

REVIEW ARTICLE

Importing deciduous wood chips from North America to northern Europe – the risk of introducing bark- and wood-boring insects

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Increasing inter-continental trade with wood chips represents a challenge for phytosanitary authorities as such trade may lead to pest introductions and invasions with huge impacts on forest ecosystems and economy. Predicting species invasions and their impacts in advance may be difficult, but improved information about potential invasive species ahead of any interceptions is an important precautionary step to reduce the probability of invasions. Here we identify bark- and wood-boring insects that have a potential to become invasive in northern Europe and that may be introduced by import of deciduous wood chips from North America. The potentially most damaging species belong to the beetle genus *Agrilus* (Buprestidae), which includes the highly damaging emerald ash borer *A. planipennis*. We give a brief presentation of this and seven other *Agrilus* species or subspecies and review factors of importance for the risk of establishment and potential economic and ecological impacts of these species. We also discuss one Scolytinae, *Hylurgopinus rufipes*. There are strong indications in the literature that some north European trees are highly susceptible to attack from the selected beetle species. We therefore conclude that because north European trees have not coevolved with these herbivores and thus may lack adequate defenses, most of the identified beetle species are likely to spread in “defense- and enemy-free space” if they are introduced to northern Europe, with considerable economic and ecological consequences.

Keywords: naïve hosts; wood-boring insects; *Agrilus*; invasive species; phytosanitary risk

Introduction

Introduction and establishment of species beyond their native range can lead to high economic costs and severe ecological damage (Brockerhoff et al. 2006b; Kettunen et al. 2008; Liebhold & Tobin 2008; Pimentel et al. 2000). Insects that bore into the bark and wood of living trees may severely impact ecosystem structure and function due to the ability of some species to kill healthy trees (Kenis et al. 2009; Gandhi & Herms 2010; Økland et al. 2011). Between 1980 and 2006, bark- and wood-borers accounted for 56% of all new insect species detected in the United States (Aukema et al. 2010). There are now more than 400 introduced species attacking woody plants in the United States alone (Liebhold et al. 1995; Mattson et al. 2007; Langor et al. 2008; Aukema et al. 2010), and a new high-impact forest pest is predicted to establish every 5 to 6 years (Koch et al. 2010). Europe has 109 nonindigenous insect species established on woody plants, including 57 species from North America and 52 from Asia (Mattson et al. 2007). A complicating factor is that species introductions often go undetected for a long time, with a lag phase that can last for years until the population suddenly grows rapidly (Mack et al. 2000).

The major pathways for introduction of bark- and wood-boring insects are trade with living plants and various commodities of non-squared wood, including wood chips (EPPO 2009; Liebhold et al. 2012). The import of wood chips to Europe is expected to increase due to growing demands for energy production (EPPO 2011b). Wood chips may be large enough to allow survival of several insect species (McCullough et al. 2007) and represent a challenge for inspectors. Økland et al. (2012) did for example show that insect detection with 90% certainty from a ship load of ~21,000 metric tons of wood chips requires a sampling volume of 27 million liters. Furthermore, phytosanitary regulations have not been updated to accommodate the recent increase in imports of biomass for bioenergy production (Kopinga et al. 2010). Import of coniferous wood chips is regulated by the European Union and several European countries to prevent the spread of the pinewood nematode, *Bursaphelenchus xylophilus*. However, import of deciduous wood chips to Europe is still largely unregulated, and except for a few species (EPPO 2005; EPPO 2011a), little is known about forest pests that could be transported from North America to Europe in these large import volumes.

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So far, no major tree-killing insects on deciduous trees have been introduced to northern Europe, but, for example, the bark beetles *Xyleborinus alni*, feeding on recently dead or dying *Salix* spp., and *Cyclorhipidion bodoanus*, feeding in hollow *Quercus* trees, have been recorded on deciduous trees in Sweden (Lindelöw et al. 2006; Lindelöw 2009). Bark- and wood-boring beetles are regularly intercepted all over the world (Humble & Allen 1998; Lindelöw 2000; Haack 2001, 2006; Brockerhoff et al. 2006a), and the EPPO (2012) reporting service frequently reports interceptions of non-indigenous bark- and wood-boring beetles from different wood commodities in Europe. The arrival and establishment of insect pests capable of killing healthy deciduous trees in Europe seem likely, due to increasing international trade volumes. One illustrative case is the recent establishment of the East-Asian emerald ash borer *Agrilus planipennis* in the Moscow region (Baranchikov et al. 2008). This species has also been introduced in North America where it exclusively attacks ash, has killed millions of trees during the last 10 years, and is threatening several endemic ash species and the functioning of whole forest ecosystems (Poland & McCullough 2006; Gandhi & Herms 2010).

In this paper, we followed a defined procedure to identify bark- and wood-boring insects with a potential to invade northern Europe (Fennoscandia, the Baltic states, and northern provinces of European Russia) through import of deciduous wood chips from North America. Wood packaging material (WPM) was not considered here, because it is already regulated through ISPM 15 (Food and Agriculture Organization 2009). We restricted our focus to bark- and wood-boring beetles, since beetles are a major and relatively well-studied group of tree-boring insects. We give a brief presentation of the biology of each identified species and review factors that may influence the risk of establishment and potential economic and ecological impacts.

Identification of high-risk species

We used the following criteria to identify bark- and wood-boring beetles to be included:

- (1) The species should not be present in Europe, so only species that are endemic to North America or are introduced to North America from areas other than Europe were included.
- (2) The species should be abundant, widely distributed, and have a northerly distribution within North America to increase the likelihood that they will be adapted to the climatic conditions in northern Europe. The geographic area of origin for potential invaders was further narrowed down to eastern North America (east of the 100th meridian, as defined by Baker

1972), since this is the most important area for export of wood chips to northern Europe.

- (3) The species should be associated with a host tree in a genus with representatives in northern Europe, since insects that are invading new areas usually colonize hosts within the same genus as in their native range (Mattson et al. 1994; Niemela & Mattson 1996; Roques et al. 2006; Mattson et al. 2007). We included all North-American deciduous tree genera that occur in Fennoscandia, which is a representative region for the tree species composition in northern Europe (Table 1).
- (4) The insect species should be a pest in its native range and be able to colonize the bark and sapwood of the trunk of living trees. To find bark- and wood-borers that are pests on the tree genera selected in (3), we searched the literature (Craighead 1950; Browne 1968; Baker 1972; Johnson & Lyon 1976; Ives & Wong 1988; Mattson et al. 1994; Solomon 1995), cross-checked with relevant databases (ISPI 2009; GISD 2012; NAFC-ExFor 2012; NAPIS 2012; U.S. Forest Service 2012; Bugwood.org 2013; EPPO 2013) and consulted experts on North American bark- and wood-borers.
- (5) The species should have behavioral, physiological, and morphological traits that favor survival through transport of raw materials for production of chipped wood, the chipping process itself, and transport of chipped wood. We searched the literature for information about survival rates in wood chips and physical dimensions of egg, larva, pupa, and imago.

After the first screening of the literature using criteria 1 to 3, the initial list contained 50 beetle species. Following criteria 4 and 5, we ended up with nine bark- and wood-boring beetle species or subspecies satisfying the selection criteria. The most important reasons for excluding species were that they were not regarded as pests, had a southerly distribution, were not considered established in North America, or most importantly, were too large to likely survive in wood chips. Eight of the selected species belong to the genus *Agrilus* (Buprestidae) and one to Scolytinae (*Hylurgopinus rufipes*). Except for the East-Asian species *A. planipennis*, all are native to North America. In *Agrilus*, the size of prepupae and pupae and the timing of pupation in the outer sapwood facilitate survival through the wood chipping process. Furthermore, survival through chipping has been experimentally documented for one of the species; McCullough et al. (2007) showed that *A. planipennis* prepupae can survive the chipping process with a 10-cm screen. The dimension of the different life stages of *A. planipennis*, including the

Table 1. Bark- and wood-boring beetles discussed in this paper, their tree hosts, distribution area in North America, and length of their life stages.

Species name	Genera prone to attack	Host tree species in north America	Known host tree species appearing in Fennoscandia	Other potential host tree species appearing in Fennoscandia	Pest distribution	Egg mm	Larva mm	Pupa mm	Imago mm
<i>Agrilus anxius</i>	<i>Betula</i>	<i>B. alleghaniensis</i> <i>B. lenta</i> <i>B. occidentalis</i> <i>B. papyrifera</i> <i>B. populifolia</i>	<i>B. maximowicziana</i> <i>B. pendula</i> <i>B. pubescence</i> <i>B. szechuanica</i>		All southern Canadian provinces, Alaska and Contiguous US except 12 southern states (Muilenburg & Herms 2012).	1.3–1.5	25	NA	6–12
<i>A. bilineatus</i>	<i>Castanea</i> <i>Quercus</i>	<i>C. dentata</i> <i>Q. alba</i> <i>Q. coccinea</i> <i>Q. ellipsoidalis</i> <i>Q. macrocarpa</i> <i>Q. prinus</i> <i>Q. stellate</i> <i>Q. velutina</i>	<i>Q. rubra</i>	<i>Q. petraea</i> <i>Q. robur</i>	Southeastern Canada. Eastern and Central US westwards to Texas and the Rocky Mountains (Haack & Acciavatti 1992).	1	25	NA	6–12
<i>A. g. granulatus</i>	<i>Populus</i>	<i>P. deltoids</i> <i>P. trichocarpa</i>	<i>P. nigra</i>	<i>P. alba</i> <i>P. balsamifera</i> <i>P. tremula</i>	From New York south to North Carolina and Louisiana, westwards to Colorado, Montana and southern Alberta, Canada (Solomon 1995).	NA	27–40	NA	7–11
<i>A. g. liragus</i>	<i>Populus</i>	<i>P. deltoides</i> <i>P. grandidentata</i> <i>P. tremuloides</i> <i>P. trichocarpa</i>	<i>P. balsamifera</i>	<i>P. alba</i> <i>P. nigra</i> <i>P. tremula</i>	New Brunswick to British Columbia. South to Pennsylvania and Arizona (Bright 1987).	1.2	30–40	NA	7.2–10.3
<i>A. horni</i>	<i>Populus</i>	<i>P. grandidentata</i> <i>P. tremuloides</i>	<i>P. alba</i> <i>P. tremula</i>	<i>P. balsamifera</i> <i>P. nigra</i>	From Massachusetts to Arizona in the US, north to Ontario and Aweme, Manitoba in Canada (Bright 1987).				
<i>A. planipennis</i>	<i>Fraxinus</i>	<i>F. americana</i> <i>F. nigra</i> <i>F. pensylvanica</i>	<i>F. angustifolia</i> <i>F. excelsior</i>		Invasive in 19 US states (Kansas, Minnesota, Iowa, Missouri, Wisconsin, Michigan, Illinois, Indiana, Kentucky, Tennessee, Ohio, West-Virginia, Virginia, Pennsylvania, New York, Connecticut, Maryland, Massachusetts, New Hampshire; USDA 2013), and the Canadian provinces of Ontario and Quebec (CFIA 2013).	1	30–36	13–17.5	13
<i>A. politus</i>	<i>Acer</i> <i>Salix</i>	<i>A. glabrum</i> <i>A. pensylvanicum</i>		<i>A. campestre</i> <i>A. platanoides</i>	Transcontinental across Canada and throughout the United States (Bright 1987).	NA	NA	NA	5–8.5

Table 1 (Continued)

Species name	Genera prone to attack	Host tree species in north America	Known host tree species appearing in Fennoscandia	Other potential host tree species appearing in Fennoscandia	Pest distribution	Egg mm	Larva mm	Pupa mm	Imago mm
<i>A. pensus</i>	<i>Alnus</i> <i>Betula</i>	<i>S. babylonica</i> <i>S. lasiolepis</i> <i>S. lucida</i> <i>S. scouleriana</i> <i>A. rugosa</i> <i>B. nigra</i>		<i>A. pseudoplatanus</i> <i>A. rubrum</i> <i>S. caprea</i> <i>A. glutinosa</i> <i>A. incana</i> <i>B. maximowicziana</i> <i>B. pendula</i> <i>B. pubescence</i> <i>U. glabra</i>	Manitoba to Nova Scotia, south to Pennsylvania and New Jersey (Bright 1987).	1.2	NA	NA	7.5
<i>Hylurgopinus rufipes</i>	<i>Ulmus</i>	<i>U. americana</i> <i>U. pumila</i> <i>Fraxinus</i> sp.			Throughout the eastern US north of Mississippi, west to North Dakota. In Canada, from New Brunswick to Manitoba (Solomon 1995)	NA	3–5	NA	2–3.5

pupal stage, was summarized by Chamorro et al. (2012), and is presented in Table 1. Maximum larval and imago lengths for the selected species are 25–40 mm and 7–11 mm, respectively, with *A. planipennis* being the longest species. Pupal size is not available for the other *Agrilus* species, but as they have smaller larvae, imagines, they probably also have shorter pupae than *A. planipennis* and should thus be well suited to survive chipping.

Besides *H. rufipes*, there are other candidates of small bark and ambrosia beetles in the curculionid subfamilies Scolytinae and Platypodinae (Wood 1982; Wood et al. 1992) that may be imported by wood chips and that has been encountered in other wood materials at ports of entry (Brockerhoff et al. 2006a; Haack 2006). Due to the extensive number of species, their complex biology, and the lack of documentation on survival in wood chips and attack on European tree species, we limited our selection to *Agrilus*, where survival in wood chips has been documented (McCullough et al. 2007), and the one candidate among the small scolytids that is known to kill deciduous trees in eastern North America (Baker 1972).

Presentation of the selected wood-borers

The selected *Agrilus* species share many morphological characteristics and have similar life cycles. The larvae make typical zig-zag-shaped tunnels in the phloem and need to feed on living or dying phloem to develop (Bright 1987; Anderson 1944). Before pupation, the larvae usually enter the outer sapwood, and the larvae of the alder birch borer *Agrilus pensus* can even bore through the stem from one side to the other (Carlson & Knight 1969). All the selected *Agrilus* species make a D-shaped exit hole on the stem and feed on various tree species for a period during their adult life. During mating, the males hover around leaves of host trees in their visual search for females and use contact pheromones to determine species and sex of potential partners (Lelito et al. 2007; Domingue et al. 2011; Lelito et al. 2011). Many *Agrilus* species have high fecundity; *A. planipennis* can lay 200 eggs (Rutledge & Keena 2012), and females of the bronze birch borer *Agrilus anxius* mate several times and may lay 375 eggs (Claire Rutledge, personal communication). The morphology and biology of the native elm bark beetle, *H. rufipes*, differs from the *Agrilus* species. *H. rufipes* constructs egg galleries in the bark, in which the larvae also pupate (Baker 1972). Winter is spent under the bark either as adults or larvae. *H. rufipes* is the primary vector in North America of the devastating Dutch elm disease (DED), which is caused by the fungus *Ophiostoma novo-ulmi* (McLeod et al. 2005). Adults can feed on healthy elms and inoculate them with DED. All the species presented below are widely distributed throughout

eastern North America and occur in a wide range of forest environments.

Bronze birch borer *Agrilus anxius* (Gory 1841) is a major pest of *Betula* spp. and can have expansive periodic outbreaks (Muilenburg & Herms 2012). The larvae need living phloem to develop (Anderson 1944), and field tests have shown that European birch species may suffer 100% mortality if attacked by *A. anxius* (Nielsen et al. 2011). The life cycle is completed in one or two years, depending on climate and host condition. Fourth instar larvae construct pupal cells in the outer sapwood, where they must overwinter and be exposed to freezing temperatures before they pupate in April to May. Adults emerge from the stems between May and July, at about 305 degree-days (base temperature 10°C, starting date January 1) in Ohio and Michigan (EPPO 2011a).

A. anxius was added to the EPPO alert list in 2010 (EPPO 2010), and a pest risk analysis was completed in 2011 (EPPO 2011a). A pest risk assessment of *A. anxius* was performed by The Norwegian Scientific Committee for Food Safety (VKM 2012) in 2012, which supported the EPPO (2011a) pest risk analysis. The EPPO (2011b) pest risk analysis concluded that there was a moderate probability of entry of *A. anxius* into Europe, a high probability of establishment, a risk of spread, and high ensuing mortality of birch throughout the PRA area with major economic consequences. The main pathway of concern for introduction into EU and Scandinavia is chipped deciduous wood. Ornamental trees, lumber, and firewood also represent a risk (EPPO 2011b).

Emerald ash borer *Agrilus planipennis* (Fairmaire 1888) is native to Far East Asia, where it is not considered a major pest on native trees (Rebek et al. 2008). The species has been introduced to North America and to the Moscow region in Russia (Baranchikov 2007; Baranchikov et al. 2008). *Agrilus planipennis* mainly kills *Fraxinus nigra*, *F. pennsylvanica*, and *F. americana* in North America, and mainly *F. pennsylvanica* in the Moscow region, but *F. excelsior* is also very susceptible (Baranchikov et al. 2008, 2009). The abundance of *Fraxinus* increases towards southern Europe, where two other potential hosts are present, *Fraxinus angustifolia* and *F. ornus*. The life cycle of *A. planipennis* is completed in one or two years depending on climate and host condition, and adults are active between May and July (Wang et al. 2010). Attacks start in the canopy and trees usually die within three years (Poland & McCullough 2006; Wessels-Berk & Scholte 2008).

Agrilus planipennis is on the NAPPO list of quarantine pests for both USA and Canada (NAPPO 2013). It was added to the EPPO alert list in 2004, and a pest risk analysis was performed in 2003 (EPPO 2005). The main pathways for introduction are plants for planting (including bonsai), untreated wood, and wood packing material

EPPO (2003a, 2003b). Firewood and wood chips are also possible pathways (Haack et al. 2010).

Twolined chestnut borer *Agrilus bilineatus* Weber, 1801 is the principal pest of *Quercus* spp. and *Castanea dentata* in North America and is reported to kill trees (Muzika et al. 2000). It primarily hastens the death of stressed trees, but may kill apparently healthy trees when population densities are high. The larval tunnels in the phloem may girdle the trunk and disrupt nutrient transport (Dunbar & Stephens 1976; Bright 1987). Attacks start in the canopy and trees may die within two to three years (Haack & Acciavatti 1992).

Granulated poplar borer *Agrilus granulatus* Say, 1823 is common in stressed native and planted *Populus* species in North America (Bright 1987; Solomon 1995). It attacks trees that are severely weakened by drought, disease, or winter injury and prefers trees growing in poor site conditions. The larva bore in the phloem and sometimes into the outer sapwood. The lifecycle is completed in one to two years. Morphologically this subspecies may be confused with the subspecies *A. granulatus liragus* (see below), but they have slightly different host preferences and are usually treated separately in the literature.

Bronze poplar borer *Agrilus granulatus liragus* Barter & Brown, 1929 attacks stressed, injured, and dying *Populus* species in North America. It prefers living phloem (Bright 1987) and causes decline and frequently death of the host (Barter 1965; Ives & Wong 1988). Attacks may spill over from weakened to healthy trees when population densities are high (Bright 1987). The life cycle is completed in one to two years, depending on temperatures and host vigor.

Aspen root girdler *Agrilus horni* Kerremans, 1900 attacks stressed and apparently healthy suckers of *Populus* spp. According to Nord et al. (1965), infestation by *A. horni* leads to the certain death of attacked suckers, especially in hybrid aspen plantations. On the experimental plots reported in Nord et al. (1965), the Eurasian species *Populus alba*, *P. tremula*, and various hybrids were most susceptible. Unlike other *Agrilus* species, *A. horni* larvae first bore down into the root phloem before they turn around and spiral upwards in the stem phloem. They pupate in the stem. The life cycle is assumed to be completed in two or more years.

Common willow agrilus *Agrilus politus* Say, 1825 mainly attacks *Salix* spp. and *Acer* spp. but is reported from several other genera as well, such as *Quercus* spp., *Corylus* spp., and *Alnus* spp. (Bright 1987; Solomon 1995). The damage inflicted on the hosts may be significant, but *A. politus* is considered to be of little economic importance in North America (Bright 1987). *A. politus* is the most widespread and polyphagous of the *Agrilus* species treated here, suggesting that it has substantial ecological plasticity and adaptability to a wide range of forest environments.

Alder birch borer *Agrilus pensus* Horn, 1891 attacks stressed *Alnus rugosa* and *Betula nigra* trees. According to Solomon (1995), *A. pensus* plays a more primary role in tree killing than its near *Agrilus* relatives. Similarly, Carlson and Knight (1969) state that *A. pensus* is a more significant tree killer than *A. g. liragus* and *A. anxius*. *Agrilus pensus* oviposits only in living trees or branches, although it seems likely that the host is under some type of stress (Bright 1987).

Native elm bark beetle *H. rufipes* Eichhoff, 1868 prefers *Ulmus* spp., mainly American elm (*Ulmus americana*) and Siberian elm (*Ulmus pumila*) (Anderson & Holliday 1999; McLeod et al. 2005), but is also registered as a minor pest on common elm (*Ulmus glabra*) (EPPO 2013). It has been reported attacking *Fraxinus* spp. (Baker 1972), but species-specific information on *Fraxinus* is lacking in the literature. This species attacks stressed trees, but summer-emergent adults are attracted to and feed on healthy elm trees (Swedenborg et al. 1988). *H. rufipes* populations can grow large during drought periods, when the beetles aggressively attack healthy trees.

Factors that may influence the risk of establishment

For a species to become invasive it needs to overcome a sequence of biotic and abiotic barriers limiting the probability that it will survive and establish a new population (Richardson et al. 2000). Biological characteristics of the species and the biotic and abiotic nature of its new environment will determine how likely it is to pass successfully through all these barriers. For most of the selected species we do not have sufficient information to do a thorough assessment of the prospects of successful establishment, so we will instead apply the general literature on species invasion to discuss the importance of the different barriers for our selected species.

Climatic similarity

Differences in climate are unlikely to stop the selected species from becoming established in northern Europe. There are many similarities between the climates of eastern North America and Europe, particularly within the continental and oceanic climate regions. As an example, both *A. anxius* and *A. planipennis* have expanded their ranges vastly within the continental climate zones. The two areas where *A. planipennis* first established in North America (Michigan) and Europe (Moscow region) have similar climates (precipitation and temperature) according to Köppen-Geiger climate maps (Peel et al. 2007). The very broad distribution of many of the selected species, especially *A. anxius*, *A. politus*, and now also *A. planipennis*, suggests that they may be adapted to colonize a wide geographic range in Europe and perhaps Asia, as long as suitable

host species are present. Northern Europe lies further north than most of the source areas in North America and will thus have a different photoperiodic regime. This could influence the establishment success of species and might be one of several factors explaining why there are relatively few invasive bark- and wood-borers in northern Europe.

Presence of the species along the pathway

Several characteristics of the selected species make it likely that living individuals will be present in the commodity pathway all the way up to arrival of wood chips in northern Europe. *Agrilus* beetles may be present in the outer sapwood of their host trees at any time of the year and are difficult to detect by visual inspection. Bark- and wood-boring beetles are usually more abundant in stressed and weakened standing trees and are thus likely to be present in wood typically used for wood chip production. Wood chips are often produced from low-quality wood such as damaged trees, salvage harvesting, or logging residues that do not meet the quality demands for lumber (Hall 2002). Even if better qualities were to be used it would be difficult to avoid the presence of bark- and wood-boring species, because they may attack apparently healthy trees and because of the large volumes that are logged by forest harvesters.

After harvesting, the wood is either chipped on site or transported to a chipping facility or port, where chips are either stored in piles or shipped directly. The survival rate of beetle pupa during chipping is influenced by the chipping screen size. The size of wood chips exported from North America corresponds well with a rather coarse screen size of 10 cm (Økland et al. 2012), which is known to allow survival of *Agrilus* pupae (McCullough et al. 2007). Simulation modeling performed by Økland et al. (2012) indicates that the chipping screen must be reduced to 6 mm or less to ensure that no *Agrilus* species will survive the chipping process. There is no ISPM standard for deciduous wood chips, and every national regulation of wood chips allows for larger than 6 mm chip thickness, including the regulations of more restrictive countries such as New Zealand (MAF 2003).

During storage and transport of wood chips, many organisms will usually die due to heat development resulting from fermentation. However, individuals may still survive in parts of the piles where temperatures stay below lethal levels or in cases where excessive heat development does not occur. On arrival to the production site, the wood chips are unloaded and stored in the open or in silos for up to several months. Most propagules, especially eggs and larva, usually die along the commodity pathway, but some prepupa, pupa, and adults may survive chipping, storage, and transport (McCullough

et al. 2007). Even with a low survival rate the numbers of survivors may be significant in large shiploads.

Propagule pressure and Allee effect

The number of individuals required to establish a new population varies from species to species and with environmental conditions. For instance, the spruce bark beetle *Ips typographus* seems to need hundreds of propagules (Liebhold & Tobin 2008), while it is assumed that the citrus longhorn beetle *Anoplophora chinensis* only needs a couple of individuals (van der Gaag et al. 2008). High propagule pressure is undoubtedly an advantage for successful establishment since it lowers the probability of extinction from stochastic events and reduces the effects of inbreeding depression and inverse density-dependent (e.g. Allee) effects (Colautti, Grigorovich et al. 2007; Lockwood et al. 2005). The propagule pressure of bark- and wood-boring insects is difficult to estimate directly because the propagules are hidden inside the host tree. However, the volume of the commodity pathway can be considered as a proxy for propagule pressure (Levine & D'Antonio 2003). The import volumes of chipped deciduous wood into Europe are increasing to meet the EU's target of obtaining 20% of its energy consumption from renewable sources by 2020 (Lins 2004). In addition to the large overall import volumes involved, wood materials usually also harbor large amounts of insects per unit volume.

In small populations resulting from low propagule pressure mate finding may be difficult, resulting in a low probability of establishment (Drake 2004; Haack 2006; Brouckerhoff et al. 2006a, 2006b). The importance of Allee effects for invasive species appears to differ significantly between insect taxa. For example, *Ips typographus* has been frequently intercepted in US ports but has consistently failed to establish, probably due to a combination of low propagule pressure and Allee effects related to mate finding and the need to mass-attack host trees (Liebhold & Tobin 2008). For *A. planipennis*, there are indications that Allee effects are not important, since the species has established itself efficiently in both Michigan, USA and the Moscow region. Furthermore, since its introduction to North-America in 2002, it has spread quickly to 19 US states (USDA 2013) and two Canadian provinces (CFIA 2013). We lack information about establishment and spread of other *Agrilus* species in new environments, but based on the similarities in their biology we may assume that they, like *A. planipennis*, may be weakly influenced by Allee effects.

Species interactions

Positive or negative interactions with other species are not believed to be crucial for establishment of North

American *Agrilus* species in northern Europe. Parasitism and other negative species interactions, such as competition, predation, and disease, tend to be highly species specific, and insects that are freed from these negative interactions can be said to experience "enemy-free space" in their new environment. This will usually increase their fitness and can result in uncontrolled population growth (Keane & Crawley 2002; Colautti, Ricciardi et al. 2004). There is little information on parasitism for our selected species, but it seems likely that they will benefit from the loss of negative interactions (i.e. the enemy release hypothesis). For example, in its native range in Asia *A. planipennis* has several known potential competitors (e.g. the bark beetles *Hylesinus cholodkovskiy*, *H. laticollis* and *H. fraxini*) and parasitoids (e.g. *Oobius agrili*, *Tetrastichus planipennisi*, *Spathius depressithorax*, and *S. generosus*) (Liu et al. 2007), whereas in North America it has only one known parasitoid, *Atanycolus cappaerti* (Cappaert & McCullough 2009) and in Russia there are so far no known parasites. Generalist predators like woodpeckers are known to forage for *A. planipennis* and other *Agrilus* species but are probably not efficient enough to hinder establishment.

Invasive species may be promoted by positive species interactions in new environments (Økland et al. 2009, 2011; Lu et al. 2011). Although this may be less important for the selected *Agrilus* species, which do not engage in group attacks and do not have fungal mutualists involved in host tree colonization, *H. rufipes* has a mutualistic relationship with DED in North America and will also benefit from this in areas where DED is present in northern Europe. *H. rufipes* did little damage in North America before DED was introduced but picked up the pathogen and became one of the main vectors of the disease. *H. rufipes* is attracted to and oviposits in trees infected by fungi and especially trees infected by DED (McLeod et al. 2005). When adults that have emerged from infected trees feed on healthy elms they inoculate the trees with the disease. If introduced, *H. rufipes* may become an efficient vector of DED in Europe, and particularly in northern Europe where the current DED vectors seem to be relatively inefficient (Solheim et al. 2011).

Naïve hosts

Local tree species tend to be adapted to attacks from local insects, but if the same insects attack so-called naïve hosts (i.e. hosts without a co-adapted history with the insect), the trees may succumb. Because naïve hosts often lack effective defenses against novel herbivores, they can be said to represent "defense-free space" for the herbivores (Gandhi & Herms 2010; Raupp et al. 2010). There are many examples showing that naïve hosts are preferred by invasive insects (Bryant et al. 1994; EPPO 1999; Glynn & Herms 2004; Bertheau et al. 2010;

Cudmore et al. 2010; Desurmont et al. 2011; Hulcr & Dunn 2011), and polyphagous insects that can colonize, feed, and develop on a range of naïve hosts can achieve rapid population growth (Bertheau et al. 2010).

In *Agrilus*, there are many examples of extensive tree killing when the insects have been introduced to new areas and encountered naïve host trees. Asian ash species within the native range of *A. planipennis* are much more resistant to attack than the North American white ash (*F. americana*), green ash (*F. pennsylvanica*), and black ash (*F. nigra*), which are readily killed by the insect (Gandhi & Herms 2010; Raupp et al. 2010). Also in Russia *A. planipennis* is killing green ash (*F. pennsylvanica*), which has been introduced from North America, as well as native European ash (*F. excelsior*) (Baranchikov et al. 2009). Similarly, native North American birch species, which have coevolved with *A. anxius*, are less susceptible to attack than introduced birch species such as Eurasian silver birch (*B. pendula*), white birch (*B. pubescence*), Sichuan birch (*B. szechuanica*), and monarch birch (*B. maximowicziana*), which all suffer 100% mortality (Nielsen et al. 2011). *Agrilus horni* attacks and kills Eurasian *Populus alba*, *P. tremula*, and various aspen hybrids (Nord et al. 1965). Bright (1987) noted that *A. horni* is “especially troublesome in orchard-like experimental plots of various *Populus* species” and was perhaps referring to attacks on trials with Eurasian *Populus* species. Introduced *Populus* species in North America are also attacked by *Agrilus g. granulatus* and *A. g. ligarius*, which attacks *P. nigra* and *P. balsamifera*, respectively (Barter 1965; Solomon 1995). The Wych elm (*Ulmus glabra*) in northern Europe lacks effective defenses against DED, but the disease has not spread as fast in northern Europe as in, for example, Great Britain. This is believed to be due to the lack of an effective vector for the disease. However, if *H. rufipes* was to be introduced to northern Europe, it could be a more effective vector than the native *Scolytus laevis*. If *U. glabra* proves to be a naïve host for *H. rufipes*, this could lead to a vicious cycle with extensive elm mortality.

The numerous examples given above suggest that naïve hosts are very likely to be an important factor promoting establishment and spread of bark- and wood-borers in northern Europe if they should become introduced. *Agrilus politus* and *A. pensus* are the only of our selected species without a documented history of causing mortality in European tree species. However, this does not necessarily mean that they are not harmful, as there are numerous examples of bark- and wood-boring insects that are not considered primary pests in their native range but are killing naïve trees in new environments (e.g. *Agrilus planipennis*) (Allen & Humble 2002; Haugen & Hoebeke 2005). It may therefore be prudent to expect that also *A. politus* and *A. pensus*

may be capable of primary attacks and benefit from naïve hosts should they be introduced.

Capability of spread

Agrilus wood borers appear to have considerable flight capacity and maneuverability, and this is likely to promote their ability to establish and spread if introduced into northern Europe. Most *Agrilus* species seem to fly only the distance needed to encounter a suitable host (Carlson & Knight 1969), and field tests have for example shown that most *A. planipennis* females fly only a few hundred meters (Mercader et al. 2009; Siegert et al. 2010). However, recent flight mill experiments demonstrate that *A. planipennis* has a considerable flight potential that even may exceed 20 km within a 24 hour period and that mated females fly almost 2.5 times further than unmated females (Taylor et al. 2010). The high flight capacity indicated by these experiments is supported by field observations. In Russia, the yearly diffusion of *A. planipennis* has been estimated to be at least 9 km (Y. Baranchikov, personal communication). From 2009 to 2012, *A. planipennis* dispersed 130 km westwards in Russia from Mozhaik to Vyazma, and it has now spread a total distance of 230 km since it was first discovered in Moscow in 2002 (Y. Baranchikov, personal communication). *A. anxius* is thought to be an equally good flyer as *A. planipennis* and is capable of a yearly diffusion of 16–32 km (Federal Register 2003). *A. anxius*' ability to follow its primary hosts through North America demonstrates good dispersal capabilities. Historically, *A. anxius* was restricted to the natural distribution area of its primary hosts, but due to extensive planting of ornamental birch species it has now dispersed southward in the United States and expanded its range vastly (Muirhead & Herms 2012). Little is known about the flight capacity of other *Agrilus* species.

According to Kaston (1939), *H. rufipes* can fly considerable distances to locate elm trees, although it normally probably only fly far enough to locate the next suitable tree (Anderson & Holliday 2003). The beetles use visual cues to seek out suitable host trees (Anderson & Holliday 2003), but it has also been shown that DED infected trees emit semiochemicals that attract *H. rufipes* (McLeod et al. 2005).

In addition to biological dispersal, human-mediated dispersal may create new satellite populations and increase the overall rate of spread of bark- and wood-borers. The spread of *A. planipennis* in the United States since its introduction around 2000 has for example been facilitated by movement of plants for planting non-squared wood (Muirhead et al. 2006) and possibly firewood (Haack et al. 2010). The relative importance of biological versus human-mediated dispersal is not known.

Potential economic and ecological impacts

Ecosystem effects

Together with climate change and habitat loss, biological invasions are considered the most important driving force of global environmental change. In the United States alone, 49% of all species listed as threatened are thought to be at risk due to competition or predation by non-indigenous species (Wilcove et al. 1998). Invasive, tree-killing bark- and wood-borers have the capacity to change tree species composition and forest structure, and thereby indirectly affect whole ecosystems. Direct and indirect ecosystem effects have been documented for several invasive forest insects, such as hemlock woolly adelgid *Adelges tsugae*, balsam woolly adelgid *A. picea*, gypsy moth *Lymantria dispar*, green spruce aphid *Elatobium abietinum*, and *A. planipennis* (Ellison et al. 2005; Lovett et al. 2006; Kenis et al. 2009; Gandhi & Herms 2010). Severe ecosystem effects are also expected if some of the most aggressive bark beetles should become introduced to new continents (Økland et al. 2011).

The current widespread killing of ash trees by *A. planipennis* in North America may affect the species communities associated with North America's 16 native ash species. By 2004, *A. planipennis* had killed approximately 15 million ash trees in eastern United States and was threatening an estimated 850 million ash trees in Michigan alone (Poland & McCullough 2006). Of the 282 plant and animal species that are estimated to be dependent on ash in North America, 43 species are clearly threatened if their host tree should be eliminated (Gandhi & Herms 2009). Tree mortality caused by *A. planipennis* leads to canopy gaps and changes in the microenvironment and understory succession (Gandhi & Herms 2010). This may in turn facilitate the establishment of invasive plants and lead to an "invasion melt-down" – the process by which one invasive species facilitates for other invasives (Simberloff & Von Holle 1999).

The introduction of *A. planipennis* in the Moscow region may pose an ecological and economic threat to European ash forests (Baranchikov 2010). Large-scale tree killing by *A. planipennis* is disrupting carbon fluxes and storage and can have global effects (Flower et al. 2012). Extensive tree killing and severe ecological consequences are also expected if *A. anxius* is introduced to northern Europe (EPPO 2011b; Nielsen et al. 2011), as potentially susceptible birch species are important and widely distributed throughout Eurasia (Hultén & Fries 1986). Effects of widespread killing of ash and birch forest in Eurasia by *A. planipennis* and *A. anxius* may include changes in the composition of the fauna and flora associated with these forests due to altered tree species composition, extinction of species dependent on ash or birch, and extensive erosion and mobilization of

carbon stores in the soil (Gandhi & Herms 2010; Økland et al. 2012). Introduction of *H. rufipes* to northern Europe could increase the spread of DED, one of the most destructive forest pathogens of all times, which has killed hundreds of millions elms in Europe and North America over the past decades (Brasier & Buck 2001). The loss of elms by DED in North America has changed the forest structure, bird densities, and diversity (Crooks 2002).

Economic impact

Introduction of *Agrilus* species and *H. rufipes* to northern Europe is likely to incur huge economic costs. The ~11,000 non-indigenous plant and animal species that are present in Europe today (DAISIE 2009) incur an estimated annual cost of €12.5 billion (Kettunen et al. 2008), and the more than 50,000 non-indigenous species in the United States carry an estimated annual cost of \$137 billion (Pimentel et al. 2000). Bark- and wood-borers are the most costly guild of non-native forest insects, with yearly costs in the United States alone estimated to \$3.5 billion in private and government expenditures (Aukema et al. 2010). *Agrilus planipennis* is the most costly of all the introduced wood-borers in the United States, incurring an estimated annual cost of \$1.7 billion. The largest expense is related to removal and replacement of dead trees. Eradication of *A. planipennis* is no longer considered a feasible strategy in North America, and land owners are instead advised to spread losses over time by protecting trees with insecticide treatments for a period or to cut losses by doing nothing (Vannatta et al. 2012).

The European ash *Fraxinus excelsior* is an important tree species throughout Europe, and its density increases southwards towards the Mediterranean region, where its range overlaps with *F. angustifolia* and *F. ornus* (Hultén & Fries 1986; FRAXIGEN 2005). *Fraxinus* is widely used as an ornamental tree in parks, graveyards, along roads, and in city streets throughout Europe. It is also a valuable timber species used for carpentry, furniture, house interiors, tools, and various sports equipment (FRAXIGEN 2005).

EPPO performed a pest risk analysis of *A. anxius* for Europe in 2011 and concluded that an introduction would cause high mortality of birch throughout the EPPO region, with major economic and environmental impacts (EPPO 2011b). This probably also applies to regions in Asia where susceptible birch species are abundant and widely distributed (Hultén & Fries 1986; Nielsen et al. 2011).

Concluding remarks

We have identified nine insects that probably have great potential to invade northern Europe through import

of deciduous wood chips from North America. The potentially most damaging species belong to the beetle genus *Agrilus*, which includes a species with a record of massive tree killing following introduction to new areas (*A. planipennis*). There are also other candidate insect groups that could be introduced via import of wood chips, but in this paper we have emphasized a group with a documented ability to survive in wood chips and a high damaging potential.

Screening for potential invaders by identifying common traits and performing risk assessments is not without difficulties. Only a few of the species that are introduced to a new region actually become established invasives, so there is always a risk of identifying false positives (Smith et al. 1999). On the other hand, the next great threat may very well be a seemingly innocuous species that does not appear in any risk assessments. Still, although it may be difficult to predict species invasions and their impacts in advance, improved information about potential invaders ahead of any interceptions remains an important preventive step to reduce the probability of invasions. It is well known that the time from the first interception of a species until effective phytosanitary regulations are in place usually is too long to prevent irreversible invasion and damage.

The most effective way of stopping biological invasions is to prevent arrival. Once an invasive species has become established, eradication is at best very difficult and costly. Presently there are no regulations of import of deciduous wood chips from North America to Europe, even though there are several North American beetle species with a clear potential to become invasive. It is probably impossible to single out trees infested by *Agrilus* during harvesting, since *Agrilus* species attack different tree species and may be found in both healthy looking and declining trees. Furthermore, since wood chips are produced from mixed forests, phytosanitary regulations of individual tree species may be impractical, and a better alternative may be to regulate the deciduous wood chip commodity as a whole.

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