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Distribution, impact and rate of spread of emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) in the Moscow region of Russia

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Surveys of ash trees along the major motorway routes leading away from the city of Moscow during July 2013 indicated that emerald ash borer (*Agrilus planipennis*) was well established up to 235 km west of the city and 220 km to the south. Over the last 4 years, the beetle has spread in these directions at an average rate of 30–41 km year^{-1}, which cannot be explained by natural dispersal alone and implies that human-assisted transport is contributing significantly to the spread of the pest, probably via the hitchhiking of adult beetles on vehicles. The European common ash (*Fraxinus excelsior*) is uncommon in Moscow and in the boreal forests to the west and north, but those trees that are present suggest that this species is not killed as rapidly by *A. planipennis* as North American ash species and that it may need to suffer a degree of stress before it succumbs rapidly to infestation. Nevertheless, *A. planipennis* is a major threat to *F. excelsior*, and south of Moscow, where the beetle has become established in natural broadleaved woodlands in which *F. excelsior* is a major component, many of the ash trees are suffering severe dieback and mortality. The abundance and almost continuous distribution of *F. excelsior* in these woodlands means that *A. planipennis* now has the opportunity to spread unhindered on a broad front to other countries in Europe.

Introduction

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is native to north-east China, Korea, Japan, Taiwan, Mongolia and the Russian Far East (Haack *et al.*, 2002; Liu *et al.*, 2003). In these regions, the beetle behaves as a minor secondary pest, attacking severely stressed and dying ash trees of the local species *Fraxinus mandshurica* Rupr. and *F. chinensis* Roxb., and it is not particularly common (Liu *et al.*, 2003; Zhao *et al.*, 2005; Wang *et al.*, 2010). *Agrilus planipennis* came to prominence in 2002 however, when it was identified as the cause of extensive dieback and death of native ash trees, particularly green ash (*F. pennsylvanica* Marsh.), white ash (*F. americana* L.) and black ash (*F. nigra* Marsh.), in southeast Michigan in the United States and in southern Ontario in Canada (Haack *et al.*, 2002; Cappaert *et al.*, 2005). The beetle had probably been introduced up to 10 years earlier with solid wood packaging material from Asia, but it was only detected once ash trees started to die on a large scale (Siegert *et al.*, 2007). The population of *A. planipennis* in North America has continued to increase and spread, and by 2012, infestations had been recorded in 19 states and in southern Quebec, as well as in Ontario, Canada (EAB Information, 2013). The beetle has killed tens of millions of ash trees over the last 10 years and has raised concerns over the future of ash in North America (Poland and McCullough, 2006; EAB Information, 2013). The cost to the US economy over the 10-year period from 2009 to 2019, in terms of tree removal and replacement alone, is expected to exceed $10 billion (Kovacs *et al.*, 2010).

North American species of ash appear to be highly susceptible to *A. planipennis,* because they have not been exposed previously to the beetle and they lack the chemical and physical mechanisms of resistance that Asian ash species have developed as a result of their close association with the beetle over a long period of evolutionary time (Rebek *et al.*, 2008). North American ash trees usually die within 5–7 years of initial attack, although some may die within 1–2 years (Knight *et al.*, 2013). The lack of co-evolved resistance in North American ash species, and the high rates of mortality that were being observed, suggested that European ash species such as *F. excelsior* L. might also be at risk should *A. planipennis* be introduced into Europe. Consequently, in 2004, the European Plant Protection Organisation (EPPO) added *A. planipennis* to its A2 list of quarantine pests, i.e. a species not present in the EPPO region, but which was likely to cause significant economic, environmental and social damage if it was introduced and against which strict regulation was required. Import restrictions on ash material and new international standards on the quality and treatment of wood packaging (ISPM 15) have greatly reduced the chances of *A. planipennis* being introduced into Europe from either east Asia or North America and, to date, there have been no reports of any interceptions of living life stages of *A. planipennis* being imported into the EU or the wider EPPO region.

In 2007 however, *A. planipennis* was reported from Moscow in Russia, where it was found to be attacking and killing large numbers of green ash, *F. pennsylvanica,* in parks and gardens, and along streets and in shelterbelts within the city (EPPO, 2007; Mozolevskaya and Izhevskiy, 2007; Baranchikov *et al*., 2008). *F. pennsylvanica* is widely planted in Moscow and other Russian cities as an ornamental tree and as a landscaping species, and in Moscow, dieback had been observed in many of the *F. pennsylvanica* since 2004 and was increasing. Specimens of an *Agrilus* species were collected in Moscow during 2003–2006, and in 2007, these were confirmed as *A. planipennis* (Baranchikov *et al*., 2008; Mozolevskaya *et al*., 2008). It is unclear how *A. planipennis* arrived in Moscow, but it may have been introduced with infested planting stock or, more likely, arrived in wood packaging material from China (Mozolevskaya and Izhevskiy, 2007; Baranchikov *et al*., 2008; Izhevskiy and Mozolevskaya, 2010).

The presence of *A. planipennis* in Moscow presents a serious threat to ash trees in Europe, particularly as there is no geographical barrier to prevent spread westwards into other European countries (Baranchikov *et al*., 2008). Initially, *A. planipennis* was confined to the centre of Moscow, but surveys carried out in 2009 found that the area of infestation had increased and that severely damaged and dying *F. pennsylvanica* were present up to 95–100 km west and south of the city centre (Baranchikov *et al*., 2010). The Moscow region is within the natural range of *F. excelsior*, which includes most of Europe from the Atlantic coast to southern Scandinavia, Finland and the Baltic States, and the European part of Russia (Nikolaev, 1981; FRAXIGEN, 2005; AgroAtlas, 2013). *Agrilus planipennis* has the potential therefore, to disperse across the whole of this region. The other European species of ash that are reasonably widespread, flowering ash (*F. ornus* L.) and narrow-leaved ash (*F. angustifolia Vahl.)*, have more southerly distributions that extend to Romania, southern Russia and the Transcaucasus, but they are planted widely outside this range (FRAXIGEN, 2005; AgroAtlas, 2013).

There is very little information on the impact of *A. planipennis* on European ash species. Volkovich (2007) (in Baranchikov *et al*., 2008) reported one *F. excelsior* killed by *A. planipennis* in Moscow and other reports suggest that *F. excelsior* is highly susceptible to attack (Baranchikov *et al*., 2010), but there is no detailed information on damage or rates of mortality for this species. As a result, there is still a great deal of uncertainty surrounding the likely future impact of *A. planipennis* on ash in Europe. Between 7 and 19 July 2013 therefore, the authors surveyed ash trees in Moscow and travelled by car along the main motorways through the surrounding region and inspected ash trees at as large a number of sites as possible, looking for damage and infestation by *A. planipennis*, to try to obtain a better picture of how the pest might be affecting *F. excelsior*, and to determine how far and how quickly it has spread since 2009.

Impact on ash trees in Moscow

Larvae of *A. planipennis* tunnel beneath the bark of ash trees and feed on the cambium and outer sapwood. The tunnels disrupt the transport of water and nutrients and effectively girdle the branches and stem, which then die above the point of infestation (Haack *et al*., 2002). The adult beetles are active from mid-May through to the end of June. They are metallic green and 8.0–13.5 mm long and slender in shape. Most live for ~3 weeks, and throughout their lives, they feed on ash foliage, chewing out small, irregular-shaped pieces from around the margins of the leaves. At least a few days of feeding are required before the adult beetles mate, and 1–2 weeks of feeding may be required before the females begin to lay eggs. The eggs are laid singly in crevices in the bark of ash trees. On hatching, the larvae tunnel through the bark and start feeding on the phloem tissues. The tunnels they produce are typically long (10–50 cm) and sinuous, and they cut backwards and forwards across the stem under the bark. (Note that the presence of *A. planipennis* larvae beneath the bark of ash trees does not result in any bleeding or dark staining on the outside of the stem, unlike attack by *A. biguttatus* on oak, *Quercus robur,* in which bleeding is often a highly visible symptom of infestation). Most larvae are fully developed by late autumn. They are white or cream-coloured, characteristically elongate and flattened, and when full-sized are 26–32 mm in length. The larvae overwinter and pupate in the following spring, in a cavity excavated in the outer sapwood or, in thicker barked trees, in the bark. The adult beetles emerge in May by chewing an exit hole through the bark. The exit holes produced by *Agrilus* species are D-shaped, with one side flat and the other side curved. Those produced by *A. planipennis* are relatively large and 3–4 mm in width. The presence of D-shaped exit holes on branches and the main stem of an ash tree is a clear indication that the tree is infested by the beetle. Further information on the life-cycle and biology of *A. planipennis* and illustrations of the signs and symptoms of attack are provided by Scarr *et al*. (2002), de Groot *et al*. (2006), McCullough *et al*. (2008), Wang *et al*. (2010) and EAB Information (2013).

In Moscow and the area immediately around the city (Moscow Oblast), *A. planipennis* has probably killed >1 million ash trees, although the exact figure will never be known (Y. Gninenko, unpublished data). Some of the dead ash trees have been removed, but the vast majority remain standing irrespective of their condition. The authors inspected a large number of these trees at as many locations in Moscow as possible in the time available and assigned each tree to one of several damage categories (Table 1). *F. pennsylvanica* was by far the most abundant ash species in the city and, although most were badly affected by *A. planipennis*, there was a range in tree condition. It was soon apparent that small trees with a diameter at breast height (DBH) of <10 cm were generally in very good condition and showed no signs of infestation. Small ash trees and small diameter branch material have also been observed to be less frequently attacked by *A. planipennis* in North America, probably because the bark is too thin for larval development (Timms et al., 2006; Wang *et al*., 2010), but it may also relate to the general vigour of young trees. In Moscow where *A. planipennis* was found in trees with a DBH of <10 cm, it was invariably on poor, dry sites, especially where the trees had been planted recently and were struggling to establish.

In contrast, only 2 per cent of medium- and large-sized *F. pennsylvanica* (i.e. trees with a DBH of 10–65 cm) were in a good condition and showed no signs of *A. planipennis* infestation (Table 1). The condition of the other 98 per cent varied and showed a sequence in the development of damage symptoms that started with a reduction in foliage density and development of dieback in the upper

Table 1 The relative condition of green ash *F. pennsylvanica* and European ash *F. excelsior* affected by *A. planipennis* in the city of Moscow in 2013. The table gives the total number of trees with a DBH of >10 cm that were observed in each damage category

	Damage category	*F. pennsylvanica*	*F. excelsior*
0	Healthy tree with a dense, full canopy (no dieback or signs of damage)	7	6
1	Foliage density reduced in the upper $\frac{1}{3}$ of the canopy; small leaves at top (no dieback)	9	1
2	Foliage density markedly reduced in the upper $\frac{1}{2}$ of the canopy, but very little dieback. No re-growth or just a few epicormic shoots on the main stem	22	-
3	Upper $\frac{1}{3}$ of main stem dead; new shoots emerging from the main stem below	118	-
4	Upper $\frac{1}{2}$–$\frac{2}{3}$ of the main stem dead; new shoots growing from the lower half of the main stem and at ground level	340	-
5	Main stem dead; new shoots from the base of the stem at ground level	424	-
6	Foliage density greatly reduced (>90% leaves lost); just a very few scattered leaves present. No re-growth or a few shoots from the stem base. Tree dying	9	7
7	Standing dead	11	-
Total		940	14

canopy, followed by the progressive dieback and death of the main stem from top to bottom until the whole tree was affected (damage categories 2–5 in Table 1). On better quality sites, or perhaps where populations of *A. planipennis* were lower, infestation and dieback did not appear to have developed quickly and the trees produced new shoots from epicormic buds on the main stem, below the section that was damaged. A similar sequence of dieback and re-growth is seen in ash trees in North America (Haack *et al*., 2002; Scarr *et al*., 2002; McCullough *et al*., 2008). In Moscow, the new shoots produced by damaged trees were often sufficiently vigorous to produce a secondary canopy, especially in trees where the upper dead parts had been removed.

The new growth on damaged trees was generally not attacked by *A. planipennis*, most likely because the maximum diameter of the stems had not reached 7–10 cm. A few D-shaped exit holes were found at the base of some of the larger epicormic shoots on a few trees, indicating that these shoots would eventually be attacked and killed, but most of the new shoots on *F. pennsylvanica* in Moscow currently remain free of attack and a second wave of infestation killing this new growth has yet to be observed.

At other sites in the city, *F. pennsylvanica* appeared to have died much more quickly, within 1–2 years, and the trees had not had time to produce epicormic growth from the main stem. Large numbers of D-shaped exit holes were visible in the trunks of these trees. However, because the roots remained alive, almost invariably new shoots had grown up from the base of the stem at ground level. There was no sign of these new shoots being attacked by *A. planipennis*, even though in trees where the main stem had died several years ago, these basal shoots had reached a height of 4–5 m and in some shelterbelts it formed a dense understorey. These trees were functionally still alive, but they had lost all value as an ornamental and landscape species.

Fraxinus excelsior is also planted in Moscow, but only in small numbers. We located 14 in the city, representing just 1.5 per cent of all of the ash trees surveyed (Table 1). No other ash species were found. This small sample did not show the same pattern of damage and dieback as seen in *F. pennsylvanica*, and it was notable that seven of the *F. excelsior* were in a very good condition and showed no obvious signs of attack by *A. planipennis*, whilst the other seven, although 20–30 m tall and growing well until recently, were currently in a very poor state and appeared to be dying quite rapidly (Table 1). A small number of D-shaped exit holes were visible in the trunks of these dying *F. excelsior*, showing that they were being attacked by *A. planipennis*, but the trees were located in an area of Tsaritsyno Park in south Moscow where other tree species were also in a poor condition and showing dieback. This suggests that additional factors were involved in the decline of *F. excelsior* at this site, and the poor condition of the trees was not due entirely to attack by *A. planipennis*.

Current distribution

Fraxinus pennsylvanica has been planted in large numbers in protective lines (against snow drift) and in shelterbelts along the main motorways and other roads leading away from Moscow. The impact of *A. planipennis* on these trees is highly visible, with most of those close to the city severely damaged or standing dead, and those further out showing progressively less damage. It is possible therefore, by travelling outward from the city, to track the development of the infestation and locate the approximate edge of the outbreak.

North-west to Tver

Roadside plantings of *F. pennsylvanica* severely damaged by *A. planipennis* were readily visible along the M10 motorway from Moscow to Klin and Novozavidoskiy. Further out, the condition of *F. pennsylvanica* was more variable, with some trees only partly dead and with new shoots arising from the lower part of the main stem. The last trees in this direction to show obvious signs of *A. planipennis* attack was a roadside planting of *F. pennsylvanica* 2 km west of Emmaus (8 km south-west of Tver) at a distance of 155 km from Moscow. (All distances are measured from the central point of the city of Moscow) (Figure 1). These trees were 6–10 m tall and showed a range of canopy condition, including some in which foliage density was reduced by 70–80 per cent. A large amount of adult *A. planipennis* feeding damage was visible on the leaves, especially in the upper canopy. In contrast, there were no signs of *A. planipennis* infestation on *F. pennsylvanica* in Tver or further along the M10 as far as Torshok.

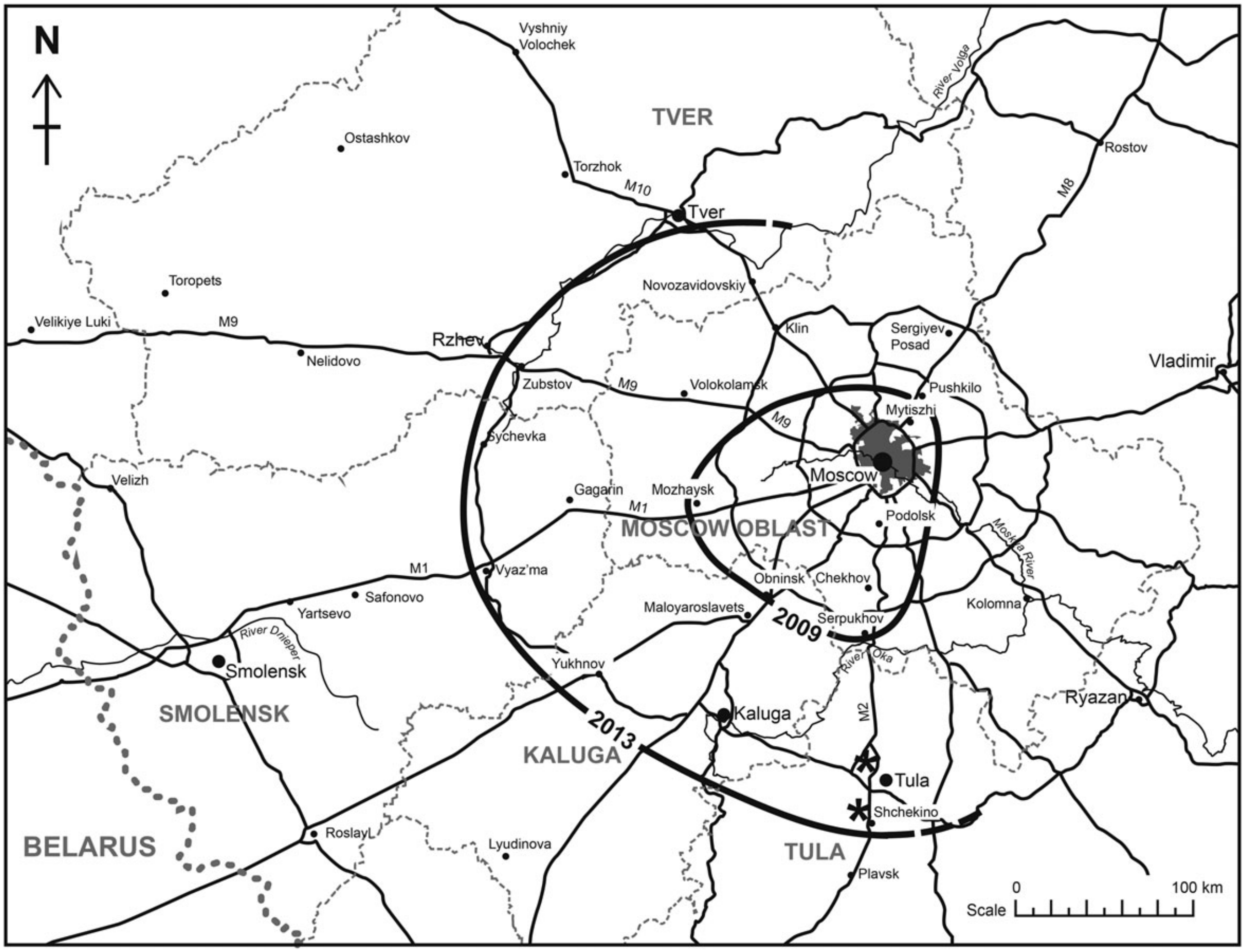

Figure 1 The distribution of *A. planipennis* in the Moscow region of Russia in 2009# and 2013, as indicated by the presence of damaged and dying ash trees. Star symbols mark the location of European ash *F. excelsior* in natural woodlands, which is mentioned in the text. #After Baranchikov *et al.* (2010).

West to Rzhev and Vyaz'ma

Going west on the M9, in the direction of Rzhev and Velikiye Luki, the furthest location where *A. planipennis* infestation could be confirmed was a row of >80 *F. pennsylvanica* (5–7 m tall) set back from the road on the west side of Zubstov, at a distance of 215 km from Moscow (Figure 1). The trees at this site showed considerable dieback and some had died, although this may have been due partly to poor site conditions rather than directly because of *A. planipennis*. Small numbers of D-shaped exit holes and *A. planipennis* larvae were found on upper branches of two trees that were felled, and adult feeding damage was evident on the foliage. There were no signs of *A. planipennis* further west in Rzhev, Nelidovo or Velikiye Luki.

Travelling south-west on the M1, severely damaged and dying *F. pennsylvanica* were seen just north of Vyaz'ma at the location reported by Baranchikov and Kurteev (2012). A further 3 km west of Vyaz'ma, at 235 km from Moscow, a single line of *F. pennsylvanica* planted along the motorway had very thin canopies and showed characteristic signs of infestation. After this point however, the motorway passed through extensive areas of natural forest dominated by Scots pine (*Pinus sylvestris* L.), aspen (*Populus tremula* L.), birch (*Betula pendula* Roth.) and willows (*Salix caprea* L., *S. cinerea* L.) in which ash was evidently very scarce, and there were no roadside plantings of *F. pennsylvanica*. Consequently, it was not possible to delimit the edge of the outbreak area any further west of Vyaz'ma. A large number of *F. pennsylvanica* were inspected at Yartsevo (335 km from Moscow), and both *F. pennsylvanica* and *F. excelsior* were observed in Smolensk (Table 2), but none of the ash trees in these towns showed any signs of attack by *A. planipennis*. The healthy status of *F. pennsylvanica* in Smolensk, outside the area occupied by *A. planipennis*, was much better than, and contrasted markedly with, the condition of this species in Moscow (Table 1).

South to Tula

Dead and dying *F. pennsylvanica* were evident along the M2 motorway up to 110 km south of Moscow, but beyond this point, there were few roadside plantings of this tree species. Twenty kilometres north of Tula, the landscape along the motorway changed from

Table 2 The relative condition of green ash *F. pennsylvanica* and European ash *F. excelsior* in Smolensk, outside the current range of emerald ash borer. Data are restricted to established trees with a DBH of >10 cm

Damage category	*F. pennsylvanica*	*F. excelsior*
Dense, full canopy. (no dieback or signs of damage)	133	104
Foliage density reduced; small amount of branch dieback	1	4
Foliage density greatly reduced; moderate-to-severe branch and stem dieback	–	1
Standing dead	–	3
Total	134	112

open countryside to a mixture of large fields and blocks of mixed broadleaved woodland, in which *F. excelsior* was a major co-dominant component. It was very noticeable however that the *F. excelsior* was in a very poor condition compared with other tree species. Over the next 30 km (160–190 km from Moscow), the canopy of half of the *F. excelsior* trees showed a 50–80 per cent reduction in foliage density and a third of the trees had lost virtually all of their foliage or had died. The remainder were in reasonably good health. Between 190 and 220 km from Moscow, to ~5 km south of Shchekino (Figure 1), the general condition of *F. excelsior* improved but was still highly variable. About half of the trees appeared healthy and in good condition, but a third had lost almost all of their foliage or were dead. The rest were intermediate.

After 220 km, almost all (90 per cent) of the *F. excelsior* were in a good condition and showed no reduction in crown density. A small number of very poor trees were present amongst otherwise healthy trees up to 240 km, and these showed some evidence of feeding damage by adult *A. planipennis*, but there were no other signs of infestation. Further south at Plavsk, both *F. pennsylvanica* and *F excelsior* were present and both trees species were undamaged and showed no signs of infestation.

The trend in the condition of *F excelsior* from Tula, where the trees were generally in a very poor state, to south of Shchekino, where most of the ash trees were in a good condition, matches the pattern of damage and the distances that *A. planipennis* has spread in other directions from Moscow (Figure 1), and indicates that the beetle is well established in the broadleaved woodlands in this area. This is very significant, because it means that the pest is now present in areas where *F. excelsior* is naturally abundant in woodland, where it has the potential to increase and spread very effectively.

Rate of spread

In 2009, the observed distribution of *A. planipennis* outside Moscow was delimited by the towns of Mytiszhi (20 km north), Bykovo (35 km south-east), Serpukhov (100 km south) and Mozhaysk (108 km west) (Baranchikov *et al*., 2010; Figure 1). By 2013, the southern boundary of the outbreak had moved 120 km further south to just south of Shchekino (Figure 1), indicating a rate of spread in this direction of 30 km year^{-1} over the last 4 years. To the west, the identifiable outer limit of the outbreak has extended by 125 km from Mozhaysk to just west of Vyaz'ma, indicating a rate of spread of 31 km year^{-1}. Baranchikov and Kurteev (2012) however observed ash trees severely damaged by *A. planipennis* at almost the same location near Vyaz'ma in 2012, a year earlier. This being the case, then *A. planipennis* must have spread along the M9 at an average rate of 41–42 km year^{-1} between 2009 and 2012. This is probably closer to the actual rate of spread in this direction compared with the estimate based on the boundary observed in 2013, which could not be placed further west because of the scarcity of ash trees between Vyaz'ma and Yartsevo.

Spread north of Moscow appears to have occurred at a slower rate. We did not search for *A. planipennis* east or north-east of Moscow, because we were interested primarily in spread to the west and south, but Baranchikov and Kurteev (2012) reported that *A. planipennis* was well established in Pushkino in 2009 and in Sergiyev-Posad, 40 km further north, 3 years later, indicating a rate of spread in this direction of 13 km year^{-1}.

A. planipennis was well established in Moscow by 2003, but it may have been introduced initially in the late 1990s (Izhevskiy and Mozolevskaya, 2010). Up to 2005, the rate of spread was estimated to be ~4 km year^{-1}, and subsequently, it has been estimated to be 10–12 km year^{-1} (Baranchikov and Kurteev, 2012). The rate of spread between 2009 and 2013 is much greater and suggests an increase in the rate at which the outbreak is expanding, at least to the west and south. The previous estimates of spread are within the natural dispersal capabilities of *A. planipennis*. Even though most adult female *A. planipennis* lay their eggs within a few hundred metres of their point of emergence (Mercader *et al*., 2009; Siegert *et al*., 2010), they have the capacity to fly up to 10 km over a period of several days (Taylor *et al*., 2010). The original outbreak of *A. planipennis* in Michigan, in the United States, spread initially at a rate of 10–11 km year^{-1}, primarily at this time through natural dispersal (Smitley *et al*., 2008). Subsequently, the *A. planipennis* outbreak in the United States has expanded at a rate of >20 km year^{-1}, and this can only have been achieved through human-assisted movements, which in North America appear to involve the transport and redistribution of firewood from infested to uninfested areas (Muirhead *et al*., 2006).

The high rates of spread of *A. planipennis* along the motorways west and south of Moscow also imply a considerable influence of human-assisted transport, but local movement of firewood is not thought to be a significant factor in this region, because ash is not generally abundant and it is not used for firewood as much as conifers or birch (Baranchikov *et al*., 2010). The dead ash trees along the motorways are not being felled and utilized. If this is the case, the only mechanism that might explain the high rate of dispersal is inadvertent hitchhiking of adult *A. planipennis* in or on vehicles travelling along these extremely busy motorways. Hitchhiking on vehicles has contributed to the spread of *A. planipennis* in North America (Buck and Marshall, 2008). In the Moscow region, this process has probably been made more effective by the practice of planting *F. pennsylvanica* along the main roads, often on marginal sites, which has provided a highly suitable host plant at the very places where the beetle is likely to be deposited.

Vyaz'ma is 230 km from the Belarus border (compared with Shchekino, which is 346 km from the Ukraine border). At the current rate of spread, *A. planipennis* should cross the border in 6–7 years of time, in ~2020. Baranchikov and Kurteev (2012) also predicted that *A. planipennis* would reach Belarus by 2020. However, the beetle might arrive earlier. In North America, *A. planipennis* has shown unexpected long distance 'jumps' of up to 100–200 km beyond the known edge of the outbreak area, presumably as a result of human-assisted movements (Muirhead *et al*., 2006; Smitley *et al*., 2008). It is quite possible therefore that isolated populations of *A. planipennis* already exist at a considerable distance outside the known area of distribution in Russia, but remain undetected.

Impact on European ash, *Fraxinus excelsior*

Only 14 *F. excelsior* were observed in Moscow and in the immediate surrounding area, and this made it difficult to obtain a direct comparison of the state of this species with that of *F. pennsylvanica*. In Moscow, half of the *F. excelsior* were in a good condition and showed no signs of infestation by *A. planipennis*, whereas the other half were in rapid decline (Table 1), albeit on a site where other tree species, not just *F. pennsylvanica*, were in a poor condition, which suggests that site conditions were also influencing the trees' condition.

Elsewhere, the only other location within the outbreak area where *F. excelsior* was found was at Zubstov, west of Moscow. Fourteen large *F. excelsior* (25–30 m tall) were found here in the central town park and along some of the streets and were in a very good condition and showed no signs of beetle attack, even though *A. planipennis* was attacking *F. pennsylvanica* <1 km away to the west. Unfortunately, there were no *F. pennsylvanica* in the same park or streets with which to make a direct comparison, but these trees and those in Moscow indicate that *F. excelsior* is not being killed immediately by *A. planipennis*, even when the beetle is present in the general area, and that it may not be as susceptible. Studies on the feeding preferences of adult *A. planipennis* on different species of ash also suggest that *F. excelsior* is not as susceptible as North American ash species, although not as resistant as Asian ash species (Pureswaran and Poland, 2009).

South of Moscow, *F. excelsior* was abundant in the mixed broadleaved woodlands near Tula and Shchekino, but *F. pennsylvanica* was not present in the same woodlands and was less frequent here along the roads, which again prevented a direct comparison being made between the two species. The condition of *F. excelsior* was highly variable, especially further south where dead and dying trees were scattered amongst trees with full, undamaged canopies. Thus here, as in Moscow and Zubstov, *F. excelsior* was not dying rapidly *en masse*, unlike *F. pennsylvanica*, and it was apparently taking longer for the majority of *F. excelsior* to succumb to infestation. The variable condition of *F. excelsior* in these woodlands may reflect a greater degree of genetic diversity amongst the ash trees in these natural populations, leading to a more variable response to infestation, or it may reflect a greater influence of competitive interactions between the trees, or small-scale variation in site quality. *Agrilus planipennis* preferentially attacks trees weakened by drought, competition or other factors (e.g. girdling) in its native range and in North America (McCullough *et al*., 2009; Tluczek *et al*., 2011), and this may play a large part in determining which trees are attacked first in woodland habitats.

Some evidence that a degree of stress might be more important in pre-disposing *F. excelsior* to attack by *A. planipennis*, compared with *F. pennsylvanica*, was provided by the trees in Tsaritsyno Park, in Moscow, where the dying *F. excelsior*, although attacked by *A. planipennis,* occurred on a site where other trees were in decline. A significant role of tree stress in determining whether *F. excelsior* is attacked by *A. planipennis* might also explain some features of how the Moscow outbreak has developed over time, particularly an apparent difference in the rate and manner in which *F. pennsylvanica* and *F. excelsior* have been killed. *F. pennsylvanica* was the main tree species affected during the first phase of the outbreak, up to 2009, and it was the mass dieback of this species that led to the discovery of *A. planipennis* (Mozolevskaya *et al*. 2008; Izhevskiy and Mozolevskaya, 2010). Subsequently, *F. excelsior* has been reported to be the one more widely attacked, and it is tempting to think that this may be related to the extreme drought that affected Moscow and a large part of European Russia in 2010 (Mokhov, 2011). Prior to the drought, *F. excelsior* was perhaps less susceptible to *A. planipennis*, and as a result, the outbreak was most noticeable amongst *F. pennsylvanica*. The drought, however, is likely to have made both *F. excelsior* and *F. pennsylvanica* more vulnerable to attack, but because *F. pennsylvanica* was already widely damaged or had died, the new wave of infestation was more noticeable amongst *F. excelsior*, which previously had not been as badly affected. If this is the case, and *F. excelsior* became susceptible mainly after the 2010 drought, then perhaps *A. planipennis* behaves more as an aggressive secondary pest toward this ash species, killing trees that might otherwise recover, but nevertheless requiring trees generally to be suffering some degree of stress before it can attack successfully.

A range of factors can induce stress in trees, making them more susceptible to attack by wood-boring insects, including abiotic factors, such as drought, water-logging and severe frost, and biotic factors, such as defoliation and disease (Wargo, 1996; Thomas *et al*., 2002). Across much of Europe, *F. excelsior* is currently being damaged by infections of the fungal pathogen *Chalara fraxinea* (teleomorph = *Hymenoscyphus pseudoalbidus*) (Pautasso *et al*., 2013). This invasive organism, first found in Poland and Lithuania in 1992, has not yet been recorded from Russia (except Kalingrad on the Baltic coast) (Forestry Commission, 2013; Pautasso *et al*., 2013). Infection with *C. fraxinea* is especially damaging to *F. excelsior*, especially young trees, which are often killed within one growing season of symptoms becoming visible. Older trees usually survive initial attacks but tend to succumb after several seasons of infection. Ash trees weakened by infection, however, are likely to be very attractive to *A. planipennis*. Consequently, once the distributions of *C. fraxinea* and *A. planipennis* overlap, as they inevitably will, the combined action of the two organisms is likely to leave very few ash trees remaining intact.

Early detection and implications for management

Low population densities of *A. planipennis* are notoriously difficult to detect and infestations typically remain unnoticed for several years until damage becomes clearly visible (McCullough *et al*., 2008; Ryall *et al*., 2011; Mercader *et al*, 2012). The boundaries of the *A. planipennis* outbreak in the Moscow region shown in Figure 1 are therefore conservative and mark the furthest extent that visible damage and definite signs of infestation were observed. The exit holes and adult feeding damage found at these locations will have been produced by beetles emerging at the site, at least one generation after the initial colonization of the trees, and these beetles will have dispersed. Therefore, *A. planipennis* is undoubtedly present a further 10 km or more beyond the identifiable edge of the distribution area, but at densities that are almost impossible to detect (Baranchikov and Kurteev, 2012).

The implication for management is that it is virtually impossible to devise a strategy that will prevent *A. planipennis* from spreading. A *cordon sanitaire* failed to prevent further spread of *A. planipennis* in Canada, even though during 2003 and 2004 every ash tree was felled up to 10 km ahead of the advancing outbreak front (Marchant, 2004, 2005). New infestations were found beyond the ash free zone almost as soon as it was created. Some of these infestations had been present at the time the zone was established, but they were inconspicuous and had not been detected during initial surveys, whilst other infestations appeared later as a result of the unintentional movement of the beetle across the zone in firewood, timber and nursery plants.

The edge of the *A. planipennis* outbreak in the Moscow region has been relatively easy to determine because of the highly visible damage to *F. pennsylvanica* along the main motorway network. Further out, e.g. west of Vyaz'ma, *F. pennsylvanica* is not as frequently planted and the edge of the outbreak is more difficult to find. To the south, the presence of *A. planipennis* is revealed by the trend in dieback and death of *F. excelsior* in the natural woodlands. However, the more variable state of the *F. excelsior* in these woodlands, especially toward the leading edge of the outbreak, makes it particularly difficult to pick out the earliest signs of infestation (canopy thinning in a small number of trees) against the normal background variation in tree condition inherent in a woodland habitat. Consequently, in these natural woodlands, the spread of *A. planipennis* is going to be particularly difficult to track and, given the continuity in the distribution of *F. excelsior* in and beyond this area, the beetle now has the opportunity to spread largely undetected on a broad front toward southern Belarus and Ukraine, which will present surveillance and monitoring programmes with an exceptionally difficult challenge.

Conclusions

The rate of spread of *A. planipennis* in the Moscow region over the last 4 years has been faster than that previously reported, and the pest is now well established 235 km west and 220 km south of the city. Current rates of spread cannot have been achieved without a significant contribution from human-assisted movements, of which hitchhiking on vehicles seems to be the most likely pathway, assisted by the presence of a highly susceptible host species (*F. pennsylvanica*) along the main roads. To the south of Moscow, *A. planipennis* has become established in natural broadleaved woodlands where *F. excelsior* is abundant. Many of the *F. excelsior* in these woodlands are suffering severe dieback and are in decline, but *F. excelsior* appears not to be as immediately susceptible to *A. planipennis* as *F. pennsylvanica*, and it may need to suffer a degree of stress before it succumbs rapidly to infestation. The long-term impact of *A. planipennis* on *F. excelsior* is expected to be significant however, especially in the future when the pest encounters ash trees that are infected with the fungal pathogen *C. fraxinea*. The consequences of the spread of *A. planipennis* for other European ash species (*F. ornus* and *F. angustifolia*) remains unknown.

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Conflict of interest statement

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