Eur. J. Entomol. **112**(4): 778–789, 2015
doi: 10.14411/eje.2015.102
ISSN 1210-5759 (print), 1802-8829 (online)

Cascading ecological effects caused by the establishment of the emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae) in European Russia

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Key words. Coleoptera, Buprestidae, *Agrilus planipennis*, *Agrilus convexicollis*, non-native species, biological invasion, common ash, EAB, Curculionidae, Scolytinae, *Hylesinus varius*, Cerambycidae, *Tetrops starkii*, Hymenoptera, Braconidae, *Spathius polonicus*

Abstract. Emerald ash borer, *Agrilus planipennis*, is a destructive invasive forest pest in North America and European Russia. This pest species is rapidly spreading in European Russia and is likely to arrive in other countries soon. The aim is to analyze the ecological consequences of the establishment of this pest in European Russia and investigate (1) what other xylophagous beetles develop on trees affected by *A. planipennis*, (2) how common is the parasitoid of the emerald ash borer *Spathius polonicus* (Hymenoptera: Braconidae: Doryctinae) and what is the level of parasitism by this species, and (3) how susceptible is the native European ash species *Fraxinus excelsior* to *A. planipennis*. A survey of approximately 1000 *Fraxinus pennsylvanica* trees damaged by *A. planipennis* in 13 localities has shown that *Hylesinus varius* (Coleoptera: Curculionidae: Scolytinae), *Tetrops starkii* (Coleoptera: Cerambycidae) and *Agrilus convexicollis* (Coleoptera: Buprestidae) were common on these trees. *Spathius polonicus* is frequently recorded. About 50 percent of late instar larvae of *A. planipennis* sampled were parasitized by *S. polonicus*. Maps of the distributions of *T. starkii*, *A. convexicollis* and *S. polonicus* before and after the establishment of *A. planipennis* in European Russia were compiled. It is hypothesized that these species, which are native to the West Palaearctic, spread into central European Russia after *A. planipennis* became established there. Current observations confirm those of previous authors that native European ash *Fraxinus excelsior* is susceptible to *A. planipennis*, increasing the threat posed by this pest. The establishment of *A. planipennis* has resulted in a cascade of ecological effects, such as outbreaks of other xylophagous beetles in *A. planipennis*-infested trees. It is likely that the propagation of *S. polonicus* will reduce the incidence of outbreaks of *A. planipennis*.

INTRODUCTION

An invasion of a non-native species of insect can by a cascading sequence of ecological effects affect the structure of an ecosystem (Kenis et al*.,* 2009). In particular, the establishment of one non-native species sometimes makes an ecosystem more likely to be invaded by other non-native species (Simberloff & Von Holle, 1999). The cascading ecological effects that resulted from the establishment of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), in European Russia is described in the present article.

Agrilus planipennis is one of the most destructive forest pests in the world (Aukema et al., 2011). This beetle originates from East Asia: Northeastern China, Korea, Japan, Taiwan and Russian Far East (Jendek, 1994; Wei et al., 2007). It was inadvertently introduced into North America in the 1990s (Siegert et al., 2014) and has destroyed tens of millions of ash trees there (Aukema et al., 2011). *Agrilus planipennis* was first collected in Europe in 2003 in Moscow (Izhevskii & Mozolevskaya, 2010). To date, more than 80% of the ash trees in Moscow have been destroyed by this pest and there are additional infestations in 11 regions in central European Russia (Orlova-Bienkowskaja, 2013, 2014a, b; Baranchikov, 2013; Straw et al., 2013), but our understanding of the ecological effect of *A. planipennis* outbreak is limited.

In European Russia *A. planipennis* develops mainly on *Fraxinus pennsylvanica* Marsh. (Baranchikov et al., 2008), which was introduced from North America about 100 years ago. It is one of the most common trees in urban plantations. In particular, it makes up about 20% of the trees in Moscow (Majorov et al., 2012; Vinogradova et al., 2010). *Agrilus planipennis* prefers some species of ash over others (Wei et al., 2007; Anulewicz et al., 2008). It is important to know if *F. excelsior* is susceptible to *A. planipennis*, because *F. excelsior* is common and an important component of the biodiversity in European forests (FRAXIGEN, 2005; Mitchell et al., 2014).

Fraxinus excelsior is rare in central European Russia, with only individual trees occurring in urban plantations. The broad-leaved forests with *F. excelsior* occur in the southern parts of European Russia, in the Kursk region in particular, where *A. planipennis* has not yet been recorded. It has, however, been detected very close to broad-leaved forests in the Tula region (Straw et al., 2013; Orlova-Bienkowskaja, 2014a). Straw et al. (2013) and Baranchikov et al. (2014) record *F. excelsior* trees damaged by *A. planipennis* in Moscow. Additional records of *F. excelsior* damaged by *A. planipennis* in Moscow, Voronezh, Tula and Orel are presented in the present article.

The insect fauna encountered on *Fraxinus* in the centre of European Russia, especially in the Moscow region, is well-described (Nikitsky et al., 1996; Mozolevskaya et al., 2010). About 20 species of insects (Coleoptera, Lepidoptera, Hymenoptera and Diptera) are common on ash. *Hylesinus varius* (Coleoptera: Curculionidae: Scolytinae) was the only species of xylophagous beetle known to develop on ash in the Moscow region before the arrival of *A. planipennis*. After the establishment of *A. planipennis*, two more species of xylophagous beetle were recorded: *Agrilus convexicollis* Redtenbacher (Coleoptera: Buprestidae) (Nikitsky, 2009; Vlasov, 2010) and *Tetrops starkii* Chevrolat (Coleoptera: Cerambycidae) (Danilevsky, 2012). It is hypothesized that the extent of the range of *A. convexicollis*, which develops in dead ash branches, has increased as a result of ash canopy decline caused by *A. planipennis* (Orlova-Bienkowskaja & Volkovitsh, 2014), but the effect of *A. planipennis* on other xylophagous beetles has not been studied.

Spathius polonicus Niezabitowski (Hymenoptera: Braconidae: Doryctinae) is the first species of parasitoid recorded attacking *A. planipennis* (Orlova-Bienkowskaja & Belokobylskij, 2014) in Europe, but there is little information about its distribution, phenology and the rate of parasitism.

The aim of this study is to analyze the ecological consequences of the establishment of *A. planipennis* in central European Russia and to answer the following questions: (1) What other xylophagous beetles develop on ash infested with *A. planipennis*?; (2) how common is the emerald ash borer parasitoid, *Spathius polonicus*, and what percentage of the emerald ash borer larvae are parasitized by this parasitoid?; and (3) how susceptible is the native European ash, *Fraxinus excelsior*, to attack by *A. planipennis*?

MATERIAL AND METHODS

574 larvae, pupae and adults of xylophagous beetles and parasitoids were collected from about 1000 trees of *F. pennsylvanica* severely damaged by *A. planipennis* at 13 localities in European Russia in 2013 and 2014 (Table 1). Parasitoids were collected from the remains of *A. planipennis* larvae found under the bark in the lower part of stems up to 1.5 m from the ground. For this purpose, the lower 1.5 m of trunks of standing trees was debarked using a chisel and hammer. Larvae and pupae of xylophagous beetles were collected from under the bark of branches and thin upper parts of stems and preserved in alcohol. Adults were collected from leaves, branches and stems. About 100 trees in the Moscow region were regularly surveyed for adults twice a week from 15.v.2014 to 19.vii.2014. Dates of additional surveys in other regions are indicated in Tables 3, 4 and 5. Sweep nets and sticky bands were used, but the most effective way of sampling was collecting from leaves by hand. All specimens (adults, larvae and pupae) were examined under a microscope in the laboratory and deposited in the author's collection.

The distributions of *T. starkii* Chevrolat (Coleoptera: Cerambycidae), *A. convexicollis* Redtenbacher (Coleoptera: Buprestidae) and *S. polonicus* Niezabitowski (Hymenoptera: Braconidae: Doryctinae) before and after the establishment of *A. planipennis* are mapped. The information about records of these insects was compiled by examining 86 literature sources and collecting data from specimens deposited in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (ZIN) and Moscow State Pedagogical University (MSPU). In addition, I mapped my records of these insects in Moscow, Yaroslavl and Lipetsk regions in summer 2013 and 2014. Seventy-three localities for *A. planipennis*, 480 localities for *A. convexicollis*, 284 localities for *T. starkii* and 8 localities for *S. polonicus* are mapped. Maps of recent finds of *T. starkii*, *A. convexicollis*, and *S. polonicus* are compared with the map of the known *A. planipennis* distribution in European Russia. The program DIVA-GIS Version 7.5 (Hijmans, 2011) was used to generate the maps.

To determine how susceptible the native *F. excelsior* is to *A. planipennis,* 34 *F. excelsior* trees were examined in four cities. The sample size was limited because *F. excelsior* is rare in central European Russia. The trees were observed from ground level.

Abbreviations used in figures: AZ – Azerbaijan, AD – Adygea, AR – Armenia, BE – Belgium, BY – Belarus, CR – Crimea, CZ – Czech Republic, DA – Dagestan, IR – Iran, IT – Italy, K – Kaluga region, KA – Karachay-Cherkessia, KE – Kemerovo region, KR – Krasnodar territory, L – Lipetsk region, M – Moscow region, NL – Netherlands, O – Orel region, PL – Poland, R – Ryazan region, RO – Rostov region, S – Smolensk region, SE – Serbia, SL – Slovakia, SP – Spain, ST – Stavropol territory, SZ – Switzerland, TA – Tambov region, TD – Tadjikistan, TU – Tula region, TR – Turkmenistan, TV – Tver region, UK – Ukraine, UZ – Uzbekistan, VL – Vladimir region, VOL – Volgograd region, VOR – Voronezh region, Y – Yaroslavl region.

TABLE 1. Locations sampled.

Localities	Coordinates	Approximate no. of trees surveyed for adults	Approximate no. of trees dissected to find larvae and pupae	No. of *A. planipennis* collected	No. of specimens of other species collected
Zelenograd, 11th district	56.00°N, 37.18°E	300	20	71	179
Zelenograd, 16th district	55.97°N, 37.16°E	100	10	36	29
Zelenograd, Georgievsky prospect	55.98°N, 37.21°E	10	10	1	5
Zelenograd, Panfilova street	55.98°N, 37.17°N	50	10	35	38
Monino	55.84°N, 38.20°E	100	0	1	3
Uzunovo	54.55°N, 38.62°E	50	0	0	3
Yaroslavl	57.63°N, 39.87°E	100	0	1	4
Moscow, VILAR	55.56°N, 37.59°E	100	20	16	13
Staraya Kupavna	55.81°N, 38.18°E	100	10	5	9
Gryazi	52.49°N, 39.93°E	20	0	0	1
Planernaya	55.92°N, 37.38°E	0	50	75	23
Povarovka	56.07°N, 37.07°E	20	10	2	9
Solnechnogorsk	56.19°N, 36.98 E	20	5	3	12
Total number		970	145	246	328

TABLE 2. Localities of *Tetrops starkii* in its native range.

Region*	No. of mapped localities	Years when collected	Sources of information
Austria	23	1888–2001	Horion, 1974; Holzschuh, 1981; Geiser, 2001, GBIF, 2013
Azerbaijan	1	pre 1928	Danilevsky, 2014
Belarus	0	pre 1997	Danilevsky, 2014
Belgium	3	2012	Drumont et al., 2012
Bosnia Herzegovina	0	pre 2010	Löbl & Smetana, 2010
Bulgaria	6	pre 1931–2005	Horion, 1974; Holzschuh, 1981; Migliaccio et al., 2007; Georgiev et al., 2005; pers. commun. by G. Georgiev
Croatia	0	pre 2010	Löbl & Smetana, 2010
Czech Republic	43	pre 1929–2007	Roubal, 1929; Holzschuh, 1981; Sláma, 1998; Hoskovec, 2007; Coleoptera Poloniae, 2014 and examined specimens from ZIN**
Denmark	5	1913–1989	Danmarks Fugle og Natur, 2014; Fagdatacenter for Biodiversitet og Terrestrisk Natur, 2007
France	40	pre 1958–2002	Horion, 1974; Schmeltz, 2002; Cocquempot, 2011
Germany	21	pre 1995	Horion, 1974; Bense, 1995
Great Britain	5	1991–1997	Welch, 2003; GBIF, 2013
Greece	0	pre 2010	Löbl & Smetana, 2010
Hungary	10	pre 1971–2003	Lőkkös, 2010
Italy	7	pre 1927–2009	Roubal, 1929; Horion, 1974; Bellavista et al., 2009; Sama & Rapuzzi, 2011; Hellrigl et al., 2012; GBIF, 2013
Ireland	0	pre 2010	Löbl & Smetana, 2010
Latvia	0	pre 2010	Löbl & Smetana, 2010
Macedonia	1	1971	Holzschuh, 1981
Moldova	1	pre 1927	Roubal, 1929
Netherlands	7	1968–2013	Horion, 1974; Waarneming.nl, 2014
Norway	4	1934–2008	Horion, 1974; GBIF, 2013
Poland	11	pre 1928–2005	Starzyk & Lessaer, 1978; GBIF, 2013; Coleoptera Poloniae, 2014
Romania	5	1895–1965	Holzschuh, 1981; Starzyk & Lessaer, 1978; Serafim, 2010
Russia, Kaliningrad region	1	2014	Pers. commun. by V. Alekseev
Russia, Krasnodar region	2	1986	Nikitsky et al., 2008; Danilevsky, 2012 and examined specimens from ZIN
Russia, Rostov region	1	1951	Examined specimens from MSPU***
Russia, Voronezh region	1	1960	Examined specimens from MSPU
Russia, Republic of Crimea	1	1910	Examined specimens from ZIN
Serbia	2	pre 1974–2009	Starzyk & Lessaer, 1978; Gnjatović & Žikić, 2010
Slovakia	28	pre 1929–1991	Roubal, 1929; Holzschuh, 1981; Sláma, 1998; Lamiaires du Monde, 2014 and examined specimens from ZIN
Slovenia	9	1926–1987	Brelih et al., 2006
Spain	1	2002	Sobrino & Sánchez, 2003
Sweden	21	1947–2013	GBIF, 2013
Switzerland	19	1951–2012	CSCF-karch, 2013
Ukraine	4	1911	Pers. commun. by A. Miroshnikov and examined specimens from ZIN

* Besides these regions *T. starkii* was recorded in Central Georgia (Starzyk & Lessaer, 1978), but Danilevsky (2014) proved that this record referred to another species. Tamutis et al. (2011) presumed, that *T. starkii* could occur in Lithuania, but there are no documented records. ** ZIN – Zoological Institute of the Russian Academy of Sciences. *** MSPU – Moscow State Pedagogical University.

RESULTS

What other xylophagous beetles develop in ash trees attacked by *A. planipennis*?

The survey of ash trees attacked by *A. planipennis* revealed that three species of xylophagous beetles are common: *T. starkii*, *A. convexicollis* and *H. varius*. *Tetrops starkii* is widely distributed in the Western Palaearctic, from Great Britain in the west to Azerbaijan in the east, and from Sweden in the north to Sicily in the south (Table 2, Fig. 1). In European Russia, it has been previously recorded only in the south: Krasnodar region, Rostov region, Voronezh region and Crimea. In central European Russia, however, it was first recorded only a few years ago, namely in the Moscow region in 2012 (Danilevsky, 2012) and in Yaroslavl in 2008 (D. Vlasov, pers. commun.), so the known distribution of *T. starkii* has recently increased by 700 km to the north. *T. starkii* was collected by the author at three localities in the Moscow region including Zelenograd, where it is a common species (Table 3, Fig. 1). In all cases, *T. starkii* were collected on ash trees severely damaged by *A. planipennis*.

Tetrops starkii is known to feed on *F. excelsior* (Starzyk & Lessaer, 1978), *F. ornus* L. (Georgiev et al., 2005) and *F.*

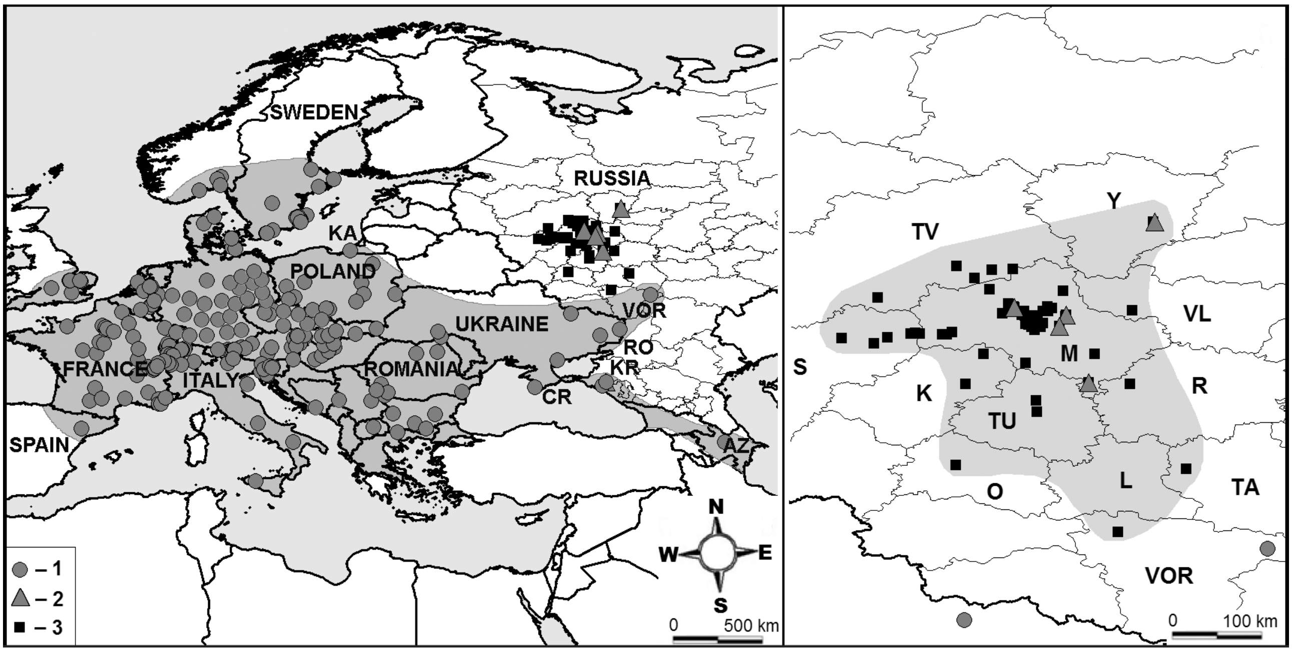

Fig. 1. The known distributions of *Tetrops starkii* (Coleoptera: Cerambycidae) and *Agrilus planipennis* (Coleoptera: Buprestidae) in Europe in 2014. Left hand map: the whole distribution, right hand map: the distribution in the centre of European Russia. 1 – records of *T. starkii* within its native distribution. 2 – localities where *T. starkii* are recorded outside its native distribution (all records for 2008–2014). 3 – localities, where *A. planipennis* are recorded. Native distribution of *T. starkii* is shaded in the left hand map and the area recently occupied by *A. planipennis* in the right hand map. Sources of information are listed in Tables 1 and 2. The localities of *A. planipennis* in Figs 1–3 are those cited by Orlova-Bienkowskaja (2014) with some new localities. Abbreviations: see "Material and methods".

angustifolia Vahl (Bellavista et al., 2009). At all localities examined in central European Russia, adults of *T. starkii* were collected on *F. pennsylvanica*. In addition, 18 pupae of *T. starkii* were collected from dead branches of *F. pennsylvanica*, which is a new host record for *T. starkii*.

In the Moscow region, adult *T. starkii* beetles were collected from late May to mid July (Table 3). Adults are active in daytime and occur on leaves both in sunny and cloudy weather and even when it is raining. Live hibernating *T. starkii* pupae were collected in winter and early spring from dead branches of *F. pennsylvanica*. It is known that in its native range *T. starkii* often occurs on the same trees as *A. convexicollis* (Starzyk & Lessaer, 1978). In the centre of European Russia, these species also coexist on *F. pennsylvanica* damaged by *A. planipennis*.

The distribution of *A. convexicollis* was recently described in detail based on the examination of 29 museum specimens and 48 literature sources (Orlova-Bienkowskaja & Volkovitsh, 2014). This species occurs in many European and Mediterranean countries, from Spain to Azerbaijan. In European Russia, it was previously recorded only in the south (Adygea, Dagestan, Karachay-Cherkessia, Krasnodar territory, Rostov region, Stavropol territory, Volgograd region and Voronezh region). Before 2007 it had not been recorded in central European Russia, but since 2007 specimens of *A. convexicollis* have been collected at 9 central European Russia localities in the Moscow, Lipetsk and Yaroslavl regions (Fig. 2, Table 4), effectively extending the northern border of the previously known distribution by approximately 665 km. In all cases but one, *A. convexicollis* was collected on ash trees with signs of *A. planipennis* infestation.

In Western Europe, *A. convexicollis* develops mainly in recently dead shoots and branches of ash trees: *F. excelsior*,

Table 3. Localities where *Tetrops starkii* was recently recorded in central European Russia.

Collection localities	Dates	No. of specimens	Source of information
Yaroslavl	21.6.2008, 18.6.2014	4 adults	One examined specimen collected by D. Vlasov and pers. commun. by D. Vlasov
Bykovo	6.2012	31 adults	Danilevsky (2012)
	2013	more than 100 adults	Pers. commun. by M. Danilevsky
Zelenograd	1.6.–3.7.2013 and 26.5–12.7.2014	57 adults	Specimens collected by the author
	19.11.2013, 27.3.2014, 16.04.2014	18 pupae	
Monino	21.6.2013	1 adult	
Uzunovo	29.6.2013	2 adults	

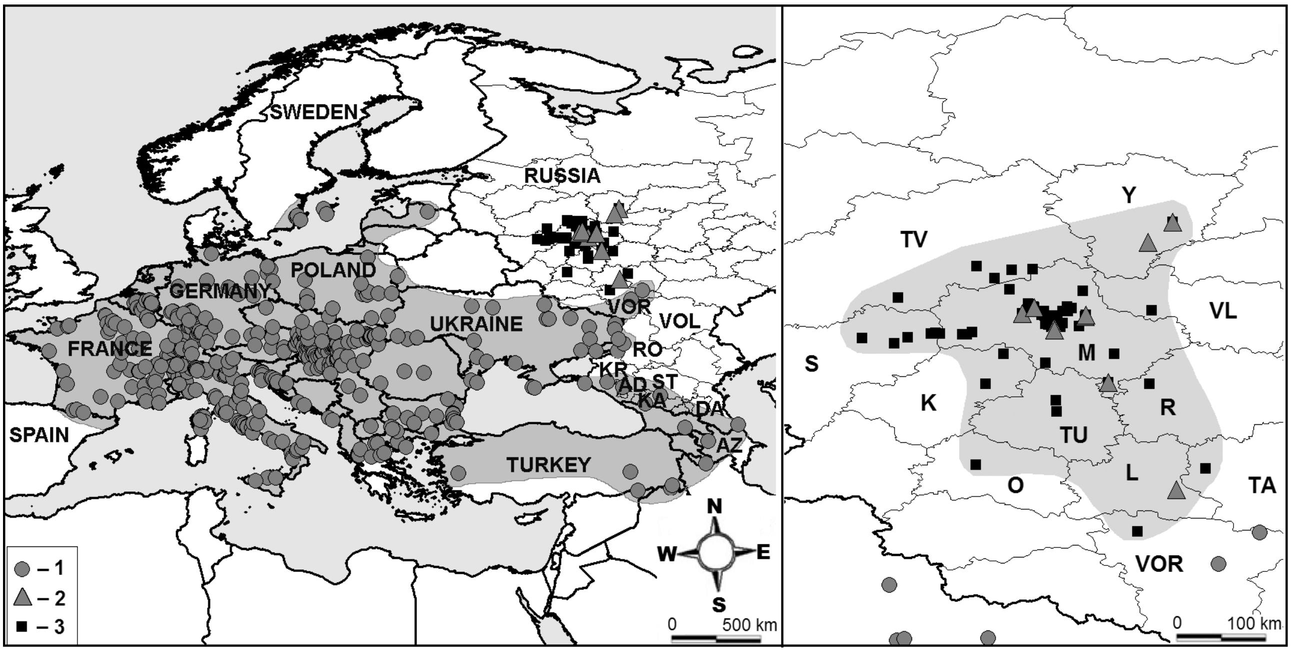

Fig. 2. The known distributions of *Agrilus convexicollis* and *A. planipennis* (Coleoptera: Buprestidae) in Europe in 2014. Left hand map is of the whole distribution, right hand map is its distribution in the centre of European Russia. 1 – records of *A. convexicollis* within its native distribution. 2 – localities where *A. convexicollis* is recorded outside its native distribution (records for 2007–2014). 3 – localities, where *A. planipennis* is recorded. Native distribution of *A. convexicollis* is shaded in the left hand map and the area recently occupied is in the right hand map. Abbreviations: see Fig. 1. The distribution of *A. convexicollis* is based on Orlova-Bienkowskaja & Volkovitsh (2014) with additional localities (see Table 4).

F. ornus and *F. oxyphylla* as well as some other plants of the family Oleaceae (Brechtel & Kostenbader, 2002). Rcently, *F. pennsylvanica* was recorded as a host plant (Orlova-Bienkowskaja & Volkovitsh, 2014). All specimens of *A. convexicollis* collected in central European Russia were on *F. pennsylvanica*. Fifteen larvae were collected from under the bark of the upper parts of the trunks of *F. pennsylvanica.* In addition, one adult beetle that died in its emergence hole was also found. The flight period of *A. convexicollis* lasts from early June to mid July (Table 4).

Hylesinus varius is a native pest of ash (Stark, 1952). The current outbreak of *H. varius* was first recorded in 2002 (Izhevskii & Mozolevskaya, 2010). In this study, larval galleries, adults and larvae of *H. varius* were recorded in trunks and branches of *F. pennsylvanica* at seven localities in the Moscow region. The percentage of trees damaged by *H. varius* is estimated to be between 10 and 60%. The adult flight period is in May. New adults were recorded in the bark from the middle of August to the end of April. *Hylesinus varius* occurs mainly in the same trees

Table 4. Localities where *Agrilus convexicollis* was recently recorded in central European Russia.

Localities	Dates	No. of specimens	Was the tree damaged by *A. planipennis*?	Source of information
Yaroslavl	2007 and 30.6.2013	4 adults	Yes	Vlasov (2010) and specimens collected by the author
Rostov (Yaroslavl Region)	2007	1 adult		Pers. commun. by D. Vlasov
Manikhino	15.6.2008	1 adult	Yes	Nikitsky (2009)
Zelenograd	1.6.2013–5.7.2013, 2.6–16.7.2014	74 adults, 12 larvae	Yes	Specimens collected by the author
Moscow, Botanical garden of VILAR	19.6.2014	3 adults, 3 larvae	Yes	
Staraya Kupavna	21.6.2013	9 adults	Yes	
Monino	21.6.2013	2 adults	Yes	
Uzunovo	29.6.2013	1 adult	Yes	
Gryazi	27.6.2013	1 adult	No	
Total number		95 adults, 15 larvae		

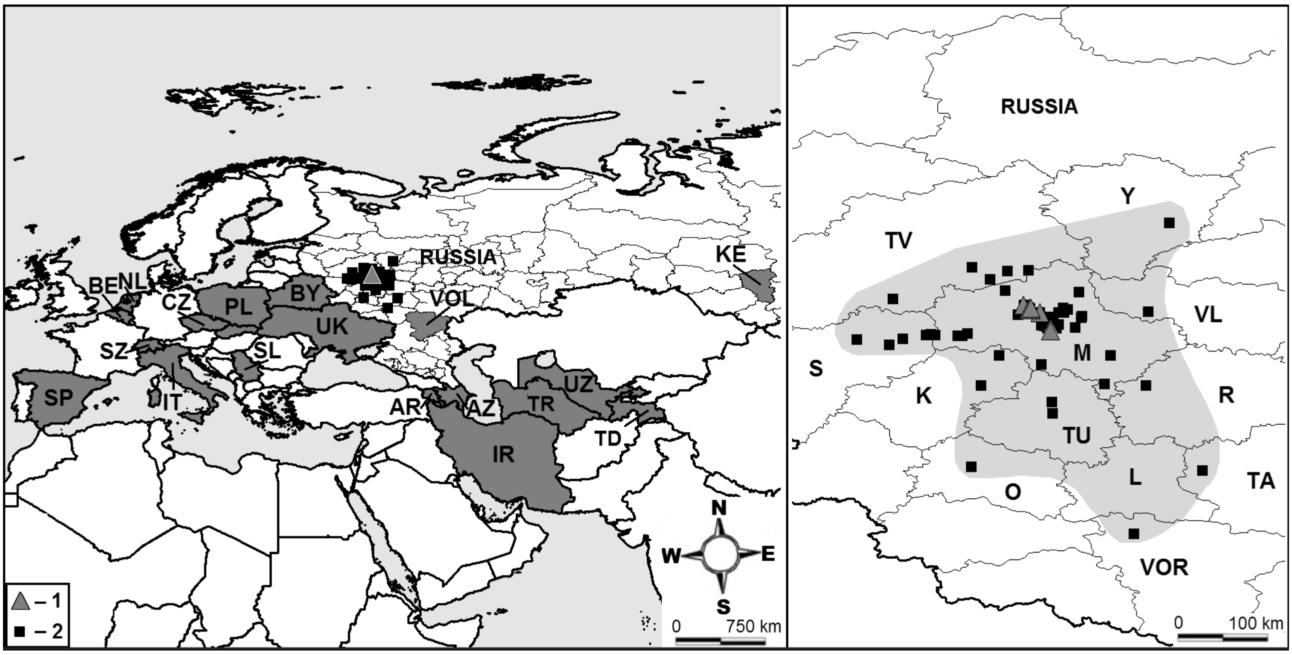

Fig. 3. The known distribution of *Spathius polonicus* (Hymenoptera: Braconidae) and the area recently occupied by *A. planipennis* (Coleoptera: Buprestidae) in Europe in 2014. Left hand map is the whole distribution, right hand map is distribution in the centre of European Russia. 1 – records of *S. polonicus* reported in 2013–2014. 2 – localities, where *A. planipennis* is recorded. Countries and regions where *S. polonicus* is recorded are shaded in the left hand map and the area recently occupied by *A. planipennis* is shaded in the right hand map. Sources of information are listed in Table 5.

as *A. planipennis*, but there are also occasionally individual trees severely damaged or even killed by *H. varius* without any signs of infestation by *A. planipennis*. The proportion of such trees in Zelenograd is about 5%.

How common is the parasitoid *Spathius polonicus* and what is the extent of parasitism of the emerald ash borer *A. planipennis* by this species?

Spathius polonicus is an ectoparasitoid of buprestid larvae (Belokobylskij, 2003). Recently, it was discovered that it can parasitize *A. planipennis* (Orlova-Bienkowskaja & Belokobylskij, 2014). *Spathius polonicus* is a widely distributed Western Palaearctic species (Fig. 3). It occurs in Spain, Netherlands, Switzerland, Italy, Poland, Czech Republic, Slovakia, Serbia, Belarus, Ukraine, Russia, Armenia, Azerbaijan, Turkmenistan, Uzbekistan, Tadjikistan, Iran (Belokobylskij, 2003) and Belgium (Belgian Species List, 2014). It had not been recorded in the centre of European Russia before 2013. The only previously known locality in European Russia is in the southeastern part: in the Volgograd region (Belokobylskij, 1989). In 2013–2014, *S. polonicus* was found at eight localities in the Moscow region (Table 5, Fig. 3). The distance between the two most distant localities is about 78 km. So *S. polonicus* is common and rather widely distributed in the region of the outbreak of *A. planipennis*.

I have collected 129 live specimens (adults in cocoons, larvae and pupae) of *S. polonicus* associated with late instar *A. planipennis* under the bark of trunks. I found the remains of 56 *A. planipennis* larvae killed by *S. polonicus* and 51 live late instar larvae. With about 50% of the specimens sampled parasitized the percentage parasitism is probably quite high. Remains of *A. planipennis* larvae killed by *S. polonicus* typically consist of the head capsule, prothorax and a pair of urogomphi connected by a thin "thread" (remains of the body) (Fig. 4). Sometimes the dead *A. planipennis* larvae found with cocoons of *S. polonicus* were not completely consumed. Up to six specimens of *S. polonicus* develop on one larva of *A. planipennis*. They can be at different stages of development. Sometimes larvae, pupae and adults in cocoons occur simultaneously on the same *A. planipennis* larva. Cocoons are built close to each other. In winter, hibernating *S. polonicus* pupae and larvae in cocoons were collected from under the bark (Table 5). Adult *S. polonicus* were captured on leaves in June–July.

What other insects are connected with *F. pennsylvanica* attacked by *A. planipennis*?

Adults of *Coeloides melanotus* Wesmael (Braconinae) are very common on leaves of *F. pennsylvanica* in the Moscow region. Seven adults of this species were reared from pieces of dead branches of *F. pennsylvanica* collected 16 April 2014. There were also larval galleries of *T. starkii* and *H. varius* in these branches. It is known that *C. melanotus* parasitizes *H. varius* (Elton, 1966). Eight larvae of *A. convexicollis* were killed by unidentified braconid parasitoids. Six pupae and 7 larvae of these parasitoids were collected. On 19 July 2014 one pupa of an unknown hymenopteran parasitoid was found within the cocoon of *S. polonicus*. Some insects, in particular *Anthonomus pomorum* L. (Curculionidae), use the galleries of *A. planipennis* or space under loose bark of *F. pennsylvanica* as a shelter. Other species use the larval galleries as a breeding site. For example, the wasp *Passoloecus corniger* Shuckard (Hy-

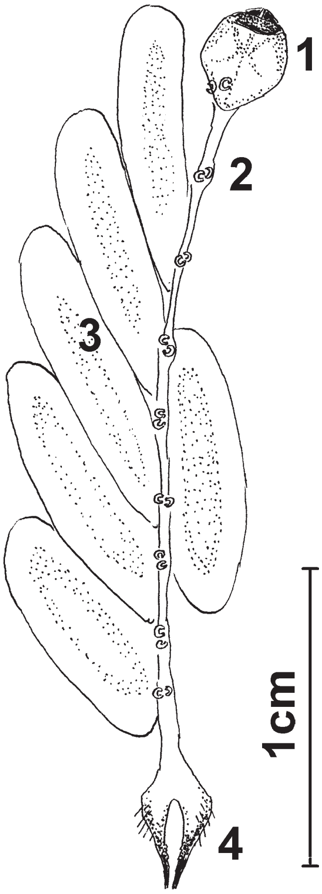

Fig. 4. Remains of a larva of *Agrilus planipennis* with cocoons of the ectoparasitoid *Spathius polonicus*. 1 – head capsule and prothorax; 2 – remains of cuticle with spiracles; 3 – cocoons of the ectoparasitoid; 4 – urogomphi.

menoptera: Sphecidae) makes nests in larval galleries of *A. planipennis* in trunks of *F. pennsylvanica*, and the smaller wasp *Passoloecus brevilabris* Wolf (Hymenoptera: Sphecidae) make nests in larval galleries of *A. convexicollis* in dead branches.

How susceptible to attack by *A. planipennis* is the native species of European ash, *Fraxinus excelsior*?

The survey of 34 trees of landscaped ash *F. excelsior* in four cities where *A. planipennis* was present revealed that 28 of them have emergence holes of *A. planipennis* (Table 6). All trees with signs of *A. planipennis* infestation were severely damaged. Many branches and sometimes the upper parts of trunks were dead. Larvae of *A. planipennis* were collected from under the bark of *F. excelsior*.

DISCUSSION

Invasive plants, which change the character of ecosystems, are termed transformers (Richardson et al., 2000). *Agrilus planipennis* is an example of such an insect. It significantly changed the community connected with *F. pennsylvanica* in central European Russia. The scheme of ecological effects connected with the establishment of *A. planipennis* is shown in Fig. 5.

It is known that *A. planipennis* thrives on *F. pennsylvanica* (Wei et al., 2007; Anulewicz et al., 2008) and readily colonizes it, causing an outbreak. Outbreaks have occurred in North America where *F. pennsylvanica* is native and *A. planipennis* is non-native (Aukema et al., 2011), in China where *F. pennsylvanica* is non-native and *A. planipennis* is native (Wei et al., 2007) and in European Russia where both species are non-native (Volkovitsh & Mozolevskaya,

Table 5. Specimens of *S. polonicus* collected with the remains of larvae of *A. planipennis* from under the bark of *F. pennsylvanica* in the Moscow region.

Locality	Date of collection	Collected specimen of *S. polonicus*	No. of *A. planipennis* last instar larvae killed by *S. polonicus*	No. of live *A. planipennis* last instar larvae and prepupae
Zelenograd, 11th district	1.–2.10.2013	12 larvae in cocoons, 1 pupa	2	8
	29.10.2013	4 larvae in cocoons, 1 pupa	1	1
Zelenograd, 16th district	30.10.2013	20 larvae in cocoons	3	4
	11.3.2014	9 adults in cocoons	1	2
Zelenograd, Georgievsky prospect	4.5.2014	2 adults in cocoons, 2 larvae in cocoons, 1 pupa	3	1
Zelenograd, Panfilova street	4.6.2014	8 adults in cocoons, 7 larvae	5	6
	19.7.2014	9 empty cocoons, 5 adults in cocoons, 2 larvae in cocoons, 4 pupae	13	9
	16.6.2014	3 empty cocoons	1	3
Planernaya	9.1.2014	5 larvae in cocoons	1	4
	10.3.2014	1 adult in cocoon, 7 larvae in cocoons	2	3
	28.4.2014	10 adults in cocoons	12	0
Povarovka	2.5.2014	3 adults in cocoons, 6 larvae in cocoons	6	1
Moscow, Botanical garden of VILAR	19.6.2014	7 adults reared from cocoons	2	9
Solnechnogorsk	21.7.2014	10 adults in cocoons, 2 larvae	4	0
Total number	–	55 adults, 7 pupae, 67 larvae	56	51

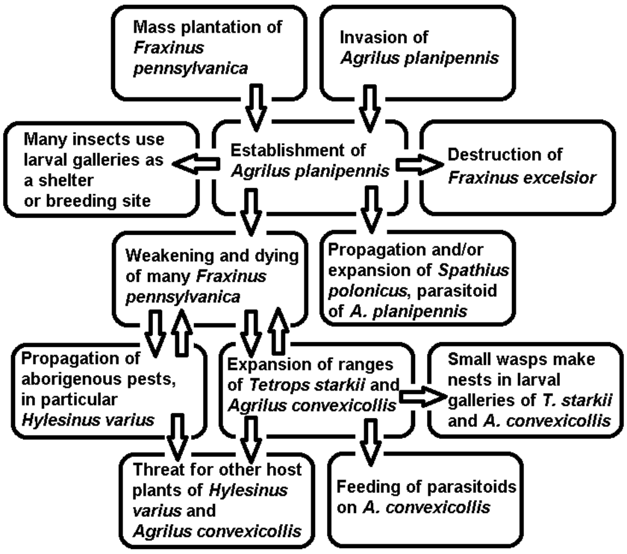

Fig. 5. Cascading ecological effects caused by the establishment of *Agrilus planipennis.*

2014). In central European Russia, the native *F. excelsior* is rare (Gubanov et al., 1992), but mass cultivation of North American *F. pennsylvanica* created a rich food supply for *A. planipennis*. This was one of the main factors aiding the establishment and quick propagation of this invasive pest. Few cases of damage to *F. excelsior* by *A. planipennis* were known before 2012. It was hoped that *F. excelsior* might be less susceptible to this pest (Baranchikov et al., 2008; Izhevskii & Mozolevskaya, 2010) but unfortunately this is not so. Many cases of infestation and severe damage of *F. excelsior* are known (Majorov et al., 2012; Straw et al., 2013; Baranchikov et al., 2014 and present study). *Fraxinus excelsior* is common in the south of European Russia, the Caucasus and central and Western Europe. It has an important role in the biodiversity of European forests (Mitchell et al., 2014), so the ecological consequences of the establishment of *A. planipennis* in Europe could be considerable.

In the Far East, *A. planipennis* often affects trees together with *Hylesinus chlodkovskyi* Berger (Yurchenko et al., 2007). In European Russia, it often affects trees together with the native pest of the same genus: *H. varius.* The establishment of *A. planipennis* was accompanied by an outbreak of *H. varius* (Izhevskii & Mozolevskaya, 2010). This outbreak was recorded after 2002, i.e. before the first specimen of *A. planipennis* was found (Izhevskii, 2007). It is possible that *H. varius* thrived because *A. planipennis* weakened the ash trees, but it is also possible that the establishment of *A. planipennis* was facilitated by an outbreak of *H. varius*. It is known that native and alien xylophagous insect species can benefit each other by weakening trees (Kenis et al., 2009). An outbreak of *H. varius* worsens the situation for ash trees and can potentially also affect lilac (*Syringa* spp.) and other host plants of this species (Stark, 1952).

Examination of the ranges and habitats of *T. starkii* and *A. convexicolis* has led me to conclude that these West-Palaearctic xylophagous beetles are not native to central European Russia. First, they were not recorded there before the establishment of *A. planipennis*, but were discovered almost immediately after the establishment of *A. planipennis*. Second, they occur only on ash trees damaged by *A. planipennis*. Third, they occur only in habitats transformed by humans, which is typical of newly established non-native beetles (Beenen & Roques, 2010). In Western Europe, *T. starkii* and *A. convexicolis* develop in dead branches of ash trees (Starzyk & Lessaer, 1978; Brechtel & Kostenbader, 2002). Probably they spread to European Russia because *A. planipennis* had weakened the ash trees growing there.

Could *A. convexicollis* and *T. starkii* have occurred unnoticed in central European Russia prior to the arrival of *A. planipennis*? It is unlikely, though impossible to prove the absence of any species of insect in any territory. However, the fauna of xylophagous beetles in the Moscow region has historically been intensively surveyed and *A. convexicollis* and *T. starkii* were not recorded (Nikitsky et al., 1996). Also, there are no specimens of *A. convexicollis* and *T. starkii* collected in central European Russia in the rich collections in the Zoological Institute (Russian Academy of Sciences), Moscow State Pedagogical University and Zoological Museum of Moscow State University, although there are many other specimens of the genera *Agrilus* and *Tetrops* and of beetles collected from ash trees, such as *H. varius.* In addition, *A. convexicollis* and *T. starkii* are conspicuous because they are neither very small nor nocturnal. They occur on the leaves of ash trees in cities where many professional and amateur entomologists live and where specialized institutions for forest science are located. Fi-

TABLE 6. Results of examinations of trees of *Fraxinus excelsior* in European Russia.

Localities	Dates	No. of trees examined	No. of trees with emergence holes	Source of information
Moscow	2013	14	7	Straw et al., 2013
Moscow, N.V. Tsitsin Main Botanical Garden	2014	64	45	Baranchikov et al., 2014
Moscow, Botanical garden of VILAR	19.6.2014	16	16	Own observations
Voronezh	12.6.2013	1	1	Own observations
Tula	5.6.2013	3	3	Own observations
Orel	4.–5.6.2013	14	8	Own observations
Total number		112	80	

nally, *A. convexicollis* and *T. starkii* were recorded at hundreds of localities in West and Central Europe before 2007, but not in the centre of European Russia. It is unlikely that they occurred but remained unnoticed in the Moscow region since the fauna of beetles in the Moscow region is as well studied as the fauna of Central Europe.

Perhaps more insects were recorded on ash and their known distribution ranges extended after the detection of *A. planipennis* because people looked harder and in more places? That is not the case. First, *T. starkii* and *A. convexicollis* were recorded in the Yaroslavl region before the data on the detection of *A. planipennis* in central Russia were published (D. Vlasov, pers. commun.; Vlasov, 2010). Second, the researchers who collected *A. convexicollis* and *T. starkii* before 2013 (D. Vlasov, E. Shankhiza, M. Danilevsky) were not surveying ash trees in connection with the establishment of *A. planipennis*.

Fraxinus pennsylvanica is very common in the centre of European Russia, so there is no reason to think that the hosts in the centre of European Russia were less suitable than in Europe. In spite of this, in the 20th century, *T. starkii* and *A. convexicollis* were recorded at several hundred localities in Central and Western Europe but not in the Moscow region and other regions of Central Russia. There are no reasons to believe that these species were more difficult to find in the Moscow region than in Central Europe, so I believe that the absence of these species in collections and lists of fauna is reliable evidence of their absence before the *A. planipennis* invasion.

What factors could facilitate the spread of *A. convexicollis* and *T. starkii* into central European Russia? First, it is well known that many insects in Europe are now spreading northward because of warming climates (Beenen & Roques, 2010). Second, the introduction of *F. pennsylvanica* created a rich food supply for these pests. The main factor is probably the weakening of ash trees by *A. planipennis* because the northern borders of their ranges shift northwards only in the region occupied by *A. planipennis*. *Agrilus convexicollis* and *T. starkii* extended their known ranges northwards by more than 600 km and just into areas recently occupied by *A. planipennis*. It is unlikely that it is just a coincidence. Larvae of xylophagous beetles can develop faster if the tree is stressed (Tluczek et al., 2011). In stressed trees, they can complete development even if the warm period is short. Therefore, if the shorter warm period was the factor limiting the northern extension of the ranges of *T. starkii* and *A. convexicollis*, the appearance of stressed ash trees could have facilitated the spread of these species to the north. Straw et al. (2013) discuss the possible influence of drought on the susceptibility of *Fraxinus excelsior* and *F. pennsylvanica*. Probably the severe drought in 2010 facilitated the current outbreak of *A. planipennis* and other xylophagous insects connected with ash trees.

It is quite possible that *T. starkii* and *A. convexicollis* could weaken *F. pennsylvanica* and therefore facilitate further propagation of *A. planipennis*. If this hypothesis is confirmed, the interactions between *A. planipennis*, *A. convexicollis* and *T. starkii* are an example of an invasion meltdown, i.e. the process by which a group of non-native species facilitate one another's invasion (Simberloff & Von Holle, 1999). *Agrilus convexicollis* and *T. starkii* are known to feed on North American *F. pennsylvanica*, therefore they could potentially become established wherever *F. pennsylvanica* is present. The appearance of *T. starkii* and *A. convexicollis*, as well as the outbreak of the native pest *H. varius*, could affect *F. excelsior* in European Russia.

The parasitoid *S. polonicus* could also be a non-native species that spread into central European Russia shortly after the establishment of *A. planipennis*. It is rather widely distributed in the West Palaearctic, but was not recorded in central European Russia until after the establishment of *A. planipennis*. It is unlikely that *S. polonicus* was introduced with *A. planipennis* because *S. polonicus* is not recorded in the native range of *A. planipennis*, although less is generally known about the ranges of Braconidae than of many beetles. As a result, it cannot be excluded that *S. polonicus* may have occurred but remained unrecorded in central European Russia before its recent discovery.

I found *S. polonicus* under the bark at all localities where I collected larvae of *A. planipennis*. Obviously this parasitoid is common in the region occupied by *A. planipennis*. The level of parasitism by *S. polonicus* seems rather high, so this parasitoid could if propagated and released be an effective biological control agent of *A. planipennis* infestations, though more precise studies are necessary to evaluate this hypothesis. *Spathius polonicus* may be suitable for biocontrol of *A. planipennis* both in Europe and North America, because it is a native of the temperate climate zone. The potential of this parasitoid for biological control needs to be investigated further.

The resulting cascade of ecological effects following the spread of *A. planipennis* may also affect other species, because *T. starkii*, *A. convexicollis* and *S. polonicus* are connected with other species of insects and plants in their native ranges. In particular, *A. convexicollis* feeds on different trees and shrubs of the family Oleaceae (Brechtel & Kostenbader, 2002) and larvae of *S. polonicus* are known to parasitize the larvae of many buprestids (Belokobylskij, 2003). In addition, there are parasitoids that parasitize *A. convexicollis* and *T. starkii*. Cascading ecological effects concern not only insects included in food chains connected with ash, but may affect some insects that use the space under loose bark as a shelter or breeding site.

Cascading direct and indirect effects of the establishment of *A. planipennis* are reported in North America (Smith, 2006; Gandhi & Herms, 2010; Herms & McCullough, 2014). The damage resulting from an outbreak of *A. planipennis* causes the formation of gaps in the canopy, changes woody debris dynamics and biogeochemical cycling, influencing both native and non-native plants. In particular, *A. planipennis* can facilitate the establishment and spread of invasive plants by creating gaps in the canopy that increase light availability while relaxing interspecific competition for space and resources.

It is known that invasion by one species can facilitate the invasion of a related species (for example, parasites) from the same region (Kenis et al., 2009), but the case considered in the present article is different. The community connected with *F. pennsylvanica* affected by *A. planipennis* is "intercontinental" and of recent origin. The host plant *F. pennsylvanica* originates from North America, while *A. planipennis* is from East Asia, *T. starkii*, *A. convexicollis* and probably *S. polonicus* are from European regions west and south of the centre of European Russia, and *H. varius* and other insects are indigenous. Ecological interactions between the members of this community are anthropogenic, because these are interactions between species that do not occur in the wild. This case illustrates that the invasion of one non-native species could indirectly affect the distributions of other species through cascading ecological effects. In other words, humanity inadvertently creates new complexes of ecologically related species and these complexes have unknown properties.

ACKNOWLEDGEMENTS. I thank M. Danilevsky (A.N. Severtsov Institute of Ecology and Evolution, Moscow), A. Miroshnikov (Russian Entomological Society, Krasnodar), D. Vlasov (Yaroslavl State Historical-Architectural and Art Museum-Reserve, Yaroslavl), V. Alekseev (Kaliningrad State Technical University, Kaliningrad) and G. Georgiev (Forest Research Institute, Sofia) for valuable information, S. Belokobylskij (Zoological Institute, St. Petersburg) for identification of Braconidae, K. Makarov (Moscow State Pedagogical University, Moscow) and M. Volkovitsh (Zoological Institute, St. Petersburg) for the possibility to study specimens from collections deposited in their respective institutes, to V. Maslyakov (All-Russian Research Institute of Medicinal and Aromatic Plants) for allowing me to collect insects in the botanical garden of this institute, and to N.W. Siegert (USDA Forest Service) and A.F.G. Dixon (University of Norwich) for linguistic corrections. The study was supported by the Russian Foundation for Basic Research (project No. 15-29-02550).

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Received April 15, 2015; revised and accepted July 13, 2015
Prepublished online October 8, 2015