

Is It Possible to Distinguish Alien Species of Beetles (Coleoptera) from Native Ones?

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Abstract—Species established outside their native ranges are termed alien. Biological invasions of beetles are poorly studied. Distinguishing between alien and native species is necessary for conservation as well as for taxonomic, zoogeographic, and evolutionary studies. It constitutes a difficult problem, but the experience of botany and some branches of zoology gives reasons to believe that it is not unsolvable. The following criteria for distinguishing alien beetle species from native ones are proposed based on the criteria developed for plants, algae, mammals, and marine invertebrates: (1) detection of an established population of the species which has not been recorded earlier in the region; (2) disjunction of the range which cannot be explained by disjunction of suitable landscapes or host plant ranges; (3) expansion of a part of the range isolated from its main part; (4) highly localized distribution in an area adjacent to a known invasion pathway; (5) establishment in other regions; (6) dependency on another non-native species (feeding on an alien host plant or animal); (7) absence of specific parasites in the given region and their presence in some other region; (8) association with anthropogenic biotopes; (9) sharp fluctuations of abundance; (10) lack of taxonomically close species in the given region and their presence in other regions; (11) detection in the region of two or more taxonomically and/or ecologically close species typical of another region; (12) presence of known vectors of invasion; (13) low genetic diversity; (14) reproduction by parthenogenesis or inbreeding. These criteria are mere indirect evidences of the alien status of a species in the given territory, because numerous exceptions exist. Usually it is impossible to recognize an alien species by a single criterion, but matching several criteria characterizes the species as an alien one with high probability.

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Beetles (order Coleoptera) comprise about 20–25% of all the living species (Zhang, 2013; Roskov et al., 2015), but papers devoted to alien beetles make up only 5–7% of all the papers on biological invasions in the special Russian and international journals (Fig. 1). Of course, these figures do not mean that beetles become established beyond their natural ranges less frequently than other organisms. The true reason of this imbalance is the insufficient level of knowledge of the biological invasions of beetles.

Beetles are constantly brought into new territories with grain, vegetables, planting stock, seeds, timber, compost, and humus; they can be inadvertently transported by vehicles and in a number of other ways, and often get established in the new territories (Beenen, 2006; Kenis et al., 2007; Roques et al., 2009; Maslyakov and Izhevsky, 2011). In most cases, however, the appearance of new species in the beetle fauna remains unnoticed (Kirkendall and Faccoli, 2010). The known alien beetle species are only the tip of the iceberg. Experts believe that the great majority of alien species

are presently considered as native ones (Beenen, 2006). In the level of knowledge of invasions, entomology drops behind many other fields of biology. For example, the fraction of phytophagous beetles considered to be alien in Moscow Province is 80 times smaller than that of adventive plants in the local flora (Maslyakov and Izhevsky, 2011; Maiorov et al., 2012) (Fig. 2).

Recognizing alien beetle species is very important in various fields of research. For adequate analysis of the genetics, physiology, ecology, and other aspects of life of a given species in a given territory, it is necessary to know if the species is a native one or it has colonized this territory as the result of human activities. The knowledge of the species' status (native or alien) is a necessary basis for taxonomic, zoogeographic, and evolutionary conclusions, and also for taking practical measures of pest control and conservation. For example, researchers looking for agents of biological control of a particular pest need to know where the native range of this pest is located (Maslya-

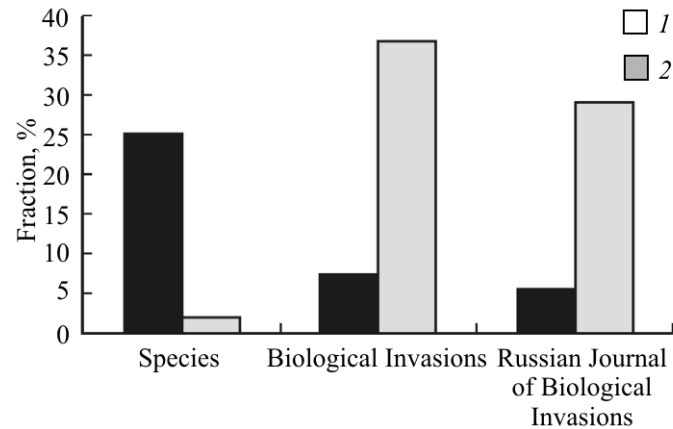


Fig. 1. The fraction of beetles among all the living species and the fraction of papers devoted to beetles in two special journals: Biological Invasions and Russian Journal of Biological Invasions. The corresponding data on ray-finned fishes are provided for comparison; 1, beetles; 2, ray-finned fishes.

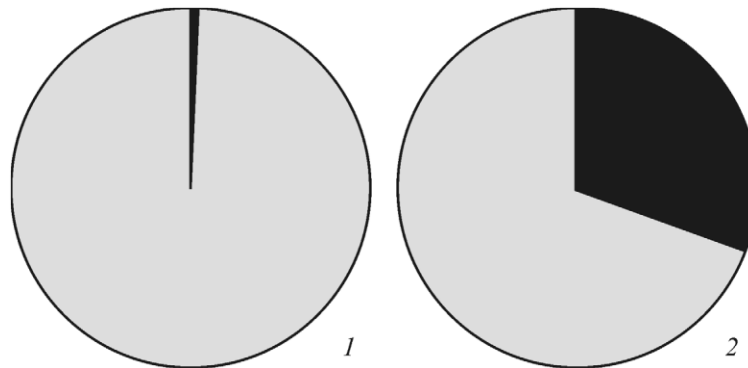


Fig. 2. The fraction of alien species in the fauna of phytophagous beetles of Moscow Province (1) and the fraction of adventive plants in the flora of Moscow Province (2) (after Maslyakov and Izhevsky, 2011; Maiorov et al., 2012).

kov and Izhevsky, 2011). This knowledge is also needed to avoid the common mistake of including the recently introduced species in the lists of protected taxa (Saveliev, 2005).

The invasions of beetles have recently attracted the attention of many researchers. Lists of alien species have been compiled for selected territories and beetle families (Beenen, 2006; Beenen and Roques, 2010; Kirkendall and Faccoli, 2010; Vlasov, 2013; Munteanu et al., 2014). Beetles are included in the databases of alien species (*Alien Insects...*, 2012; *NOBANIS*, 2014; *DAISIE*, 2014). However, no special criteria of alienness have been developed for beetles, since the biology of insect invasions still remains at the initial stage of data accumulation, and some general conclusions have only started to be drawn (Maslyakov and Izhevsky, 2011).

In many cases, only the species having an established “reputation” of invaders are regarded as aliens. Experts note that beetle species are usually

added to the lists and databases of alien organisms with hardly any justification (Kirkendall and Faccoli, 2010). On the other hand, common and familiar species tend to be automatically categorized as native. In order to abandon such a subjective approach in favor of the scientifically valid one, the criteria of alienness should be developed (Webb, 1985; Pushkarov, 2012).

The smaller are the representatives of a given taxon, the more difficult it is to recognize some of them as aliens. This tendency was ironically expressed as the “small rule of invasion ecology: If you are small you are native” (Wyatt and Carlton, 2002). Revealing alien species of beetles is a fairly complicated task. Even after a thorough investigation, it may be difficult to state with confidence that the species recorded for the first time in a given territory is an alien one, and not merely a native species which had been overlooked previously (Prisnyi et al., 2013). It is only rarely that the exact moment of invasion can be recorded and the

subsequent establishment of the species can be observed.

However, the absence of direct evidence of the alien origin of some species does not mean that these species should be considered native “by default,” or that the problem should be abandoned as unsolvable. The experience of botany and some branches of zoology shows that the problem of recognizing alien species can be solved. The criteria suitable for revealing alien forms have been developed for many groups, in particular higher plants, marine invertebrates, and algae (Webb, 1985; Chapman and Carlton, 1991; Boudouresque and Verlaque, 2002; Zvyagintsev et al., 2011; Maiorov et al., 2012). Since every rule has exceptions, none of the criteria can provide absolute proof of the alien origin of a species; still, applying several criteria to a particular species often helps the researcher to determine its most probable status.

The criteria of alienness proposed independently for different taxa are quite similar, this fact obviously reflecting some common trends of the invasion process. At the same time, the complexes of criteria also show differences determined by the specific ecological features of different groups and their specific types of relationships with man. In particular, groups of organisms differ in the pattern of biotopic distribution of alien species (Pyšek et al., 2010). The methods of revealing alien forms among other taxa cannot be mechanically applied to beetles. Instead, specific criteria suitable for beetles should be developed.

This work has the following goals.

- (1) To attract the attention of coleopterists to the problem of development of the criteria for revealing alien species.
- (2) To propose the ways of solving this problem based on the summarized experience of botany and other fields of biology.
- (3) To demonstrate the validity of ecological, geographic, phylogenetic, and other criteria of alienness by the examples of some indisputably alien beetle species.
- (4) To show how the complex of criteria can be used to estimate the status (native or alien) of species in non-obvious cases.

The terminology used in this communication mostly follows that of Maslyakov and Izhevsky (2011).

THE CRITERIA OF ALIENNESS OF A SPECIES

1. *The Finding of a Sustainable Population of the Species in the Territory Where It Had not been Recorded Before*

If the flora or fauna of a particular region is well studied, the appearance of a new, previously unrecorded species will indicate that the species has migrated into the region from elsewhere. This approach is used to establish the alien status of the species of mammals (Khlyap et al., 2008), higher plants (Webb, 1985), marine invertebrates (Chapman and Carlton, 1991), and algae (Boudouresque and Verlaque, 2002).

Unfortunately, the fauna of beetles is very incompletely studied, the faunistic lists being available only for individual regions and some beetle families. Therefore, this criterion can be applied only in such obvious cases when the alien species causes great economic damage and cannot remain unnoticed. A good example is the emerald ash borer *Agrilus planipennis* Fairmaire, 1888 (Buprestidae). Until the beginning of the XXI century this species was recorded only in East Asia; later, since 2002, it started to be recorded in North America, and since 2003, in Moscow. Mass reproduction of this pest during the last decade manifested itself as an entomogenic disaster, resulting in the death of a considerable part of ash trees in Moscow Province (Orlova-Bienkowskaja, 2013a). Experts are certain that *A. planipennis* is an established alien species (Volkovitsh and Mozolevskaya, 2014).

The findings of single specimens may be incidental and cannot indicate the establishment of the species. For example, sporadic findings of *Harmonia axyridis* (Pallas, 1773) (Coccinellidae) in Belgorod Province, *Leptomona russica* (Gmelin, 1790) (Chrysomelidae) in Orenburg Province, and *Paridea angulicollis* (Motschulsky, 1854) (Chrysomelidae) in Primorskii Territory are no proof of invasion of these species (Bieńkowski and Orlova-Bienkowskaja, 2013; Orlova-Bienkowskaja, 2013b; Orlova-Bienkowskaja and Bieńkowski, 2014). Still, such findings should be recorded, so that later, if the species is really established in the given territory, the time of its appearance can be determined. The initial stages of active dispersal of invasive plant species are usually poorly documented (Vinogradova et al., 2010), and the corresponding data on beetles are even scarcer. For example, the invasive ladybird *Harmonia axyridis* was first recorded in Moldova only after it had become a common species

in the whole territory of that country (Yazlovetsky and Sumenkova, 2013).

Historical records serve as one of the main criteria for recognizing adventive plants. The absence of a given species in the old floristic lists and herbaria indicates that it did not grow in the territory in question (Webb, 1985). The archeophytes (ancient invaders) may be a dubious group while the alien status of most of the neophytes (recent invaders) is fairly easy to establish (Maiorov et al., 2012). During analysis of the flora, the arbitrary boundary between ancient and recent invaders is usually drawn at the year 1500 (Vinoogradova et al., 2010), and in case of the mammalian fauna, at 1700 (Khlyap et al., 2008). Unfortunately, almost no faunistic lists of beetles have been preserved from the past centuries. Therefore, the boundary between ancient and recent invaders should be placed no earlier than the middle of the XIX century, when the first reviews of beetles were compiled (e.g., Dejean, 1837; Gemminger and Harold, 1868–1876).

The situation is aggravated by the difficulty of identification of beetle species and the scarcity of experts. A species may be absent in the earlier lists simply because the researchers failed to identify it. For example, the common and widespread leaf beetle *Cryptocephalus bameuli* Duhadelborde, 1999 (Chrysomelidae) remained unrecorded in European Russia for a long time because it was not differentiated from a close species *Cryptocephalus flavipes* Fabricius, 1781 (Bieńkowski, 2009).

However, such examples constitute an exception rather than the rule. The skepticism of some entomologists who believe that every finding of a species previously unrecorded in European Russia should be attributed to incompleteness of the previous records cannot be accepted. Material from European Russia was collected by hundreds of professional entomologists and thousands of amateurs. The Zoological Institute of the Russian Academy of Sciences and the Zoological Museum of Moscow State University possess extensive collections of beetles which quite fully represent the regional fauna. Therefore, new findings, especially those made in the best studied central parts of the region, are more likely to indicate invasion than to reflect the incompleteness of previous collections.

The native status of the species may be indicated by its having been found during archaeological excavations (Vlasov, 2012) or by its presence in the bottom sediments (Nazarov and Rasnitsyn, 1984). The use of

archaeological data to reconstruct the history of formation of the fauna is a highly promising direction of research. However, a situation is possible when the species inhabited a given territory in the remote past, then became extinct there, and after that re-colonized the territory. In invasion biology such species are commonly regarded as aliens, since they resemble true invaders in their ecological traits and the manner of interaction with the native communities (Khlyap et al., 2008).

2. Disjunction of the Range which Cannot be Explained by Disjunction of Landscapes or Ranges of host plants

If the range of the species consists of several isolated areas, then one of these areas may be its native range, and the others, the results of invasion (Webb, 1985; Chapman and Carlton, 1991). Most beetles established outside their native distribution areas have disjunctive ranges. For example, the ambrosia beetle *Xylosandrus germanus* (Blandford, 1894) (Curculionidae, Scolytinae) is distributed in East Asia, Europe (including European Russia), and North America (Kirkendall and Faccoli, 2010). Its primary range lies in Asia while the inhabited territories in Europe and North America represent secondary ranges.

Of course, disjunction of the range is not always related to invasion. A disjunctive range may be produced naturally, if the species becomes extinct within the greatest part of its range but is preserved in some isolated areas. Some insects whose recent distribution is restricted to the territories with relict floristic complexes have reduced their ranges during the advance of the glacier. On the contrary, some cold-loving species were widespread in the glacial epoch, and after the warming they remained only in Asia, in the north of Europe, and in the European mountains (Gorodkov, 1984).

In entomology there is a prevalent notion that the currently observed ranges of beetles are quite ancient (Kryzhanovskij, 2002). Their boundaries are usually explained by the events accompanying the continental plate movement or glaciations. However, the examples of the Colorado potato beetle, the emerald ash borer, and many other invasive species show that beetles can colonize whole continents in mere decades. It is evident that the recent ranges of many beetles are quite young.

Having discovered a disjunctive range, researchers often consider it to be relict, totally ignoring the possi-

bility of invasion. This approach was shown to be invalid, in particular, for marine invertebrates (Chapman and Carlton, 1991) and dragonflies (Kharitonov, 2012). The relict nature of disjunction should be proved by morphological, genetic, ecological, and other data. Genetic drift and natural selection produce differences between populations from different parts of the range in the course of prolonged isolation. For example, the populations of the ladybird *Harmonia axyridis* occurring west of Lake Baikal clearly differ in morphological and genetic parameters from the populations living east of the lake (Lombaert et al., 2011). By contrast, if the individuals from different parts of the disjunctive range reveal no significant differences, there is no reason to consider the relict status of the disjunction.

Application of this alienness criterion to beetles is difficult because their ranges are insufficiently studied. The absence of material from the territory separating the two studied parts of the range may produce the false appearance of a disjunction. Gorodkov (1981) noted that “although it is virtually impossible to give absolute proof of the absence of a particular insect in a certain territory, there are several ways of clarifying the range boundaries.” He proposed the following methods.

(1) Mapping of the available material for the whole taxon to which the species in question belongs. The absence of records of a given species in the regions where the related species have been collected will make the negative information more reliable.

(2) Comparison of the ranges of two or more biologically and (often) taxonomically close species that usually co-occur in the collections. If one of such species is regularly found in the given territory while the other is not found at all, then the absence of the latter species cannot be attributed to insufficient sampling.

(3) Mapping of the localities in which the species was specially sought but was not found, onto its known range.

The range maps are now much more complete and precise than they were in the recent past. The study of ranges has reached an unprecedented level due to the development of computer-assisted methods of storage and processing of faunistic information, and also the appearance of publicly available mapping systems, such as DIVA-GIS (www.diva-gis.org). The reliable records of species confirmed by experts

are accumulated in international databases, in particular, the Global Biodiversity Information Facility (www.gbif.org). In addition, the literature of the XVII–XX centuries has become available online (www.biodiversitylibrary.org, etc.) and is now being used in the studies of long-term dynamics of ranges (Orlova-Bienkowskaja, 2012; Prisnyi et al., 2013).

3. *Expansion of a Part of the Range Isolated from its Main Part*

This is one of the most reliable criteria (Chapman and Carlton, 1991; Boudouresque and Verlaque, 2002). If individuals of a given species were first found only within a small area distant from the main part of the range, and later recorded over a larger territory, then we are most likely observing the process of colonization of suitable territories after a recent invasion.

For example, the weevil *Lignyodes bischoffi* Blatchley, 1916 (Curculionidae) and the flea beetle *Epitrix hirtipennis* (Melsheimer, 1847) (Chrysomelidae), which were brought from America into Europe in the second half of the XX century, have been gradually expanding their secondary ranges and have already reached Russia (Arzanov, 2013; Orlova-Bienkowskaja, 2014b). The first European locus of the emerald ash borer was recorded in Moscow in 2003, and by 2014 this species has colonized nearly all the central regions of European Russia (Orlova-Bienkowskaja, 2014a).

4. *Local Distribution in a Region Adjoining the Invasion Pathway*

The range boundaries of native species are usually determined by the boundaries of natural zones or landscapes (Kryzhanovskij, 2002). By contrast, the distribution of invasive species is often limited by artificial factors: for example, an alien species of marine invertebrates may inhabit only that particular harbor into which it was introduced (Chapman and Carlton, 1991), while an alien algal species may grow only in the vicinity of a particular aquaculture farm (Boudouresque and Verlaque, 2002). In a similar way, the secondary range of an invasive beetle is sometimes restricted to a small territory adjacent to the point of introduction.

For example, the Trans-Siberian Railway provides the pathway along which many species expand far beyond their native ranges into the uncharacteristic landscapes. The typically steppe-dwelling Central

Asian leaf beetle *Pallasiola absinthii* (Pallas, 1773) (Chrysomelidae) has penetrated into the taiga zone of Western Siberia along the Trans-Siberian Railway but has not become established in the natural landscapes of that zone, so that its distribution is restricted to a strip 10–20 m wide along the railway (Dubeshko and Medvedev, 1989). In a similar way, many European beetle species introduced in North America were originally established in harbors and colonist settlements (Bain and King, 2009).

5. Establishment in Other Regions

Although invasion is a stochastic process, the set of species which have been able to establish themselves outside their natural ranges is by no means random (Karatayev et al., 2009). Some organisms have a propensity for colonizing new territories due to the specific traits of their behavior and biology (Chapman and Carlton, 1991). The invasive abilities of a species depend on a variety of natural and anthropogenic factors many of which remain unknown; however, if a given species has managed to colonize one region, it may with a fairly high probability colonize another region. This trend was demonstrated for algae (Boudouresque and Verlaque, 2002), and seems to be valid for beetles as well.

The ladybird *Harmonia axyridis*, already mentioned above, can be considered as an example. The first established populations of this species were discovered in North America in 1988. Since that time, its global expansion has been observed (Brown et al., 2011). By 2014 *H. axyridis* has spread over 50 countries of Europe, Asia, North and South America, and Africa (EPPO, 2014). Recently, the wave of its expansion has covered European Russia, the Caucasus, and Southeast Kazakhstan (Orlova-Bienkowskaja, 2014c, 2015b; Ukrainsky and Orlova-Bienkowskaja, 2014).

6. Trophic Association with Another Alien Species

A considerable part of alien phytophagous insects feed only on cultivated and adventive plants and do not switch over to feeding on native plant species (Beenen, 2006; Pyšek et al., 2010). For example, the ragweed leaf beetle *Zygogramma suturalis* (Fabricius, 1775) introduced from North America to Russia feeds exclusively on the adventive ragweed *Ambrosia artemisiifolia* L. (Kovalev et al., 2013).

Native species sometimes feed on adventive plants (Aistova et al., 2014), but such plants never become

their only trophic resource. At the same time, feeding on native plants cannot be considered as evidence of the native origin of a species. For example, the Colorado potato beetle *Leptinotarsa decemlineata* (Say, 1824) in European Russia consumes not only cultivated plants of the family Solanaceae but also the native bittersweet nightshade *Solanum dulcamara* L. (Medvedev and Roginskaya, 1988), while the emerald ash borer feeds on the native European ash *Fraxinus excelsior* L. (Maiorov et al., 2012; Orlova-Bienkowskaja, 2015a).

7. The Absence of Specific Parasites and Predators in the Given Region and Their Presence in Some Other Region

It is known that in the new regions, the invasive species often get released from the pressure of their specific predators and parasites (Elton, 1960). This tendency was observed in many taxa including beetles. For example, the low level of parasitism is believed to be one of the most important factors of the Colorado potato beetle outbreak in Europe (Chernyshev, 2012).

However, the presence of parasites of a certain species in a given region cannot indicate the native status of that species. For example, the emerald ash borer *Agrilus planipennis* in Moscow is parasitized by *Spathius polonicus* Niezabitowski, 1910 (Hymenoptera: Braconidae), the level of infestation reaching 50% (Orlova-Bienkowskaja and Belokobylskij, 2014).

8. Association with Anthropogenic Biotopes

Organisms of alien origin often prefer anthropogenic biotopes. In particular, many alien marine invertebrates develop on the bottoms of ships (Chapman and Carlton, 1991) as well as in places subjected to thermal or some other kind of anthropogenic pollution (Zvyagintsev et al., 2011). Alien species of mammals most frequently colonize habitats associated with human dwellings (Khlyap et al., 2008), while adventive plants grow in agrocenoses and settlements (Webb, 1985).

The predominant association of alien species with anthropogenic biotopes can be also observed for insects (Pyšek et al., 2010). It is largely determined by the fact that species directly associated with human economic activities are more likely to be dispersed by man (Kenis et al., 2007). Besides, anthropogenic biotopes have low resistance to invasions due to the low

pressure of predators, parasites, and competitors (Elton, 1960; Kenis et al., 2007).

Anthropogenic communities serve as outposts and refugia for alien beetle species. For example, a study of the beetle fauna in compost heaps in North Europe showed that 34 species were recent invaders from the south; only 12 of them were established in natural communities, the rest being found only in compost (Ødegaard and Tømmerås, 2000).

Some dendrophilous beetles can be found in parks far beyond their own native ranges and the native ranges of their food plants. For example, the viburnum leaf beetle *Pyrrhalta viburni* (Paykull, 1799) (Chrysomelidae), feeding exclusively on arrowwood, occurs in the south of Saratov Province where arrowwood grows only in artificial plantings (Bieńkowski, 2011).

On the other hand, the presence and even mass development of a species in the natural biotopes cannot be regarded as proof of its native origin. For example, the four-eyed fir bark beetle *Polygraphus proximus* Blandford, 1894 (Curculionidae: Scolytinae) destroys fir trees in the natural taiga communities of Western Siberia (Krivets, 2012; Kerchev, 2014).

9. Sharp Fluctuations of Abundance

Establishment of a species in a new territory usually starts with a latent phase during which the species has low abundance. Then an outbreak occurs, often followed by an abrupt decline of abundance, after which another abrupt increase may be recorded. This pattern was observed in many taxa, such as higher plants, marine algae, gastropods, and insects (Webb, 1985; Boudouresque and Verlaque, 2002; Simberloff and Gibbons, 2004; Maslyakov and Izhevsky, 2011). The sharp fluctuations reflect the fact that interactions between the alien species and the native community require a certain time to balance (Simberloff and Gibbons, 2004).

A good example of sharp fluctuations of abundance within the secondary range is given by the population of the scarlet lily beetle *Lilioceris lili* (Scopoli, 1763) (Chrysomelidae) on the British Isles. This beetle was first introduced into England in the first half of the XIX century and became a common species in the outskirts of London (Stephens, 1839). Then it disappeared completely for reasons unknown, and reappeared 100 years later (Fox Wilson, 1943). At present, *L. lili* has spread over all the counties of Great Brit-

ain, inflicting heavy damage to floriculture and the native natural communities (Salisbury, 2003).

10. The Absence of Related Species in the Native Fauna and Their Presence in Some Other Region

A species alien to the given region often has no close relatives in the local fauna, but such relatives are present in the territory of its origin. This criterion was proposed during a study of invasive crustaceans in California (Chapman and Carlton, 1991), and can also be applied to beetles. For example, the fauna of European Russia includes only two representatives of the American subtribe Doryphorina: the Colorado potato beetle accidentally brought from America, and the ragweed leaf beetle introduced deliberately (Kovalev and Medvedev, 1983).

11. Simultaneous Recording of Two or More Taxonomically and/or Ecologically Close Species Typical of Another Region

Sometimes, not one species but a complex of closely related species participate in invasion. For example, three species of North American ragweeds of the genus *Ambrosia* were recorded in the center of European Russia (Maiorov et al., 2012). Three North American species of the genus *Epitrix* (Chrysomelidae) and two Asian species of the genus *Anoplophora* (Cerambycidae) have established themselves in Europe (EPPO, 2014). It appears that the conditions favoring invasion of one species in the given region may also facilitate invasion of its close relatives.

12. The Presence of Known Vectors of Invasion

During analysis of the species' status, the presence of vectors of invasion, i.e., possible ways of its individuals getting into other regions, should be taken into account (Webb, 1985). Dozens of typical vectors of invasion are known for beetles (Maslyakov and Izhevsky, 2011). For example, adults of *Harmonia axyridis* often aggregate in parked vehicles in search of wintering shelters, and can thus be transported over considerable distances (Korotyayev, 2013). Weevils of the genus *Otiorhynchus* (Curculionidae) develop on plant roots in the soil, and are often transported with planting stock (Balalaikins and Bukejs, 2011).

Analysis of the historical vectors of invasion is helpful in the studies of adventive flora. For example, many plant species are known to have dispersed along the Great Silk Road, some others spread along the

migration paths of nomadic tribes, while the weeds associated with specific cultivars followed them in their dispersal (Afanasiev and Laktionov, 2008). Beetles are also likely to have used these ways of dispersal, but the historical vectors of their invasion remain completely unstudied.

13. Low Genetic Diversity

The populations of a species forming outside its native range often have low genetic diversity. This trend was demonstrated for higher plants (Webb, 1985), marine invertebrates (Boudouresque and Verlaque, 2002), and insects (Tsutsui et al., 2000). Due to the founder effect, such populations may lack some of the genotypes present in the native range. For example, the coffee berry borer *Hypothenemus hampei* (Ferrari, 1867) (Curculionidae: Scolytinae), which has spread to all the regions of the world where coffee is grown, was shown to have an extremely low level of genetic diversity (Andreev et al., 1998). In North America, the populations of the introduced Asian longhorn beetle *Anoplophora glabripennis* (Motschulsky, 1853) (Cerambycidae) have lower genetic diversity as compared to the populations in China (Carter et al., 2010). In some cases, a decrease in genetic diversity is reflected by the narrower range of morphological diversity. For example, *Harmonia axyridis* is represented by only one color morph in its secondary South African range, whereas dozens of color morphs exist within its native Asian range (Stals, 2010).

If two populations of a species are geographically isolated but genetically identical, there is good reason to suggest that one of them is invasive by origin. If these populations had originally belonged to the native range and become isolated as the result of extinction in the intermediate territories, they would have accumulated genetic differences due to geographic isolation (Boudouresque and Verlaque, 2002).

14. The Ability to Reproduce by Parthenogenesis or Inbreeding

During invasion into a new region, the population almost always passes through the phase of very low abundance, which entails a number of problems. First, finding mates may be difficult at low density. Second, close breeding may lead to inbreeding depression (Kirkendall and Faccoli, 2010). The species that typically reproduce by parthenogenesis or inbreeding are immune to such problems and therefore have a propensity for invasion. In particular, the parthenogenetic

weevil *Ottiorhynchus smreczynskii* Cmoluch, 1968 (Curculionidae) is currently expanding its secondary range in Europe (Balalaikins and Bukejs, 2011), while more than half of the alien bark beetle species in the European fauna are characterized by close breeding (Kirkendall and Faccoli, 2010).

EXAMPLES OF REVEALING ALIEN SPECIES BASED ON A COMPLEX OF CRITERIA

The invasion biology of beetles lies at the intersection of three disciplines: entomology, biogeography, and ecology. The alien status can be recognized by a complex study of the distribution, ecology, and other features of the species. The criteria of alienness considered above are not absolute, and a species matching one of them may still be a native one; however, compliance with several criteria would indicate its alien origin quite reliably. Such a complex approach is widely used in research of other taxa (Webb, 1985; Chapman and Carlton, 1991; Zvyagintsev et al., 2011). A native species is unlikely to match several criteria of alienness. For example, if we assume that the probability of chance compliance with one criterion is 20%, then the probability of chance compliance with six criteria will be about 4% (Fig. 3). In other words, if a species matches six of the above criteria, the probability of it being alien is about 96%.

The ambrosia beetle *Xyleborus pfeilii* (Ratzeburg, 1878) (Curculionidae: Scolytinae) gives an example of the species whose alien status in Europe was detected by a complex of criteria. This beetle used to be considered a native one, but Kirkendall and Faccoli (2010) performed a complex analysis of its features and concluded that the species had been brought to Europe from Asia before the XIX century. The cited authors observed that according to its morphological traits, *X. pfeilii* belongs to the *volvulus-perforans* species group that is distributed in Asia and has no other representatives in Europe (our criterion 10). The species has a clearly disjunctive range (criterion 2). A possible vector of its invasion was shipment of timber from the Far East (criterion 12). The ability of *X. pfeilii* to establish itself outside the native range was confirmed by its recent invasion into North America (criterion 5).

A similar example is provided by the scarlet lily beetle *Lilioceris lili*. Analysis of its biology and range dynamics allowed us to conclude that this leaf beetle was also of Asian origin and that it was brought into

Europe several centuries ago (Orlova-Bienkowskaja, 2012).

Criterion 2: until the beginning of the XX century *L. lili* had a disjunctive range consisting of the Asian and the West European subranges separated by a vast territory where the species was not found. The absence of *L. lili* in collections from the greatest part of European Russia and Western Siberia cannot be attributed to insufficient material, since the distribution map of the closely related species *Lilioceris merdigera* (Linnaeus, 1758) compiled from the same XIX-century sources reveals a continuous range of the latter species (the method of comparison of ranges of related species; see Gorodkov, 1981).

Criterion 3: since the beginning of the XX century until recently, the European range of the species has been expanding in the northern and eastern directions.

Criterion 5: *L. lili* became a common and widespread species on the British Isles and in North America where it appeared in the 1940s.

Criterion 6: *L. lili* feeds almost exclusively on cultivated plants of the genus *Fritillaria*. Its occasional findings on wild lilies in Europe are of secondary nature, similar to the findings of the Colorado potato beetle on wild plants of the family Solanaceae.

Criterion 8: in Europe, *L. lili* can be found almost exclusively in gardens and flowerbeds. Despite being common, the species was only sporadically recorded outside the artificially planted areas.

Criterion 10: the genus *Lilioceris* as a whole is of Asian origin, and the great majority of its species occur in Asia.

Criterion 12: the vector of invasion of *L. lili* is shipment of lily bulbs with soil.

The third example is that of the weevil *Barynotus moerens* (Fabricius, 1792) (Curculionidae) (Orlova-Bienkowskaja, 2009).

Criterion 1: the species is distributed in Western Europe. It was first recorded in European Russia in 1999, and since that time it has been regularly found in Solnechnogorsk District of Moscow Province.

Criterion 2: *B. moerens* has a disjunctive range, the territory of its distribution in Moscow Province being isolated from its Western European range.

Criterion 8: *B. moerens* was recorded only in anthropogenic biotopes, mostly in urban waste lots and along the highway.

Criterion 10: the great majority of species of the genus *Barynotus* occur in Western Europe. Only one species besides *B. moerens* is present in European Russia.

Criterion 12: the larvae of *B. moerens* develop on plant roots in the soil. It is known that beetles with this type of development are often transported together with planting stock.

Criterion 14: all the individuals found in Moscow Province for 15 years (over 50 ind.) were females. Some populations of the species are known to reproduce by parthenogenesis (Lundmark and Saura, 2006); it is highly probable that the population of Moscow Province is also parthenogenetic.

The leaf beetle *Chrysolina eurina* (Frivaldszky, 1883) (Chrysomelidae) in European Russia matches six criteria of alienness (Orlova-Bienkowskaja, 2013c).

Criterion 1: the species has been found in European Russia since the beginning of the XX century.

Criterion 2: its range consists of three small isolated areas. Such a range disjunction is unlikely to have a relict nature, because in Europe *Ch. eurina* inhabits plain territories rather than relict or mountain landscapes.

Criterion 6: *Ch. eurina* feeds only on the tansy, which is considered an archeophyte in Europe.

Criterion 8: the beetle occurs almost exclusively in roadside waste lots.

Criterion 10: *Ch. eurina* belongs to the group of species distributed almost exclusively in Siberia.

Criterion 12: the species is usually found along roads, which may serve as its invasion pathways.

In some cases, even one criterion may be sufficient for revealing the invasive origin of a species. For example, *Psylliodes hyoscyami* (Linnaeus, 1758) (Chrysomelidae) feeds only on the henbane *Hyoscyamus niger*, which is regarded as an archeophyte (Medvedev and Roginskaya, 1988; Afanasiev and Laktionov, 2008). The henbane is believed to have been introduced in the ancient times from the Mediterranean region, as a medicinal plant. Correspondingly, *Ps. hyoscyami* should also be considered an alien species in European Russia.

One more interesting example is that of the beaver beetle *Platypsyllus castoris* Ritsema, 1869 (Leiodidae:

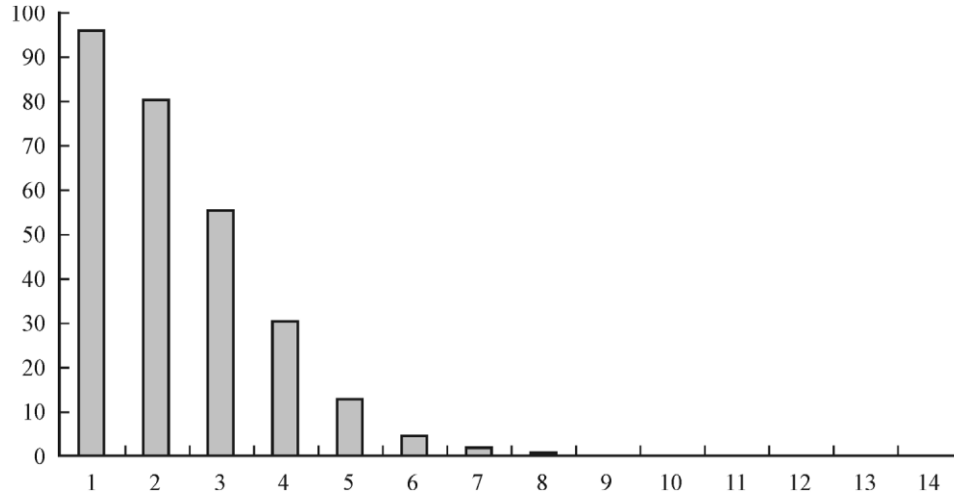


Fig. 3. Probability of misidentification of a native species as an alien one (vertical axis) depending on the number of criteria matched (horizontal axis). The probability of the species accidentally matching one criterion is arbitrarily taken as 20%.

Platypsyllinae), a specific ectoparasite of beavers (Peck, 2006). The Eurasian beaver *Castor fiber* L., 1758 is considered to be an alien species in European Russia, because its population was almost completely destroyed by the end of the XIX century and later restored by introduction from the remaining fragments of its former range (Khlyap et al., 2008). Thus, the beaver beetle should also be regarded as an alien species in those regions where the beavers had been eliminated. Another hypothesis assumes that the beaver beetle may have been brought into Europe during introduction of the North American beaver *Castor canadensis* Kuhl, 1820, since the beetle was first recorded in Europe on North American beavers kept in the zoo (Peck, 2006). In the opinion of Peck (2006), this assumption should be tested by comparative genetic analysis of *P. castoris* from Europe and America.

Analysis is particularly difficult in those cases when the species expands not into some remote region but into the territory adjoining its native range (Beenen, 2006). For example, the jewel beetle *Agrius convexicollis* Redtenbacher, 1849 (Buprestidae), developing on drying ash branches, has been until recently recorded only in Western and Central Europe and in the south of European Russia, but since 2007 the species started to appear in the central part of European Russia and became a common inhabitant of ash trees infested with *Agrius planipennis* (Orlova-Bienkowskaja and Volkovitsh, 2014). The outbreak of *A. convexicollis* was evidently determined by the appearance of a great number of dying ash trees. It is not clear, however, whether *A. convexicollis* should be regarded as an alien or a native species with expanding range.

CONCLUSION

Thus, the problem of recognizing alien beetle species is a very important and difficult one, but the experience from other branches of biology shows that it can be solved. A complex study of geographic distribution, ecology, phylogeny, genetics, and other aspects of a species allows the researcher to determine its status (alien or native) with a certain degree of confidence. If the species matches several criteria of alienness, it is most likely alien.

The majority of data on alien beetles refers to terrestrial phytophagous species, mostly pests of cultivated plants. It is quite possible that the above criteria will need to be considerably adjusted before applying them to predatory and aquatic beetles and those associated with manure. The proposed criteria are by no means complete or indisputable. The invasion biology of beetles is a new direction of research that currently has more questions than answers. I would feel that my goal has been achieved if the problem addressed in this communication provoked a discussion among the experts in different groups of beetles.

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