations and underrepresented distribution of the species used for comparison with simulation outputs. The former would lead to the overestimation of needed proportion of long-distance dispersed seed, while the second to its lower estimates. Even though such bias can be hidden in the presented results, the data in this study are the best that are available. Another issue potentially results from the fact that only flowering plants were clearly detected on aerial photographs. Therefore, the lag owing to the existence of vegetative plants (rosettes) outside the identified patches in the beginning of simulations might cause a delay in the modelled invasion dynamics compared to the observed data. However, this difference is only minor because the life span of the species is short, with the majority of plants flowering in their 3rd to 5th year (Pergl *et al.*, 2007).

Nevertheless, aerial photographs also provide a good way of analysing the role of landscape structure in shaping the patterns of long-distance dispersal and allow the use of habitat-specific models of species' population dynamics. Although the model used in the present study was based only on stochastic non-directed long-distance dispersal at a large scale, the results demonstrate the importance of relatively small but significant amounts of seed that are dispersed over long distance across the landscape. The advantage of our long-distance dispersal model is its simplicity, by using uniform random dispersal that fits the relatively small area of homogeneous landscape without strong corridors. However, in contrast to a pilot study by Nehrbass *et al.* (2007), our approach shows that reliable estimates of long-distance dispersal can be obtained only if environmental heterogeneity is taken into account. At the Arnoltov study site, which was used in both studies, the estimated values of long-distance dispersed seed are 5.0–7.5% (this study) and 2.5% (Nehrbass *et al.*, 2007). This difference is likely to result from different population growth model (matrix vs. IBM) based on different population data, with the latter overestimating local dispersal at the expense of random dispersal (Nehrbass *et al.*, 2006).

The interplay between the dispersal of species and landscape structure affects the dynamics and survival of many species (e.g., Hanski, 1999; Soons & Ozinga, 2005; Trakhtenbrot *et al.*, 2005). In our study, the variation in the fraction of long-distance dispersing seeds that provides the best fit to the prediction of observed spread was attributable to the suitability of landscape to invasion, determined by land-use structure. Bearing in mind that a more rigorous statistical analysis was constrained by the low number of study sites, the results, nevertheless, strongly suggest that the fraction of long-distance dispersed seed needed to account for the observed invasion dynamics decreases as the proportion of the landscape made up of habitats that are suitable for invasion increases. In addition to identifying the fraction of dispersed seeds over long distances as critical, the simulations also showed that the level of long-distance dispersal significantly differs among individual study sites, even among those that experience similarly low levels of human pressure. This emphasizes the crucial role of habitat (and its invasibility) in plant invasions (Chytrý *et al.*, 2008a, 2008b) and indicates that in disturbed landscapes where a large proportion of area is covered by suitable habitats, the long-distance seed dispersal needed for a successful invasion needs to be much lower than in landscapes that are less disturbed. This highlights the smaller size of the window of opportunity for invasion for alien species in undisturbed habitats and increased potential of highly disturbed habitats that are generally suitable to invasion and exposed to a higher propagule pressure (Catford *et al.*, 2009; Davis, 2010). However, although the dispersal along streams and roads is crucial for this species (Pyšek *et al.*, 2008), these pathways are unlikely to play a role in our study sites owing to their relatively small area and the absence of the respective dispersal vectors. In addition, as these dispersal modes increase the availability of seeds at sites far away from the seed source, our results are rather conservative estimates of the study species' spread patterns.

The results of this study point to an important conclusion for management of both invasive and rare native species (see e.g. Trakhtenbrot *et al.*, 2005; Jongejans *et al.*, 2008). While the general recommendation is that the eradication of invasive species should first target satellite rather than central populations (Moody & Mack, 1988), our results indicate the importance of monitoring as large an area as possible. It needs to be noted that 1% of the seed set of an average *H. mantegazzianum* plant represents about 200 highly germinable seeds (Moravcová *et al.*, 2006; Perglová *et al.*, 2006). In the context of sustainable management of large infestations of *H. mantegazzianum* where complete eradication is unrealistic, our results show that reduction in the seed set even at small amounts is likely to significantly affect the invasion dynamics. This can be extrapolated to other invasive species where control methods focus on reducing the seed set; the results of our study suggest that the more important effects of such methods may be in decreasing the number of seeds that are available for dispersal to a large distance from mother plants rather than in simply reducing the total seed set.

In this paper, we present a case study of an invasive species, invasion dynamics of which was modelled by incorporating long-distance seed dispersal. The study also indicates how linking long- and short-term population studies can improve the application of spatially explicit models that are currently in use. Based on the results, it is concluded that long-distance dispersal is an important component of the population dynamics of a species in the early phase of invasion, even at relatively small (regional) scales. Furthermore, by using the model species *H. mantegazzianum*, it was possible to show that the effects of long-distance dispersal on population dynamics can be demonstrated without direct measurements of dispersal events if long-term observations on a species distribution and land-use change accompanied by detailed population data are available. But, it has to be kept in mind that the data presented and conclusion drawn in this study are only valid for the scale used here and the species studied, while at different landscapes and for species with different dispersal mechanisms and life history, the effect of long-distance dispersal might be different. Therefore, our conclusions can only be generalized to a limited group of monocarpic perennial species in a comparable habitat that reproduce by seed, are extremely prolific and lack any specialized dispersal mechanisms, such as some other invasive Apiaceae (e.g., *Myrrhis odorata*, *Imperatoria ostruthium, Angelica archangelica*); more case studies covering a wider range of species with different life histories and addressed at a variety of spatial scales are needed.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Map of the study sites.

Appendix S2 Results of simulations of the sites.

Appendix S3 Results of sensitivity analyses.

BIOSKETCH

Jan Pergl is with the Institute of Botany in the Academy of Sciences of the Czech Republic, and his research focuses on population ecology of invasive plant species, modelling their spread and macroecological patterns of biological invasions. He is actively involved in management and policy issues linked to invasive species in the Czech Republic. The authors are members of a group studying various aspects of biological invasions in Europe. In recent past, they were involved in major international projects of European Union addressing biological invasions such as GIANT HOGWEED, ALARM, DAISIE and PRATIQUE.

Author contributions: J.P., T.H. and P.P. designed research and wrote the paper, J.P., J.M. and I.P. collated the data, J.P. and T.H. analysed the data.

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