

Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years

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Abstract

Globalization is triggering an increase in the establishment of alien insects in Europe, with several species having substantial ecological and economic impacts. We investigated long-term changes in rates of species spread following establishment. We used the total area of countries invaded by 1171 insect species for which the date of first record in Europe is known, to estimate their current range radius (calculated as $[\text{invaded area}]^{0.5}/\pi$). We estimated initial rates of radial spread and compared them among different groups of insects for all years (1800–2014) and for a subset of more recent decades (1950–2014). Accidentally introduced species spread faster than intentionally introduced species. Considering the whole period 1800–2014, spread patterns also differ between feeding guilds, with decreasing spread rates over residence time in herbivores but not in detritivores or parasitic species. These decreases for herbivorous species appeared mainly in those associated with herbaceous plants and crops rather than woody plants. Initial spread rate was significantly greater for species detected after 1990, roughly 3–4 times higher than for species that arrived earlier. We hypothesize that the political changes in Europe following the collapse of the Iron Curtain in 1989, and the further dismantling of customs-checkpoints within an enlarged European Union (EU) have facilitated the faster spread of alien insect species. Also, the number of species first recorded in the Eastern Bloc of the politically-divided Europe before 1989 was lower than for the rest of Europe. A detailed analysis of six recent invaders indicated a dominant role of long-distance translocations related to human activities, especially with the plant trade, in determining rates of spread.

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Keywords

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Introduction

Biological invasions by alien species involve a series of discrete, consecutive phases (Blackburn et al. 2011; Lockwood et al. 2013). After the arrival and establishment phases, invading species begin to spread by expanding their range into suitable environments. Although alien species have been arriving and establishing for several centuries, a large fraction are still spreading and likely to exhibit non-equilibrium or transient population dynamics as they move into new areas (Paini et al. 2010). Given that the spread of many species is ongoing—even for alien species established long ago—understanding this process is critical for predicting and managing the impacts of invasions.

The spread of alien species is driven by demographic and ecological processes, including population growth and dispersal (Hastings et al. 2005; Hui et al. 2011). Consequently, both intraspecific and interspecific variation in rates of spread will result from factors that affect either process. Several studies have investigated how environmental heterogeneity can influence spread in invading species either by affecting population growth rates (e.g., Sharov et al. 1999) or dispersal (e.g. Skalski and Gilliam 2000). However, few studies have examined variation in spread rates among species, and even fewer have considered differences between functional groups such as feeding guilds (e.g. Liebhold et al. 2013), residence time (Wilson et al. 2007), or ecological or geopolitical context of invasion.

In Europe, the rate of establishment of alien insect species has nearly doubled over the last few decades, increasing from an average of 10.9 species per year for the period 1950–1974 to an estimated 19.6 species per year for 2000–2008 (Roques 2010). Most alien insect species in Europe were introduced accidentally, with only 14 % of introductions being intentional, most of these for biological control (Rabitsch 2010; Hajek et al. 2016); this pattern is similar for other world regions (Kumschick et al. 2016). This recent influx of alien insects appears to comprise predominately herbivores (Roques 2010), which is probably related to recent changes in trade practices, especially the increased magnitude in the movement of live plants globally (Liebhold et al. 2012; Eschen et al. 2014; Essl et al. 2015). Given these trends, it is important to know whether there has been a parallel increase in rates of spread within Europe.

Many alien insect species first reported in Europe since the late 1990s have spread extremely rapidly, invading most of the continent within a few years. For example, the western seed bug, *Leptoglossus occidentalis* (Hemiptera: Coreidae), a native of North America, was first observed in 1999 in northeastern Italy. The insect now occurs from Portugal to Russia and from North Africa to Scandinavia, as well as in China, Japan and Korea (Lesieur 2014). Similar rapid spread has been observed in several other species associated with woody plants, such as the chestnut gall wasp, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae; first detected in 2002 in Italy; Avtzis and Matošević 2013), the honeylocust gall midge, *Obolodiplosis robiniae* (Diptera: Cecidomyiidae; detected in 2003 in Italy; Skuhrová and Skuhrový 2009), the elm zig-zag sawfly, *Aproceros leucopoda* (Hymenoptera: Argidae; detected in 2003 in Poland; Blank et al. 2010), and the box tree moth, *Cydalima perspectalis* (Lepidoptera: Pyralidae; detected in 2006 in Germany; Bella 2013). Rapid spread has also been observed in crop pests recently detected in Europe, such as the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae; detected in 2006 in Spain; Desneux et al. 2010) and the vinegar fly, *Drosophila suzukii* (Diptera: Drosophilidae; detected in Italy in 2008 but already present throughout most of Europe; Cini et al. 2012). The predatory Harlequin ladybeetle, *Harmonia axyridis*, has invaded most of Europe since its discovery in 1991 in Belgium (Brown et al. 2011). Several species associated with palm trees, such as the palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) and the palm moth, *Paysandisia archon* (Lepidoptera: Castniidae), have also expanded their ranges rapidly across the Mediterranean Basin since the early 2000s (Sauvard et al. 2010; Lopez-Vaamonde et al. 2010), as did the gall makers, *Ophelimus maskelli* and *Leptocybe invasa* (Hymenoptera: Eulophidae) (Hurley et al. 2016), and the psyllids, *Acizzia jamatonica* and *Glycaspis brimblecombei* (Hemiptera: Psyllidae; Mifsud et al. 2010; Bella and Rapisarda 2013) associated with *Eucalyptus*. In contrast, for unknown reasons some species have not spread at all since their establishment, despite apparently favourable conditions. An example is the poplar-feeding ambrosia beetle, *Megaplatypus mutatus* (Coleoptera: Curculionidae) that was reported in 2000 in southern Italy (Sauvard et al. 2010).

The vast majority of insect pests, even those that have been present since 1800, appear to be still actively spreading. Nonetheless, analysis of spread rates needs to account for the potential declines due to habitat filling, and also should be interpreted with some caution because the available data rarely describe the whole invasion process since the initial introduction or arrival (Williamson et al. 2005). Recorded dates of discovery can be a poor proxy for the timing actual introduction, given detection or reporting lags (Solow and Costello 2004). The discovery process is closely linked to effort allocated to detecting established alien species in the invaded region (Costello et al. 2007)—detection effort is highly likely to vary across time and space, partly as a function of available funding.

The political and economic structure of the European continent has changed radically over the last three decades, with profound implications for the movement of invading species. The fall of the Berlin wall in 1989 resulted in increased commerce and travel between Eastern and Western Europe. In 1992, the Maastricht Treaty promoted the free circulation of people and goods, resulting in the dismantling of custom checkpoints at internal national borders within the European Union in 1993. These events, coupled with the successive addition of countries to the European Union in 2004 (Cyprus, Czech Republic, Estonia, Hungary, Latvia, Lithuania, Malta, Poland, Slovakia, Slovenia) and in 2007 (Bulgaria, Romania), likely have provided enhanced opportunities for the spread of introduced insects. Chiron et al. (2010) showed that these socio-political changes influenced patterns of bird introductions in Europe but had a limited impact on spread, with only 12 % of the 121 introduced species having spread from the original country of introduction to a neighbouring country. However, no analyses have explored whether these political changes have affected rates of spread of alien insects.

In this study, we use recently collated data from the DAISIE and EASIN databases (see “Materials and methods”) to test whether the rate of spread of alien insects: (1) has accelerated in the last few decades in a way that is consistent with expectations given changes in the socio-political situation in the European Union; (2) varies depending on the region of a species’ first record in Europe; (3) varies by insect feeding guild, or by host type for phytophagous species (woody vs. non-woody plants), or the mode of introduction (intentional vs. unintentional).

Materials and methods

A barrier to characterizing patterns in the spread of alien insects is the lack of standardized historical survey data. Data on historical patterns of spread are largely limited to a few species with high levels of economic impact that were first detected in the last 20 years (Cini et al. 2012; Bella 2013). Instead, we exploit data from two recent general inventories of alien species in Europe. The DAISIE database (Delivering Alien Species Inventories in Europe), launched in 2008, provides historical invasion data at the country level for the species introduced to Europe after 1700 (DAISIE 2009; www.europe-aliens.org). More recently, the EASIN catalogue (European Alien Species Information Network) additionally provided year and country of species’ first record in Europe (Katsanevakis et al. 2015; <http://easin.jrc.ec.europa.eu/>). Neither of these databases includes detailed distributional data, and in some cases dates of first recorded establishment in each country are not available, particularly for species that were first detected before 1990. Nevertheless, a coarse characterization of the rate of spread of alien insects since their first record in Europe can be effectively estimated from these data.

We extracted the current distribution of all alien insects known to have established in Europe from the DAISIE and EASIN databases, which were updated to reflect the situation in late 2014. Only species alien to the whole of Europe (including the Canary Islands and Madeira) were considered; species whose native distribution included part of the European continent (Lambdon et al. 2008) were excluded even if these species were considered alien in some parts of Europe. The dataset contained a total of 1418 species. We discarded species for which certain data were missing: 138 species that lacked a date of first record; 86 species recorded only from greenhouses; 9 species present only in Russia, with a range extending to Asia; and 14 species first recorded before 1800 (as their first record date is uncertain). This reduced the dataset to 1171 species (list in Supplementary Material S1) for which the date of first record in Europe was known, along with their presence/absence as of 2014 in each of the 41 countries of geographic Europe and (considered separately) 12 major islands or archipelagoes (Balearics, Corsica, Canaries, Crete, Faeroe, Ionian islands, Madeira, North Aegean islands, Sardinia, Sicily, South Aegean islands, Svalbard).

Species’ spread over time since the first record in Europe was calculated following Liebhold et al. (2013) as invasion radius = $\sqrt{\text{area}}/\pi$. The slope of the regression line obtained by regressing invaded range radius against time since first detection provides an estimate of the mean radial rate of spread (Gilbert and Liebhold 2010; Liebhold et al. 2013; Tobin et al. 2015). Such estimates can be used to test for differences in the spread rate of alien insects that might reflect their mode of introduction (intentional vs. accident) aspects of their biology such as their feeding guild. For each insect species we calculated the total area of the invaded countries using the surface area data provided by EUROSTAT (<http://ec.europa.eu/eurostat>). This area in many cases overestimates the invaded range because each species may have invaded only a portion of each country. However, it was not possible to obtain finer resolution data for most alien insects.

We expect the rate of radial expansion to slow over time as species spread to fill their suitable habitat in Europe: when a species has spread to occupy its entire suitable habitat, the rate of radial expansion will decline to zero (Shigesada and Kawasaki 1997). To accommodate this, we used a modified form of the Beverton–Holt function to model the relationship between invasion radius and time since first record. This function allows for a slowing rate of radial spread, which approaches zero as a species approaches its full radial occupancy:

$$\text{Invasion radius} = \frac{ax}{1 + ax/b} + c \quad 1$$

where x is number of years since first recorded presence and a , b and c are parameters to be estimated from the data. Parameter a measures the initial rate of radial expansion, b is the asymptotic value of the invasion radius (the radius when all suitable habitat has been occupied) and c is an intercept parameter that estimates the initial radius of occupancy corresponding to the area of the first country colonized. Other functions would also be suitable to model radial spread. In particular, a logistic function could model both a slow-down in rate of spread as species neared full occupancy, along with an increasing initial rate of spread, which might be expected due to a lag-phase. We chose Eq. 1 because: (a) there was no evidence of obvious lag phases in our data (see “Results”), perhaps due to the rather coarse measure we used to calculate change in area of occupancy over time (i.e., at a country scale) and (b) Eq. 1 usually provided a better fit to the data than a logistic function.

We compared this initial spread rate (parameter a , Eq. 1, which unbiased with respect to currently colonized area) among species that were intentionally vs. unintentionally introduced, and among species belonging to different feeding guilds. Feeding guilds were as follows: 1 detritivores, 2 herbivores, and 3 parasites and predators. The herbivorous species were further separated into those associated with woody vs. non-woody (herbaceous) plants. We also tested for differences in initial spread rate among insect orders. To compare initial rates of spread, we fit Eq. 1 to the full data set and to subsets of the data corresponding to the different guilds above using a Bayesian framework in JAGS (Plummer 2003), implemented in the R package jagsUI. We specified uninformative priors for all of the parameters to be estimated. Parameters a , b and c were given priors of mean zero and variance 10,000 on a log scale (with the log transformation used to ensure that the resulting parameter values were positive). Variance terms were given assigned a uniform prior in the range 0–100 based on the standard deviation. Models were run with three chains and a burn-in of 10,000 iterations followed by 10,000 further iterations, which were extended if the chains had not converged. Convergence was checked using the Gelman–Rubin statistic, and models were run until all parameters had values of the Gelman–Rubin statistic <1.1. For each parameter, we extracted the mean and 95 % credible intervals from the resulting

posterior distributions.

To determine whether initial rates of spread have changed over time, potentially in response to recent socio-political changes in Europe, we extracted data from a subset of the DAISIE database comprising 760 insect species first recorded in Europe between 1950 and 2014. Of these 760 species, the date of first record in every invaded country was available for 455 species (list in Supplementary Material S2), from which we could calculate the change in invasion radius over time. We excluded the 238 species were recorded in just one country and thus provided no information on change in radial occupancy over time. For the 217 species that remained, we examined whether initial spread rates exhibited an increase over time. We accomplished this by categorizing these 217 species into three groups based on the year in which they were first recorded in Europe: 1950–1969, 1970–1989 and 1990–2009. These periods were selected because they roughly correspond to the main socio-political events having affected Europe: Cold War, divided Europe before the collapse of the Iron Curtain, and enlargement of the European Union. For the species in each period we estimated the initial rate of spread by fitting Eq. 1 to the data and estimating parameter a . The data comprised a time series for each species documenting the increase in invasion radius over time as species colonized new countries. To account for the fact that the series of data points for each species were not independent, we fitted a hierarchical model in which we estimated separate a , b and c parameters for each species. These species-level parameters were assumed to be drawn from independent normal distributions having means equal to the overall mean for each parameter, and variances estimated from the data. We fitted this model in JAGS (Plummer 2003) using the same uninformative priors as above, running three chains with a burn-in of 10,000 iterations followed by 10,000 further iterations, and with convergence checked as above. Using the same statistical method, we compared the initial spread rate among species for which the first record was from: 1. Central Europe; 2. Eastern Europe; 3. Southern Europe; and 4. Western Europe; these parts were defined on the basis of geographic, historical, cultural and political settings that can be assumed to affect the spread of alien species and that have previously been shown to differ for, e.g. plant invasions (Chytrý et al. 2009).

We also calculated and compared annual spread patterns of six emblematic species that were detected in Europe since the late 1990s and rapidly invaded the entire continent: elm zig-zag sawfly, *Aproceros leucopoda*; box tree moth, *Cydalima perspectalis*; chestnut gall maker, *Dryocosmus kuriphilus*; western conifer seed bug, *Leptoglossus occidentalis*; honeylocust gall midge, *Obolodiplosis robiniae*; vinegar fly, *Drosophila suzukii*.

Results

Figure 1 shows the radial spread since the first record in Europe for 1171 alien insect species that were detected in Europe since 1800. Mean initial radial range expansion was estimated at 3.3 km year⁻¹ (95 % credible intervals: 2.5–4.4), although this rate of range expansion has slowed with time since introduction (Fig. 1). Spread patterns differed significantly between intentionally ($n = 138$; Fig. 2a) and accidentally introduced species ($n = 1033$; Fig. 2b), with accidentally-introduced species having a faster initial spread rate of 3.5 (2.6–4.7) vs. 1.1 (0.7–1.6) km year⁻¹ for intentional introductions (Fig. 2c). Patterns of spread also differed between feeding guilds, with radial spread tending to decrease over residence time in herbivores ($n = 597$; Fig. 3b) but remaining approximately constant for detritivores ($n = 249$; Fig. 3a) and parasitic species ($n = 325$; Fig. 3c). However, the mean initial spread rate did not differ statistically among guilds, partly due to large variance in spread among herbivores and parasitic species, which contrasts with detritivores (Fig. 3d). The pattern of decreasing rates of herbivore spread appears to be dominated by species associated with herbaceous plants ($n = 200$; Fig. 4a), while invasion radius constantly increased over time in the woody plant-associated species ($n = 397$; Fig. 4b). The mean initial spread rate was higher in species associated with herbaceous plants (4.8 [2.9–8.3] vs. 1.9 [1.9–5.1] km year⁻¹ for woody plant-associated species), but this difference was not significant due to high within-group variance (Fig. 4d). Among insect orders, Coleoptera showed the largest mean initial spread rate (7.0 [4.1–11.7] km year⁻¹), followed by Hemiptera (5.0 [3.2–7.6] km year⁻¹), with Hymenoptera having the lowest initial spread rate (2.0 [1.4–3.1] km year⁻¹; Fig. 5).

Fig. 1

The extent of radial spread of alien insect species recorded in Europe from 1800 to 2014 as a function of time since first record. Radial spread was calculated as $\sqrt{\text{area occupied}}/\pi$. The grey circles show the raw data for all 1171 species; the black circles show the average value for radial spread in each decade; the black line represents the fit of the modified Beverton–Holt function (Eq. 1) to the data with 95 % credible intervals shown as dotted lines

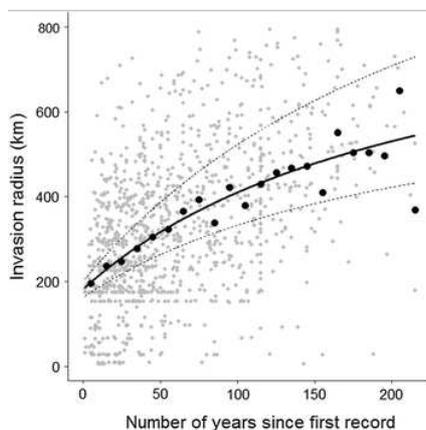


Fig. 2

The extent of radial spread of alien insect species recorded in Europe from 1800 to 2014 as a function of time since first record for a

intentional and **b** unintentional introductions. Radial spread was calculated as $\sqrt{\text{area occupied}}/\pi$. The *grey circles* show the raw data; the *black circles* show the average value for radial spread in each decade; the *black lines* shows the fit of modified Beverton–Holt functions (Eq. 1) to the data with 95 % credible intervals shown as *dotted lines*. **c** estimates of initial spread rate (parameter a in Eq. 1) and 95 % credible intervals for intentional and unintentional introductions

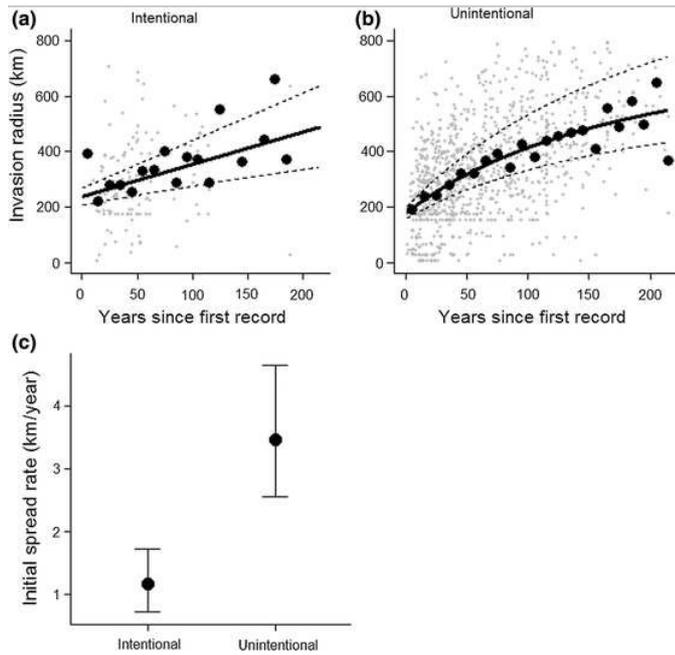


Fig. 3

The extent of radial spread of alien insect species recorded in Europe from 1800 to 2014 as a function of time since first record for **a** detritivores, **b** herbivores and **c** parasites and predators. Radial spread was calculated as $\sqrt{\text{area occupied}}/\pi$. The *grey circles* show the raw data; the *black circles* show the average value for radial spread in each decade; the *black lines* shows the fit of modified Beverton–Holt functions (Eq. 1) to the data with 95 % credible intervals shown as *dotted lines*. **d** Estimates of initial spread rate (parameter a in Eq. 1) and 95 % credible intervals for detritivores (*Det*), herbivores (*Herb*) and parasites and predators (*Par*)

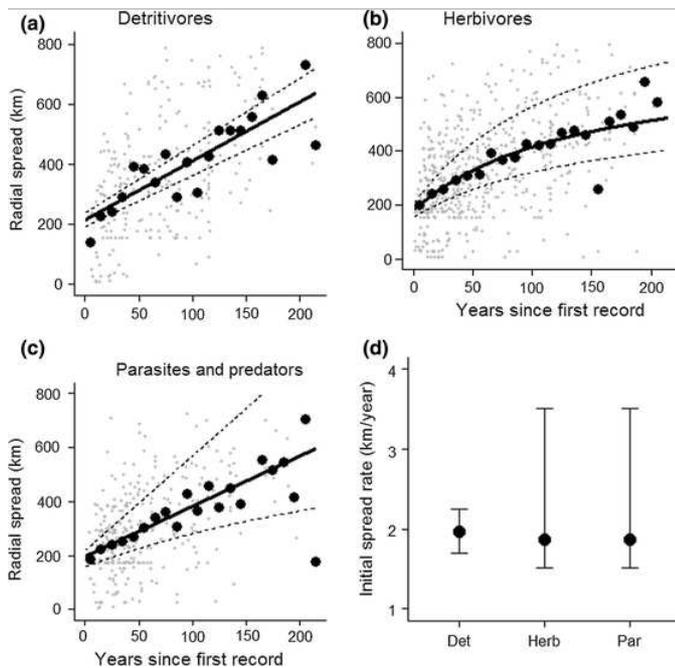


Fig. 4

The extent of radial spread of alien insect species recorded in Europe from 1800 to 2014 as a function of time since first record for **a** herbivores associated with non-woody plants and **b** herbivores associated with woody plants. Radial spread was calculated as $\sqrt{\text{area occupied}}/\pi$. The *grey circles* show the raw data; the *black circles* show the average value for radial spread in each decade; the *black lines* shows the fit of modified Beverton–Holt functions (Eq. 1) to the data with 95 % credible intervals shown as *dotted lines*. **c** estimates of initial spread rate (parameter a in Eq. 1) and 95 % credible intervals for herbivores associated with non-woody and woody plants

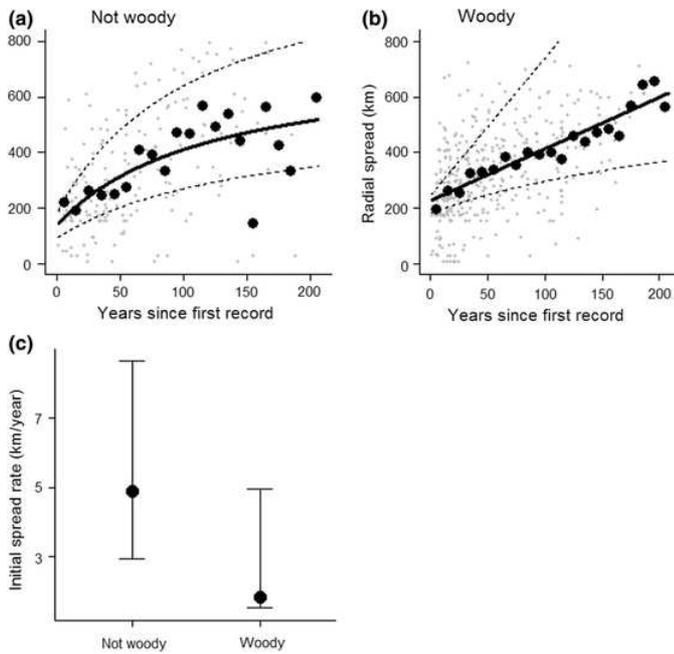
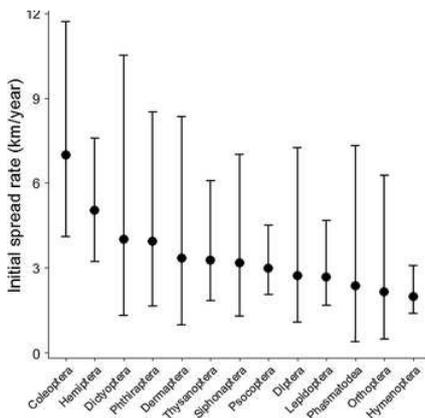


Fig. 5

Estimates of initial spread rate (parameter a in Eq. 1) and 95 % credible intervals for alien insect species recorded in Europe from 1800 to 2014 in relation to insect orders



The patterns changed slightly when only species that were newly detected during the most recent period (1950–2014) were considered (Fig. 6). Radial spread patterns differed significantly between periods (Fig. 7). Although the estimate had wide credible intervals, the initial spread rate of alien species first recorded after 1989 was significantly higher (37.0 [23.7–60.7] km year⁻¹) than for species first recorded from 1970 to 1989 (12.1 [8.8–17.5] km year⁻¹) (Fig. 7d). Recently detected species also exhibited a larger initial spread rate than the species first recorded during the period 1950–1969 (6.5 [5.1–8.4] km year⁻¹; Fig. 7d). Most alien species were first recorded in southern and western Europe (49.7 and 27.8 %, respectively), and only a few were first reported from other regions (central Europe 12.5 %; eastern Europe 7.1 %; northern Europe 2.9 %). The species first established in central, northern and eastern Europe during the period 1950–2014 tended to exhibit a faster initial spread rate than the alien insects first established in southern Europe but there was a wide overlap in the credible intervals (Fig. 8).

Fig. 6

Invasion patterns of alien insect species recorded in Europe from 1950 to 2014: radial spread was calculated as $\sqrt{\text{area occupied}}/\pi$. Some of the species showing high rate of initial spread are abbreviated as follows: *Aj* *Acizzia jamatonica*, *Al* *Aproceros leucopoda*, *Cp* *Cydalima perspectalis*, *Ds* *Drosophila suzukii*, *Dk* *Dryocosmus kuriphilus*, *Ee* *Eretmocerus eremicus*, *Gb* *Glycaspis brimblecombei*, *Ha* *Harmonia axyridis*, *Li* *Leptocybe invasa*, *Lo* *Leptoglossus occidentalis*, *Or* *Obolodiplosis robiniae*, *Om* *Ophelimus maskelli*, *Pa* *Paysandisia archon*, *Rf* *Rhynchophorus ferrugineus*, *Ta* *Tuta absoluta*

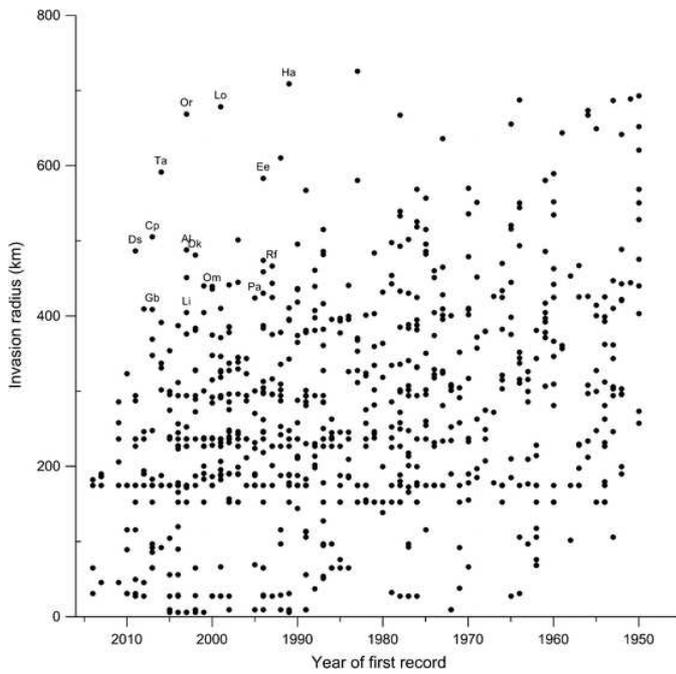


Fig. 7

Plot of radial spread over time since first record for 238 insect species recorded in Europe since 1950 that have colonized more than one country (*grey lines*) grouped by arrival period: **a** 1950–1969, **b** 1970–1989 and **c** 1990–2009. The *black lines* show the fit of modified Beverton–Holt functions (Eq. 1) to the data with 95 % credible intervals shown as *dotted lines*. **d** Estimates of initial spread rate (parameter a in Eq. 1) and 95 % credible intervals for species that arrived during the three periods

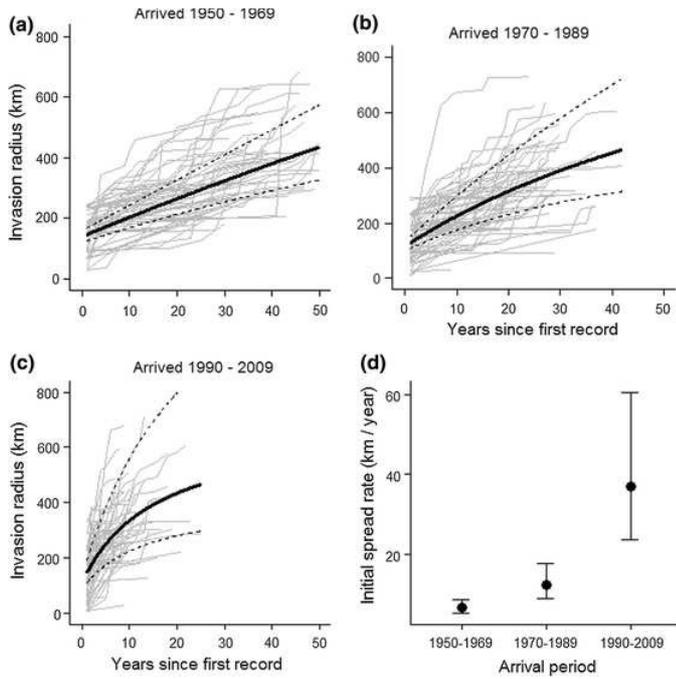
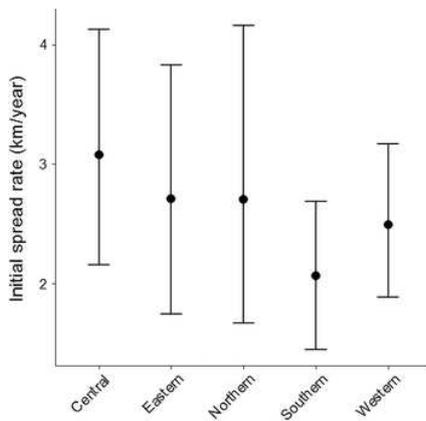


Fig. 8

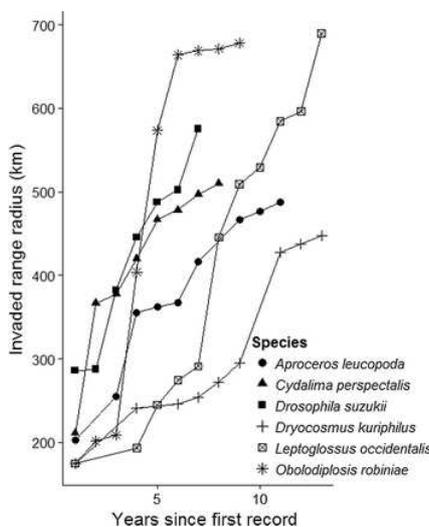
Estimates of parameter a (initial rate of radial spread, see Eq. 1) by region of introduction for species first recorded in Europe between 1950–2014



Several recently-detected species have spread much faster than others and colonized the major part of the European continent within 5 and 10 years following their first record (Fig. 6). Comparison of their spread patterns revealed differences in the rates of their spread once detected (Fig. 9). The fruit fly *Drosophila suzukii* showed a generally linear yearly increase in invasion radius. In contrast, the other five highlighted species all showed a dramatic increase in their invasion radius in certain years, which largely exceeded their potential flight capabilities. However, the years of dramatic increase in invasion radius varied: 454 km year⁻¹ between 4 and 6 years after the first record for the honeylocust gall midge, *Obolodiplosis robiniae*; 254 km year⁻¹ between 6 and 7 years, and again 131 km year⁻¹ between 11 and 13 years after the first record for the gall wasp *Dryocosmus kuriphilus*; 154 km year⁻¹ between 9 and 10 years after the first record for the North American seed bug, *Leptoglossus occidentalis*; 155 km year⁻¹ between 2 and 3 years after the first record for the box moth, *Cydalima perspectalis*; and 100 km year⁻¹ between 3 and 4 years after the first record for the elm sawfly, *Aproceros leucopoda*.

Fig. 9

Yearly spread pattern of six alien insect species having rapidly invaded Europe since the late 1990s. Elm zig-zag sawfly, *Aproceros leucopoda* (14 countries colonized in 2015); box tree moth, *Cydalima perspectalis* (23 countries colonized); chestnut gall maker, *Dryocosmus kuriphilus* (15 countries colonized); western conifer seed bug, *Leptoglossus occidentalis* (36 countries colonized); honeylocust gall midge, *Obolodiplosis robiniae* (32 countries colonized); vinegar fly, *Drosophila suzukii* (23 countries colonized)



Discussion

This study represents the first attempt to characterize variation in the rate and extent of spread for a large number of alien insect species recorded in Europe since 1800. Although caution should be taken to the use of date of first published record as a proxy for the record of introductions (Solow and Costello 2004; Costello et al. 2007), significant differences in initial spread rates were detected for several of the groups studied. For example, spread rates were faster for accidentally introduced species than for intentionally introduced (primarily biocontrol) insects. Feeding guild was important too whilst considerable variation was observed across insect orders, with Coleoptera and Hemiptera on the rapid end of the spread rate continuum and Orthoptera and Hymenoptera on the slow end. Perhaps most striking, however, was the finding of vastly elevated spread rate among insects introduced most recently (1990–2009), threefold higher than in the preceding 20 year period and 5.7-fold faster than during the period between 1950 and 1969. This pattern strongly suggests the hypothesis that changes in patterns and volumes of trade, particularly those related to the socio-political changes in Europe, may be a principle driver in the movement and spread of recent invaders. This hypothesis is outlined in detail below.

In alien plants, species with longer residence times tend to be more widespread (Rejmánek 2000; Pyšek and Jarošík 2005; Pyšek et al. 2015). A similar pattern is observed for insects (Fig. 1), but it does not correspond to a full saturation of the space available for invasion. Thus, only 11 of the 1171 (0.9 %) alien species recorded since 1800 have thus far invaded all of Europe (invasion radius >750 year⁻¹; Fig. 1). For species first detected after 1950, none have invaded all of Europe and only 30 of 761 (3.9 %) have invaded half of Europe (invasion radius >563 year⁻¹; Fig. 6) within 10 years of their first record. However, it is important to consider that since all species have

specific climatic and environmental requirements, the entire European territory is unlikely to be suitable for all species, e.g. continental or alpine regions would be unsuitable for insects associated with palms, eucalypts and other tropical/subtropical plants introduced to Europe. This may also explain why species first established in central-, northern and eastern Europe during the period 1950–2014 tend to exhibit a faster initial spread rate to the West and South than any of the alien insects first established in southern Europe.

Intentionally introduced species appeared to invade, on average, a smaller area than those introduced accidentally, and their initial spread rate was about three times lower than rates exhibited by the latter group. Apart from a few species reared as pets or for silk production that have escaped or been released into the wild, most of the intentionally introduced insects were released for biological control (Rabitsch 2010) and most of these were introduced after the 1950s (Roques 2010). Releases usually took place in selected environments depending on the specific purposes for which they were intended. It is thus not surprising that their expansion has been more limited on average than for accidentally- introduced species. This may in part explain differences in the spread rates between insect orders (Fig. 5), where the lowest initial spread rate is observed in Hymenoptera: about half (48.1 %) of alien Hymenopterans in Europe have been intentionally released for biological control, whereas this percentage ranged from 0 to 4 % in the other insect orders. Conversely, as Pyšek et al. (2011) suggested for alien plants, unintentionally introduced insect species are likely pre-adapted for dispersal and may tend to spread more effectively as a result.

The existence and duration of a lag phase, where the invading population has an initial slow period of growth that is followed by rapid expansion, is often difficult to distinguish from the later phases of invasion in the case of unintentionally introduced species. This lag phase appears to be variable among and within taxonomic groups (Aikio et al. 2010), lasting centuries for woody plants (Kowarik 1995) and decades for herbs (Pyšek and Prach 1993), but it is probably shorter for insects. Essl et al. (2011) observed that current numbers of alien insect species in Europe are better explained by contemporary rather than by historical indicators of socioeconomic activities, suggesting that lag times between introduction and establishment are shorter for insects than for other groups of organisms. They hypothesized that insect mobility facilitates the exploration of habitats and hence likely accelerates naturalization because barriers between suitable habitats and the actual places of introduction could be more easily overcome. Lag phases in recent insect introductions are apparently very short, particularly for those species detected in Europe since the late 1990s and that have spread rapidly throughout much of the continent (Fig. 89). It is likely that their arrival in Europe preceded their first detection by a few years but once detected, the majority of these species exhibited very rapid spread. Lag phases between discovery and the initiation of spread were only observed in the bug *Leptoglossus occidentalis* (4 years) and in the gall midge *Obolodiplosis robiniae* (3 years).

Spread patterns of herbivores, the most numerous group of insect invaders in Europe (51 %), generally differ from those of other feeding guilds, with a noticeable decline in speed with increasing residence time, although initial spread rate did not differ among guilds (Fig. 3). However, this decline appeared to be mainly present in species associated with herbaceous plants and crops. Spread rates of species associated with woody plants more closely resembled those of detritivorous species, whose invasion radius constantly increased over time. Many detritivorous species are believed to be disseminated with imported stored products (Roques 2010), whereas phytophagous species are mostly associated with the trade of living plants and, thus both could be easily moved with human activities. The ever-increasing trade in woody ornamental plants (Richardson and Rejmánek 2011; Eschen et al. 2014), as well as the generalized use of wood packaging material, could explain the constant increase in the mean invasion radius for insects related to woody as compared with herbaceous plants. This is coherent with spread rates observed in insect pests of plantation forestry, which exhibit incredibly rapid spread and facile jump-dispersal—even among continents—suggesting that human aided movement is important for some species, particularly those associated with commercial trees (Garnas et al. 2016; Hurley et al. 2016). Liebhold et al. (2013) did not detect differences in the rate of spread of alien borers, foliage feeders, and sap feeders invading the forests in the USA.

Our analyses identified significant increases in spread rates over time for species arriving since 1950. The mean initial spread rate of species detected after 1990 was around four times higher than for species detected during the decades following the 2nd World War (1950–1969), and three times higher than for species detected during the period 1970–1989. We hypothesize that the opening of borders to movement and trade enabled by the collapse of the Iron Curtain in 1989, the dismantling of internal custom checkpoints within the European Union in 1993, and successive enlargements of the EU in 2004 and 2007, could have facilitated the immediate spread of alien insect species. However, we cannot exclude the alternative hypothesis that the increased attention to alien species during recent years is responsible for these results, with greater efforts being put into the rapid detection of aliens at the country level. Chiron et al. (2010) found that the Cold War and its resulting commercial alliances in Eastern vs. Western blocks led to contrasting patterns in the numbers, composition and origin of birds introduced into each of these two socio-political European blocks. The results of the present study show that 71 alien insect species were first recorded in eastern Europe during the period 1950–1989 compared to 332 species first recorded during the same period in western Europe. Although these numbers could have been partly biased by differences in research facilities and publication opportunities between the East and the West, it is likely that the restrictions on international trade would have limited introductions of alien species to eastern Europe.

Six of the species that were detected only recently, and that appear to have spread more rapidly than others (Figs. 6, 9), share a common feature: spread is enhanced both by short-range active dispersal and human-mediated long-distance translocation, quite likely with infested nursery or crop stock. Rapid long-distance movements, over hundreds of km per year, however, were not identical between these species. Whereas the gall midge *Obolodiplosis robiniae* expanded by more than 450 km between the fourth and sixth year after its first record, such a long-range expansion was observed only after a decade in the chestnut gall wasp, *Dryocosmus kuriphilus*. These differences may be a consequence of chance associations with human transport vectors, which of course also interact with looser regulations around cross-border movement and trade. Wermelinger and Skuhrová (2007) stated that the spread of *O. robiniae* on black locust probably occurred mainly through human movement or the transport of plant material rather than via active dispersal. The decisive role of the motorway network in the spread of this gall midge in Slovakia was mentioned by Skuhrová et al. (2007) who showed that adults or infested leaves with pupae may be transported over large distances on the wheels and other parts of motor vehicles. Blank et al. (2010) considered that passive dispersal with traded material of elm plants for horticulture or forestry might be a major pathway for the elm

sawfly, *Aproceros leucopoda*. Similarly, the box tree moth, *Cydalima perspectalis* was first recorded from nurseries in many countries such as the Netherlands (Van der Straten and Muus 2010), and the United Kingdom (Mally and Nuss 2010), and it probably expanded to the Black Sea coast with *Buxus* exports from European nurseries on the occasion of the Olympic games in Sochi, Russia (Karpun and Ignatova 2013). However, the spread process could be even more complex, such as for *Leptoglossus occidentalis*, an invasive true bug native to Western North America, combining active dispersal of the adults, long-distance transport of eggs and maybe larvae within Europe with plant materials, and multiple introductions into different European regions including a bridgehead (global source) population in Eastern North America (Lesieur 2014; Garnas et al. 2016).

AQ2

The results of this study point to unrestricted horticultural trade in Europe as a key driver of alien insect spread. Such trade has increased dramatically as the political barriers in Europe have fallen and free movement of living plants and plant products has grown exponentially. Plant trade is likely to facilitate long-distance movement of alien insects and increases likelihood of the introduction of phytophagous species. It is important to recognize that once an introduction has occurred, the further spread within Europe, but also to adjacent regions and to other parts of the world, is facilitated, by for example ‘bridgehead effects’ where pests and pathogens move increasingly rapidly once established in areas outside their native range subsequent to the establishment of key populations (or bridgeheads) that become important exporters of invasive pests to other regions (Garnas et al. 2016). Actions such as those called for in the Montesclaros Declaration (<http://www.iufro.org/science/divisions/division-7/70000/publications/montesclaros-declaration/>), which calls for restrictions in plant trade have arisen from concerns regarding the growing numbers of alien invasive insects (and pathogens) moving throughout Europe. Mechanisms to reduce rapidly growing alien insect and pathogen ranges in Europe and globally (Wingfield et al. 2015) should be considered and implemented at all stages from improved biosecurity measures, surveillance and eradication activities to diligent management and control actions.

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Electronic supplementary material

Supplementary material S1. List of the 1171 alien insect species for which the date of first record in Europe was known, including taxonomic details (insect order), date of first record in Europe, total surface invaded in Europe by 2014, intentionality of the introduction (I: Intentional; U: Unintentional), feeding regime (DET: Detritivorous species; PAR: Parasites and Predators; PHY: Phytophagous species), and type of host plants for phytophagous species (W: woody plants and woody material; NW: herbaceous plants and crops). (XLSX 99 kb)

Supplementary material S2. List of the 455 alien insect species first recorded in Europe following 1950, and for which the date of first record in every invaded country is known. (XLSX 99 kb)

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