Between Ash Dieback and Emerald Ash Borer: Two Asian Invaders in Russia and the Future of Ash in Europe

Dmitry L. Musolin*[1], Andrey V. Selikhovkin[1,2], Dmitrii A. Shabunin[3], Viacheslav B. Zviagintsev[4] and Yuri N. Baranchikov[5]

[1] *Department of Forest Protection, Wood Science and Game Management, Saint Petersburg State Forest Technical University, Institutskiy per., 5, Saint Petersburg, 194021 Russia*

[2] *Department of Biogeography and Environmental Protection, St. Petersburg State University, Universitetskaya nab. 7-9, St. Petersburg, 199034, Russia*

[3] *Department of Selection, Reforestation and Chemical Thinning, Saint Petersburg Forestry Research Institute, Institutskiy av., 21, St. Petersburg, 194021 Russia*

[4] *Department of Forest Protection and Wood Science, Belarusian State Technological University, Sverdlova str., 13a, Minsk, 220050, Republic of Belarus*

[5] *Department of Forest Zoology, V.N. Sukachev Institute of Forest, Federal Research Center «Krasnoyarsk Science Center of the Siberian Branch of the Russian Academy of Sciences», Akademgorodok 50, Krasnoyarsk, 660036, Russia*

** Corresponding author: musolin@gmail.com, tel. +7 921 325 9186*

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Abstract

Four ash species are native to Russia (*Fraxinus excelsior*, *F. angustifolia*, *F. chinensis*, *F. mandshurica*) while *F. pennsylvanica* was introduced from North America. Ash forests cover 666 300 ha (0.1% of total forest area of Russia) and constitute a volume of 77.91 mln m^3. Ash is widely used in the greening of populated places, around fields and along inter-city roads. We review the current situation with two recent invaders – ash dieback fungus *Hymenoscyphus fraxineus* (Ascomycota) and emerald ash borer *Agrilus planipennis* (Coleoptera). *Hymenoscyphus fraxineus* was likely accidentally introduced from Asia to Western Europe, expanded its range eastward and by 2014 reached Moscow, whereas *A. planipennis* was accidentally introduced from Asia to Moscow Region, expanded its range in all directions but most noticeably southwards. By 2012, *A. planipennis* reached Smolensk Region bordering Belarus, and by 2013, Voronezh Region bordering Ukraine. At least between Belarus and Moscow city, the ranges of invaders overlap. Both species are a threat to the native as well as introduced ash in Europe. We list known records of two invaders in Russia (as of 2016) and for *A. planipennis* also review food plants, seasonal cycle, dispersal, parasitoids and susceptibility of different ash species. We analyze the synergetic effect of two invaders on ash in the area of overlapped ranges and potential losses of biological diversity associated with ash decline and conclude that the future of ash in Europe is precarious. The following directions of actions in Eurasia are proposed: (1) studies of resistance mechanisms to both agents in Asian ash species (first of all, *F. chinensis* and *F. mandshurica*) and hybrids between Asian and European or North-American ash species, (2) studies on selection of resistant ash forms and hybrids (to both agents), (3) controlled introduction of resistant Asian ash species, (4) slowing down of expansions of *A. planipennis* to Western Europe and *H. fraxineus* within Russia, (5) studies of natural control agents, (6) monitoring of invasions and sanitary condition of ash, and (7) studies on synergetic effect of *H. fraxineus* and *A. planipennis* on ash.

Keywords: *Agrilus planipennis*, ash, ash dieback, Buprestidae, *Chalara fraxinea*, emerald ash borer, forest, forest health, *Fraxinus*, *Hymenoscyphus fraxineus*, pathogen, forest pests, plant resistance

"In terms of invasive forest pests, emerald ash borer may well represent a worst-case scenario."
D. A. Herms and D. G. McCullough (2014)

Introduction – Ash species in Russia

The genus *Fraxinus* L. (ash; Oleaceae) currently consists of 48 accepted tree and shrubby species widely distributed in the tropical and temperate regions of the Northern Hemisphere (Wallander 2012). Three species have wide European distribution: European, or common, ash *Fraxinus excelsior* (L.), Caucasian, or narrow-leaved, ash *F. angustifolia* (Vahl), and South European flowering, or manna, ash *F. ornus* (L.). Among these three species, *F. excelsior* is the most spread ash in Europe (FRAXIGEN 2005, Wallander 2008, 2012).

There are four native ash species in Russia: European ash *F. excelsior*, Caucasian ash *F. angustifolia*, Chinese, or Korean, ash *F. chinensis* (Roxburgh), and Manchurian ash *F. mandshurica* (Hance) (Bulygin 1991, Bulygin and Yarmishko 2000, Usoltsev 2001, Alekseev and Sviazeva 2009). It should be noted that in the earlier Russian literature four other species were sometimes listed that otherwise are considered synonyms, subspecies or variations of the four above mentioned species:

– *F. coriariifolia* (Scheele) as a synonym of *F. exelsior* (Wallander 2012) or subspecies *F. exelsior coriariifolia* (Scheele) Bois (Tree Names 2015),
– *F. oxycarpa* (Willdenow) as a subspecies *F. angustifolia oxycarpa* (Willdenow) Franco et Rocha Afonso (Wallander 2012),
– *F. rhynchophylla* (Hance) as a subspecies *F. chinensis rhynchophylla* (Hance) E. Murray (Wallander 2012),
– *F. densata* (Nakai) as a subspecies *F. chinensis rhynchophylla* (Hance) E. Murray (The Plant List 2013).

As in Western and Central Europe, in Russia, European ash *F. excelsior* is the most widely spread ash species, often dominant in broad-leaved forests in the European Russia and the Caucasus (Bulygin and Yarmishko 2000, Usoltsev 2001). The northern range limit of this species is close to the line Saint Petersburg – Tikhvin – Kostroma – Nizhniy Novgorod (Tkachenko 1952, Timofeev and Dylis 1953). In the East, European ash does not reach the Volga River being limited by Eastern borders of basins of rivers Sura and Khoper (Tkachenko 1952). This species is naturally well regenerated by sprouting. Pure stands, however, are rare. European ash is drought-tolerant and thermophilic and, thus, is often damaged in cold winters. It grows well only on soils rich in lime on overflow lands. The species is widely and actively used for planting of field-protecting belts in central and southern parts of the European Russia.

Caucasian ash *F. angustifolia* is mostly distributed in the Caucasus and in the Crimea. It is smaller in size than *F. excelsior* and has narrower leaves.

Chinese ash *F. chinensis* is distributed in the Russian Far East, in particular in south of Primorye Territory. It often covers dry mountainous slopes (Bulygin and Yarmishko 2000, Usoltsev 2001).

Manchurian ash *F. mandshurica* is up to 35 m in height and up to 1 m in diameter. It is also distributed in the Russian Far East along valleys of rivers, on gentle slopes of hills and rich soils (Tkachenko 1952, Bulygin and Yarmishko 2000).

Green, or red, ash *F. pennsylvanica* Marshall was introduced from North America. It is currently widely used, especially its cold-tolerant forms, for greening in cities and towns in the taiga zone of Russia (Timofeev and Dylis 1953, Bulygin and Yarmishko 2000). One of its numerous forms, namely *F. pennsylvanica* var. *lanceolata* (Borkhausen) Sargent is used for forest cultivation and greening in the steppe and forest-steppe zones in the southern part of the European Russia (Bulygin and Yarmishko 2000) because this form is not only cold- and drought-tolerant but also withstands high soil salinity (Timofeev and Dylis 1953). This ash is often planted in parks, alleys, and along inter-city roads (Bulygin and Yarmishko 2000).

Ash forests cover more than 666 300 ha (about 0.1% of total forest area of Russia) and have volume of about 77.91 mln m^3 (Table 1). These forests usually have a comparatively low stand timber volume (117 m^3 per ha; State Forest Registry 2014).

Distribution of ash forests over the country is far from uniform (Table 1). Such forests are mostly concentrated in two regions of the Russian Federation, namely, central and southern parts of the European Russian (including the Caucasus), and the Russian Far East.

About 264 300 ha of ash forests (i.e., forest lands with ash as a dominant tree species), which is ca. 40% of all Russian ash forests, are concentrated in European Russia. We probably have to add to this number thousands of hectares of *F. pennsylvanica* and to a somewhat lesser degree *F. excelsior* stands in a form of field-protecting belts and along-inter-city-road plantings, the size of which is difficult to estimate. In the north of European Russia and close to the European ash natural range (in Novgorod, Pskov, and Leningrad Regions), the species covers not more than 300 ha of forest lands, but in cities such as Saint Petersburg (and further south – e.g. in Moscow), ash is often and widely used for greening.

Most of the Russian ash forests and, consequently, ash timber volume is concentrated in the Russian Far East (more than 60% in terms of land and more than 65% of timber volume; Table 1).

In the broad-leaved forests of the steppe-forest zone of the European Russia, *F. excelsior* tends to expand its dominance and the area of ash forests increases. Together with maple *Acer platanoides* L. and linden *Tilia cordata* Miller, ash replaces old oak *Quercus robur* L. stands (Chebotarev and Chebotareva 2015).

Specific plant biomass of ash is 1.5 times higher in the western and southwestern parts of European Russia than in Eastern and Western Europe (Usoltsev 2002). Such forest stands are very good food resources for potential forest pest and pathogen invaders, including those from the Far East of Eurasia.

The disjunction of ash range in Siberia can be easily overcome by existing and sometimes numerous ash trees in form of parks, alleys, field-protecting belts, and along-intercity-road's plantings in and around populated settlements of different sizes. For example, Green ash *F. pennsylvanica* and Manchurian ash *F. mandshurica* are widely used in Novosibirsk, Barnaul, Tyumen', Yekaterinburg, Krasnoyarsk, Irkutsk, and many other cities and towns. These ash species can well withstand harsh climatic conditions of Siberia.

The vast area occupied by several native and introduced ash species in the European Russia and existing Ural-Siberian "corridor" of planted ash in addition to commercial transfer of resources and materials between different regions of Russia have created good pre-conditions for potential expansion of invasive pests and pathogens associated with ash from the Russian Far East to the European Russia first and then further to Central and Western Europe.

Insects and fungal pathogens associated with ash in Russia

In total, more than 5,000 species of insects associated with forest and urban trees and shrubs are known in Russia (Pests of forest 1955, Maslov et al. 1988, Catalogue 2008, Fauna Europaea 2015). Among them, trophic linkages with ash are known for at least 168 species, what seems to be close to the average number expected for forest tree species. Of these species, 45 can be considered more or less specialized dendrophagous insects and 28 monophagous species of *Fraxinus* (A. V. Selikhovkin, D. L. Muslin, unpublished data). Some of them (mostly, beetles) can strongly affect condition of an ash stand, whereas most of other species colonize only weakened, dying or even dead trees.

Fungal pathogens (and more general – mycobiota) of ash are poorly studied and has never been properly reviewed in Russia. Local, but mostly relatively old literature, lists only 16 largely most common fungal pathogens known to damage ash in Russia and 19 additional species of fungi associated with a wider range of trees including ash (Kuz'michev et al., 2001, 2004, A. V. Selikhovkin, D. L. Musolin, unpublished data). These records need further confirmation.

More species of insects and fungal pathogens associated with ash are known from southern and south-eastern parts of the European Russia as well as from the Far East and Primorye than from other parts of the country. These observations suggest high probability of invasions of pests and pathogens from both west and east.

Ash dieback fungus *Hymenoscyphus fraxineus* in European and Asian parts of Russia

As mentioned above, in Russia species of the genus *Fraxinus* grow both in the European part and Far East. For the European Russia, *F. excelsior* is a native species. It is susceptible to the ash dieback disease caused by *Hymenoscyphus fraxineus* (T. Kowalski) Baral et al. (≡ *Chalara fraxinea* T. Kowalski, = *Hymenoscyphus pseudoalbidus* Queloz et al.) (Baral and Bemmann 2014, Baral et al. 2014). The disease quickly kills ash in many countries in Western Europe. It is currently believed that the pathogen was accidentally introduced into Western Europe (likely Poland or one of the Baltic countries) in about 1995 with plant materials (likely, introduction of Manchurian ash *F. mandshurica* (Kowalski 2006, Baral and Bemmann 2014, Drenkhan et al. 2014). As of June 2016, there are several findings of this pathogen in Russia, both in its European and in Asian parts.

In the European part of Russia, *H. fraxineus* was registered for the first time in 2011 in Saint Petersburg, where ash leaf petioles with apothecia of the fungus were found by Dr. T. Kirisits in the Botanical Garden (Dendrarium) of Saint Petersburg State Forestry Technical University and Botanical Garden of Botanical Institute of Russian Academy of Sciences (Gross et al. 2014, McKinney et al. 2014). Despite the pathogen presence, the decline of trees was not obvious at that time and it is not observed now (2016; D. A. Shabunin, unpublished data). The presence of *H. fraxineus* in the Botanical Garden of Saint Petersburg State Forestry Technical University was also confirmed by Drs R. Vasaitis and R. Drenkhan in 2011–2013 (Musolin et al. 2014).

Table 1. Distribution of forest stands (with ash as the main tree species), its area and total growing stock in different subjects (i.e., constituent territories) of the Russian Federation (State Forest Registry 2014)

Administrative divisions of the Russian Federation (by federal district, region [oblast', or province] and territory [krai])	Forest stands with ash as the main tree species	
	Area, thousand ha	Total growing stock, mln m^3
Central Federal District	59.3	9.45
Belgorod Region	9.5	1.04
Bryansk Region	2.2	0.39
Kaluga Region	1.7	0.41
Kursk Region	16.5	2.92
Lipetsk Region	1.3	0.15
Moscow Region	0.3	0.04
Oryol Region	1.6	0.28
Ryazan Region	0.2	0.03
Smolensk Region	1.4	0.26
Tambov Region	0.4	0.05
Tver Region	0.2	0.03
Tula Region	7.9	2.18
Voronezh Region	16.1	1.67
Northwestern Federal District	7.2	1.31
Kaliningrad Region	7.0	1.28
Novgorod Region	0.1	0.01
Pskov Region	0.1	0.02
Southern Federal District	91.2	7.90
Astrakhan Region	8.8	0.68
Krasnodar Krai	31.6	3.80
Republic of Adygeya	6.5	0.95
Republic of Kalmykia	0.4	0.01
Rostov Region	14.8	1.25
Volgograd Region	29.1	1.21
North Caucasian Federal District	46.3	4.64
Chechen Republic	5.3	0.50
Kabardino-Balkarian Republic	3.0	0.36
Karachayevo-Cherkessian Republic	2.8	0.24
Republic of Daghestan	4.6	0.33
Republic of Ingushetia	4.0	0.34
Republic of North Ossetia – Alania	2.5	0.32
Stavropol Krai	24.1	2.55
Privolzhsky (Volga) Federal District	60.3	3.58
Chuvash Republic	2.8	0.15
Nizhni Novgorod Region	0.7	0.08
Orenburg Region	11.2	0.54
Penza Region	4.2	0.57
Republic of Bashkortostan	0.8	0.06
Republic of Marij El	0.3	0.05
Republic of Mordovia	6.2	0.49
Republic of Tatarstan	0.3	0.04
Samara Region	10.2	0.57
Saratov Region	23.5	1.02
Ulyanovsk Region	0.1	0.01

Table 1. (Continued)

Administrative divisions of the Russian Federation (by federal district, region [oblast', or province] and territory [krai])	Forest stands with ash as the main tree species	
	Area, thousand ha	Total growing stock, mln m^3
Far Eastern Federal District	402.0	51.03
Amur Region	0.6	0.06
Jewish Autonomous Region	3.1	0.30
Khabarovsk Territory	85.1	10.27
Primorye Territory	313.2	40.40
Ural Federal District	0.0	0.00
Siberian Federal District	0.0	0.00
RUSSIAN FEDERATION	666.3	77.91

In 2012, ash dieback was recorded in tree stands of the natural monument Dudergof Heights near Saint Petersburg (59°41′52″ N, 30°08′01″ E; Figure 1A; Shabunin et al. 2012). Identification of *H. fraxineus* was confirmed by nuclear DNA sequencing and PCR with a species-specific primer (Figure 2; Shabunin et al. 2012). A mass declining of trees at this site was noted. The fungus caused wilting of branches in adult trees and undergrowth of ash. Different parts of trees were affected to different degree. At some plots, the dead trees without bark were observed in 2012. The entire range of declining trees was seen: from barely affected to declining and dead ones. According to our estimates in Dudergof Heights, tree dying-off process has been going on for at least 5 years. Also, degradation of tissues of a dead tree takes some time. Taking this into consideration, we can assume that the pathogen appeared there no later than in 2005.

In addition to Dudergof Heights, the disease was detected in the State Nature Reserve The Northern Coast of the Neva River Bay near Saint Petersburg in 2013. However, there were no dead ash trees there. In this case, decline of crowns was less than 20%. The ash seed regeneration sized up to 2 m was affected by the disease more than any other age group of ash trees (D. A. Shabunin, unpublished data).

In 2014, Belarusian researchers carried out a survey of ash stands planted along the federal route M1 from the border of Russia with Belarus to Moscow. By that time, in Belarus, more than 54% of ash stands had died most likely because of ash dieback caused by *H. fraxineus* (Zviagintsev et al. 2014), whereas in the European Russia, records of *H. fraxineus* had only been occasional (Shabunin et al. 2012, Baral and Bemmann 2014, Musolin et al. 2014). The survey demonstrated that the road-side alleys were dominated by planted introduced green ash *F. pennsylvanica* and in particular by *F. pennsylvanica* var. *lanceolata*. Native European ash *F. excelsior* was observed only as individual trees on the territory of the park of the Moscow State Forest University (currently named Mytishchi Branch of Bauman Moscow State Technical University; Mytishchi district, Moscow Region) and was only occasionally found in the roadside hedgerows and in forest stands adjacent to the federal route M1 (Zviagintsev et al. 2015).

Visual diagnostics of ash condition identified symptoms of ash dieback everywhere along the federal route M1 from the border of Russia with Belarus to Moscow. The proportion of damaged last-year shoots ranged from 10 to 90%. For precise identification pure cultures of the pathogen were obtained from infected tissues of branches. After two months of cultivation with decreasing temperature, phialides typical for *C. fraxinea* were formed. According to the results of Amplified Fragment Length Polymorphism analysis of pure cultures, species-specific restriction band patterns typical for *H. fraxineus* were identified and it was subsequently confirmed by sequencing (Zviagintsev et al. 2015).

According to these studies, *H. fraxineus* is distributed everywhere along the federal route M1 from the border of Russia with Belarus to Moscow Region and the invasion reached Moscow City at least a few years ago (Zviagintsev et al. 2015). It is interesting to note that the recent studies focused on genus *Hymenoscyphus* in the Moscow Region did not report *Hymenoscyphus albidus* (Gillet) W. Phillips or *H. fraxineus* (Miliokhin and Prokhorov 2007).

A special survey focused on *H. fraxineus* was additionally carried out in the Main Botanical Garden of the Russian Academy of Sciences (Moscow) in 2015. Molecular genetic analysis of nine samples of *F. excelsior* with typical dieback symptoms did not reveal the presence of *H. fraxineus* genetic material. On affected branches and buds five taxa of micromycetes were identified: *Phoma glomerata* (*Corda*) Wollenw. et Hochapfel (dominant, de-

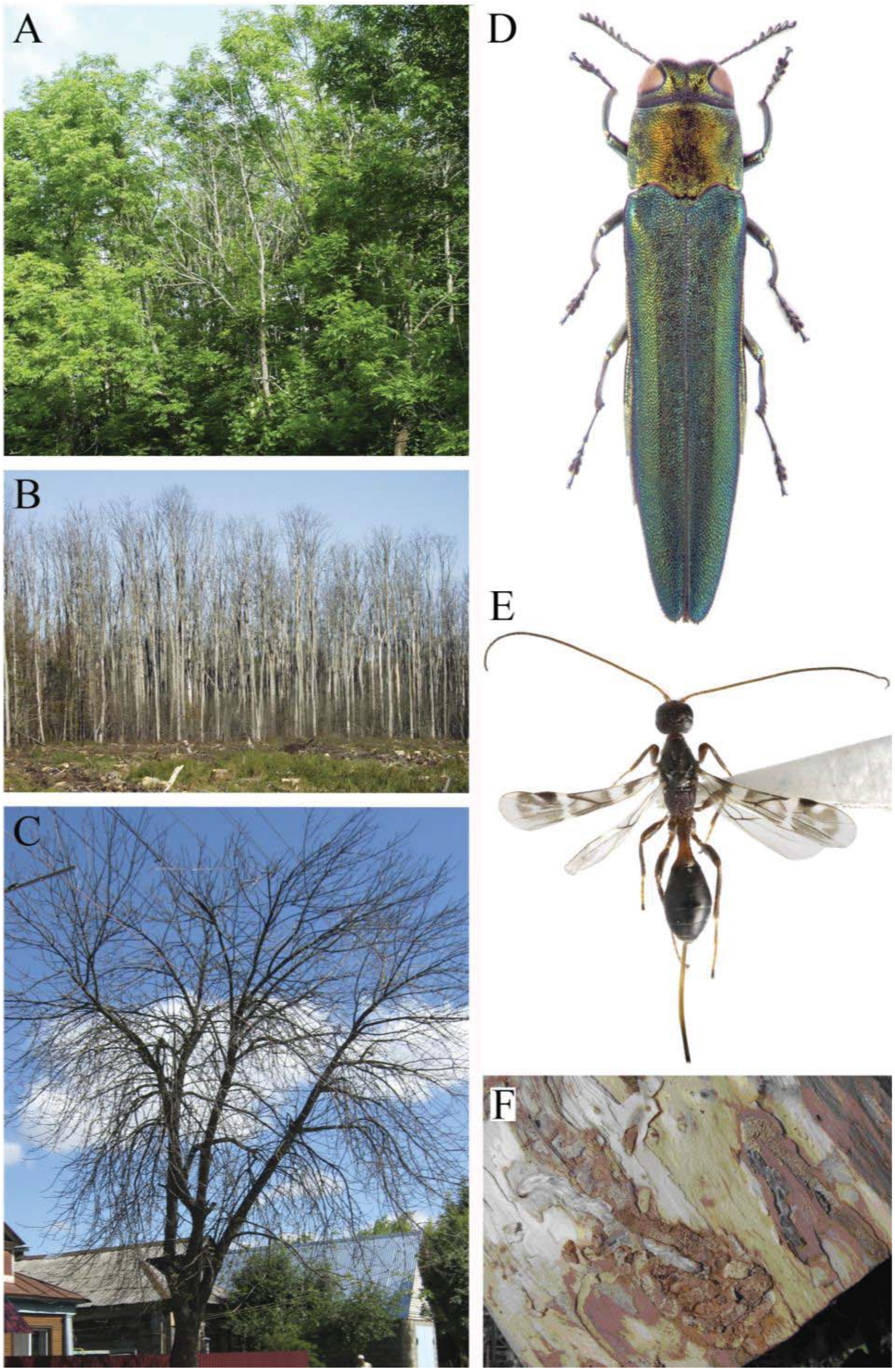

Figure 1. A: The decline of ash in the tree stands of the natural monument Dudergof Heights near Saint Petersburg, 2012 (photo by D. A. Shabunin). **B:** The decline of ash in Kaliningrad Region, 2005. Dead ash tree stand on the background and the sanitary cutting of ash trees on the foreground (photo by D. A. Shabunin). **C:** An ash tree killed by emerald ash borer *Agrilus planipennis*, Voronezh city, Voronezh Region, 2013 (photo by Dr. M. J. Orlova-Bienkowskaja, with permission). **D:** Emerald ash borer *Agrilus planipennis*. The specimen was collected on *F. excelsior* in small town Manihino, Istrinskiy district of Moscow Region on 15 July, 2006 by E. V. Shanhiza (size 10.5 mm; photo by Dr. K. V. Makarov, with permission). **E:** Wasp *Spathius polonicus*, a parasitoid of emerald ash borer *Agrilus planipennis* (photo by Dr. K. V. Makarov, from Orlova-Bienkowskaja and Belokobylskij, 2014, with permission). **F:** Cocoons of emerald ash borer *Agrilus planipennis* parasitized by *Spathius galinae*, under bark of an ash tree, south of Primorye Territory (photo by Dr. G. I. Yurchenko, with permission)

Figure 2. Apothecia of *Hymenoscyphus fraxineus* (from Shabunin et al. 2012; photo by D. A. Shabunin)

tected in 66% of samples), *Cryptococcus* sp., *Eutypa* sp., *Alternaria* sp. and a new undescribed species close to genus *Cryptococcus*, but not *H. fraxineus* (L. G. Seraia, V. B. Zviagintsev, unpublished data).

Recent studies of ash stands in the Voronezh Region revealed their good sanitary condition (Chebotarev and Chebotareva 2015), although outbreak foci of emerald ash borer have been reported in Voronezh city (Orlova-Bienkowskaja 2014a).

Ash forests in the European part of Russia never occupy large areas. Instead, *Fraxinus* spp. are often only secondary mixture species in forest stands. Therefore, decline of ash may often go unnoticed. However, the situation in the Kaliningrad Region was exceptional. In contrast to many other regions, European ash formed pure forest stands there. In 2005, a mass mortality of ash was observed (Figure 1B; Zhigunov et al. 2007). Declining ash stands were surveyed in five forest enterprises. Excavation and examination of root systems of ash trees demonstrated that ash trees with only initial signs of decline in 50–70% were already affected by *Armillaria lutea*. In some cases, the fungus had time to affect 50% of the root system of a particular tree and to form fruit bodies, but the tree crown had to be classified as “having no signs of weakening”. The survey showed that the cause of ash trees mortality was the damage to their root system from rot caused by *A. lutea*. An important feature of the disease development is high speed of tree mortality. The forest stands died within one year. There were no trees with different stages of decline, as it is typical for ash dieback disease caused by *H. fraxineus*. Such observation confirms the conclusion that *A. lutea* was the principal cause of ash stands mortality in Kaliningrad Region. The root rot caused by *A. lutea* was detected in all surveyed plots of ash and in the vast majority of plots of oak and even in one plot of aspen. The causes of massive outbreak of *A. lutea* in the region remain unclear.

In 2005, the signs of crown damage by *H. fraxineus* were not found. The current state of ash forests in the Kaliningrad Region is unknown.

In the natural forests of north-western and central regions of the European Russia ash species are not numerous (Table 1). They are represented by small scattered stands or mixed with other tree species. Consequently, natural forest stands cannot be considered sufficiently reliable transmission vector or media of *H. fraxineus* from the western border of Russia to the eastern part of the *F. excelsior*’s range. It is most likely that ash trees widely and actively planted along the inter-city roads and agricultural fields greatly promoted spread of *H. fraxineus* from the western border to Moscow and likely further eastward.

Currently, the expansion of another Far Eastern invader, namely emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is observed in ash stands in Moscow and several nearest administrative divisions (see below). Unfortunately, emerald ash borer disguised the traces of dieback caused by *H. fraxineus* in Moscow.

As mentioned above, two ash species, namely Chinese ash *F. chinensis* and Manchurian ash *F. mandshurica*, are naturally distributed in the Far East region of Russia (Bulygin 1991, Bulygin and Yarmishko 2000, Usoltsev 2001). Our studies demonstrate that none of these two species is susceptible to ash dieback caused by *H. fraxineus* (D. A. Shabunin, unpublished data). We examined several stands of *F. mandshurica* in Terneiskiy district of Primorye Territory and along the route Khabarovsk – Dalnerechensk – Rudnaya Pristan’ – Amgu (federal routes A370, A179, A181, and local roads). Even though *H. fraxineus* was detected in the collected samples, the decline of ash was not recorded. On October 14, 2015, we found an anamorph state of the fungus (*Chalara fraxinea*) in the vicinity of Plastun settlement in Terneiskiy district of Primorye Territory (45°06' N, 135°26' E) on fallen leaves of *F. mandshurica* (D. A. Shabunin, unpublished data).

A perfect stage of *H. fraxineus* on *F. mandshurica* was also collected on August 17, 2005 in the Nature Reserve Kedrovaya Pad’ (Khasanskiy district of Primorye Territory) by E. S. Popov (Baral and Bemmann 2014).

There is also a record of findings of *H. fraxineus* (as *H. pseudoalbidus*) among seven species of *Hymenoscyphus* in the Far East of Russia by Dr. A. V. Bogacheva (exact location and date are not reported; Bogacheva 2015).

Furthermore, presence of *H. fraxineus* was confirmed by molecular methods in green leaves from crowns of *F. mandshurica* from three locations in Primorye Territory (46°37' N, 134°56' E; 46°37' N, 135°23' E; 44°36' N, 134°52' E). The presence of *H. fraxineus* on non-symptomatic ash suggests a possible role of the species as an endophyte in its native environment (Marčiulynienė et al. 2013, Cleary et al. 2016).

Thus, the findings of *H. fraxineus* in different locations in the Russian Far East give a basis for a preliminary conclusion that the fungus is widespread in the region and it is likely that the Russian Far East is a part of the species' native range.

Overall, the condition of the ash forests in Russia and the status of *H. fraxineus* are poorly studied and further research is urgently needed.

Morphological features of **Hymenoscyphus fraxineus** *collected in Russia*

Studies of *H. fraxineus* collected in ash stands in the natural monument Dudergof Heights near Saint Petersburg (Shabunin et al. 2012) revealed that some features of our material differ from those documented in the original description (Baral et al. 2014). In the fungus samples, a heterospory was noted in ascospores and in conidia. This phenomenon has not been recorded before. Shabunin et al. (2012) described the specimens and discussed the revealed differences in ascospores.

In the Russian Far East specimens (from fallen ash leaves), the *C. fraxinea* conidiophores were also observed under conditions of a moist chamber. Conidiophores appeared only on leaf plates. The fungus did not contaminate the rachises and did not form black stroma. On the same leaf rachises, fructifications of different fungi were also seen (*Cladosporium* spp., *Alternaria* sp.). In these specimens, one more type of conidia was observed. The conidia were hyaline elongated, cylindrical, rounded at the upper end and truncated at the lower end, 5.9–6.8 x 1.8–2.2 µm (Figure 3). Thus, heterospory was found in both perfect and imperfect stages of the fungus.

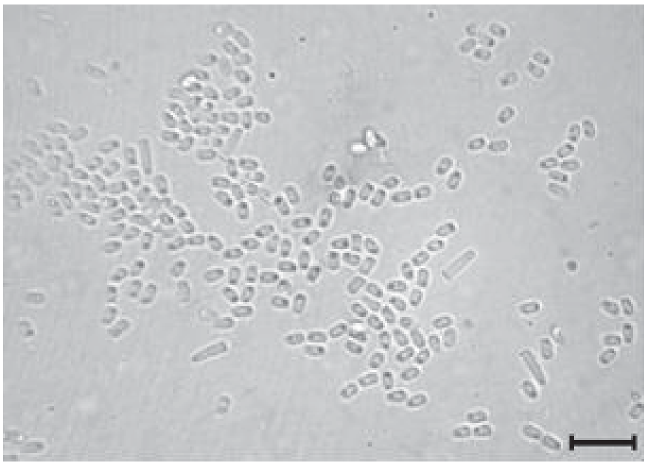

Figure 3. Conidia of *Chalara fraxinea*. The specimen was collected in Terneiskiy district of Primorye Territory (bar = 10 µm; photo by D. A. Shabunin)

Emerald ash borer *Agrilus planipennis*

Whereas currently *H. fraxineus* is spreading from Western Europe to the Central Russia, another extremely important enemy of ash, a beetle emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae; Figure 1D), is moving in the opposite direction. This species has demonstrated its devastating potential as a pest of ash: in North America, the beetle was accidentally introduced to the region of the Great Lakes in the late 1980s or early 1990s and already by 2015 the invasive North American range of the pest has covered 24 states of USA and two Canadian provinces. Currently, emerald ash borer is the most damaging forest pest in USA: the annual damage caused by this species exceeds 3 billion US dollars (Haack et al. 2015).

Native and invasive ranges and food plants

Outside Russia the native range of *A. planipennis* covers 9 provinces of North and North-Eastern China, Taiwan, Japan (from Hokkaido to Shikoku), and South Korea (Volkovitsh and Mozolevskaya 2014).

Within its native range, the buprestid is known to feed on different species of ash. In Japan and South Korea, *Juglans mandshurica* Maxim., *Pterocarya rhoifolia* Siebold et Zucc., and *Ulmus davidiana* Planch. were reported as food plants of *A. planipennis*, but these records need to be re-checked because at least in USA in the experimental host range studies emerald ash borer failed to complete development on species of *Ulmus*, *Juglans*, and *Carya* (Anulewicz et al. 2006). Within its invasive (i.e., secondary) ranges in North America and Europe (Russia), the beetle feeds exclusively on different species of ash (Yurchenko et al. 2007, Herms and McCullough 2014, Volkovitsh and Mozolevskaya 2014).

Before the beginning of the current millennium, *A. planipennis* was known to exist only in the territory of the Russian Federation due to limited records. All of them were from the southern part of Primorye Territory where a limited number of specimens were collected in 1935–1999 (Alexeev 1979, Jendek 1994, Yurchenko et al. 2007, Volkovitsh and Mozolevskaya 2014). In 2004, the species was found at the south of Khabarovsk Territory on a waste area ranging from the city of Khabarovsk and its vicinity to the village of Dzonki (100 km from Khabarovsk down along the Amur River; Yurchenko 2010).

Previously, being a very rare species in the Russian Far East, *A. planipennis* was associated exclusively with weakened and dying local Manchurian ash *F. mandshurica* and Chinese ash *F. chinensis*. The harmful activity of the buprestid in that region was first noticed in 2004: *A. planipennis* appeared to be the main factor of dieback of introduced North American Green ash *F. pennsylvanica* on the streets of Vladivostok city (Yurchenko 2010), where rather mature trees with stem diameter of 20–40 cm were infested. Detailed study of dead trees of introduced North American ash in parks and arboretum in Khabarovsk demonstrated that they had been killed by emerald ash borer within the preceding 5–10 years at the age of 28–35 years (Yurchenko 2010).

In European Russia, first beetles of *A. planipennis* were collected in June of 2003 on streets of Moscow (Volkovitsh and Mozolevskaya 2014). Within the next two years, a few more beetles were found. In 2005, these samples were identified as *A. planipennis* by Dr. A. V. Alexeev (А. В. Алексеев), a leading Russian expert on Buprestidae (Izhevskii and Mozolevskaya 2010). It was finally recognized that emerald ash borer was responsible for the recent intensive ash weakening and dieback all over Moscow city (Baranchikov et al. 2008, Mozolevskaya et al. 2008). Within the following years, the pest was quickly spreading from Moscow in all directions. In 2006, 10 beetles were collected as far as 30 km to the west of the Moscow Ring Highway (Volkovitsh and Mozolevskaya 2014). In 2009, ash trees killed by the buprestid were found in many settlements of Moscow Region; the most westward location of ash dieback was registered in Mozhaisk, 100 km from Moscow (Baranchikov et al. 2010b). In 2010, the beetle was found in Kaluga Region, in 2012 – in Smolensk and Ryazan Regions (Baranchikov and Kurteev 2012, Baranchikov 2013), in 2013 – in Vladimir (Baranchikov 2013), Tver, Tula, Oryol, Voronezh, Yaroslavl, and Tambov Regions (Figures 1C, 4 and 5; Orlova-Bienkowskaja 2014a,b). Thus, currently (as of June 2016), the invasive range of *A. planipennis* covers territory of 11 administrative divisions of the Russian Federation (Figure 6).

Figure 4. Galleries of emerald ash borer *Agrilus planipennis* larvae under bark of a dead ash tree, Pushkino city, Moscow Region, 2016 (photo by D. L. Musolin)

It is important to note that in these regions ash (as an exclusive food plant of emerald ash borer) can be found almost only as artificially planted trees in cities, towns and other populated places, along roads and highways, and in field-protecting tree belts. Native stands of the European ash *F. excelsior* are very rare and limited in size in these regions. Nevertheless, in 2014, an outbreak of *A. planipennis* was for the first time recorded in a natural stand of *F. excelsior* in Moscow Region (Smirnov 2014). The situation will likely become much worse if and when the pest reaches the neighboring Kursk, Belgorod, Rostov, Volgograd, and Saratov Regions, where proportion of ash stands is as high as 3–7% of the total forest area (Figure 6).

Figure 5. Emergence holes of emerald ash borer *Agrilus planipennis* adults on bark of an ash tree, Oryol city, Oryol Region, 2013 (photo by Dr. M. J. Orlova-Bienkowskaja, with permission)

In 2011, *A. planipennis* was mentioned in a review paper as being reported in Sweden (Dobrowolska et al. 2011). The same information was recently repeated in another review (Thomas 2016) and caused a panic in Western Europe (Marshall 2016). However, further investigation revealed that the specimen had been incorrectly identified and, thus, as for 2016, *A. planipennis* is not recorded in Sweden (EPPO 2016, Skovsgaard 2017).

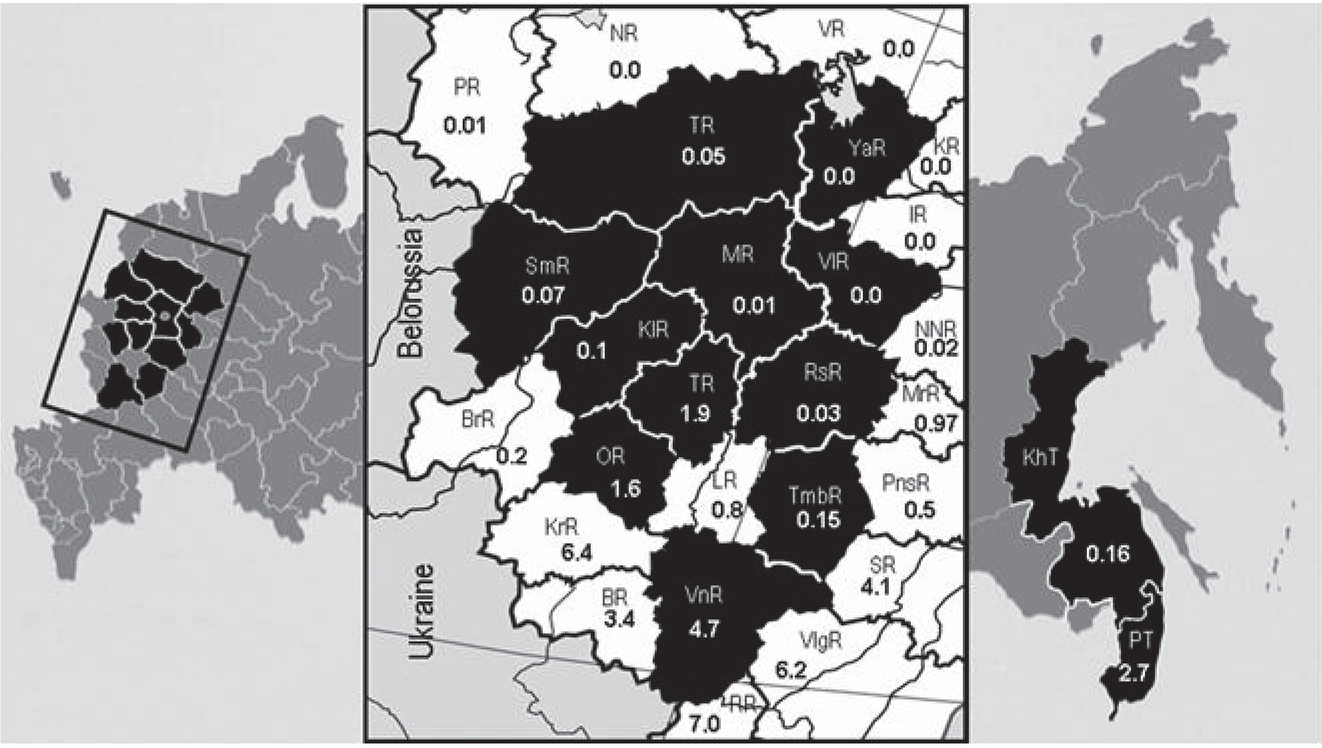

Figure 6. The current distribution of emerald ash borer *Agrilus planipennis* in the Russian Federation. The regions where *A. planipennis* has been recorded are shown in black. Figures refer to the proportion (in percent) of ash forest in the total forest area of each administrative division (State Forest Registry 2014), thus estimating food resources for the monophagous pest. Administrative divisions: In the native range: KhT – Khabarovsk Territory, PT – Primorye Territory; In the invasive range: PR – Pskov Region; NR – Novgorod Region; VR – Vologda Region; TR – Tver Region, YaR – Yaroslavl Region, KR – Kostroma Region, SmR – Smolensk Region, MR – Moscow Region, VlR – Vladimir Region, IR – Ivanovo Region, NNR – Nizhny Novgorod Region, BrR – Bryansk Region, TR – Tula Region, KR – Kaluga Region, RsR – Ryazan Region, MrR – Republic of Mordovia, KrR – Kursk Region, OR – Oryol Region, LR – Lipetsk Region, TmbR – Tambov Region, PnsR – Penza Region, BR – Belgorod Region, VnR – Voronezh Region, SR – Saratov Region, RR – Rostov Region, VlgR – Volgograd Region

Seasonal cycle

In Moscow Region flight of *A. planipennis* starts at the very beginning of June after accumulation of approximately 240 degree-days of the effective temperatures calculated using a tentative lower developmental threshold of 10°C, data from Orlova-Bienkowskaja and Bieńkowski (2016) and local weather data (WeatherArchive.ru 2016). The mean accumulated sum of effective temperatures (240 degree-days) (further confirmed by the timing of the flight beginning in Moscow Region in 2013–2014) is rather close to 250 degree-days of effective temperatures calculated for the population of the species from Michigan, USA (Brown-Rytlewski and Wilson 2004). In Michigan and Canada, the flight period continues for 3–6 weeks (Bauer et al. 2004, Lyons et al. 2004). Females feed on leaves of ash for 10–14 days before copulation (Rodriguez-Saona et al. 2007). Eggs are laid into cavities on the ash bark individually or in small groups and larvae hatch in two weeks at a temperature of 25°C. Larvae build curved and oriented along the stem galleries which widen towards their ends and filled with sawdust (Figure 4). The species has four larval instars. In the cooler climates of the most parts of the invasive range the complete larval development takes two years, whereas in the warmer regions (e.g., Tianjin, China) most individuals complete development within one year (Orlova-Bienkowskaja and Bieńkowski 2016). Larvae spend the 1st winter in their earlier instars and the 2nd winter as pre-pupae in sapwood (if the bark is thin) or in the outer bark (if the bark is thick). In Michigan, USA, pupation starts from mid-April to beginning of May and first new-generation adults emerge in three weeks (Bauer et al. 2004).

Rates of dispersal

To predict expansion of an invasive pest, it is necessary to know its possible spreading rates. There are many approaches and methods of calculation, estimation or modelling of rates of invasive species' range expansion (Tobin et al. 2015). Validation of these methods and confirmation of results require numerous and repeated records over a wide area around the secondary range center during several years. Such data are not yet available for the invasive range of emerald ash borer in the European Russia. Published data on new records (e.g., Volkovitsh and Mozolevskaya 2014) help us understand the current species' distribution, but characterize mostly activity of researchers rather than that of the invasive pest. The first published regional records of an invader might be well behind the actual year of the first appearance of the pest if the absence of the pest was not carefully checked in the previous years. Thus, Straw et al. (2013) estimated the rate of expansion of *A. planipennis* as 40 km/year based purely on two literature records: the species was reported in 2009 in Mozhaisk (Baranchikov et al. 2010a) and in 2012 in Vyazma (Baranchikov and Kurteev 2012) which is located 130 km from Mozhaisk. However, the cited papers did not prove or even mention that the reported years were the first years when the species appeared in these towns.

In 2014, Y. N. Baranchikov and colleagues carried out a detailed observation of ash stands at the western front of emerald ash borer invasion along the federal route M1 between Mozhaisk and Smolensk (Baranchikov et al. 2016). The westmost mass localization of dead ash trees with emergence holes of the buprestid's adults was found in Vyazma (the same location as two years before that). Samples in the form of stem disk (cross section) were taken from dead ash trees (diameter of 12–14 cm) and healthy ones (from the nearest location where there were no signs of emerald ash borer, 18 km east of Vyazma). Analysis of the samples using dendrochronological cross-dating of dead trees (Cybis Dendrochronology 2014) allowed to conclude that all ash trees died very quickly (there was no decrease of radial increment a year preceding the dieback). It demonstrated that the first ash trees died in 2010 whereas all the rest of the trees in the sampled group (i.e., 90%) died in 2011 (Baranchikov et al. 2016).

Table 2. Estimations of rates of emerald ash borer *Agrilus planipennis* dispersal (within its invasive ranges)

Observation (location)	Speed of distribution	Reference
Reconstruction based on the dendrochronological methods (USA)	a slow phase – 6.5 km/year a fast phase – 20.0 km/year	Siegert et al. 2014
Movement of point of 40% canopy thinning, 2003–2006 (USA)	10.6 km/year	Smitley et al. 2008
Movement of visible canopy thinning (USA)	14.6 km/year	Gandhi et al. 2007
Reconstruction based on the dendrochronological methods (Russia)	10.0–12.0 km/year	Baranchikov et al. 2016

It was recently demonstrated in Michigan, USA, that noticeable damage caused by *A. planipennis* might be recorded only 10–15 years after the first appearance of the invader in a forest stand (Siegert et al. 2014). Thus, we can assume that emerald ash borer was introduced in Moscow circa 1990. It took the invader approximately 20 years to reach Vyazma. Based on these data, it was possible to roughly evaluate a mean rate of the front of invasion spreading westwards as 10–12 km/year. This figure is close to similar estimations previously done in the US (Table 2).

It should be mentioned that the single- or double-row planting of ash trees along roads (highways) is likely to increase the dispersal rates of the invader. Similarly, increase of the dispersion degree of food plants (by protecting of some trees with insecticides or by pre-emptive ash removal) might also increase the probability of long distance dispersal of emerald ash borer (Mercader et al. 2011).

Parasitoids

So far, it is known that in the Russian Far East, *A. planipennis* is naturally controlled by a species of egg parasitoid *Oobius* sp. (Hymenoptera: Encyrtidae) and three species of larval ectoparasitoids: *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), *Atanycolus nigrivensis* Voinovskaja-Krieger (Hymenoptera: Braconidae: Braconinae), and *Spathius galinae* Belokobylskij et Strazanac (Hymenoptera: Braconidae: Doryctinae) (Belokobylskij et al. 2012, Duan et al. 2012). It seems that the last species, namely recently described *S. galinae*, turned out to be the most effective parasitoid of emerald ash borer (Figure 1F). The species is preadapted to the climatic conditions of the northern regions of USA and southern regions of Canada which made it possible to start a release of this braconid in North America in 2015 (Anonymous 2015) and gave some perspective of the use of this agent to control emerald ash borer in both North America and Europe.

It was also noticed that in the invasive ranges, local parasitoids recently started to infest *A. planipennis.* In North America, at least 24 species of local Hymenoptera have been recorded to parasitize emerald ash borer, although so far with a very low efficacy (Taylor et al. 2012). In Europe, braconid *Spathius polonicus* Niezabitowski (Hymenoptera: Braconidae: Doryctinae) turned out to play an important role in the control of emerald ash borer (Figure 1E). This specialized parasitoid feeds only upon buprestids and occurs over a wide range from Kazakhstan to Spain. In some locations in Moscow Region, this parasitoid is reported to be responsible for mortality of 50% of *A. planipennis* larvae (Orlova-Bienkowskaja and Belokobylskij 2014). Two other braconids, namely, *S. exarator* (L.) and S. *rubidus* (Rossi), were also recorded in Europe. These widely polyphagous species feed on insects from different orders and occur over the entire Palaearctic. *Spathius rubidus* occurs in North America as well (Gninenko and Klyukin 2014).

Susceptibility of different ash species to emerald ash borer

Not all ash species are equally susceptible to emerald ash borer. Detailed examination of the ash collection in the Main Botanical Garden of the Russian Academy of Sciences (Moscow) was carried out in 2014 and revealed that only two Asian ash species, namely, Chinese ash *F. chinensis* and Manchurian ash *F. mandshurica*, were resistant to emerald ash borer. Some Asian ash species in the collection died in 2010–2014, but these trees did not have any signs of infestation by *A. planipennis.* At the same time, the pest buprestid killed trees of both North-American (*F. pennsylvanica* and *F. americana*) and European ash species (*F. excelsior*, *F. angustifolia* and *F. ornus*; Figure 7). Death of three European ash species mostly or completely was caused by *A. planipennis*. This finding strongly suggests that the fate of the European ash species will be bleak when the pest spreads further west (Baranchikov et al. 2014).

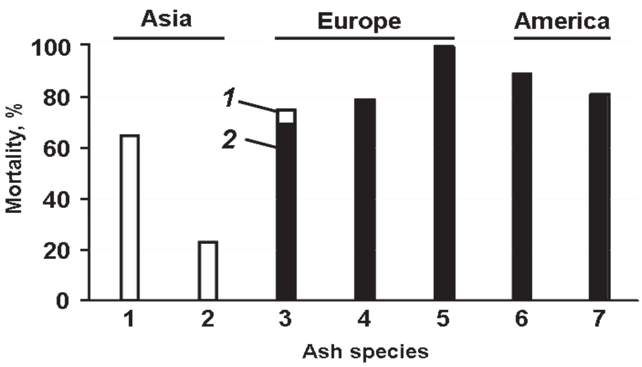

Figure 7. Mortality of Asian, European, and American ash (*Fraxinus*) in the Main Botanical Garden of the Russian Academy of Sciences (Moscow) in 2010–2014. *1* – dead trees without any signs of infestation by *A. planipennis*; *2* – dead trees with galleries and/or emergence holes of *A. planipennis*; 100% – all specimens of each ash species in the collection (see *n* below); continents of origin of ash species are shown above the histogram. Species of *Fraxinus* (number of specimens in the collection in 2010): 1 – *F. chinensis* (*n* = 35), 2 – *F. mandshurica* (*n* = 20), 3 – *F. excelsior* (*n* = 64), 4 – *F. angustifolia* (*n* = 19), 5 – *F. ornus* (*n* = 3), 6 – *F. pennsylvanica* (*n* = 54), 7 – *F. americana* (*n* = 37) (data from Baranchikov et al. 2014)

A similar conclusion was reached by our American colleagues who experimentally studied American, European, and Asian ash species in the plantation in Michigan, USA, in 2010–2014. They revealed that *A. planipennis* killed 95.0–100.0% of three European ash species (*F. excelsior*, *F. angustifolia*, and *F. ornus*) and 35.0–100.0% of five American ash species (*F. pennsylvanica*, *F. nigra*, *F. latifolia*, *F. americana*, and *F. quadrangulata*). At the same time, mortality of Asian *F. mandshurica* and a hybrid *F. nigra* x *mandshurica* was only 20.0% (Herms 2015). The nature of resistance of Asian ash species to emerald ash borer is currently under intensive study, but far from sufficient understanding (Villari et al. 2016).

Ash dieback fungus and emerald ash borer: Overlap of ranges and relationships between two invaders

As demonstrated above, the secondary ranges of ash dieback fungus *H. fraxineus* and emerald ash borer *A. planipennis* have overlapped at least along the federal route M1 from the border of Russia with Belarus to Moscow. We do not know yet how far *H. fraxineus* has penetrated into surrounding forests and residential places, whereas *A. planipennis* have been recorded in numerous cities and towns (Orlova-Bienkowskaja 2014a, b) as well as at least one natural ash stand (Smirnov 2014).

It has been reported that the emerald ash borer readily attacks ash trees that had been weakened by disease, fire or girdling (Herms and McCullough 2014), so trees previously infected by *H. fraxineus* would have a higher risk of being attacked by the pest. Emerald ash borer infests ash trees with diameter more than 5 cm (EPPO 2013) but leaves their epicormic shoots uninfested (Orlova-Bienkowskaja 2014b). In response to infestation, most of the attacked and dying ash trees start to produce massive epicormic shoots that, together with young trees, are not suitable for development of the borer's larvae. It has also been noticed that ash epicormic shoots are more heavily infected by *H. fraxineus* than branches in tree crowns (Zviagintsev et al. 2015). Low resistance of epicormic shoots and young trees to the fungus that can result in fast development of disease and death of a tree has been reported in other regions as well (Pliūra et al. 2011, Schumacher 2011, Yaruk and Zviagintsev 2015). Thus, putting together these observations, we expect that a cumulative effect of two invaders on ash in the zone of overlapped ranges will be devastating for both native and introduced from North America ash species.

It should be mentioned, however, that in basically all populations of all non-Asian ash species, individual trees demonstrate resistance to invaders. Incidence of resistance towards *H. fraxineus* is significantly higher (1.0–5.0%; Klooster et al. 2014) than that to *A. planipennis* (about 0.1%; McKinney et al. 2014). These trees are precious material for selection of resistant ash. It has never been studied whether resistance to the two invaders has anything in common.

Two invaders damaging ash and potential losses of biological diversity

Ash plays an important role in natural communities in different regions of the world. Thus, according to the U.S. National Vegetation Classification, 16 species of *Fraxinus* form or function as important components in

150 plant community types (Wagner and Todd 2015). In the UK, the European ash *F. excelsior* is a part of 61 plant community types and at least 953 species of biota are identified as having some associations with this species (Mitchell et al. 2014).

Reasonably comprehensive estimation of damage that might be caused to local biodiversity by complete loss of ash has never been done. However, in a few countries such damage has been preliminary estimated (Table 3). Thus, extinction of ash in the UK will likely destroy food resources of at least 46 obligatorily or highly associated with ash monophagous insect species, mostly lepidopterans and hemipterans (Table 3; Littlewood et al. 2015). According to two similar studies carried out in USA, mono- and oligophagous insects associated with *Fraxinus* also mostly belong to Coleoptera, Lepidoptera, and Hemiptera (Table 3; Gandhi and Herms 2010, Wagner and Todd 2015). Our list of insects associated with *Fraxinus* in Russia (A. V. Selikhovkin, D. L. Musolin, unpublished data) consists of 168 species and strongly dominated by coleopteran and lepidopteran species (Table 3; polyphagous species are also included). The total number of species is much higher than those reported for the UK and USA (Table 3), but it should be kept in mind that in the different studies, different approaches and procedures were applied.

It should be mentioned that direct effect of emerald ash borer on abundance and diversity of particular species or ecological guilds of biota has never been fully estimated. Some researchers expect that limitation of food resource will directly lead to elimination of phytophagous animals. However, Gandhi and Herms (2010) stressed that elimination of ash in stands would affect diverse guilds of ash-associated arthropods differently. Seed-feeders, folivores, sap-feeders, leaf-miners, and gall-makers will likely experience more or less linear population decline as ash mortality increases. Seed-feeders might suffer first as seed production declines quickly in ash trees infested by *A. planipennis*. On the other hand, when emerald ash borer increases availability of suitable hosts, populations of wood-borers and bark beetles that colonize and utilize declining and dead ash trees will likely initially increase (Gandhi and Herms 2010). This theoretical prediction was recently very well supported by field observations in Russia: European species of ash-associated xylophagous beetles *Agrilus convexicollis* Redtenbacher (Coleoptera: Buprestidae) and *Tetrops starkii* Chevrolat (Coleoptera: Cerambycidae) have noticeably expanded their natural ranges towards east and inhabited stands of *F. pennsylvanica* and *F. excelsior* previously weakened by emerald ash borer (Orlova-Bienkowskaja 2015).

Table 3. Structure of phytophagous insect fauna associated with *Fraxinus* in the UK, USA and Russia

Order	Number of phytophagous insects species associated with ash in different countries (number of species per order and percentage in the total) [1]							
	UK[2]		USA[3]		USA[4]		Russia[5]	
	species	percent	species	percent	species	percent	species	percent
Coleoptera	3	6.5	<u>18</u>	<u>25.7</u>	24	25.8	<u>70</u>	<u>41.6</u>
Diptera	7	15.2	11	15.7	9	9.7	4	2.4
Hemiptera	<u>12</u>	<u>26.1</u>	17	24.3	<u>25</u>	<u>26.9</u>	20	11.9
Hymenoptera	3	6.5	5	7.1	3	3.2	7	4.2
Lepidoptera	<u>18</u>	<u>39.2</u>	<u>19</u>	<u>27.2</u>	<u>32</u>	<u>34.4</u>	<u>62</u>	<u>36.9</u>
Thysanoptera	3	6.5	0	0.0	0	0.0	1	0.6
Orthoptera	0	0.0	0	0.0	0	0.0	4	2.4
Total	46	100.0	70	100.0	93	100.0	168	100.0

1 – for each country, two insect orders with the highest numbers of species are underlined;
2 – for UK, data from: Littlewood et al. (2015). Monophagous species (only *Fraxinus* as a food plant) and oligophagous species (*Fraxinus* and 1–3 other genera as food plant) are counted;
3 – for USA, data from: Gandhi and Herms (2010). Monophagous species (only *Fraxinus* as a food plant) and oligophagous species (*Fraxinus* and 1–3 other genera as food plant) are counted;
4 – for USA, data from: Wagner and Todd (2015);
5 – for Russia, data from: A. V. Selikhovkin, D. L. Musolin, unpublished data. Not only monophagous and oligophagous but also polyphagous species are included.

Conclusions: the future of ash in Eurasia - if any

As demonstrated above, two Asian forest invaders quickly spread in Russian ash stands: *H. fraxineus* was likely accidentally introduced first to Western Europe and is now expanding its range eastward, whereas *A. planipennis* was as well accidentally introduced first to Moscow Region and is now expanding its range in all directions but most noticeably southward (where host plant becomes more readily available) and westward. At least between the Republic of Belarus and Moscow (i.e., over Smolensk and Moscow Regions) the ranges of two invaders overlap. Taking into consideration that both invaders are devastating and that they have already almost wiped out European and North American ash species in Western Europe (*H. fraxineus*) and North America (*A. planipennis*), the synergetic effect of the two actors is likely to be fatal to local ash.

As D. A. Herms and D. G. McCullough (2014, p. 23) put it when reviewing the impact of emerald ash borer on trees and people, “the future of the ash resources in North America is precarious”. We can say the same about the fate of ash in Europe, twice as much.

Based on the presented review of the current situation between two centers of invasions, we believe that the urgent efforts in Eurasia should be focused on the following issues:

- studies of resistance mechanisms to both agents in Asian ash species (first of all, Chinese ash *F. chinensis* and Manchurian ash *F. mandshurica*) and hybrids between Asian and European or North-American ash species,
- studies on selection of resistant ash forms and hybrids (to both agents),
- controlled introduction of resistant Asian ash species,
- slowing down of expansion rates of emerald ash borer to Western Europe and ash dieback within Russia,
- studies of natural control agents,
- detailed monitoring of invasions and sanitary condition of ash in forest stands, residential places, botanical gardens (arboreta), and road-side plantings, and
- studies on synergetic effect of *H. fraxineus* and *A. planipennis* on ash.

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