BIODIVERSITY RESEARCH

The distribution of range sizes of native and alien plants in four European countries and the effects of residence time

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ABSTRACT

Aim Do the statistical distributions of range sizes of native and alien species differ? If so, is this because of residence time effects? And can such effects indicate an average time to a maximum?

Location Ireland, Britain, Germany and the Czech Republic.

Methods The data are presence or absence of higher plants in mapping units of 100 km² (Ireland and Britain) or *c.* 130 km² (Germany and the Czech Republic) in areas varying from 79 to 357 thousand km². Logit transforms of range sizes so defined were tested for normality, and examined by ANOVA, and by loess, ordinary least square (OLS) and reduced major axis regressions.

Results Current range sizes, in logits, are near normally distributed. Those of native plants are larger than those of naturalized neophytes (plants introduced since 1500 AD) and much larger than those of casual neophytes. Archaeophytes (introduced earlier) have range sizes slightly larger than natives, except in Ireland. Residence time, the time since an invasive species arrived in the wild at a certain place, affects range sizes. The relationships of the range of naturalized neophytes to residence time are effectively straight in all four places, showing no significant curvature or asymptote back to 1500, though there are few records between 1500 and 1800. The relationships have an r^2 of only about 10%. Both OLS regressions and reduced major axes can be used to estimate the time it takes for the range of a naturalized neophyte to reach a maximum.

Main conclusions Established neophytes have smaller range size distributions than natives probably because many have not yet reached their maximum. We estimate it takes at least 150 years, possibly twice that, on average, for the maximum to be reached in areas of the order of 10^5 km². Policy needs to allow for the variation in rates of spread and particularly the long time needed to fill ranges. Most naturalized neophytes are still expanding their ranges in Europe.

Keywords
Archaeophytes, biological invasions, Europe, native plants, neophyte spread, range size, residence time.

INTRODUCTION

Range size is an important and dynamic characteristic of a species. The statistical properties, such as means, of sets of range sizes reflect the distribution of biodiversity. The differences in range sizes between species have been studied for different taxonomic groups, different habitats, different biogeographical regions, by latitude, longitude, trophic group, body size, dispersal ability, abundance and genetic variation (Gaston, 2003). Surprisingly, the difference between alien and native species and between classes of aliens has scarcely been studied. Here we consider these comparisons for higher plants in four European areas, thereby controlling for most of the other comparisons that have been made.

It has become widely recognized that residence time, the time from the first record in the wild until now, is an important determinant of the present geographical range sizes of alien plants in the country in which they have escaped or been released (Rejmánek, 2000; Kühn & Klotz, 2003; Wu *et al.*, 2003; Castro *et al.*, 2005; Hamilton *et al.*, 2005; Pyšek & Jarošík, 2005; Rejmánek *et al.*, 2005; Lambdon & Hulme, 2006; Essl, 2007; Wilson *et al.*, 2007). Residence time is by no means the only determinant of range size (Kühn *et al.*, 2004). Pyšek & Jarošík (2005), for instance, found the proportion of the variance in range associated with residence time, r^2, to vary in 15 examples from 4.1 to 39.6% with a median of 18.7%. Cadotte *et al.* (2006), Richardson & Pyšek (2006) and Pyšek & Richardson (2007) have reviewed the known effects of residence time.

There are two implications from the importance of residence time that deserve more study. The first is that the ranges of alien plants are likely to be smaller on average than the ranges of natives because most aliens are likely to be still increasing their range. The second is that it should be possible to estimate how long it takes for the average range size of aliens to reach a maximum. There is little published evidence on these two implications. On the first, Williamson (1998) and Williamson & Gaston (1999) showed, both for all aliens and for naturalized aliens, that the range measured in hectads, 10 km × 10 km grid squares, of alien plants in Britain is much smaller than the range of natives. On the second implication, Guo *et al.* (2006) show an approach to an asymptote in North America after about 400 years, and fitted an asymptote to their Eastern Asian data from 100 years; those latter data seem to us to be more complex than that, still increasing at 600 years residence time. In both cases they used quite large political units for determining range. Williamson (2002) showed that only eight of 30 'interesting' (sic) British alien plants showed no significant increase between 1958 and 1988 and two of the eight are the only archaeophytes in the set. That indicates that the time to reach maximum range in Britain is measured in centuries.

In Europe, there are data sets giving the range of native and alien plants measured in small mapping units of around 100 km^2, and also information of the date at which aliens were introduced and found in the wild. Here we examine the three points above: the statistical distribution of range size for various categories of aliens and for natives, the importance of residence time in determining range and the time it takes for aliens, on average, to cease spreading. We use data from four European areas: from west to east, Ireland, Britain, Germany and the Czech Republic. The aim of this paper is to quantify those three points.

METHODS

Data sets

For each area we used a data set containing information on the current distribution of native and alien plant species measured in number of mapping units. For Britain and Ireland, the size of the grid square is 10 km × 10 km, 100 km^2, a hectad (Williamson *et al.*, 2006). In Germany and the Czech Republic, units of 10′ longitude × 6′ latitude (Schönfelder, 1999) are used, about 130 km^2, varying from 118 to 140 km^2 (Kühn *et al.*, 2003). The status of species is either native or alien; aliens are either archaeophytes, introduced before 1500 AD, or neophytes, introduced later, and also either casual or naturalized (Pyšek *et al.*, 2004). We have taken the status given in the data sets, but other workers might want to assign a few of the species differently. The distinction between casual and naturalized can be fuzzy (Williamson *et al.*, 2005), as can be deciding which species are archaeophytes (Preston *et al.*, 2004). Table 1 gives the number of species in different categories in each country in our data.

Irish data

We used the 1987–1999 distributions from the CD of the *New Atlas* (Preston *et al.*, 2002). Unlike the *New Atlas* we treated hybrid species with at least one alien parent as alien, following Pyšek *et al.* (2004). Some species are alien in Ireland but native in Britain and are called native in the text of the *New Atlas* though shown red (for alien) on the maps of Ireland. We have taken these as alien. We derived a list of Irish archaeophytes by taking all species that are naturalized in Ireland from the British archaeophyte list (Preston *et al.*, 2004) and discussed in Williamson *et al.* (2008) the criteria used and the validity of this approach. Alien status and first record date were taken from Milbau & Stout (2007). We only used neophyte species with a first record date (Table 1). The number of hectads is 1007; the area is about 84,000 km^2.

Table 1 Number of native and alien species for which the data were available. 'Natives' are the total number of grid-mapped species. 'Archaeophytes' include a few casual species. 'Dated' are the number of species with a first record date.

	Natives Total	Archaeophytes Total	Naturalized neophytes		Casual neophytes		All taxa
			Total	Dated	Total	Dated	
Ireland	1027	95	254	254	259	259	1635
Britain	1571	153	511	488	960	103	3195
Germany	2550	251	388	136	139	23	3328
Czech Republic	799	144	123	123	445	445	1511

British data

As for Ireland, we used the 1987–1999 distributions from the CD of Preston *et al.* (2002). Species recorded as native in some hectads and alien in others were called natives. Archaeophytes are those in Preston *et al.* (2004). Information on the status of neophytes and the date of the first record were taken mainly from Hill *et al.* (2005) supplemented by Clement & Foster (1994). There are 2837 hectads in Britain, including the Isle of Man but not the Channel Islands; the area of Britain so defined is about 229,000 km^2.

German data

For ranges, we used the FLORKART data base (http://www.floraweb.de) maintained by the German Federal Agency for Nature Conservation for the German Network for Phytodiversity (Kühn *et al.*, 2003) with records up to 2001. Status and the date of the first record come from the BIOLFLOR data base (Klotz *et al.*, 2002), http://www.biolflor.de/. The number of mapping units is 2995; the area is about 357,000 km^2.

Czech data

The status of alien species was taken from Pyšek *et al.* (2002). The number of mapping units recorded up to 2005 for both alien and native species was from a working data base of the national flora held at the Department of Invasion Ecology, Institute of Botany, Průhonice, which is not publicly available. It was compiled using the national data base of floristic literature FLDOK (Institute of Botany Průhonice), national floras (Hejný & Slavík, 1988–1992; Slavík, 1995–2004; Kubát *et al.*, 2002) and atlases (Slavík, 1986–1990, 1998) and also the primary literature (see Pyšek *et al.*, 2002). We only used neophyte species with a first record date, 568 of them (Table 1), and natives for which there is a grid map, 799 of 2750. There are 682 mapping units, and the area is about 79,000 km^2.

Statistical points

Our statistical work generally follows standard procedures (Sokal & Rohlf, 1995) that need not be described here. Most of our calculations were done in R (R Development Core Team, 2006) though some were done in Minitab 13. Four points perhaps need some explanation:

Logits

Following Williamson & Gaston (1999), range size was transformed to logits, which are $\log(p/q)$, where p is the proportion of mapping units occupied out of the total available in the area and q the proportion unoccupied. The totals are given in data sets, above. Logits have the additional advantage that they produce comparisons of the proportion of the area occupied which is appropriate for our data as all four areas are in the European temperate zone with a range of habitats characteristic of that zone and of comparable sizes.

Normality testing

The Ryan–Joiner test (available in Minitab) looks at the probability that the correlation of the normit (i.e. normal scores) and the measure being studied is significantly different from unity, rather than from zero as in standard correlation tests. It is equivalent to the Shapiro–Wilks *W*-test, described fully in section 7.2.1.3 of NIST/SEMATECH (2006).

Loess curves

These are locally weighted scatterplot smoothers and are calculated as locally weighted polynomial regressions over a span of values. They can be thought of as a development of moving averages and are described fully in section 4.1.4.4 of NIST/SEMATECH (2006). The loess line can also be called a loess regression.

Reduced major axis

In the relationship of residence time and range, both the response and the explanatory variables have errors. In ordinary least square (OLS, model I) regression, the predictor variable is treated as precise and only the response variable is assumed to have error. We therefore also use a model II regression approach, the reduced major axis (RMA), sometimes called the standard major axis, as the two variables are standardized, and the geometric mean regression, as the line is the geometric mean of the regressions of *x* on *y* and of *y* on *x* (Sokal & Rohlf, 1995). The line is also the first principal component of a principal components analysis of the correlation matrix of *x* and *y*. The slope is given by the ratio of the standard deviations of the two variables with the sign of their correlation. This equals b_{OLS}/r_{xy}, where b_{OLS} is the OLS slope and r_{xy} the Pearson correlation coefficient. The RMA has the same standard error and so r^2 as the OLS regression, but is necessarily steeper. We use both OLS and RMA to estimate the time needed for the average range size of neophytes to come to a maximum. We assume the maximum to be the average range size of natives. Our reasons for making this assumption, which use the results on current distribution and residence time, are given after those results.

RESULTS

Current distributions

The distribution of range sizes by country and status is summarized in Fig. 1. The results of tests of normality for logits are given in Table 2; logarithmic and square-root transformations and the raw data give unsatisfactory fits.

There are sixteen sets in Fig. 1 each of a different size (Table 1). A two-way ANOVA by country and status is therefore over different size sets but indicates that all statuses and all countries are significantly different and that there is significant interaction between them. The highly significant interactions make it easier to interpret a one-way ANOVA of all sixteen sets. Using Tukey
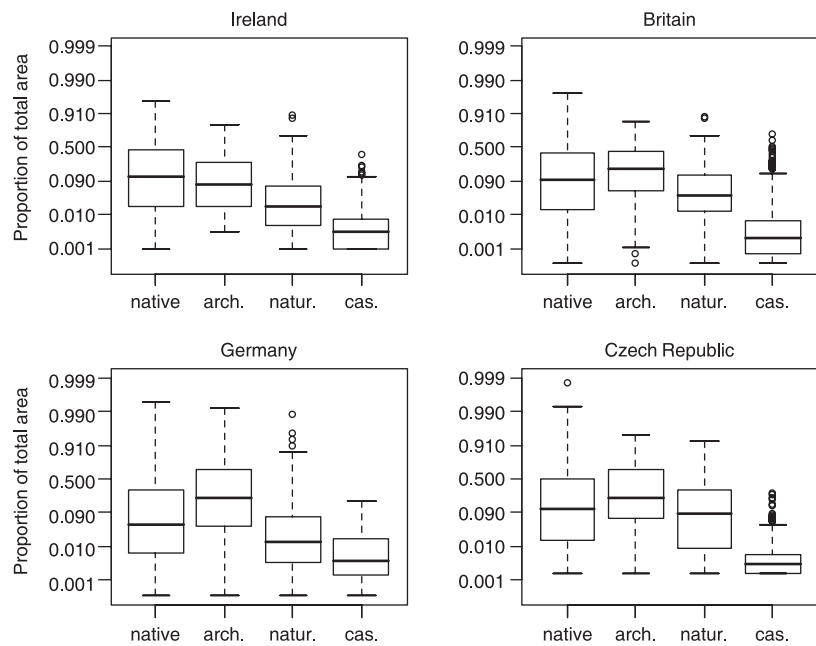
Figure 1 Box and whisker plots on a logit scale of the range sizes as a proportion of the total mapping units of natives, archaeophytes, naturalized neophytes and casual neophytes.

Table 2 Statistics of normality fits for logits. These are Ryan–Joiner statistics, equivalent to Shapiro–Wilks. In each cell, correlation coefficient values are given (of normit against logit value) followed by, in parentheses, the probability of a good fit to a straight line. Probabilities in bold are not significant (the fit is good), the one in italics almost so. The effect of sample size on the probabilities is obvious, but it can also be seen that the correlation coefficient is > 0.99 for all natives and all naturalized neophytes, except the (non-significant) correlation of Czech naturalized neophytes.

Country/status	Native	Archaeophyte	Naturalized neophyte	Casual neophyte
Ireland	0.9948 (< 0.01)	0.9940 ($>$ **0.1**)	0.9942 (*0.0435*)	0.9763 (< 0.01)
Britain	0.9960 (< 0.01)	0.9796 (< 0.01)	0.9981 ($>$ **0.1**)	0.9838 (< 0.01)
Germany	0.9928 (< 0.01)	0.9969 ($>$ **0.1**)	0.9922 (< 0.01)	0.9959 ($>$ **0.1**)
Czech Republic	0.9941 (< 0.01)	0.9782 (< 0.01)	0.9894 (**0.0519**)	0.9681 (< 0.01)

Table 3 Five groups found from a one-way ANOVA of 16 country-status sets (from 4 countries × 4 statuses). The sets are listed in descending order of mean range size. Note that the order of countries is different in each status but the order of status is the same in all countries except for the inversion of Irish archaeophytes and natives. The mean percentage occupancy, from logits, is given for each set.

Group A:	German archaeophytes 21.3, Czech archaeophytes 19.9, British archaeophytes 14.1.
Group B:	Irish natives 11.5, Czech natives 11.1, British natives 8.4.
Group C:	Irish archaeophytes 7.9, Czech naturalized neophytes 7.1, German natives 5.6, British naturalized neophytes 4.1.
Group D:	Irish naturalized neophytes 2.0, German naturalized neophytes 1.8.
Group E:	German casual neophytes 0.46, Irish casual neophytes 0.36, Czech casual neophytes 0.33, British casual neophytes 0.29.

comparisons from that to group together sets that are not significantly different produces five groups of sets (Table 3). All the sets in groups E (casuals) and D (Irish and German naturalized neophytes) are significantly different from all other sets. Groups A to C though form a continuum which was separated by making group A contain all sets not significantly different from the most widespread set (German archaeophytes) and group C all those not significantly different form the least widespread (British naturalized neophytes), leaving group B in the middle

with its sets all not significantly different from each other but also, in some cases, not significantly different from some sets in either group A or group C.

These groupings confirm what can be seen in Fig. 1. Archaeophytes, other than in Ireland, are the most widespread and form group A. The next largest ranges are found in natives (group B), though German natives (in group C) are rather restricted. After those come naturalized neophytes, though the Czech and British (in group C) are significantly more widespread than the Irish and
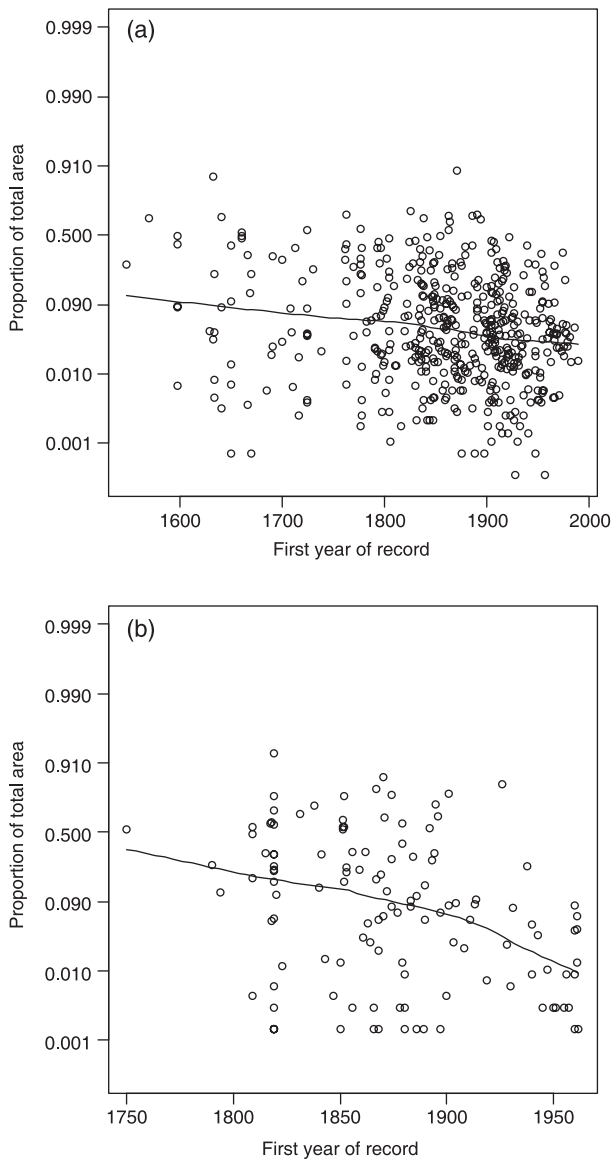
Figure 2 Current range on a logit scale as a proportion of the total mapping units of British (a) and Czech (b) naturalized neophytes against the first record date. Loess regression lines were fitted using a span of 0.9.

German (group D) and then, with much the smallest ranges, all the casual sets (group E). The anomalous positions of Irish archaeophytes and German natives (both in group C) explain the strong interactions found in the two-way ANOVA. As the order of countries is different in each status, it makes no sense to order the countries using all statuses, which, statistically, is another factor in the interaction terms in the two-way ANOVA.

Residence time effects

The relationship of residence time to range size was studied in bivariate plots. Here we present the results just for naturalized neophytes; we also examined the effect in casuals and in total neophytes but such plots were uninformative. As can be seen in
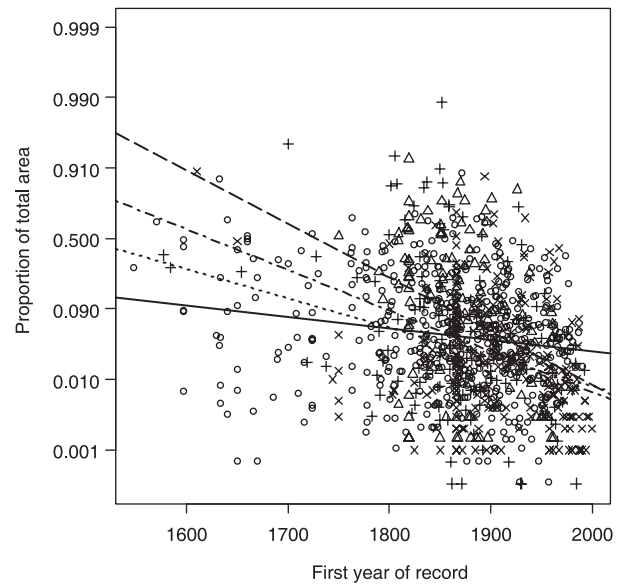

Figure 3 Linear regressions of current range size on first record date of naturalized neophytes for Ireland, Britain, Germany and the Czech Republic. Range sizes are expressed as the proportion of the total mapping units on a logit scale.

Czech Republic Dashed line Δ
Germany Dot-dash line +
Ireland Dotted line ×
Britain Solid line ◯

Figs 2 and 3, the relationship is fairly weak, so the first question is, is it straight or curved? That was examined with loess regressions; two results are shown in Fig. 2. In all areas, there is a slight indication of a flatter slope with the older dates. The majority of introductions, as can be seen, are in the 19th and 20th centuries, so the slopes for the older dates are based on fewer data. However, fitting OLS regressions to the data, before and after the most obvious break point, showed no significant change of slope, so we fitted one regression to the whole of each data set.

The lines for OLS regressions for the four areas are shown in Fig. 3.

All the regressions are significant, and the coefficients of determination (r^2) vary only from 3.1 to 13.2% (Table 4, which also gives the RMA slopes). Table 5 shows that the regression for Britain is significantly flatter than that of the others, which do not differ among themselves. It might be thought that the British result comes from the appreciable numbers of early introductions with small ranges, obvious in Fig. 3, but the loess results in Fig. 2(a) show that the British slope is flat up to the start of the 21st century. The consensus, as far as that is possible with four data sets, is that r^2 is about 10% for naturalized neophytes in European countries, the median figure in our results.

A regression gives the best prediction from known data. However, in our data the uncertainties in the first record date are probably higher than those in range size. Range size is necessarily a minimum; some localities may have been missed. Date is usually also often regarded as the latest, leading to the phrase 'minimum residence time'. In many cases it may be too early, in

Table 4 Results of linear (OLS) regression and reduced major axis (RMA) analyses of logit (naturalized species range) against first record date.

	Intercept	SE	Slope	SE	P	r^2
Linear regression						
Ireland	6.1758	1.6501	−0.0041	0.0009	< 0.001	0.083
Britain	1.6074	0.7598	−0.0016	0.0004	< 0.001	0.031
Germany	9.3560	2.3881	−0.0058	0.0013	< 0.001	0.132
Czech Republic	13.1044	3.6167	−0.0076	0.0019	< 0.001	0.113
Reduced major axis						
Ireland	25.6461	1.6501	−0.0144	0.009		
Britain	15.6228	0.7598	−0.0091	0.0004		
Germany	28.2384	2.3881	−0.0159	0.0013		
Czech Republic	41.1199	3.6167	−0.0225	0.0019		

SE, standard error.

Table 5 Probabilities of the post hoc multiple comparisons of the regressions in Table 4, from an ANCOVA analysis.

	Ireland	Britain	Germany
Britain	0.0053		
Germany	0.15	0.000021	
Czech Republic	0.20	0.000019	0.22

that the date needed is the first date from which the species starts to spread. In the Czech flora (Williamson *et al.*, 2005), over half the species with good statistical patterns of spread (28 of 50) show a lag, determined rigorously (not from arithmetic plots) from 7 to 154 years with a median of 41 years (Williamson, in press).

The time needed to complete spreading

The second implication from the importance of residence time for range size is that it should be possible to estimate how long it takes, on average, for naturalized neophytes to complete their range, and for mean range size to come to a maximum. If plots such as those in Fig. 2 showed an asymptote then an estimate would follow immediately, but in our data they do not. The mean range size will, however, not increase indefinitely but come to some maximum which will be higher than the present mean. There are several ways in which the maximum can be estimated.

A rather weak method is to compare the upper whiskers and particularly the uppermost points (extremes) for natives and naturalized neophytes in Fig. 1. These whiskers will contain fast spreading neophytes that have completed their spread. In all cases the neophytes are lower than the natives, which suggests that the eventual mean for neophytes will be less than the native mean. The same conclusion comes from the British plants introduced before 1700. Britain is the only area with an appreciable number of such species (see Fig. 3). These will have been in

Britain around 250 years longer than the median British established neophyte (from *c.* 1650 to *c.* 1900). Their mean abundance is 7.2% compared with (Table 3) 4.1% for all British naturalized neophytes and 8.4% for British natives. As will be seen below, 250 years is possibly a mid to high estimate of the time to maximum range, so tentatively, the limiting mean range of British neophytes is unlikely to be larger than the mean range for natives and could be a touch smaller.

A different approach is to consider the range of habitats of the different statuses. This approach requires a translation from a habitat distribution to a mapping square distribution. Archaeophytes have rather special habitats, considered more fully in the Discussion, and that translates generally (Fig. 1) into a higher median than for other groups but with a relatively short upper whisker. Neophytes are known to occupy a wider range of habitats, approximately those of natives, but with a different spectrum of abundances. Succinctly, neophytes are commoner in human-affected and riparian habitats, natives in unproductive habitats. Crawley (1987), using 37 types of habitat, shows that difference from the percentage of alien species in different British habitats, though his figures include archaeophytes. Pyšek *et al.* (2005), for arable weeds in the Czech Republic, show that archaeophytes have the most distinct habitat requirements, while neophytes are close to, but different from, natives. It could be argued that, as with archaeophytes, the high occupancy of man-modified habitats by neophytes would lead to a mean range size greater than that of natives. Or it could be argued that because of their scarcity in widespread unproductive habitats, neophytes would be more restricted than natives. It is possible that the answer would be different in, for example, Scotland with much mountainous habitat than in England with little. Many botanists, noting the ubiquity of ruderal vegetation, will probably prefer the first argument. Without the translation from habitats to mapping squares, it is not possible to decide which argument is right.

Taking all these arguments together, an assumption that neophytes will match natives will be near the truth and allows comparable estimates to be made across all four countries. With that assumption, it is possible to estimate the time to full range

Table 6 Estimates of the time for the mean range size of naturalized neophytes to reach a maximum, from the ordinary least square (OLS) and reduced major axis (RMA) results in Table 4.

	Years from OLS		Years from	
	Regression	SE	RMA	SE
Ireland	290	42.64	151	17.02
Britain	351	57.98	177	23.75
Germany	166	16.94	145	15.60
Czech Republic	160	14.02	141	12.26

SE, standard error.

for neophytes by estimating the time for the mean neophyte range to match the mean native range.

In Table 6 there are eight estimates of the time needed to reach maximum mean naturalized neophyte range size. These are from four countries and two lines (OLS regressions and RMA). Six of the eight estimates cluster around 150 years, the other two, the British and Irish regression estimates, are around twice that. Note that the four RMA estimates agree much more closely than the regression ones. Tentatively, it seems that the time to maximum range in a European country-sized area may well be around 150 years but could be around twice that, 300 years or more.

DISCUSSION AND CONCLUSIONS

The relative size of native and alien ranges from largest to smallest is (Table 3): archaeophytes (except in Ireland), natives, naturalized neophytes and casuals. Irish archaeophytes come between natives and neophytes. In that ordering, only the position of archaeophytes requires special explanation. Casual neophytes are very restricted in range in all four areas and are of course not spreading of their own accord. The difference between casual and naturalized means that data on these statuses should be kept separated. Naturalized neophytes have ranges more nearly matching those of natives but still significantly smaller in all cases, partly because they have mostly not yet filled their ranges.

Archaeophytes, many of which have been in western and central Europe for thousands of years, will be in equilibrium with their environment so might be expected to have the same range distribution as natives. That they have larger ranges, on average, is likely the result of their special habitat requirements. They are primarily arable weeds especially of warmer soils (Pyšek *et al.*, 2005) and loess soils (Kühn *et al.*, 2003). That also explains the anomalous ranges of Irish archaeophytes, as arable land is well known to be much more restricted in Ireland than in the other areas and loess is also scarce there.

A minor anomaly is that the mean range size (but not the maximum, Fig. 1) of German natives, measured as a proportion of the mapping units, is smaller than those of the other countries (Table 3). Germany has also the highest native species richness in our data (Table 1) and the largest area, stretching from the Alps to the North Sea, so there is greater opportunity for specialization on local habitats (see also Korsch, 1999).

As noted in the Introduction, residence time is an important determinant of range size. We found coefficients of determination ranging from 3.1 to 13.2%. Among these, the flattest, British, slope is significantly different from the others. With four data sets, it is not possible to say if that is an anomaly or just part of the natural range of slopes. There are of course effects of country size, mapping unit size and the survey methods in all countries, but none of these seem likely to explain the effect, nor have we found any other plausible explanation, such as types of plants introduced, or variation in habitat heterogeneity, which seems comparable across all four areas. There are not enough such studies yet to do more than guess at the reason for these small r^2s, but we considered more species in more sampling units than any previous study.

Two implications of the importance of residence time were mentioned in the Introduction: the relative size of native and alien ranges, and the possibility of estimating the average time it takes an alien to fill its range. Our results for the first implication, discussed above, are somewhat more complicated than has been indicated before. On the second implication, our extensive data on range size and residence time mean we can estimate that, on average, naturalized alien plants (in areas varying from 80,000 to 360,000 km^2) take at least 150 years to fill their range and possibly twice that, 300 years (Table 6). Similar numbers can be derived from Braithwaite *et al.* (2006): 313 years from the regression of 17-year range size change on residence time for neophytes recorded reliably in 2×2 km squares, and 176 years for the median residence time of such neophytes showing no significant change of range size from 1987 to 2004.

Although not helpful in managing individual species, both implications need to be allowed for in formulating policy. The importance of the second for policy, based on our results, is set out in Diversitas (2008). There is much variation in rates of spread, as shown by our small coefficients of determination, and the average time to fill a range is long. Rapid spreaders need to be identified quickly so that action can be taken against them. Plants introduced in the last century with smallish ranges and slow spread now may nevertheless, in time, become widespread and possibly troublesome species. The present distribution is not necessarily a guide to the future and monitoring programmes need funding alongside control programmes.

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