

# On the rates and patterns of spread of alien plants in the Czech Republic, Britain, and Ireland<sup>1</sup>

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**Abstract:** The rates and patterns of spread of 63 species in the Czech Republic and seven in Britain and Ireland were determined from quadrat records, *mapovací pole* (11- × 12-km mapping zones in the Czech Republic), and 10- × 10-km hectads in Britain and Ireland. Species that have straight sections on logarithmic, square root, and arithmetic plots were found; the last group (10 of them) are generally casuals. Straight square root plots (52 found) are expected from Fisher-Skellam reaction diffusion models, with logarithmic equivalents (36 found) where the dispersal kernel has a thicker tail or where spread involves scattered colonies. The greater frequency of the straight square root plots is unexpected. The straightness of so many plots shows that there is no significant variation in recorder bias. About a third of the species showed lags, and many species showed a later slowing of the rate of spread, called here bends. Lags may indicate an initial casual phase as well as slower growth; bends, a lack of further areas to spread to. Typically, with much variation, areas of occupancy double in about 10 y (logarithmic mode) or spread at about 2 km·y<sup>-1</sup> (square root mode). Both speeds indicate that most spread is from human activity. The reasons for the major phenomena—the occurrence of the two types of spread predicted by models, their distinctness, and the distribution in rates—may reflect economic and landscape features as well as biological ones. The straightness, speed, and patterns found are all new results for invasion biology.

**Keywords:** Britain, Czech Republic, data transformations, Ireland, patterns of spread, rates of spread.

**Résumé :** Les taux et patrons de dissémination de 63 espèces de plantes vasculaires de la République tchèque et de sept autres espèces de Grande-Bretagne et d'Irlande ont été déterminés à l'aide de quadrats de 11 × 12 km (République tchèque) et de 10 × 10 km (Grande-Bretagne et Irlande) couvrant les différents pays. Lorsqu'on additionne les quadrats où l'espèce considérée est présente en fonction du temps, la courbe d'accumulation qui en résulte devient droite à une échelle arithmétique, logarithmique, ou lorsqu'on fait la racine carrée du nombre de quadrats. Les espèces pour lesquelles une droite est obtenue à l'échelle arithmétique (10 cas) sont en général des espèces adventices. Les 36 cas où une droite est obtenue par transformation logarithmique des données correspondent en outre à des situations où les espèces se disséminent grâce à des colonies qui sont très éloignées les unes de autres. Les droites obtenues grâce à une transformation des données à l'aide d'une racine carrée (52 cas) concordent avec les prédictions des modèles de Fisher-Skellam, mais il est surprenant qu'elles soient aussi abondantes. Le fait que l'on peut tracer des droites chez la plupart des espèces indique qu'il n'y a pas de variation significative quant au biais associé à la récolte des données. On trouve chez environ le tiers des espèces un décalage entre les premières observations et le moment à partir duquel l'espèce agrandit de façon sensible son aire de répartition. Ce décalage peut indiquer la présence d'une phase avec introductions accidentelles et sans conséquence ou d'une phase de croissance lente de la population. On observe aussi chez plusieurs espèces un ralentissement du taux de dissémination après une période de forte croissance. Cela pourrait être associé au fait que ces espèces ont alors beaucoup moins de nouveaux territoires à conquérir. En général, quoique cela varie beaucoup selon les espèces, l'aire occupée par une espèce introduite double à tous les 10 ans (patron logarithmique) ou s'agrandit de 2 km par année (patron avec racine carrée). Il est probable que les activités humaines contribuent fortement à la dissémination de ces espèces. En fait, les patrons de dissémination s'expliqueraient autant par les caractéristiques économiques et paysagères des pays concernés que par les caractéristiques biologiques des espèces.

**Mots-clés :** Grande-Bretagne, Irlande, patrons de dissémination, République tchèque, taux de dissémination, transformation des données.

**Nomenclature:** Stace, 1997; Kubát *et al.*, 2002.



<sup>1</sup>Rec. 2004-09-27; acc. 2005-01-25.

Associate Editor: Claude Lavoie.

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## Introduction

There have been many studies on the rate of spread of one or a few species of alien plant, but rather few (Williamson, Preston & Telfer, 2003) on many species (reviewed in Pyšek & Hulme, 2005). Spread is the stage of invasion that is most easily modelled and most accessible to quantitative analysis (Williamson, 1996). Most of the classical studies of spread were of animals or pathogens (Elton, 1958; Murray, 2001; Okubo & Levin, 2001); there have been comparatively few studies of plants. Yet it is in principle easier to study quantitatively the spread of a set of plants than a set of animals using the voluminous records of naturalists and professionals. We offer here a brief and approximate summary of what is known about mathematical models of spread, considering only analytical models over homogeneous space. The numerous recent simulation and landscape specific models are not considered. For a wider review, see Pyšek and Hulme (2005).

The standard analytical, homogeneous model of spread is the set of reaction-diffusion equations known as the Fisher-Skellam model. These equations predict that, from a point of introduction, a species will spread out circularly at a constant speed, with a wave front though not an edge (Williamson, 1996). So the square root of the area of occupancy will increase linearly. That remains true in more elaborate models with age-structure (*i.e.*, with separate dynamics for each age class) (Neubert & Caswell, 2000). The model assumes that the tail of the dispersal distribution is normal (Gaussian). It is now well established that many species have dispersal kernels with fatter, longer tails (Williamson, 2003) that reflect, amongst other things, interesting and important new patterns of long-distance dispersal (Cain, Nathan & Levin, 2003). Kot, Lewis, and van den Driessche (1996) showed that such leptokurtic tails can lead to an accelerating rate of spread, with functional forms varying from steeper than exponential to less steep. Shigesada and Kawasaki (1997) reviewed various other models, involving in particular scattered colonies, that also lead to an accelerating rate that, in their models, is always of exponential form. Such accelerating models can be reasonably linear on a logarithmic scale depending on how close they are to an exponential rate of spread, though none of those authors show log-linear plots of their results. Biologists have frequently plotted the logarithm of the area of spread against time and sometimes found that to be linear (Pyšek, 1991; Pyšek & Prach, 1995; Pyšek & Hulme, 2005). It should be noted that in none of the published models of spread will the simple, untransformed plot of area against time be linear. In the reaction-diffusion case, the square root of area against time will be linear. In the fat-tailed and scattered colony models, the logarithm of area against time may be linear.

There are some important complications in practice that, to our knowledge, have not yet been modelled analytically. Perhaps the two most important are multiple origins and the effect of boundaries. By multiple origins we mean that the spread may start from several places, not just one. Preston (1988), for instance, showed a minimum of four points of introduction, possibly seven, of *Epilobium*

*ciliatum* in England before 1929. The extra three could conceivably have spread from his fourth point. If so, his map for 1949 showed that subsequent spread was from points three and four only. The first two introductions did not spread, though the first, at least, was persistent. It seems likely that if the points of introduction are sufficiently separated in space or time, the pattern of spread, *i.e.*, the shape of the curve of area against time, will be much the same as for a single introduction, but this needs further study.

Areas such as the Czech Republic and the islands of Britain and Ireland are finite, with clear land and sea boundaries, respectively. Invasions in practice take place predominantly within such boundaries because of the pattern of human activities that affect them. It is obvious that the observed pattern of spread, the pattern within the boundaries, will change once a species reaches one of these boundaries. However, unlike, say, density-dependent population growth, there need be no effect on the pattern of spread until the boundary is reached. In practice, it is reasonable to expect that the pattern of rate of increase of area will be constant until a boundary is reached and will then slow down. Again, this needs further study, but as the relation of the point of introduction to the boundary has many possibilities, a simple analytical solution seems unlikely.

Here we consider the rate and pattern of spread over many years, up to centuries, of a fairly large set of aliens in the Czech Republic and a much smaller set in Britain and Ireland. In both cases, we use records by quadrats, of 133 km<sup>2</sup> and 100 km<sup>2</sup>, respectively, rather than using range maps. Such quadrats give a much better measure of the “area of occupancy” than maps that indicate only the outer edge of the “extent of occurrence” (Gaston, 2003); quadrats also avoid the uncertainties of area and overlap associated with using “locality” records. Using quadrats to study the spread of alien species is not new (Usher, 1986; Perrins, Fitter & Williamson, 1993; Williamson, Preston & Telfer, 2003) but has not been used to study sets of species over many years. This approach allows the comparison not only of the rate of spread over many species but also of the type of spread and the contrast between that and what is predicted by models.

## Methods

### THE CZECH DATA SET

Data on the distribution of 63 alien species (Tables I and II) of the Czech flora, over time and by locality, were assembled from major floral works and published floristic papers for the Czech Republic, compendia on the distribution of alien plants (Hejný *et al.*, 1973; Jehlík, 1998), herbarium collections (BRNM, BRNU, CB, COM, HR, Liberec, LIT, MJ, PL, PR, PRC, Příbram, ROZ, Sokolov), and unpublished floristic records. Published records provided 53.4%, herbaria 37.4%, and unpublished records 9.1% of the total data (Pyšek, Prach & Mandák, 1998). Woody plants were deliberately excluded because their dynamics are different from those of herbs, and, more importantly, in floristic records it is usually impossible to distinguish remnants of planting from self-seeding.

TABLE I. Summary of the types and rates of spread found in the Czech Republic for those species straight in part on square root or logarithmic plots. The other species are shown in Table II. Species are listed alphabetically. Invasion status (cas = casual, nat = naturalized, inv = invasive) is based on the definitions of Richardson *et al.* (2000) and Pyšek *et al.* (2004) and was taken from Pyšek, Sádlo, and Mandák (2002). Total number of quadrats from which the species was reported up to 1995 is given (maximum possible: 679). Spread type: 'sqrt/log' indicates that both square root and log plots are straight in overlapping parts of the plots of transformed cumulative number of quadrats over time; 'log→sqrt' indicates straight on log early on but straight on sqrt later. The presence of a lag phase is indicated; '?' indicates that it was not possible to assess the presence of a lag phase unequivocally. For each type of transformation, the start and end year of the straight section of the plot and  $r^2$  are shown. Rate of spread is expressed as doubling time (years for the cumulative number of occupied squares to double) for log-transformed data and in  $\text{km} \cdot \text{y}^{-1}$  for square-root transformed data (see text for details of the calculations).

Species	Status	Number of quadrats	Spread type	Lag phase	1 <sup>st</sup> record	Logarithmic					Square root				
						Start	End	$r^2$	Slope	Doubling time (y)	Start	End	$r^2$	Slope	Spread rate ( $\text{km} \cdot \text{y}^{-1}$ )
<i>Abutilon theophrasti</i>	cas	48	log		1894	1895	1984	96.7	0.0174	17.28					
<i>Acorus calamus</i>	nat	330	log→sqrt	?	1791	1825	1887	98.2	0.0227	13.27	1887	1895	99.5	0.0915	1.27
<i>Amaranthus blitoides</i>	nat	64	log		1932	1932	1975	96.1	0.0369	8.17					
<i>Amaranthus powellii</i>	inv	129	sqrt	yes	1855						1930	1995	99.2	0.1490	2.07
<i>Amaranthus retroflexus</i>	inv	312	sqrt	yes	1788						1816	1995	99.7	0.0919	1.28
<i>Artemisia annua</i>	nat	46	sqrt		1891						1891	1913	96.2	0.0955	1.33
<i>Artemisia verlotiorum</i>	nat	8	log		1895	1947	1995	90.7	0.012	25.04					
<i>Bidens frondosa</i>	inv	226	log→sqrt	yes	1900	1924	1935	89.9	0.0571	5.27	1946	1978	98.9	0.2819	3.92
<i>Bunias orientalis</i>	inv	178	sqrt	yes	1856						1895	1995	99.6	0.1114	1.55
<i>Cannabis ruderalis</i>	inv	15	log		1868	1868	1995	97.4	0.0104	28.96					
<i>Consolida orientalis</i>	nat	57	sqrt	yes	1897						1951	1986	99.3	0.1239	1.72
<i>Conyza canadensis</i>	inv	354	sqrt	yes	1789						1844	1995	99.0	0.1206	1.67
<i>Chenopodium botrys</i>	nat	55	sqrt		1804						1804	1975	98.9	0.0378	0.53
<i>Chenopodium pumilio</i>	nat	38	sqrt	?	1894						1896	1995	98.8	0.0417	0.58
<i>Corydalis lutea</i>	nat	73	sqrt	yes	1886						1933	1995	99.3	0.0722	1.00
<i>Cuscuta campestris</i>	inv	50	sqrt/log	?	1883	1924	1954	95.6	0.0256	11.77	1924	1985	98.8	0.0883	1.23
<i>Digitalis purpurea</i>	inv	170	log		1853	1853	1900	95	0.0251	12.00					
<i>Echinocystis lobata</i>	inv	51	log		1911	1928	1950	95.1	0.0356	8.45					
<i>Elodea canadensis</i>	inv	271	sqrt	?	1878						1885	1995	99.4	0.1178	1.64
<i>Epilobium ciliatum</i>	inv	311	log		1960	1960	1973	99.5	0.1337	2.25					
<i>Galinsoga ciliata</i>	inv	272	sqrt/log	yes	1901	1926	1944	98	0.0495	6.08					
<i>Galinsoga parviflora</i>	inv	337	sqrt		1867						1880	1985	99.7	0.1436	1.99
<i>Geranium pyrenaicum</i>	inv	250	sqrt		1810						1823	1952	99.6	0.0935	1.30
<i>Heracleum mantegazzianum</i>	inv	232	log	yes	1877	1936	1989	98.9	0.0327	9.21					
<i>Hordeum jubatum</i>	nat	45	sqrt/log	yes	1880	1971	1995	94.9	0.0278	10.83	1971	1995	93.2	0.1518	2.11
<i>Impatiens glandulifera</i>	inv	324	sqrt/log	yes	1896	1934	1940	96	0.0658	4.58	1934	1995	98.5	0.2633	3.66
<i>Impatiens parviflora</i>	inv	342	sqrt/log	yes	1816	1870	1886	96.6	0.071	4.24	1870	1995	97.2	0.1305	1.81
<i>Iva xanthiifolia</i>	nat	34	sqrt		1947						1947	1987	97.0	0.1202	1.67
<i>Juncus tenuis</i>	inv	359	sqrt	yes	1851						1925	1941	99.3	0.2841	3.95
<i>Kochia scoparia</i>	inv	43	log		1901	1930	1984	96.8	0.0229	13.15					
<i>Lupinus polyphyllus</i>	inv	273	sqrt/log		1895	1895	1918	97.9	0.0656	4.59	1895	1943	99.2	0.1973	2.74
<i>Matricaria discoidea</i>	inv	372	log→sqrt	yes	1851	1874	1898	97.6	0.0479	6.28	1898	1995	98.3	0.1207	1.68
<i>Mimulus guttatus</i>	inv	97	sqrt		1853						1877	1956	97.6	0.0728	1.01
<i>Oenothera biennis</i>	inv	347	log→sqrt	yes	1738	1848	1892	95.8	0.0233	12.94	1892	1973	98.8	0.0904	1.26
<i>Oxybaphus nyctagineus</i>	nat	10	sqrt/log	yes	1843	1930	1995	92.2	0.0077	39.02	1930	1995	90.8	0.0224	0.31
<i>Panicum capillare</i> s.l.	nat	31	sqrt	yes	1940						1967	1989	98.0	0.1461	2.03
<i>Reynoutria japonica</i>	inv	298	sqrt/log		1892	1892	1911	91.6	0.0689	4.37	1892	1995	98.8	0.1492	2.07
<i>Reynoutria sachalinensis</i>	inv	136	sqrt		1869						1951	1995	98.9	0.1632	2.27
<i>Rudbeckia laciniata</i>	inv	150	sqrt/log		1859	1859	1892	95.2	0.0396	7.59	1859	1911	97.7	0.1135	1.58
<i>Rumex triangulivalvis</i>	nat	22	sqrt		1943						1943	1973	92.7	0.0859	1.19
<i>Setaria faberi</i>	nat	39	log		1961	1961	1973	97.3	0.0935	3.22					
<i>Sisymbrium volgense</i>	nat	53	sqrt/log		1960	1960	1969	97.8	0.1477	2.04	1960	1977	98.4	0.3161	4.39
<i>Sisyrinchium angustifolium</i>	nat	32	sqrt/log		1863	1863	1910	87.3	0.0197	15.27	1863	1957	95.9	0.0445	0.62
<i>Solidago canadensis</i>	inv	226	log		1838	1838	1892	86.2	0.0221	13.65					
<i>Solidago gigantea</i>	inv	231	log→sqrt		1851	1851	1893	88.6	0.0248	12.40	1893	1995	97.3	0.1018	1.41
<i>Teledkia speciosa</i>	inv	82	sqrt	yes	1834						1951	1995	98.1	0.1034	1.44
<i>Trifolium hybridum</i>	nat	409	log→sqrt		1809	1809	1854	92.6	0.0239	12.60	1885	1995	99.6	0.1217	1.69
<i>Veronica filiformis</i>	inv	87	sqrt		1938						1938	1979	99.9	0.1777	2.47
<i>Veronica persica</i>	inv	368	log		1810	1810	1861	93.3	0.0204	14.70					
<i>Xanthium spinosum</i>	nat	83	sqrt/log		1840	1840	1854	94.2	0.0741	4.02	1840	1854	90.5	0.1471	2.04

Only spontaneous occurrence in the wild was considered. In total, 26,462 localities were collated. The definition of locality is that in the original records; almost all records are at least 500 m apart. For each locality, information on the year of observation was taken from the

original source. If the year of observation was not provided by the original author, the year of publication was used. As shown in previous papers on *Heracleum mantegazzianum* (Pyšek, 1991; Pyšek & Prach, 1993), the year of publication corresponds closely to the year of



TABLE II. Summary of the types and rates of spread found in the Czech Republic for those species not shown in Table I, *i.e.*, those species that were either straight on arithmetic plots or on none of the three types of plot (arithmetic, square root, logarithmic). See the caption of Table I for further details.

Species	Status	Spread type	Number of quadrats	1 <sup>st</sup> record
<i>Amaranthus albus</i>	nat	arith	123	1893
<i>Amaranthus viridis</i>	cas	arith	13	1964
<i>Ambrosia artemisiifolia</i>	inv	none	37	1834
<i>Ambrosia trifida</i>	cas	arith	12	1963
<i>Chenopodium foliosum</i>	cas	arith	20	1837
<i>Commelina communis</i>	cas	arith	43	1940
<i>Helianthus annuus</i>	cas	arith	9	1968
<i>Hirschfeldia incana</i>	cas	arith	20	1956
<i>Lactuca tatarica</i>	cas	arith	15	1957
<i>Panicum dichotomiflorum</i>	cas	arith	10	1970
<i>Panicum miliaceum</i>	nat	arith	17	1975
<i>Rumex patientia</i>	nat	none	23	1861
<i>Sorghum halepense</i>	cas	none	40	1927

observation since 81% of records are published within five years of the observation. The proportion of localities published significantly decreased with the observation/publication interval ( $Y = 1.22X^{-0.072}$ ,  $r^2 = 0.81$ ,  $P < 0.0001$ ).

For each locality, latitude and longitude were found on a map, and the locality assigned to a quadrat, *mapovací pole* in Czech, which means mapping zone, in a system widely used in Central European phytogeography (Schönfelder, 1999). This system uses a grid of 10' (longitude)  $\times$  6' (latitude), which at 50° N is 12.0  $\times$  11.1 km or 133.2 km<sup>2</sup>. The total number of such quadrats in the Czech Republic is 679 (Slavík, 1998).

Previous work (Pyšek, 1991; Pyšek & Prach, 1995; Pyšek *et al.*, 1998) showed how floristic data, systematically gathered over an area for a long time, may be used to reconstruct the pattern of a species invasion on a regional geographical scale. There are, however, some limitations to floristic data that should be emphasized. Delisle *et al.* (2003) have discussed these limitations too. The prime requirement for a successful retrospective analysis of species spread is a sufficient intensity of floristic research. This is met here by the strong, long-term, floristic tradition in the Czech Republic (Pyšek, Sádlo & Mandák, 2002; Pyšek & Prach, 2003). If systematic recording of the flora is carried out, and the same data sources are used for the whole species set analyzed, it can be assumed that the more common a species is, the more often it is recorded (Pyšek & Prach, 1993). Quadrat records can be expected, in such circumstances, usually to give a good measure of the spread of each species.

The data are cumulative quadrat records for each species, so the data sets can never decrease. Some records are available every year from early in the 19<sup>th</sup> century, so the database is a matrix of the number of quadrats by species and year. The last record year is 1995. In addition, we had information on taxonomy, life form (annual, etc.), clonality, whether sexual, propagule size, first month of flowering, habitats (natural or affected by humans), deliberate or accidental introduction, and Grime strategies (Grime, Hodgson & Hunt, 1988). Except for the dates, habitat type, and the mode of intro-

duction, all these data are biological, which is an important point when the results are interpreted. We have no economic data for the individual species.

#### THE BRITISH DATA SET

The distribution of both native and alien plants in the islands of Britain and Ireland has been surveyed by a mass effort on three occasions, producing what are now called the old atlas (Perring & Walters, 1962), the sample survey (Palmer & Bratton, 1995), and the new atlas (Preston, Pearman & Dines, 2002). All recorded the presence of species in hectads, the 10-  $\times$  10-km quadrats of the British and Irish transverse Mercator grids. The old and new atlases surveyed every hectad, but the sample survey covered only a systematic set of one in every nine, producing sampling areas of 30  $\times$  30 km. Consequently, counts from the sample survey have been multiplied by nine. The old atlas has been taken as 1958, the sample survey as 1988 (Williamson, 2002), and the new atlas as 1999. Channel Islands data have been ignored.

Both the sample survey and the new atlas note hectads where a species has not been recorded recently. For the sample survey, hectads are coded as old atlas only, sample survey only, or both. For the new atlas, records pre-1970 but not since and 1970-1986 inclusive but not since are distinguished from the current records, 1987-1999. A measure of turnover has been calculated from the new atlas data as the percentage of pre-1987 records of all records. For the calculations of rate of spread all records have been used, since that is comparable to the Czech data.

In addition to the three time points given by the three atlases, the new atlas gives for neophytes the date of the first record in the wild. The old atlas gives the known distribution for five species at a stated time between the first record and 1930. So for those species there are five time points in Britain. For three species, one of them among the five just mentioned, old records from the literature, herbaria, and in the databases of the Biological Records Centre have been collated, making it possible to give hectad counts in various other years (Bangerter & Kent, 1957; 1962; Scurfield, 1962; Bangerter & Kent, 1965; Preston, 1988). Altogether that makes seven species (see Table III) whose spread can be analyzed, a set one ninth the size of the Czech set. All occur in Britain and in Ireland and, in all cases, the Irish population derives from the British one. That allows separate analyses, when the Irish data justify them, of the British data, the Irish data, and the combined data. In three cases the Irish populations are so new as not to justify analysis.

#### STATISTICAL METHODS

For each species in each country three graphs were plotted, the number of records against time (the arithmetic plot), the square root of the number of records against time (the square root plot), and the logarithm (base 10) of the number of records against time (the logarithm plot). This is a simple and quick way to see which transformation best linearizes the data. Williamson and Brown (1986) and Williamson (1996) showed this for data on the muskrat, *Ondatra zibethicus*, in Europe. In some cases

TABLE III. Summary of the types and rates of spread found in Britain and Ireland. See Table I for explanation. The number of hectads is the number recorded up to 1999, from Preston, Pearman, and Dines (2002), the new atlas. The total number of hectads with records in the new atlas is 2,837 for Britain and 1,007 for Ireland, 3,844 for both, excluding the Channel Islands (off the coast of Normandy, France).

Species	Place	Status	Number of hectads	Spread type	Lag phase	1st record	Logarithmic					Square root				
							Start	End	r <sup>2</sup>	Slope	Doubling time (y)	Start	End	r <sup>2</sup>	Slope	Spread rate (km·y <sup>-1</sup> )
<i>Buddleja davidii</i>	Britain	nat	1,434	sqrt	?	1920						1922	1999	99.8	0.5121	6.18
<i>Cardaria draba</i>	Britain	inv	1,160	sqrt	yes	1802						1879	1999	99.6	0.2212	2.67
<i>Cardaria draba</i>	Britain	inv	1,199	sqrt	yes	1802						1879	1999	99.6	0.2248	2.71
	and Ireland															
<i>Cardaria draba</i>	Ireland	inv	39	sqrt		1879						1879	1999	96.3	0.0404	0.49
<i>Epilobium ciliatum</i>	Britain	inv	2,005	log→sqrt	yes	1891	1920	1959	99.2	0.0644	4.67	1959	1999	88.2	0.6163	7.43
<i>Epilobium ciliatum</i>	Britain	inv	2,405	log→sqrt	yes	1891	1920	1959	99.2	0.0644	4.67	1959	1999	88.0	0.7095	8.56
	and Ireland															
<i>Epilobium ciliatum</i>	Ireland	inv	400	log	yes	1958	1969	1999	94.0	0.0896	3.36					
<i>Galinsoga ciliata</i>	Britain	nat	524	sqrt	yes	1909						1939	1999	91.4	0.2873	3.47
<i>Galinsoga parviflora</i>	Britain	nat	429	sqrt	yes	1890						1939	1999	98.1	0.2481	2.99
<i>Senecio squalidus</i>	Britain	nat	1,495	sqrt/log	?	1794	1794	1999	97.9	0.0162	18.57	1899	1999	99.3	0.3326	4.02
<i>Senecio squalidus</i>	Britain	nat	1,570	sqrt/log	?	1794	1794	1999	98.2	0.0163	18.52	1899	1999	99.5	0.3369	4.07
	and Ireland															
<i>Senecio squalidus</i>	Ireland	nat	75	sqrt/log		1899	1899	1999	95.0	0.0168	17.97	1899	1999	84.3	0.0788	0.95
<i>Veronica filiformis</i>	Britain	inv	2,013	sqrt		1927						1927	1988	98.3	0.7171	8.66
<i>Veronica filiformis</i>	Britain	inv	<b>2,401</b>	sqrt		1927						1927	1988	98.4	0.7727	9.32
	and Ireland															
<i>Veronica filiformis</i>	Ireland	inv	397	sqrt		1939						1939	1999	98.7	0.2882	3.48

Or 2,410?

extra plots were made using shorter periods of time. All these hundreds of plots were examined both by looking at them at an acute angle and by using a transparent gridded ruler to determine, admittedly subjectively, which parts of the plots were straight. As will be seen below, lags in the earlier part, and slowing down (bends) in the later part, sometimes going to an asymptote, meant that the straight section was usually, but not invariably, only part of a plot. A regression was then calculated for each straight section, sometimes checked by calculating regressions from other subsets of the data. The same result could have been produced by a computer search, as used for instance by Pyšek and Prach (1993), but this method is flexible and quicker, both important properties, and allows for surprises in the data like the arithmetical straightness discussed below.

For each regression the r<sup>2</sup> value was noted. It is not used in any significance test as the data have strong autocorrelations and have been selected to be the best set. The corrections needed for those are controversial and were avoided. Almost all r<sup>2</sup> values were more than 0.9. Shorter series, or data where there was obvious quantization, i.e., sets that started with many years of one or two records, inevitably tended to have lower r<sup>2</sup>.

For ease of interpretation, the logarithmic slopes are also expressed as doubling times, while the square root slopes are expressed as kilometres per year. The formula for the first is log<sub>10</sub>2/slope; for the second it is slope times the average distance to the next quadrat. The average was taken over the eight neighbouring quadrats.

### Results and discussion

The status of the 63 Czech species, using the terminology of Richardson *et al.* (2000) and Pyšek *et al.* (2004), is given in Tables I and II. They are all neophytes

(introduced after the year 1500) and are a highly representative sample of the Czech alien flora, 27.5% of the total naturalized and invasive neophytes (Pyšek, Sádlo & Mandák, 2002). They come from 25 families, with Asteraceae being 27.0%, Poaceae 9.5%, Amaranthaceae 7.9%, and Scrophulariaceae, Polygonaceae, and Chenopodiaceae 6.3% of the species. Fourteen families are represented by a single species. Most of the species are annuals (47.3%) and polycarpic perennials (35.1%), while 43.0% of the species come from the Americas, 31.6% from Asia, 19.0% from Europe, and 5.1% from Africa; one species is Australian.

Of the seven British and Irish neophytes, four, *Epilobium ciliatum*, *Galinsoga ciliata* (now called *quadriradiata* in Britain), *Galinsoga parviflora*, and *Veronica filiformis*, are in the Czech set used here and their status is given in Tables I and III. *Buddleja davidii* is a casual in the Czech Republic but naturalized in Britain, while *Cardaria draba* (*Lepidium draba* in Britain) is invasive in both (Preston, Pearman & Dines, 2002; Pyšek, Sádlo & Mandák, 2002). The seventh species, *Senecio squalidus*, apparently arose in the 18<sup>th</sup> century in the Oxford Botanic Garden, originating by selection from a Sicilian hybrid (Williamson, 2002), and so is in our view a neophyte (Pyšek *et al.*, 2004). At present it is a British and Irish endemic neophyte.

The main results of the regression calculations, the invasive status, the first recorded date, and the dates used for the regression modes are, for the Czech data, in Tables I and II and, for the British and Irish, in Table III. There is much variation in the pattern of spread. In the Czech data, 10 species were straight on an arithmetic plot (Figure 1a), 20 only on a square root plot (Figure 1b), 12 straight more or less simultaneously on both square root and logarithmic plots (sqrt/log species), six straight initially on a logarithmic plot and later on a square root one (log → sqrt species), and 12 only on a logarithmic plot (Figure 1c),

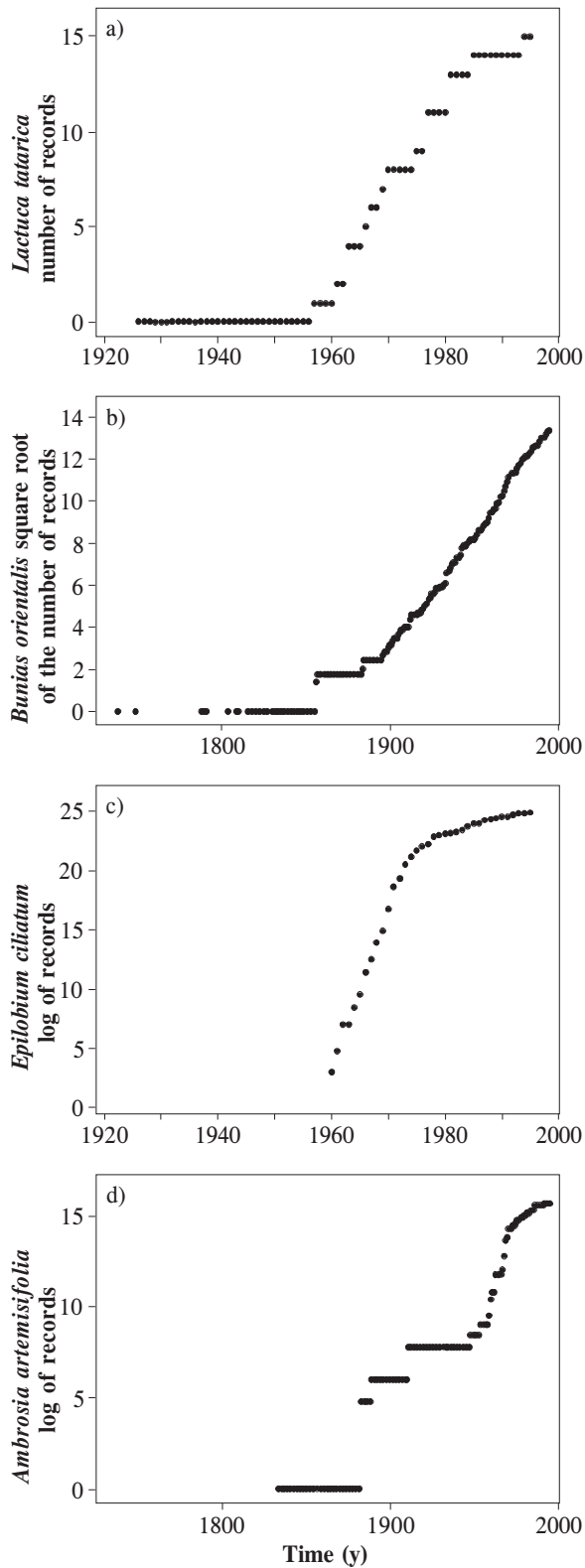


FIGURE 1. Examples of the spread patterns found in the Czech records of *mapovaci pole* (or mapping zones): a) straight arithmetic plot, bending over towards the end, *Lactuca tatarica* (Asteraceae); b) straight square root plot, with lag, *Bunias orientalis* (Brassicaceae); c) straight logarithmic plot, with bend, *Epilobium ciliatum* (Onagraceae); and d) a record not straight on any plot, *Ambrosia artemisiifolia* (Asteraceae), shown here as a logarithmic plot.

leaving just three that were not recognizably straight on any part of any plot (Figure 1d). Of the six log → sqrt species, in four the two phases abutted and in two there was a period of indeterminate type between the phases. For the sqrt/log species, all species but one started the two modes simultaneously. Normally, each species continued much longer in the square root mode. The range of the modes was 6 to 66 y (median 22 y) for the logarithmic but 15 to 126 y (median 57 y) for the square root. Nevertheless, in three species the span of the two modes was identical. It is remarkable that almost all species were straight for part of the time on at least one plot. This is unexpected and important, as it shows two things. First, there is a lack of variable bias such as was found by Delisle *et al.* (2003). Second, species behave in a mathematically fairly simple way despite the vagaries of environmental heterogeneity. The significantly greater frequency of the square root mode than the logarithmic one is also an important finding given the current emphasis on thicker tails, discussed above. It suggests that species more often spread smoothly rather than by jumping about.

In the British data, five species were straight only on the square root plots. *Epilobium ciliatum* is a log → sqrt species. On the data available, *Senecio squalidus* had a straight square root plot with a lag of about a century and a straight logarithmic plot with no lag. However, some unpublished data (S. Harris, Druce Herbarium, Oxford) suggest that *S. squalidus* too is a log → sqrt species and that the apparently straight logarithmic phase in our data is an artefact.

The four species found in **Czech and British** data sets have compatible patterns. *Galinsoga parviflora* and *Veronica filiformis* are square root species in both, *Galinsoga ciliata* is a sqrt/log species in the Czech Republic and a square root one in Britain, and *Epilobium ciliatum* is a logarithmic species in the Czech Republic and a log → sqrt one in Britain.

All that encourages us to think that there is some clear biological explanation for the different modes. However, the only mode for which we have a fairly clear biological explanation is the arithmetic one. None of the models discussed in the introduction lead to such a mode. Of the 10 species showing this mode, eight are casuals, and, conversely, of the 10 listed as casual in Tables I and II, eight are straight on part of their arithmetic plots. A simple model suggests why casual species might be straight, for a while, on an arithmetic plot. Consider a species cultivated widely and escaping rather rarely but with a constant probability. Then, if each escape is to a new quadrat (remember that this is cumulative data), the record will show a constant linear increase that will taper off, bend, once the records have become sufficiently numerous to start overlapping (Figure 1a). On that view, an arithmetic increase is a progressive accumulation of records, not an indication of a mode of spread. With this explanation it should be remembered that the distinction between casual and naturalized is not absolute. Most naturalized species have casual colonies, the proportion varying between species. This produces a continuum that is **measured** crudely by the turnover **measure** we have used with British plants. Consequently, an exact fit between the classification of neophytes and their pattern of spread is not to be expected.

OK?  
Could you rephrase without using the word measure twice?



The square root and logarithmic modes are both expected from models. It is evident that both occur quite frequently, the square root mode being the commoner of the two. In view of the emphasis recently on fat tails and long-distance dispersal (Cain, Nathan & Levin, 2003; Williamson 2003), that is an unexpected and important finding. The transition from logarithmic to square root in  $\log \rightarrow \sqrt{\text{species}}$  is not unexpected. On a scattered colony model the initial spread would be logarithmic. As the quadrat records increase there will be less and less space in a finite bounded area for a new colony: all spread will be from old colonies, and the mode will become a square root one. The surprise is that the transition, in four cases out of six, is sudden. Nevertheless, there is no explanation in the factors studied here as to why some species behave logarithmically and some in the square root mode. All the tests we tried produced no statistically significant result. In the genera *Amaranthus*, *Ambrosia*, and *Veronica* there are species of both types, which suggests there is no major biological difference between the types, nor is there any obvious difference in type of habitat or mode of dispersal.

The sets of slopes for both the logarithmic and square root plots are well behaved statistically, unimodal, and slightly skewed, another indication of a lack of variable bias. As doubling time is related to the inverse of the slope for logarithms, the logarithms of **both those** are linearly related and they are also normally distributed. The square roots of the slopes for the square root plots are also normally distributed (Shapiro-Wilk tests in both cases). Doubling times vary between 2.04 and 39.02 y, with a median of 10.02 y (Figure 2). The rates in kilometres per year vary from 0.31 to 4.39 (median 1.67) in the Czech data but up to 8.66 in the British data (Figure 3). All tests using the variables mentioned above proved negative with three exceptions considered below. We have found no general explanation for the variation in the rates. However, the general size of the rates, particularly obvious in those in kilometres per year, and their continuation linearly over many years, suggest that the spread depends to a great extent on human activities, but we have no good measure of those. Long-distance dispersal by biological methods typically shows rates an order of magnitude less than those found here (Cain, Nathan & Levin, 2003). The character of the landscape, as it interacts with the biology of the species, may well be important, particularly its diversity and dissection. Again, we have no good measures of these features. We have, though, three positive results that may reflect landscape features.

The first positive result on rates is shown in Figure 2. There is a significant negative relationship ( $P < 0.001$ ) between the logarithm of doubling time and the date of introduction for perennial species in the Czech Republic. This, of course, relates only to those species with straight logarithmic plots. The newer introductions are apparently spreading faster. This could be an artefact from increasing recorder activity, but such an explanation fits uneasily with the effects being seen in the 19<sup>th</sup> century as well as the 20<sup>th</sup> century. The simplest non-artefactual explanation, the explanation we prefer, is that the landscape has changed. Increased population density and economic

activity have made the landscape more suitable for this set of alien plants. We have no measure of landscape suitability, so that explanation is, for the moment, just a hypothesis. It does fit with the only positive explanation of spread found by Williamson, Preston, and Telfer (2003), namely that congeneric species with similar landscape requirements had similar rates of spread and, conversely, different congeneric rates of spread went with different landscape requirements.

The second positive result is that the rate in Britain in kilometres per year (for square root species) is inversely related to our measure of turnover (the proportion of hectads with **records** that did not have a **record** during the new atlas survey). The correlation coefficient is  $-0.803$  ( $P = 0.03$ ), a remarkable result with only seven points. In Fisher-Skellam theory, the rate of spread is proportional to the intrinsic rate of increase multiplied by the dispersion coefficient (Williamson, 1996). If a species has a high turnover, that will reduce its rate of increase. So, other things being equal, the relationship we have found would be expected. What would not be expected is that the other things, other factors, across species are not sufficiently variable to hide the relationship.

The third and last positive result is shown in Figure 3 and again relates to spread in species with straight (in part) square root plots. The figure shows (note the position of the medians *versus* the ranges of the variables) that the rate of spread in Britain is faster than that in

of both what?

Could you rephrase without using the word record twice?

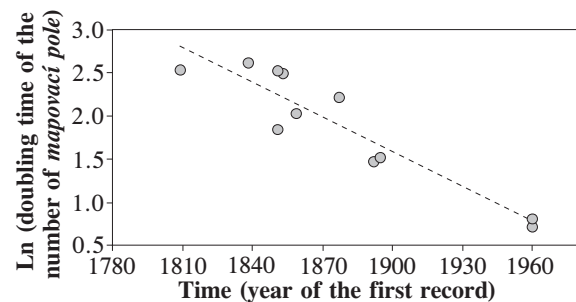


FIGURE 2. The relationship, in the Czech data, between the **ln doubling time** in the number of *mapovaci pole* (or mapping zones) and the first record of an alien perennial plant species. The relationship is statistically significant ( $P < 0.001$ ).

OK?

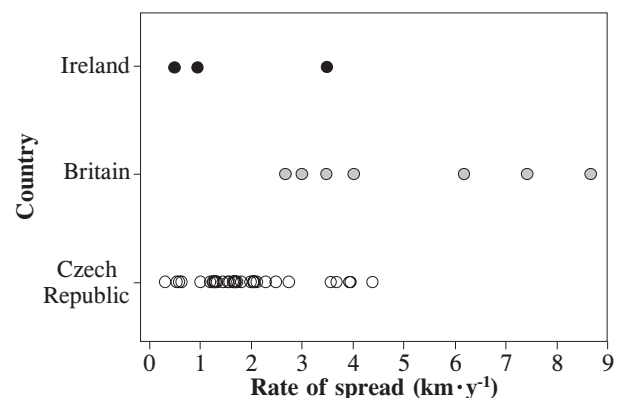


FIGURE 3. Rates of spread of alien plants in the Czech Republic, Britain, and Ireland.

either Ireland or the Czech Republic and that the rates in the latter two are not appreciably different. It is easy to confirm that numerically, *e.g.*, analysis of variance gives  $F_{2, 45} = 19.19$  ( $P < 0.001$ ). Before attempting an explanation, first ask if the pattern is an artefact. While the species in the three sets are not the same, they are overlapping sets. The two species of *Galinsoga*, neither with an appreciable presence in Ireland, have rather similar rates of spread in Britain and the Czech Republic. *Impatiens glandulifera* may also have a similar rate in Britain and the Czech Republic, though the data have been calculated in different ways (Usher, 1986; Perrins, Fitter & Williamson, 1993; Pyšek & Prach, 1995), and there are different rates in Bavaria and Slovakia (Pyšek & Prach, 1995). Only *Veronica filiformis* shows the pattern across the three countries (8.66 in Britain, 3.48 in Ireland, 2.47 in the Czech Republic). On the other hand, none of the 30 species in the Czech Republic have a rate matching *Epilobium ciliatum* or *Buddleja davidii* in Britain, and, further, both *Senecio squalidus* and *Cardaria draba* have spread much more slowly in Ireland than in Britain (0.95 versus 4.02 and 0.49 versus 2.67, respectively). The differences could be an artefact of the activity of botanists. Such an explanation is difficult to reconcile with the differences shown by the species, with the year by year increases in the Czech data (Figure 1) and with much of the British and Irish data coming from coordinated surveys across both islands. The remarkable linearity of the plots also argues against an artefact.

If there really are differences between the three countries, what might be the cause? One possible factor is the area available, which is also in a sense an artefact. As can be seen in Table III, rates for Britain and Ireland combined are, in all four cases, somewhat larger than those for Britain alone. This is because the spread in Ireland is secondary, always starting from Britain, and so added to the spread in Britain. Provided there are several foci, a larger area will in general produce a faster rate when spread is measured as area of occupancy. Britain is about 229,000 km<sup>2</sup>, Ireland about 84,000 km<sup>2</sup>, the Czech Republic 79,000 km<sup>2</sup>. There are also marked differences in population density. In 1991 there were about 235 people·km<sup>-2</sup> in Britain (higher for England where most of the spread has been), 130 people·km<sup>-2</sup> in the Czech Republic, and 60 people·km<sup>-2</sup> in Ireland. All that is consistent with the first positive result above: the rate of spread depends on economic (Perrings, Williamson & Dalmazzone, 2000) and landscape factors as well as on biological ones.

There are two further points to mention. As can be seen in the tables, it is unusual for the straight section of a plot, on whatever transformation, to cover the whole history of an alien's spread. There is often a lag initially, *i.e.*, any period before a plot becomes straight, and there is often a bending over of the plot, a bend, after the straight period. The bends are to be expected as the species come to their geographical limits. Some seem to have come to an asymptote. But, as noted in the introduction, there are no models predicting particular shapes for the bends, so we have not tried to fit curves to the bends. The species with bends have no characters that we have

found to distinguish them from those without, as would be expected.

The lag phase is more interesting. An important point is that it is usually hard to identify correctly on arithmetic plots. On these plots, all these species straight on logarithmic or square root plots will be concave upwards, appearing misleadingly to have a lag. To be sure that there is a lag, all three plots, or their computational equivalents, need to be examined. Lags may come in many forms but often indicate a casual phase before the species starts spreading spontaneously. In the cumulative records we are dealing with, there can be casual records of individuals that die out, but the record continues. These are indistinguishable in such records from casual records of species that persist at a place without reproducing or spreading. If there are a number of casual occurrences, then from the analysis above it would be expected that the lag phase would be straight on an arithmetic plot, and that seems to be so for some species. In other cases, the rate of increase in the lag phase is not linear on any plot. A species may fail to spread initially for many reasons, such as wrong habitat, accidents, wrong genotype. Again, we have no way of distinguishing those in our records. Consequently, in Table I, we have just marked those 19 species that we are fairly confident have a lag and a further four that may have. That suggests that about one species in three shows a lag. There is some indication that species showing a lag started to spread earlier, by about 25 y, than those without a lag. This effect is not quite significant ( $P = 0.072$ , *t*-test) but, if it exists, applies throughout the 19<sup>th</sup> and 20<sup>th</sup> centuries.

## Conclusion

This study shows the benefits, frustrations, and surprises that come from studying many species simultaneously and from studying more than one country. From our discussion of models, it might have been expected that several species would show a mixture of square-root and logarithmic types of spread, and so would be straight on neither plot. This seems to be rare: 60 of the 63 Czech species had plots that were straight on one transformation or another. It is quite surprising and important that so many produced plots straight in part. The straightness argues against any explanation based on the activity of botanists.

Our analyses produced rather few clear explanations. It would seem that casual species are straight on arithmetic plots and that straight parts of arithmetic plots indicate casualness. The degree of casualness as measured by turnover seems to influence the rate of spread. Despite the clear difference in the models, we are unable to explain why many species have straight square root plots and slightly fewer but still many have straight logarithmic plots, but the models do indicate why we have found some species first straight on the logarithmic plot and later straight on the square root one but none *vice versa*. Our results suggest that economic and landscape factors are important in determining the rate of spread. Conceivably, they are also behind the different types of spread. Appropriate measures of economic, social, geographic, and other non-biological factors are needed.



The three major positive findings are surprising and important for the study of biological invasions. They are: 1) almost all species have plots that are straight in part on some transformation, 2) the rate of spread is almost always fast and probably a result of human activity rather than simple biology, and 3) straight square root plots are commoner than straight logarithmic ones, implying that steady, if fast, spread is more common than jumps, though both are important.

### Acknowledgements

We thank I. Ostrý and J. Wild for technical support. This study was supported by the European Union within the FP 6 Integrated Project ALARM (GOCE-CT-2003-506675) and by grant no. 0021620828 from MŠMT Cr from the Ministry of Education of the Czech Republic. P. Pyšek was supported by grant no. 206/03/1216 from the Grant Agency of the Czech Republic and by institutional long-term research plan no. AV0Z6005908 and project no. KSK6005114, both funded by the Academy of Sciences of the Czech Republic. V. Jarošík was supported by grant MSM 113100004 from the Ministry of Education of the Czech Republic. We also thank S. Harris for allowing us access to his *Senecio squalidus* data and J. Pitchford for comments especially on mathematical points.

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