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Comparing the rate of invasion by *Heracleum mantegazzianum* at continental, regional, and local scales

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ABSTRACT

This paper compares the rate of invasion of *Heracleum mantegazzianum* (Apiaceae), a Caucasian species invading Europe, at three spatial scales (continental, regional, and local). The rate of invasion was evaluated using inclusion curves, by plotting the cumulative number of invaded countries against time on the continental scale of Europe, number of occupied grid cells at the regional scale of the Czech Republic, and invaded area inferred from a series of aerial photographs taken at the local scale over a period of 49 years in the Slavkovký les region, Czech Republic. Time of 50% inclusion (with 95% confidence intervals, CI) of invaded countries, occupied grid cells, and invaded area was assessed. The invasion was slowest at the continental scale (62 years, CI = 53–70) and did not differ significantly between regional (16 years, CI = 10–20) and local (22 years, CI = 19–24) scales. Our results indicate that there are two different mechanisms of spread acting together in this system, namely human influences and natural spread, and the relative influence of these mechanisms appears to change in an inverse proportion from the largest to the smallest scale. At the local scale, under suitable habitat conditions, the process is driven by biological traits of the species related to dispersal. At the continental and regional scales, humans played a crucial role in the invasion of *H. mantegazzianum* by planting it as a garden ornamental. At these scales, human-mediated dispersal seems to have been the major driver of spread, responsible for creating dispersal foci in the initial phases of invasion. Species traits played an important role in local spread, resulting in the colonization of new sites.

Keywords

Biological invasions, Czech Republic, giant hogweed, Europe, *Heracleum mantegazzianum*, horticulture, invasion rate, long-distance dispersal, scale.

INTRODUCTION

Biological invasions are characterized by remarkable spatio-temporal dynamics with many species having extended their distribution range from a single region to much of the globe within the last century (Weber, 2003; Daehler, 2006; Palmer, 2006; Richardson & Pyšek, 2006). To establish a large range in a short time requires efficient and fast spread; range size is closely related to the dynamics of spread. How fast a species can spread is an attractive topic of research and there is a lot of information on this in the literature. Pyšek & Hulme (2005) concluded, based on a review of spatio-temporal dynamics of over 100 taxa from studies undertaken worldwide, that average rates of local spread reported for invasive species in the literature range from 2 m year^{-1} to a maximum of 370 m year^{-1}. At regional scales, invasive species rarely move across the landscape as a continuous front and both local and long-distance dispersal (LDD) determine spatial patterns (Higgins & Richardson, 1996; Higgins *et al*., 2003; Nathan, 2003; Richardson, 2006); maximum values of the rate of spread recorded for alien species are many times higher than the mean (Richardson & Brown, 1986; Rouget *et al*., 2001; Pyšek & Hulme, 2005). This indicates that a hierarchy of processes operating at different temporal and spatial scales determines the dynamics of biological invasions and the estimate of spread of alien species, expressed in absolute terms, depends on the size of the area monitored (Pyšek & Hulme, 2005). The problem with such global data sets is that they are obtained by using different methods and are thus difficult to analyse using standard statistics. They provide a rough idea of the rate of spread, but in order to obtain a deeper insight into the effect of scale, it is more informative to analyse the invasion of individual species.

One invasive alien species that has been studied in detail recently is *Heracleum mantegazzianum*. For several reasons, detailed historical information on the distribution of this species

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is available, especially for European countries where floristic research is sufficiently intensive. *Heracleum mantegazzianum* is attractive enough for botanists to record it because of its alien origin, fast spread, and conspicuousness (Pyšek, 1991; Pyšek *et al.*, 2007c). Furthermore, this species was the subject of the European GIANT ALIEN project, which yielded comprehensive information on its biology, ecology, and distribution (Pyšek *et al.*, 2007a). Finally, floristic data allow a retrospective analysis of the spread of *H. mantegazziaum* in the Czech Republic and UK (Pyšek, 1991; Pyšek & Prach, 1993; Collingham *et al.*, 2000; Williamson *et al.*, 2005); if such data are systematically gathered over an area for a long time, they may be used to reconstruct the pattern of invasion of individual species on a regional geographical scale (e.g. Pyšek & Prach, 1995; Delisle *et al.*, 2003).

The detailed information necessary to determine the rate of invasion of species at different scales is largely missing (Pyšek & Hulme, 2005), which makes *H. mantegazzianum* a unique model species, for which the invasion dynamics at various scales can be compared. Quantitative investigations of invasive species across multiple scales are needed, but translation of anecdotal information into generalization remains limited by technical shortcomings in data acquisition (Mack *et al.*, 2007). This paper approaches the monitoring of an invasive species from a hierarchical perspective with data gathered at more than one spatial scale. Such approach has the potential to improve predictions (Mack *et al.*, 2007) and integrate landscape attributes into invasion dynamics (Pyšek & Hulme, 2005). The present paper therefore compares the rate of invasion of *H. mantegazzianum* at three spatial scales (continental, regional, and local) and discusses the factors that may underlie the differences observed among the scales studied. Our hypothesis is that if the spread at continental and regional scales (i.e. the two where human-mediated dispersal is involved) depended exclusively on the processes of local dispersal, the rate of spread would be the same.

METHODS

Study species

Heracleum mantegazzianum Sommier & Levier (Apiaceae) is native to the southern slopes of the Western Greater Caucasus, where it grows in tall herb meadow communities, forest clearings, and forest margins in the upper forest belt (Otte *et al.*, 2007). The species is invasive or naturalized in many European countries, central Russia, Canada, and the USA (Tiley *et al.*, 1996; Page *et al.*, 2006; Jahodová *et al.*, 2007). *Heracleum mantegazzianum* is a monocarpic perennial plant flowering usually in the third to fifth year (Pergl *et al.*, 2006) with a flowering stem between 200 and 500 cm tall. Flowers are arranged in compound umbels, the terminal umbel is the largest – up to 80 cm in diameter – with satellite and other umbels on branches. Flowers are insect-pollinated, hermaphrodite, and protandrous, but geitonogamous selfing between umbels is possible (Perglová *et al.*, 2006). In the invaded range of Central Europe, flowering occurs from June to July, followed by sequential ripening of fruits. A single plant is capable of producing a large number of oval-elliptical, broadly winged fruits (mericarps), which are connected in pairs and split when mature (Moravcová *et al.*, 2005). An average plant produces *c.* 20,000 fruits, with a maximum of around 50,000 (Perglová *et al.*, 2006, 2007). Seeds germinate early in spring a few days after the snow melts (Pergl *et al.*, 2007) and cold stratification is necessary for germination. On average, 91% of the seed germinates in the laboratory (Moravcová *et al.*, 2005). Seeds of *H. mantegazzianum* form a short-term persistent seed bank, and a small proportion (about 1%) of the fruits remain viable in the soil for at least 3 years (Krinke *et al.*, 2005; Moravcová *et al.*, 2006).

Heracleum mantegazzianum was introduced into Europe as a garden ornamental in 1817, when it appeared on the seed list at Kew Botanic Gardens, London. In 1828, the first population was recorded growing wild in Cambridgeshire, England. Ranked according to the date of introduction, the UK was followed by the Netherlands, Switzerland, Germany, Ireland, Denmark, and Czech Republic (Nielsen *et al.*, 2005; Jahodová *et al.*, 2007). In the Czech Republic, the species was first introduced to the Slavkovský forest region in the western part of the country as a garden ornamental, and first collected in the wild in 1877, having escaped from the nearby the site of initial cultivation (Pyšek *et al.*, 2007c).

Data

The rate of invasion by *H. mantegazzianum* at the continental scale of Europe was assessed based on data from Nielsen *et al.* (2005) and updated using distribution mapping within the DAISIE project (www.europe-aliens.org). Although the present distribution in 50 km grid cells is available (Jahodová *et al.*, 2007), the dates of the first records for individual grid cells are not. For that reason the temporal dynamics of the invasion of Europe was reconstructed using dates of the first records for individual countries and plotting the cumulative number of invaded countries against time.

Reconstruction of the invasion at the regional scale was based on the date of occurrence in 578 geo-referenced sites, obtained from the botanical literature up to 1996 (Pyšek & Pyšek, 1994, updated). This information on distribution was transferred to a mapping system commonly used in European phytogeographical mapping, based on a grid of 10′ (longitude) × 6′ (latitude), which at 50° N is 12.0 × 11.1 km or 133.2 km^2 (Schönfelder, 1999; Williamson *et al.*, 2005). In total, there are 679 grid cells in the Czech Republic. To express the rate of invasion, the cumulative number of grid cells in which the species was recorded up to a given year was plotted against time.

The rate of invasion at the local scale for the Slavkovský les region, where the species was first introduced into the Czech Republic, was measured using historical aerial photographs, which record the invasion by this species in study plots from the very beginning. *Heracleum mantegazzianum* is easily detectable on aerial photographs taken at the time of flowering or early fruiting, from June to August (Müllerová *et al.*, 2005; Pyšek *et al.*, 2007c). The size of the invading population of *H. mantegazziaum* was monitored in 10 plots of 60 hectares (750 × 800 m) on seven sampling dates between 1947 and 1996 (see Müllerová *et al.*, 2005, for details), and the rate of invasion expressed as increase in total invaded area over time.

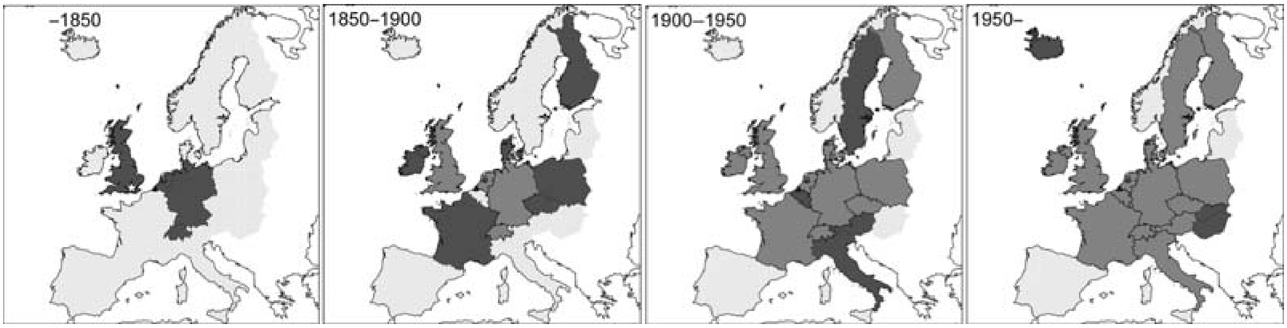

Figure 1 Invasion of Europe by *Heracleum mantegazzianum*, expressed in terms of the reported occurrence in individual countries (data from Nielsen *et al.*, 2005). See Fig. 3a for a plot of the invasion dynamics. The location of first introduction to Europe (Kew Gardens, UK) is indicated by ☆. ■ countries invaded in the given period; ▨ countries invaded up to the end of the given period; □ area considered. Note that *H. mantegazzianum* is also reported from in Norway and Estonia, but these countries are not considered because the date of introduction is unknown.

Table 1 Parameters of the three scales at which the invasion by *Heracleum mantegazzianum* was studied.

Scale	Location	Study area (km^2)	Measure (units invaded)	First record (in cultivation)
Continental	Europe	9,900,000	No. of countries	1828 (1817)
Regional	Czech Republic	78,000	No. of grid cells	1877 (1862)
Local	Slavkovský les	600*	Hectares	1957 (n.r.)

*Total area of the region in which the sample plots of 60 ha were located. n.r., not relevant.

Statistical analysis

To overcome the problems that the distribution data are cumulative and expressed in a different unit at each scale (records, grid cells, and hectares, respectively), the rates of invasion were compared by using inclusion curves (Pyšek *et al.*, 2003). The use of inclusion curves also circumvents the problem of a potential lack of independence between errors in the models, because the inclusion curves represent a type of survival analysis, in which the cumulative total of the distribution data at each scale corresponds to a cohort, of which the proportion of cumulative data at each time stands for the survival. At each scale, the inclusion curves consisted of plots of the cumulative data against years since the beginning of invasion, scaling them proportionally to the cumulative total for each scale. The curves were then analysed with GLIM (version 4; Francis *et al.*, 1994) by specifying binomial errors and logit link function, $\ln (p/1 - p)$, where p for each point of each curve was the proportion the cumulative data represent of their total. The cumulative distribution data were the response variable and the time since the beginning of invasion the explanatory variable. The logit link functions were stored in two vectors: one to identify the cumulative distribution data, and the second their total, giving a binomial denominator. Overdispersion of binomial errors was checked by comparing residual deviance with residual degrees of freedom (Crawley, 1993, p. 273). The shape of the curves was assessed by stepwise adding of powers to the explanatory variable. If an addition caused a significant ($P < 0.05$) reduction in unexplained deviance, the term was kept in the model (e.g. Crawley, 1993).

To compare the inclusion curves among scales, the estimated time of 50% inclusion, t_{50}, with 95% confidence interval (CI) was calculated for each curve, by employing Fieller's theorem (Collet, 1991; Crawley, 1993, pp. 275–278). When t_{50} of inclusion curves did not overlap in CI (lower limit–upper limit), the curves differed in time of 50% inclusion among scales, and their invasion rates were considered statistically different.

RESULTS

Rate of invasion

Parameters of the three scales are summarized in Table 1. At the continental scale, the species was first recorded as an escape from cultivation in Europe in 1828 in the UK and since then it has spread across a large part of Europe. At present it is reported from 19 countries (Fig. 1) and the increase in the number of invaded countries was linear (Fig. 3a). Visual inspection of maps drawn at 50 years intervals suggests that at the continental scale, the species spread to the south-east more or less along a continuous invasion front (Fig. 1).

At the regional scale of the Czech Republic, *H. mantegazzianum* was first recorded as planted in 1862 and in the wild in 1877. Up to the present, it has spread into 33.3% of mapping grids (Fig. 2). The invasion at this scale exhibits a distinct lag phase, with rapid exponential increase in the number of grid cells occupied after the 1970s (Fig. 3b; see also Pyšek & Prach, 1993; Pyšek *et al.*, 2007c).

At the local scale, the species was first recorded in the plots studied in 1957 (see Müllerová *et al.*, 2005; Pyšek *et al.*, 2007c,

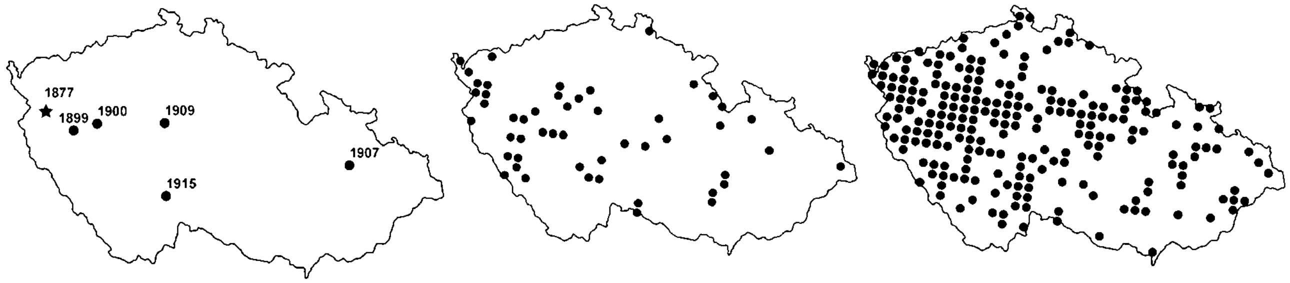

Figure 2 Invasion of the Czech Republic by *Heracleum mantegazzianum*. Reported occurrence in grid cells (mapping quadrats) of *c.* 11 × 12 km is shown. See Fig. 3b for a plot of the invasion dynamics. The location of the first introduction into the country (★) and dates of early records are indicated.

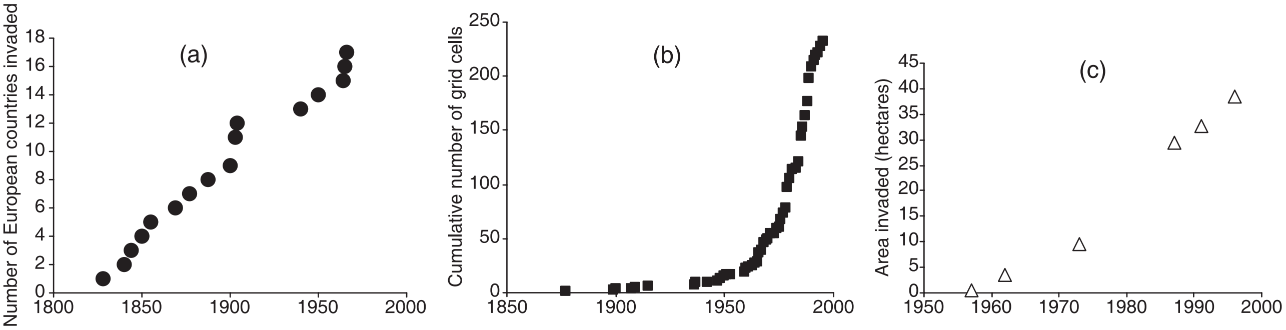

Figure 3 Invasion rates of *Heracleum mantegazzianum* at three different scales, expressed as the increase in the (a) number of countries invaded at the European scale, (b) cumulative number of grid cells at the regional scale of the Czech Republic, and (c) the area invaded at the local scale of the Slavkovský les area (summary values from 10 plots).

Table 2 The rates of invasion by *Heracleum mantegazzianum*, evaluated by inclusion curves (t_{50}), which describe the time of 50% invasion at continental (dates of the first records for individual countries), regional (number of grid cells in which the species was recorded), and local (area invaded, ha) scale. The t_{50} values (years) followed by the same letter overlap in confidence intervals CI (lower limit–upper limit) and do not differ significantly ($P < 0.05$) in invasion rates. Inclusion curves are fitted by stepwise polynomial regression where a is the intercept, b_1 and b_2 are the linear and quadratic term of time, respectively, and R^2 is the total variance explained by the model (%).

			Inclusion curves			
Scale	t_{50} (years)	CI of t_{50}	a	b_1	b_2	R^2 (%)
Continental	61.56 a	52.67–70.46	–2.10	0.034	–	94.5
Regional	15.85 b	9.89–20.14	–2.98	–0.087	0.0011	95.6
Local	22.02 b	19.33–24.54	–3.67	0.17	–	96.4

for aerial photographs documenting invasion of study plots) and has exhibited a steady increase in the area invaded (Fig. 3c).

Comparison of the rate of invasion among the three scales by inclusion curves (Table 2) indicates that the invasion was slowest at the continental scale (62 years, CI = 53–70) and did not differ significantly between the two smaller, regional (16 years, CI 10–20) and local (22 years, CI 19–24) scale.

DISCUSSION

Invasion potential of *Heracleum mantegazzianum*

Heracleum mantegazzianum is a species with enormous invasion potential, which has many characteristics traditionally attributed to a successful invader (Pyšek & Richardson, 2007), such as very high production of readily germinating seeds some of which persist for several years in a short-term persistent seed bank (Moravcová *et al.*, 2005, 2006). It has been estimated that a single population covering about 99,000 m^2 in the Slavkovský les region produces 1.4 billion seed annually. Furthermore, effective self-pollination resulting in good quality seed and seedlings (Perglová *et al.*, 2006, 2007), and dispersal by human activities, water, and wind (Moravcová *et al.*, 2007) contribute to the invasion potential of *H. mantegazzianum*. In this species, it seems to be a combination of several superior traits that makes it such a good invader, for which the term 'master of all traits strategy' has been suggested (Pyšek *et al.*, 2007b). These traits also enable the species to escape from cultivation soon after introduction into an area. The two regions for which data are available, UK and Czech Republic, are markedly similar in the time period between introduction into cultivation and first report of an escape, 11 and 15 years, respectively.

The data summarized in the review of Pyšek & Hulme (2005) allow for a rough comparison of the rates of spread of *H. mantegazzianum* with other species. At the regional scale of the Czech Republic, the value obtained for this species was about average in the data set of 31 naturalized neophytes (Williamson *et al.*, 2005). However, if the actual invaded area at a local scale is used as a measure for comparison, the invasion of study region of Slavkovský les by *H. mantegazzianum* proceeded at a similar rate to that of the most aggressive invasive species elsewhere (Pyšek *et al.*, 2007c), such as *Tamarix* species in the south-western USA (Robinson, 1965; Zavaleta, 2000). Previous studies at the local (Pyšek & Pyšek, 1995; Müllerová *et al.*, 2005) and regional (Pyšek & Prach, 1993; Pyšek, 1994) scales indicate that *H. mantegazzianum* is only limited to a very limited degree by the character of the invaded vegetation or specific site conditions; once there are suitable habitats in the landscape, it spreads at a constant and rather high rate (Pyšek *et al.*, 2007c).

Rate of invasion at different scales

This study extends previous work on the invasion dynamics of *H. mantegazzianum* (Pyšek, 1991; Pyšek & Prach, 1993; Müllerová *et al.*, 2005; Pyšek *et al.*, 2007c) to the scale of Europe and is based on the fact that for all three scales – local, regional and continental – there is an information on (i) the beginning of the invasion in the study area, and (ii) the point of introduction. The rate of invasion of *H. mantegazzianum*, as recorded at the three scales, increases from the continental to regional and local. However, it needs to be borne in mind that the local scale reflects invasion dynamics in terms of population size and the two larger scales relate to geographical distribution. Moreover, for local (Fig. 3c) and regional (Fig. 3b) scales the units of area are uniform (hectares and numbers of grid cells with equal areas, respectively) and therefore comparable in relative terms, while for the continental scale (Fig. 3a) the country areas are of unequal sizes. The question thus arises, to what extent can the data at three scales be compared? Despite these constraints, we believe that the conclusion about the slowest rate of spread at the continental scale is robust. For scales ranging from hectares to millions of square kilometres (Table 1), different measures need to be used and comparison is only possible if based on statistically standardized (relative) measures of spread. Moreover, this result is conservative; distribution data based on invaded countries, as used at the largest scale in our study, yield a higher estimate of the rate of spread than would be the case if precise data on actual invaded area were available for the whole continent, similar to that available for the finest, local scale. Yet the invasion of Europe by *H. mantegazzianum* was the slowest of the three scales.

Data that allow the rate of spread of the same invasive species to be compared at several scales are extremely rare (Pyšek & Hulme, 2005; Mack *et al.*, 2007). A case study of *Mimosa pigra* in Australia indicated faster invasion at the finer of two scales (Lonsdale, 1993). On the local scale, measured by invaded area, the doubling time over the 6-year period of study averaged out at 1.2 years. Across the study region as a whole, the doubling time for numbers of infestations was much slower, 6.7 years, probably because of the separation of plant major habitats by eucalypt savannas that *M. pigra* colonizes less readily (Lonsdale, 1993).

The explanation of Lonsdale (1993) for the faster rate of invasion of *M. pigra* at the smaller scale depends on the invasibility of habitats that form the landscape matrix relevant to each scale. Particular habitats differ strongly in their invasiveness (e.g. Chytrý *et al.*, 2005; Stohlgren *et al.*, 2006; Sádlo *et al.*, 2007) and at the continental scale, there are large areas that are unsuitable, such as forests, mountain ranges, or large rivers (Richardson *et al.*, 2000), which act as barriers to LDD. At the local scale, in our study system, the proportion of invasible land is high (Müllerová *et al.*, 2005) and barriers to dispersal are less effective, since compact areas of, for example, forest can be bypassed by the spreading of fruits along roads and water courses more effectively than at the national scale. The same is true for the intensively managed landscape of the Czech Republic at the regional scale. It can be therefore assumed that the proportion of invasible area decreases with increase in scale from local/regional to continental, which may be one reason for a decrease in the relative rate of invasion. That in our study *H. mantegazzianum* spread at the regional scale at the same rate as locally in the region of its introduction to the country indicates that the constraints imposed to its spread by landscape features and availability of suitable habitats were similar at both scales (Pyšek *et al.*, 2007c).

The role of humans in the invasion by *Heracleum mantegazzianum*

It is suggested that LDD events are largely driven by extrinsic factors (Higgins *et al.*, 2003). The invasion of Europe by *H. mantegazzianum* was closely associated with its human-mediated dispersal as a garden ornamental. Not only was the species introduced to the continent via this pathway, but it soon became popular among gardeners, and seeds were exchanged and planted in botanic gardens and in the grounds of important estates (Jahodová *et al.*, 2007). This mechanism operated at both the continental scale of Europe (Tiley *et al.*, 1996; Jahodová *et al.*, 2007) and regional scale of the Czech Republic (Pyšek, 1991; Pyšek *et al.*, 2007b), but not at the local scale, where the invasion also resulted from an initial planting in the region, which, however, had no effect on the subsequent spread of the species (Müllerová *et al.*, 2005).

Collingham *et al.* (2000) found no evidence of significant spatial autocorrelation using distribution data for the UK and suggested that the pattern they observed reflects the importance of long-distance anthropogenic dispersal in the initial phase of the invasion. In the UK, as in the Czech Republic, *H. mantegazzianum* was spread over long distances as a garden ornamental in the early stages of the invasion. This resulted in the establishment of new sites, which subsequently acted as foci for further spread (Pyšek, 1991; Pyšek *et al.*, 2007c). Moreover, the pattern and dynamics of invasion in different countries seems to be very

Table 3 Parameters of the long-distance dispersal of *Heracleum mantegazzianum* at the local scale in the Slavkovský les region, Czech Republic. Numbers of the localities correspond to those used in previous papers (Müllerová *et al.*, 2005; Pyšek *et al.*, 2007c). For each 750 × 800 m plot, beginning of invasion; years between the first two sampling dates; the distance between the margin of *H. mantegazzianum* population at the first sampling time and the most distant plant at the second sampling date (LDD); maximum potential dispersal distance defined as the distance between the point of introduction and most distant point of the study plot (Potential LDD); and proportion of the potential LDD realized by the first dispersal event (Relative LDD) are shown.

Locality	Beginning of invasion	Years	LDD (m)	Potential LDD (m)	Relative LDD (%)
2	1973	14	204	497	41.0
3	1957	5	475	533	89.2
6	1987	4	531	779	68.1
8	1962	11	260	474	55.0
9	1973	14	583	761	76.6
11	1973	14	476	574	82.9
13	1973	14	165	654	25.2
15	1987	4	97	514	18.9
16	1962	11	52	393	13.3
Mean			315.9		52.2

similar, as indicated by almost the same rate of spread calculated for the Czech Republic and UK, although based on different methods, i.e. reconstruction using floristic records and repeated mapping, respectively (Pyšek *et al.*, 2007c).

The role of long-distance dispersal

To address properly the issue of LDD and its effect at different scales, we need to think of LDD in relative terms. At the local scale of the 750 × 800 m plots monitored in our study, with an average annual spread of 10.8 m year^{-1} (Müllerová *et al.*, 2005), a seed that is dispersed 500 m from the parent plant is a dispersal event of similar magnitude, in terms of invasion dynamics, to the one over several hundred of kilometres at the regional scale of the Czech Republic. The measures of relative LDD can be inferred, with reasonable precision, only for the local scale. At this scale, our data are reliable for capturing the beginning of the invasion because plots were monitored in detail, and individual plants identified on aerial photographs. The plots were located in sections of landscape more or less isolated by forest and scrub, which minimizes the probability of this species invading the monitored plots from elsewhere (Müllerová *et al.*, 2005). At this scale, the dispersal events at the early stage of invasion accounted on average for 52.2% of the potential dispersal distance (see Table 3 for definition) and this spread was realized in 4–14 years. The potential for LDD is illustrated by two plots with a short interval between the first two sampling dates, where the species spread across 89.2% and 68.1% of the potential distance in 5 and 4 years, respectively (Table 3). The detailed monitoring available for the local scale indicates that such relatively 'long-distance' dispersal events are common and the available space is rapidly filled.

Unfortunately, at larger scales dispersal events cannot be inferred from the observed pattern of spread. Dispersal is only one of the events that must happen for spread to occur and spread is the result of realized dispersal observed over time. The floristic data recorded over time at larger scale do not provide appropriate metrics of LDD. Year-to-year data are mostly not available and the distance between two subsequent records (e.g. 1900–07 in Fig. 1) might have resulted from a single dispersal event but also from several unrecorded events. Even if such data were available, the direction of the invasion would be uncertain, i.e. what is the source population for the one recorded next year and in which direction it is located.

At larger scales, invasive species can spread over large distance by a single or a few LDD events (Batianoff & Franks, 1997; Foxcroft *et al.*, 2004), but we can only hypothesize about the difference between regional and local scales in this respect. The invasion of Europe by *H. mantegazzianum* was slower and appears to have the character of an invading front (Fig. 1), which points to less efficient LDD than in the case of the regional scale of the Czech Republic (Pyšek & Hulme, 2005). It is probable that in the past, communication between garden centres in Europe was more intensive between neighbouring countries, because gardeners in the 19th and the beginning of the 20th century were less likely to exchange plant material with very distant regions. However, this was not the case at the smaller, regional scale as documented by the origin of the earliest records of *H. mantegazzianum* in the Czech Republic (Pyšek, 1991). Most of these early records can be traced to garden centres and there is an additional evidence that garden centres have played an important role in the invasion of this country by other alien species (Mandák *et al.*, 2004).

Differences in the pattern of invasion at different scales

It has been proposed that spread involving LDD can be described by power law dispersal distributions (Shaw, 1995; Kot *et al.*, 1996; Cannas *et al.*, 2006). This leads to some concrete predictions that can be compared with the field data. For instance, it implies an exponential increase in the invaded area with time (Kot *et al.*, 1996). This is the case at the regional scale of the Czech Republic

(Fig. 3b), but the increase in the number of invaded European countries does not follow an exponential curve (Fig. 3a). The pattern of invaded grid cells at regional scale resembles those obtained from numerical simulations using a power law dispersal function and those displayed by invader species whose seeds are wind dispersed (Shaw, 1995; Cannas *et al.*, 2006). That the local scale (Fig. 3c) is not consistent with exponential behaviour can be explained by the fact that species started to spread in the region after it has gone through a lag phase (Pyšek, 1991, 1994) and the invasion was realized in a landscape matrix composed of habitats majority of which was suitable for invasion (Pyšek *et al.*, 2007c). The differences in the invasion curves depicted in Fig. 3 are indicative that different mechanisms of spread dominate the process at different spatial scales.

This suggests that there are probably two different mechanisms of spread acting in this system, namely human influences and natural spread, and the relative influence of these mechanisms appears to change in an inverse proportion from the largest to the smallest scale. With increasing scale the size of the study area (hence, the space available for invasion) increases over several orders of magnitude but the capacity of the plant to spread over a given distance, determined by natural factors (namely spread by water courses and plant traits), is the same at all scales. At the local scale, the process is driven by species' biological traits related to dispersal (Moravcová *et al.*, 2006, 2007). At the continental and regional scales, human-mediated dispersal seems to be the major driver of spread, especially in the initial phase of invasion, when it was responsible for creating isolated foci (Pyšek, 1991; Collingham *et al.*, 2000). Traits relating to dispersal are important for local spread and affect the colonization of new sites. The rejection of the null hypothesis on the same rate of invasion at the two larger scales, had the local processes resulting from natural factors been all that were operating, therefore points to a different role of human-mediated LDD. Nevertheless, it must be noted that the crucial role of dispersal by humans at the regional and continental scale probably decreased with time as the invasion proceeded. Theoretically, as population size increases within areas, propagule pressure increases, automatically increasing the probability of LDD events, not only via human-mediated means, but simply because there are more seeds available for LDD (Rouget & Richardson, 2003). Unfortunately, with current data and for the two large scales addressed here, the effect of propagule pressure as a regional driver of invasions (Rouget & Richardson, 2003; Wilson *et al.*, 2007) cannot be factored out.

This study is based on a thoroughly researched invasive species for which historical information on invasion dynamics is available; we are not aware of any other plant species for which such detailed distribution data are available at scales ranging from local to continental (see Mack *et al.*, 2007). Even for this species, our study has shown that even better data are needed to fully understand the mechanisms operating in the course of invasion at different scales. The significance of long- as opposed to short-distance dispersal is insufficiently recognized also in the conservation context, and taking LDD into consideration can improve conservation management decisions (Trakhtenbrot *et al.*, 2005). The scarcity of LDD and its inherent uncertainty render it difficult to define, observe, and quantify, but there are promising tools based on proxies (Nathan *et al.*, 2003; Trakhtenbrot *et al.*, 2005). Collating historical data on other invasive plant species besides *H. mantegazzianum* is a challenge for researchers. Comparative analysis of invasion dynamics at a range of spatial scales has much potential to contribute crucial information to invasion ecology.

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