

Climate change and invasions by nonnative bark and ambrosia beetles

Deepa S. Pureswaran^a, Nicolas Meurisse^{b,c}, Davide Rassati^d,
Andrew M. Liebhold^{e,f}, and Massimo Faccoli^d

^aCANADIAN FOREST SERVICE, LAURENTIAN FORESTRY CENTRE, QUEBEC, QC, CANADA ^bSCION (NEW ZEALAND FOREST RESEARCH INSTITUTE), ROTORUA, NEW ZEALAND ^cBETTER BORDER SECURITY (B3), LINCOLN, NEW ZEALAND ^dDEPARTMENT OF AGRONOMY, FOOD, NATURAL RESOURCES, ANIMALS AND THE ENVIRONMENT (DAFNAE), UNIVERSITY OF PADUA, LEGNARO, ITALY ^eUSDA FOREST SERVICE NORTHERN RESEARCH STATION, MORGANTOWN, WV, UNITED STATES ^fFACULTY OF FORESTRY AND WOOD SCIENCES, CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE, SUCHDOL, CZECH REPUBLIC

1 Introduction

Bark and ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) are a prominent group of insects that include important pest species, many of which have successfully established outside their native range (Brockerhoff & Liebhold, 2017; Hulcr & Stelinski, 2017; Lantschner, Corley, & Liebhold, 2020). Their cryptic nature and intimate association with bark and wood enable them to be accidentally transported within and among continents via trade of plants, timber, raw wood, wood products, and associated wood packaging materials (Haack, 2001; Meurisse, Rassati, Hurley, Brockerhoff, & Haack, 2019; Rassati, Haack, Knížek, & Faccoli, 2018). Furthermore, their resistance to dehydration and food deprivation and their thermal plasticity improves their likelihood of survival during long-distance transportation (Renault, Laparie, McCauley, & Bonte, 2018). More than 120 species are known worldwide to be established outside their native range (Gomez, Rabaglia, Fairbanks, & Hulcr, 2018; Hulcr & Dunn, 2011; Kirkendall & Faccoli, 2010; Lantschner et al., 2020; Rabaglia et al., 2019), some of which pose economic and ecological threats to urban stands, natural forests and commercial plantations in invaded areas (Hulcr & Dunn, 2011). These species, however, represent only a small fraction of the world scolytine fauna described so far (i.e., about 6000 species). This could be related to the relatively small number of scolytines transported internationally, either because these are rare species in their native range, or due to the lack of connections between their native range and foreign countries (Brockerhoff & Liebhold, 2017; Seebens et al., 2018). On the other hand, there are indications that not all species in the pool of scolytines circulating globally are able to establish in new areas. This can be explained by climatic differences among geographic regions (Marini et al., 2011), reduced host availability in the location of arrival (Colunga-Garcia, Magarey, Haack, Gage, & Qi, 2010), or a generally poor ability for

a few introduced individuals to establish a permanent population (i.e., Allee effects) ([Økland et al., 2019](#); [Tobin, Berec, & Liebhold, 2011](#)).

Understanding the drivers behind invasion success is essential to develop tools to predict which species are more likely to become invaders or which geographic areas are more prone to invasions, thereby minimizing the ecological and economic impacts and improving management of invading insect populations ([Liebhold & Tobin, 2008](#)). In general, the invasion success of nonnative species depends on three sets of factors: (1) propagule pressure—i.e., number of individuals introduced and number of introduction events per unit time into a new habitat ([Brockerhoff, Kimberley, Liebhold, Haack, & Cavey, 2014](#); [Tobin et al., 2011](#)); (2) invasiveness—i.e., the biological, behavioral and ecological traits of the species that determine its invasion capacity in term of survival and reproductive performance ([Kolar & Lodge, 2001](#)); and (3) invasibility—i.e., the biotic and abiotic characteristics of the receiving area that affect the establishment of new species ([Fridley, 2011](#)). Components of global change, including expanding international trade and movement of people, climate change, and other long-term anthropogenic modifications of ecosystems exert multiple influences on these factors ([Ramsfield, Bentz, Faccoli, Jactel, & Brockerhoff, 2016](#)). Directly or indirectly, they can profoundly alter the rates of entry and establishment of nonnative organisms.

Despite the implementation of improved phytosanitary measures, international trade and travel are still associated with substantial pest movement worldwide ([Brockerhoff & Liebhold, 2017](#); [Haack et al., 2014](#); [Hulme, 2009](#)). For several pest species, global movement is responsible for high propagule pressure at ports of arrival ([Meurisse et al., 2019](#)). Propagule pressure is considered a key driver of biological invasions ([Simberloff, 2009](#)), and while specific numbers of individual organisms transported on different pathways and associated arrival rates are largely unknown, the simultaneous arrival of a large number of individuals is more likely to lead to establishment than intermittent arrivals of single individuals ([Drake & Lodge, 2006](#)). For most species, this relationship between entries and probability of establishment is expected to be nonlinear, with rapidly increasing chances of success as founding populations become larger, due to stochasticity and Allee effects ([Tobin et al., 2011](#); [Grégoire, 2018](#)). Analyses using interception data as a proxy for propagule pressure have illustrated how changes in arrival rate relates to rapid changes in establishment probabilities ([Brockerhoff et al., 2014](#)).

Suitable climatic conditions, in contrast, constrain the ability of species to establish in any given receiving area. Insect activity, development and mortality are directly or indirectly (i.e., via associated symbionts) dependent on temperature and humidity ([Lantschner, de la Vega, & Corley, 2018](#); [Milbau, Stout, Graae, & Nijs, 2009](#)). For many species, it is the degree of similarity between geographic regions that determines invasion success ([Marini et al., 2011](#); [Venette, 2017](#)). For the same reason, climate profiles have been found to be good predictors of the long-term establishment probabilities and distribution patterns across invaded areas for forest insects and their natural enemies ([Fischbein, Lantschner, & Corley, 2019](#); [Lantschner, Atkinson, Corley, & Liebhold, 2017](#); [Lantschner et al., 2018](#)). The effect of climate is typically dependent on the intrinsic biological and ecological features of insect invaders. Certain species may establish only under certain

climatic conditions, or their population dynamics may be more sensitive to extreme weather conditions, whereas other species might be less influenced by climate and thus able to invade wider geographic areas. In fact, some species can undergo climatic niche shifts that enable invasion beyond the climate niche they occupy in their native range (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). Such variability in species climatic tolerance has been seen within the scolytines, notably between groups of species that differ in life history traits (Marini et al., 2011; Rassati, Faccoli, Haack, et al., 2016).

The scolytines are generally divided into two main guilds according to their feeding habit, namely, bark beetles and ambrosia beetles (Kirkendall, Biedermann, & Jordal, 2015). Bark beetles have relatively high host-specificity and build their galleries primarily in the phloem, or less frequently, in the sapwood from which they acquire nutrients (Kirkendall et al., 2015). Ambrosia beetles are in contrast, mostly generalist in host-range as they farm fungi that they vector and cultivate within wood galleries that they live in and feed on them as both larvae and adults (Batra, 1966). Ambrosia beetles are more diverse and numerous in wet and warm areas of the world (i.e., tropical areas), whereas bark beetles are more homogeneously distributed (Gohli & Jordal, 2017). From a taxonomic point of view, ambrosia beetles are a polyphyletic assemblage of independent clades that have evolved the ability to cultivate symbiotic fungi within wood galleries. These include several genera not only within the Scolytinae but also within the Platypodinae (Hulcr & Stelinski, 2017). In this chapter, we do not consider the Platypodinae, which includes about 1400 species of tropical and subtropical ambrosia beetles (Jordal, 2014).

At the continental scale, the geographic distribution of native bark and ambrosia beetles is affected by climatic variables such as temperature and rainfall (Marini et al., 2011; Rassati, Faccoli, Haack, et al., 2016; Reich, Lundquist, & Acciavatti, 2014). For nonnative species, the effect of climatic variables is more evident for ambrosia beetles than for bark beetles. Mean annual temperature and rainfall were strong predictors of ambrosia beetle species richness and species composition in invaded areas but had little effect on bark beetle invasions (Marini et al., 2011; Rassati, Faccoli, Haack, et al., 2016). The lower dependency of bark beetles on climatic conditions may allow them to expand their range in most areas where their host trees occur and establishment in distant regions would be mostly constrained by propagule pressure. However, these results are based on studies carried out at a continental scale, and the effect of climate on bark and ambrosia beetle invasions can differ depending on the spatial scale of the analysis. It is known from studies conducted at smaller scales, for example, that temperature can affect the development of both bark and ambrosia beetles and that of their fungal symbionts (Dodge & Stouthamer, 2021; Six & Bentz, 2007; Umeda & Paine, 2019; Yang, Wang, Li, Wang, & Jiang, 2010; Chapter 10), that can in turn affect their population dynamics (Bentz et al., 2010).

It is thus likely that changes in future temperature and rainfall regimes can affect any step of the bark and ambrosia beetle invasion process, from their predisposition to become invaders to their ability to establish and spread in invaded areas. However, the precise role of climate change on bark and ambrosia beetle invasions is still lacking in the literature. In general, the extent to which their invasion success can be attributed in part or completely to climate change remains unclear. Further, it is important to

consider the interactions of climate change with other components of global change that contribute to invasions, such as increasing trade and transport worldwide.

In this chapter, we explore the impact of climate in combination with other aspects of global change on different phases of the invasion process in bark and ambrosia beetles, i.e., predisposition to invade, transport, arrival, establishment, and spread (Fig. 1). We provide examples where climatic factors have aided the establishment and spread of nonnative species. We review the literature that predicts the impacts of climate change on invasion potential by species yet to establish in new regions of the world. Further, we identify gaps in current knowledge of the precise impacts of climate change on invasions by bark and ambrosia beetles. We suggest avenues for future research that can enhance our understanding of climate change on invasions, to improve predictions on climate-induced impacts by nonnative species.

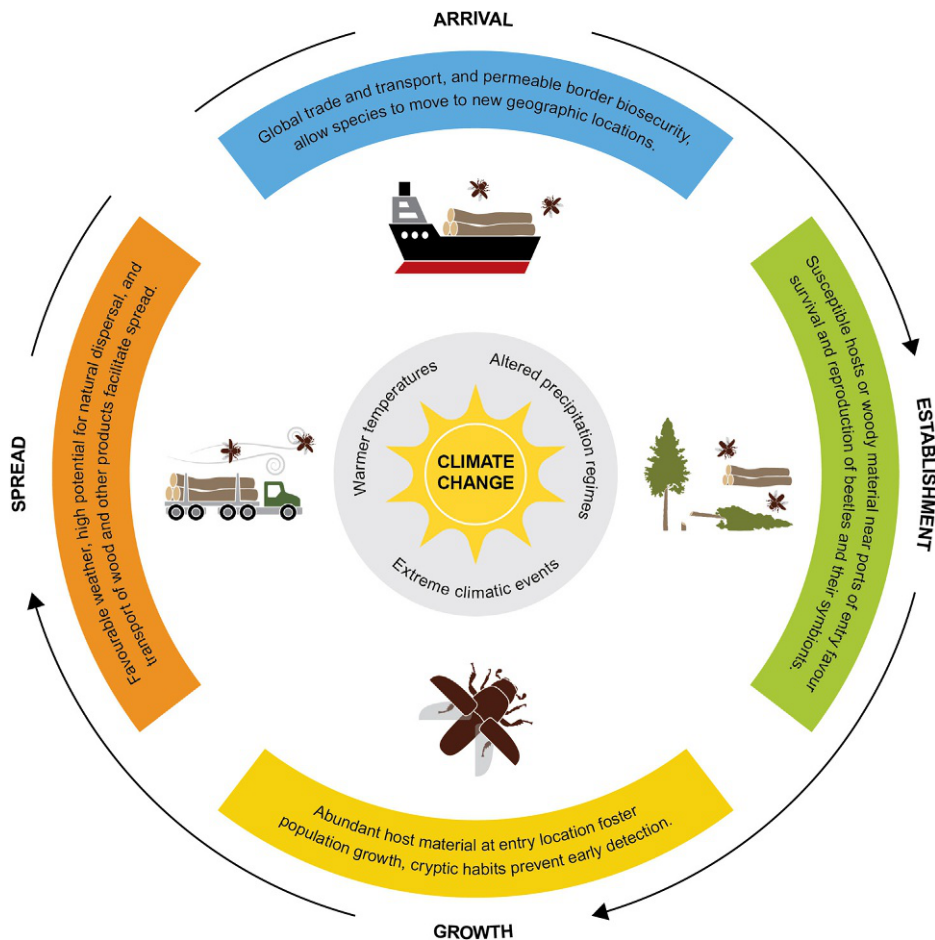


FIG. 1 Factors facilitating the four phases of invasion by bark and ambrosia beetles.

2 Key terms and concepts

Several terms, including alien, exotic, introduced, nonindigenous, immigrant, and nonnative, have been used interchangeably when discussing species invasions. This wide range of terminology and their various subjective implications have caused dispute, confusion, and debate in the invasive species literature (Valéry, Fritz, Lefeuvre, & Simberloff, 2008). We have provided a list of terms and their definitions (Text Box 1), but we restricted our usage in this chapter to “nonnative species” when referring to species that have colonized regions in which they do not normally occur.

3 Factors predisposing bark and ambrosia beetles as invaders

Certain biological traits are overrepresented among nonnative species that have successfully invaded new areas (Price & Jain, 1981; Pyšek & Richardson, 2008). For example, sib-mating, parthenogenesis, or clonal reproduction are traits shared by several successful invaders, allowing a single foundress to rapidly initiate colonization of a new area and benefit from a relatively low risk of predation (Gohli & Jordal, 2017). Such reproductive traits tend to be associated with species invasiveness because they reduce Allee effects arising from mate-finding failure, a key limiting factor for successful establishment of nascent populations (Liebhold & Tobin, 2008). Reproductive traits also explain observed patterns of historical invasions within the scolytines (Lantschner et al., 2020; Marini et al., 2011). While sib-mating is relatively uncommon in bark beetles (where most species outbreed, i.e., females locate mates at the entrance of a new gallery), it is relatively frequent in ambrosia beetles [where approximately half of the species inbreed, i.e., females mate with their brothers in maternal galleries (Kirkendall et al., 2015)]. Further, inbreeding species overcome the inbreeding depression that potentially occurs in outbreeding species when mating partners are too closely related (Andersen, Jordal, Kambestad, & Kirkendall, 2012; Peer & Taborsky, 2005) and are therefore relatively unaffected by genetic setbacks associated with small founder populations. For plants, it has been generally proposed that species that have restricted niches or ranges in their native range are less successful invaders than species that are common and widespread (Pyšek et al., 2009). This might also be valid for bark and ambrosia beetles, and abundance in the native range would be a good predictor of invasiveness. The ambrosia beetle *Xyleborinus saxesenii*, for example, is ubiquitous in its very large native range, inhabiting diverse environments ranging from conifer and broadleaf forest areas to urban-dominated landscapes (Marchioro et al., 2020; Rassati, Faccoli, Petrucco Toffolo, Battisti, & Marini, 2015). Consequently, this beetle species is now widespread as a nonnative species worldwide (Lantschner et al., 2020). On the contrary, *Heteroborips cryptographus* has a limited distribution in its native range and has never been intercepted or introduced into other regions. *Heteroborips* species excavate their brood galleries under bark rather than in wood like other Xyleborini and hence have a narrow host range strictly confined to a few species of aspen (*Populus* spp.) (Mandelstam, Petrov, Smith, & Cognato, 2019), which

TEXT BOX 1 Definition of key terms.

- **Native species.** A species living within its natural range as a naturally occurring and self-sustaining population (observed in historical times), including the area which it can reach and occupy using its natural dispersal systems. Synonym: indigenous.
- **Nonnative species.** A species or lower taxon that is not native to an area and that has entered by human agency, either intentionally or accidentally, into the area. A species that has entered an area through natural means is generally not considered a nonnative species but a species extending its natural range. Synonyms: nonindigenous, alien, exotic.
- **Entry.** Movement of a species or lower taxon into an area where it is not yet present, or present but not widely distributed. Synonym: arrival.
- **Establishment.** The process of a nonnative species population perpetuating in a habitat in the area it has entered, by successful reproduction. A single generation of reproduction can generally be considered establishment, provided the offspring have a likelihood of continued survival.
- **Introduction.** The entry and establishment of a species into an area where it is nonnative, through movement by human agency, either directly from an area where the species is native, or indirectly (by successive movement from an area where the species is native through one or several areas where it is not).
- **Invasive species.** Nonnative species whose introduction and/or spread cause ecological, environmental, and/or economic damage.
- **Established species.** Nonnative species that have sustained populations over several reproductive cycles and are not necessarily invasive in their novel ecosystem.
- **Spread.** Expansion of the geographical distribution of a species or lower taxon within an area.
- **Incursion.** Isolated population recently detected in an area, not known to be established, but expected to survive in the near future. Note distinction with invasion where the isolated population has established and started spreading.
- **Invasion.** Spread of a nonnative species to areas outside sites of introduction. Invasion may occur in various ecosystems and habitats, i.e., natural, seminatural, artificial, and with various consequences, i.e., positive, negative, and neutral.
- **Invasiveness.** Propensity of nonnative species to invade a new area. Traits that explain differences among species in invasiveness include ability for long-distance dispersal (by natural means or human agency), to establish with small numbers of propagules, and in diverse environments.
- **Invasibility.** Susceptibility of an area of introduction to invasion by a nonnative species. Environmental characteristics that explain differences in invasibility among habitats include community structure and disturbance factors.
- **Pest.** A species or lower taxon of plant, animal, or pathogenic agent injurious to plants or plant products.

would explain the confined presence of *H. cryptographus* in its native range and its inability to successfully invade other regions. Similarly, the pine bark beetle *Carphoborus marani* is a climatically restricted species occurring only in southern Greece (Lieutier, Mendel, & Faccoli, 2016). Although *C. marani* infests *Pinus halepensis*, a pine species

broadly diffused across the Mediterranean Basin, the beetle finds climatic conditions suitable for its development only in a restricted region of the Greek mainland. This might explain why it has never been intercepted nor established in other regions.

The regional distribution and abundance of phytophagous insects in their native range is primarily determined by the availability of suitable hosts and by their own climatic tolerance. In the context of climate change, certain species may have the potential to become more abundant, either as a result of increased availability of suitable host material or the existence of favorable climatic conditions, or both (Williams & Liebhold, 2002). This greater abundance results in higher probabilities that these species enter the global source pool of nonnative species for introduction elsewhere (i.e., increases propagule pressure) (Pyšek et al., 2009). For bark and ambrosia beetles, a wider distribution and higher abundance in the native range might result in a higher risk of contamination of exported round wood or wood-packaging material (see Section 4). Depending on their biology, beetle colonization can occur in the field soon after tree felling, at temporary storage locations before transportation to final destination or at shipping points; although phytosanitary treatments may eliminate contamination, wood may become infested at shipping points, especially if bark residuals are still present (Dodds, DiGirolomo, & Fraver, 2019; Haack & Petrice, 2009; Meurisse et al., 2019; Ostrauskas & Tamutis, 2012; Siitonen, 1990). Climate change can also influence nonnative species' probability of finding suitable hosts and environmental conditions in new areas, as well as potentially affect several biological and ecological traits of a given species, such as virulence, performance, or feeding habits, which can in turn increase their abundance (Ayles & Lombardero, 2000; Bentz & Jönsson, 2015; Jönsson, Appelberg, Harding, & Barring, 2009; Volney & Fleming, 2000) and their likelihood of being transported elsewhere.

4 Transportation and arrival

Introduction of nonnative organisms, including forest insects, outside their native range has increased worldwide during the 19th and 20th centuries (Brockhoff & Liebhold, 2017; Seebens et al., 2017, 2018). Global species movements have further accelerated in the last few decades, associated with intensified and more rapid transportation of contaminated traded commodities, sea and air vessels, and international passengers (Hulme, 2009; Seebens et al., 2017), concurrently with increasing connections to new source pools (Seebens et al., 2018). Within the scolytines, long-distance transportation primarily results from individuals hidden in live woody plants, inside fresh, seasoned, or processed timber, in association with wood packaging material (i.e., dunnage, crating, pallets, or drums) and other types of wood products (e.g., furniture, wooden toys, or craft items) (Brockhoff, Bain, Kimberley, & Knížek, 2006; Meurisse et al., 2019). Adult beetles are also transported via the “hitchhiking” pathway—i.e., they may be accidentally moved while associated with nonhost material. Examples include movement on the external and internal surfaces of transport vehicles (air, maritime, or land), or associated with shipping containers, trailers, or other traded items (ranging from large size vehicles and machinery,

to smaller size containerized or bulky items). It is plausible that such hitchhiking individuals may travel undetected over long distances, protected from adverse climatic conditions. Movement of bark and ambrosia beetles in association with international travelers is probably less common. Such transport might be restricted to occasional hitchhikers entrapped with outdoor equipment (e.g., camping gear), or contamination of personal items either as hitchhikers or infested wood material (e.g., woodcrafts).

Most scolytines also disperse actively or passively over long distances (Chase, Kelly, Liebhold, Bader, & Brockerhoff, 2017; Meurisse & Pawson, 2017). Nonetheless, flying individuals tend to be quickly diluted within the wider environment; hence, this mode of movement is only likely to play a role in short-distance range expansion or long-distance invasions of inbreeding and parthenogenetic species (i.e., ambrosia beetles). Traded commodities therefore remain the most likely mode of long-distance transportation for scolytines. Among the most likely pathways, importation of round wood has been the subject of several assessments of invasion risk (EPPO, 2020; USDA, 1992, 1993, 2003). For instance, in 2014 international trade was 133.5 for industrial round wood and 9.3 million m³ for fuelwood (Allen, Noseworthy, & Ormsby, 2017), and intercontinental trade of fresh-wood is generally considered one of the major and most risky pathways of woodboring beetle dispersal (Meurisse et al., 2019). Interception data provide additional evidence of bark and ambrosia beetle associations with traded wood items. In Finland, Siitonen (2000) identified 23 species of scolytines intercepted on Russian round wood imports (among 43 bark- or wood-boring beetle species). In the USA, Haack (2006) analyzed records of species intercepted from imported wooden commodities and packaging materials and reported 40 scolytine genera intercepted between 1985 and 2000. In New Zealand, Brockerhoff et al. (2006) identified 103 bark and ambrosia beetle species on sawn timber, logs, and other wooden imports and packaging material (intercepted between 1950 and 2000).

Despite accumulating documentation of such associations between commodities and scolytine interceptions, actual entries and establishments are only rarely attributable to clearly identified pathways, and the mode of arrival is often inferred based on biology or other information. Records of scolytines intercepted during inspections of imported cargo document imported wood and wood packaging material as primary pathways (Brockerhoff et al., 2006; Haack, 2001). At the fluvial port of Brussels in Belgium, Piel, Gilbert, Franklin, and Grégoire (2005) captured *Ips typographus* in unexpectedly high numbers, indicating that some individuals might be entering the city with imported spruce timber from Russia or the Baltic States. At another Belgian port, individuals of the nonestablished nonnative species, *Ips duplicatus*, were captured on quays where large volumes of imported spruce had been stored (Piel, Grégoire, & Knížek, 2006). Similarly, in Italy, nonnative bark and ambrosia beetles were trapped more commonly at or near ports of entry that handled high volumes of imported commodities (Rassati et al., 2015).

Patterns of global trade are also constantly shifting (Hulme, 2009; Roques, 2010), driving changes in pathways and source species pools (Turbelin, Malamud, & Francis, 2017; Westphal, Browne, MacKinnon, & Noble, 2008). International exchange of wood products,

for instance, is affected by fluctuations in demands for timber needs and regional changes in wood production (Kastner, Erb, & Nonhebel, 2011), including climate change (Reyer, 2015). Large quantities of wood made available, induced for instance by sudden and unexpected strong climatic events, can greatly affect the international timber markets by creating new commercial flows across countries and continents (FAO, 2004) and increasing the risk of movement and introduction of new nonnative species (Roques, 2010). In the case of catastrophic storms or droughts, these effects can also be amplified due to large quantities of dying or dead trees in affected forests or of timber in temporary storage, which are more likely to be contaminated with beetles before export (see Section 8 on European storms and the Siberian heatwave).

Other long-term changes in global transport of people and commodities, some of them related to climate change, may also play a role in future invasions by scolytines. Some of the global patterns of biological invasions observed worldwide relate to changing patterns of international trade, such as increase in live plant and other exports from Asia to other continents (Roques, 2010; Turbelin et al., 2017). Likewise, the dominance of established nonnative forest insects of Asian origin has increased in recent decades in North America (Brockerhoff & Liebhold, 2017; Langor, DeHaas, & Foottit, 2008; Liebhold, Brockerhoff, & Kimberley, 2017) and Europe (Roques et al., 2019), but not in Australia (Nahrung & Carnegie, 2020) or New Zealand (Brockerhoff et al., 2006; Brockerhoff & Liebhold, 2017). Changes in global trade patterns can be gradual or relatively quick. Notably, economic relationships and trade agreements have the potential to rapidly modify trade volumes in certain pathways, and therefore, their associated pest movements. Trade bans associated with phytosanitary regulation, or alternatively, elevated costs to avoid such bans, have for instance been identified as critical factors affecting trade destinations for log export (Self & Turner, 2009; Turner, Buongiorno, Zhu, & Prestemon, 2007).

Other influences of climate change on the dispersal of organisms between countries can generally result from flow-on effects (Luck et al., 2014). Existing trade routes could be disrupted as more frequent storm conditions are expected in some regions, whereas new routes such as the Northwest Passage could open because of rapid loss of perennial sea ice in the high Arctic. Climate change-related or not, constantly evolving trade routes may drive significant changes in the identity and numbers of forest insects transported globally. These changes could result from shifts in origins, destinations, or contamination levels of transported commodities and from shifts in survival during transit. Gray (2017) used a modelling approach considering different trade routes to show the combined effects of trade ship itineraries and global warming on risk of gypsy moth invasions. Highly fluctuating temperatures under certain routes may have profound impacts on the number of individuals arriving at the destination and their development stage (i.e., the propagule pressure is relevant for potential establishment). Variation in survival and developmental rates during transit can also be expected for travelling bark and ambrosia beetles, including impacts on diapause or emergence periods.

Climate change effect on the seasonality of trade and transportation of potentially infested plants or woody material is another concern. Colunga-Garcia, Haack, Magarey,

and Borchert (2013) investigated how live plants exported from around the world to North America contribute to propagule pressure of agricultural and forest pests at different USA ports. Their results show striking seasonal variation in plant imports for the northernmost entry locations usually associated with significant reductions in import volumes in the spring months. With climate change, it is a possibility that less strict seasonality in some countries will affect annual plant import cycles, hence annual peaks in pest arrivals may be affected. The exact consequences of such seasonal changes of pest entries on establishment remain difficult to predict. For instance, reduced propagule pressure could be expected in certain areas, while expanded durations for pest entries may increase the probability of matching a suitable climate for establishment.

5 Establishment and population growth

Analyses performed at the continental scale indicate that the likelihood of establishment in an invaded area is primarily a function of import volume for bark beetles, but that it is also strongly affected by climate suitability for ambrosia beetles (Marini et al., 2011). Even though bark beetles are less restricted by climatic factors than ambrosia beetles (Marini et al., 2011; Rassati, Faccoli, Battisti, & Marini, 2016), the number of bark beetles able to establish outside their native range is disproportionately lower than that of ambrosia beetles (Lantschner et al., 2020). The reason for this pattern is still unclear, although host availability with fewer species suitable for colonization by monophagous bark beetle species could be a driving factor. However, we can foresee that climate change will affect the likelihood of establishment of both bark and ambrosia beetles in the future.

Bark beetles of the genera *Ips* and *Dendroctonus* have been frequently intercepted outside their native regions (Haack, 2001, 2006), but except for a few (see Text Box 2 on *Dendroctonus valens*), most of these species are yet to successfully establish. Of particular interest is the Eurasian spruce bark beetle, *I. typographus*, which was intercepted in North America 253 times between 1985 and 2005 (Haack, 2006), currently stands at 727 interceptions worldwide (Turner et al., 2021), with no record of establishment to date despite suitable hosts being largely distributed across the continent. *I. typographus* can reproduce in six North American spruce species, Engelmann spruce (*Picea engelmannii*), red spruce (*P. rubens*), black spruce (*P. mariana*), white spruce (*P. glauca*), Sitka spruce (*P. sitchensis*) (Økland, Erbilgin, Skarpaas, Christiansen, & Långström, 2011), and Lutz spruce (*P. lutzii*) (Flø, Norli, Økland, & Krokene, 2018), a hybrid of Sitka and white spruce. Its primary native host in Europe, Norway spruce, is also widely planted as an ornamental tree throughout much of eastern North America where climatic restrictions are not limiting for *I. typographus* establishment. Most *Picea* habitats in North America are predicted to have high climatic suitability for establishment of *I. typographus* currently (2011–40) and throughout the century (Bentz et al., 2019). Its failure to establish so far could be attributed to aggregation behavior and polygamy that require a critical threshold of individuals infesting a tree to ensure population growth (Sun, Yang, Sweeney, & Gao, 2006). With climate change, warmer temperatures could favor *I. typographus* establishment and population growth throughout the continent due to decreasing winter mortality in

TEXT BOX 2 The red turpentine beetle.

The red turpentine beetle, *Dendroctonus valens*, infests pines in North America and parts of Central America where it is a secondary pest, rarely killing healthy trees (Eaton & Lara, 1967). Following its establishment in China, since the 1980s, it is estimated to have killed over 10 million pine trees. Favorable ecological conditions such as escape from natural enemies, presence of evolutionarily naive hosts (Zhang, Chen, & Zhang, 2002) and changes in associations with fungal symbionts (Taerum et al., 2013) have enabled its establishment and spread. In cooler regions of its native range, *D. valens* is semivoltine or univoltine, but it can be bivoltine or multivoltine in warmer regions (Smith, 1971). Forestry practices such as monoculture plantations of *P. tabuliformis* in areas affected by several consecutive years of warm winters and drought have favored spread of *D. valens* in China (Yan et al., 2005). With climate change, the average maximum temperature in China is expected to increase from 17°C to 19.8°C, and the minimum from 6.2°C to 6.9°C over the next 30 years (He, Ge, Wang, Wen, & Zong, 2015). Northern China is also warming at a higher rate than the south (Piao et al., 2010). *D. valens* is therefore predicted to expand its range northward and westward (He et al., 2015) posing a serious threat to China's pine forests.

northern regions (higher probability of univoltinism) and accelerating larval development and population growth in southern regions (higher probability of bivoltinism) [see Chapters 4 (Netherer & Almuth Hammerbacher) and 6 (McNichol et al.) for more ecological information on *I. typographus*].

Dendroctonus rufipennis is an example of a North American bark beetle that holds potential for establishment in Europe. Recent studies indicate that this species can successfully reproduce in Norway spruce (Isitt et al., personal communication), while model simulations predict that interspecific facilitation could occur between introduced populations of *D. rufipennis* and native populations of *I. typographus*, potentially increasing the frequency and severity of outbreaks in the context of invasions in Europe (Økland et al., 2011). In addition, the mountain pine beetle *D. ponderosae*, a highly aggressive pest of *Pinus* spp. in western North America, although never intercepted to date in Europe, has been intercepted 292 times in South Korea and five times in Japan (Turner et al., 2021), and could potentially colonize many pine-growing regions outside its range. For instance, Scots pine forests between 55 and 65°N in parts of Sweden and Finland would be particularly vulnerable in the event of a successful invasion by this species (Bentz et al., 2019). As the climate warms, predictions indicate climatic conditions at high elevations and latitudes in Europe would become even more suitable for *D. ponderosae*. A continued shift northward of the optimum habitat is predicted until the end of the century, after which a decline is predicted at almost all latitudes (Bentz et al. Chapter 2; Bentz et al., 2019). The fact that none of the three species discussed above have successfully established to date probably reflects the presence of strong Allee effects related to overcoming host defenses; the result is that large numbers of beetles would have to be present for populations to colonize host trees and establish.

If trees are weakened by climatic stress such as drought, fires, or windstorms, the success of invaders and their outbreaks would be further enhanced (Branco, Brockerhoff,

Castagneyrol, Orazio, & Jactel, 2015) (Chapters 7–9). Due to climate change, weather anomalies, extreme climatic events, and severe fluctuations in local weather are becoming increasingly common (Diffenbaugh, Singh, & Mankin, 2018; Wuebbles et al., 2016). There is also evidence that such climatic stresses have strong effects on tree physiological processes, including their growth and chemical defenses (Holopainen et al., 2018), which can in turn make them more susceptible to colonization by both native and nonnative scolytines (La Spina, De Cannière, Dekri, & Grégoire, 2013; Ranger, Reding, Schultz, & Oliver, 2013; Ranger, Schultz, Frank, & Reding, 2019). For many ambrosia beetles, the production of stress volatiles such as ethanol act as an attractant, predisposing trees under physiological stress to high levels of attack (Ranger, Reding, Adesso, Ginzler, & Rassati, 2021). For example, *Xylosandrus germanus* and *X. saxesenii* showed high abundance in sites where trees were weakened by abiotic stressors, such as frost (Barnouin et al., 2020; La Spina et al., 2013) or windstorms (Bouget & Noblecourt, 2005).

6 Spread of established populations

The effects of climate change on range expansions of native bark beetles have been discussed in Chapters 2–5 and 9. Nonetheless, native range expansion in forest insects has been precisely ascertained and related to climatic variables only in a few cases that include relatively well studied bark beetle species (Pureswaran, Roques, & Battisti, 2018) such as *Dendroctonus ponderosae* (Logan & Powell, 2001), *D. frontalis* (Ungerer, Ayres, & Lombardero, 1999), *D. rufipennis* (DeRose, Bentz, Long, & Shaw, 2013), *I. typographus* (Marini, Ayres, Battisti, & Faccoli, 2012; Temperli, Bugmann, & Elkin, 2013), and *Ips amitinus* (Økland et al., 2019). Climatic factors implicated in these range expansions include warm winter temperatures and extreme weather events as consequences of global climate change. Similar consequences can be expected as the climate warms and following initial establishment of nonnative bark and ambrosia beetles. The potential for bark beetles to disperse long distances on their own enables natural spread under suitable conditions of wind and temperature. For example, *D. valens*, established in China, has spread rapidly from Shanxi province to the adjacent provinces of Hebei and Henan (Yan, Sun, Don, & Zhang, 2005) (Text Box 2). *D. valens* is a strong flier with high dispersal capacity up to about 15km across the landscape (Wang, Wang, Han, Liu, & Liu, 2002). High dispersal rates also increase gene flow and genetic diversity that can aid the invasion process. In addition, northern China suffered warmer than normal winter temperatures in the decades following the introduction of *D. valens* in the early 1980s until its first outbreak in 1999 (Li, Chang, Song, Wang, & Chang, 2001; Miao et al., 2001). Drought conditions in *Pinus tabuliformis* plantations at the time are considered to have accelerated the spread of *D. valens* in China. Certain effects of climate change, as illustrated in the case of *D. valens*, have the potential to accelerate regional expansions by nonnative bark beetles.

Natural dispersal potential in ambrosia beetles appears to be limited compared to bark beetles, but climate change might favor the occurrence of multiple generations. In the tribe Xyleborini, which includes several species established in nonnative regions, including *Xylosandrus crassiusculus* (Text Box 3), males are often unable to fly and mating takes place with

TEXT BOX 3 The granulate ambrosia beetle.

The granulate ambrosia beetle *Xylosandrus crassiusculus*, of Asian origin, is a highly polyphagous pest of stressed trees (Ranger et al., 2016). Within the last several decades, it has reached most tropical and subtropical areas of the world, as well as several countries in temperate regions (Gugliuzzo et al., 2021; Storer, Payton, McDaniel, Jordal, & Hulcr, 2017). In North America, it was first reported in South Carolina in 1974 and is now established in 33 continental and the southern part of the Canadian province of Ontario (Gomez et al., 2018; Rabaglia et al., 2019). In Europe, it was first reported in Italy in 2003, and then spread in Spain, Slovenia, and France (<https://www.cabi.org/isc/datasheet/57235>). Nonetheless, both in North America and Europe, its further spread appears to be limited by climatic conditions. *X. crassiusculus* has never or sporadically been recorded, for example, in the central or northern part of Canada or northern Europe, nor in forests located at higher altitudes (Rassati, Faccoli, Battisti et al., 2016), where climate is likely unsuitable for its development and that of its fungal symbiont *Ambrosiella roeperi*. An increase in temperatures due to climate change might allow this species to expand its invasion range in the near future.

sibs in natal galleries (Kirkendall, 1983). Part of the mated females overwinter in the natal gallery and disperse the following spring to new trees. They can potentially disperse over long distances (≥ 200 m), although shorter distances of tens of meters appear more common (Werle, Sampson, & Reding, 2017). Nonetheless, warm spring weather in the southern United States enables ambrosia beetles to have two main flight periods, the first brood dispersal in early spring and a second brood in late summer (Werle, Chong, Sampson, Reding, & Adamczyk, 2015) allowing populations to spread farther each year. In the context of climate change, increased late summer heat could also increase physiological stress of trees and make them more susceptible to attack by the summer generation of dispersing females.

Invasions by bark and ambrosia beetles are also facilitated by forestry practices such as the widespread planting of nonnative tree species (Wingfield, Brockerhoff, Wingfield, & Slippers, 2015). Plantations of nonnative tree species have been widely established in several continents due to their high productivity. Much of that productivity can be attributed to “enemy release”—i.e., their tendency to have relatively few insects and pathogen species associated with them in their nonnative range. For example, extensive plantings of nonnative pines in the southern hemisphere create habitats for many scolytine species in regions that would otherwise possess no suitable host trees. However, over time and despite constant biosecurity efforts to prevent pest arrivals, it appears inevitable that freedom from pests would disappear as specialist herbivores and pathogens invade (Hurley et al., 2016; Wingfield et al., 2015; Withers, 2001). Nonnative tree species sometimes become more susceptible to colonization by native insects and pathogens than native tree species, especially in the presence of combined biotic and abiotic stressors. In experiments with reciprocal plantations of pine in Canada and Sweden, Fries (2017) found that Scots pine native to Europe (new associates) were attacked at higher rates by the mountain pine beetle, *D. ponderosae*, in British Columbia, Canada, than the native lodgepole pines (old associates that coevolved with the beetle). Planting lodgepole pine was of interest in Sweden because of its high productivity and ability to tolerate harsh environmental

conditions compared to Scots pine (Elfving, Ericsson, & Rosvall, 2001; Fries, 1993). However, should *D. ponderosae* establish in Europe, both lodgepole and Scots pine would be at risk of outbreaks (Rosenberger, Venette, Maddox, & Aukema, 2017) even in the absence of the added stress of climate warming.

The greater European spruce beetle, *Dendroctonus micans*, has slowly expanded its range throughout western Europe over the past 100 years favored by previous establishment of spruce plantations across the continent (Bright, 1976; Mayer et al., 2015). *D. micans* was also introduced to Great Britain in the 1980s (Fielding & Evans, 1997; Grégoire, 1988). Its spread in Great Britain has been attributed to increased trade in round wood timber, trees weakened by consecutive years of drought and planting of nonnative Sitka spruce rather than Norway spruce on sandy soils in which Sitka spruce suffers from moisture deficit (Fielding & Evans, 1997). Similar reasons have been proposed to explain the observed patterns of spread in western France (Pauly & Meurisse, 2007). The recent rapid spread of *I. amitinus* native to southern Europe into areas of northern Europe has posed somewhat of an enigma (Økland et al., 2019). This species co-occurs in outbreaks with *I. typographus* and is in fact preadapted to cold climates. Its recent spread to northern Europe has been attributed to reforestation that created contiguous spruce forests in the northern part of central Europe, rather than climatic conditions becoming more suitable (Økland et al., 2019).

7 Impact of climate change on fungal associates

Molecular phylogenetic evidence reveals that during two periods of global warming (c.50 million and 21 million years ago) in the Cenozoic era, expanding tropical forests favored the radiation and diversification of fungal farming groups of scolytine beetles (Jordal & Cognato, 2012). Present day global warming may similarly trigger an expansion of tropical and/or warm climate forests that can expand the geographic ranges of fungi and their beetle vectors. In addition, serendipitous and novel associations between beetles and fungi are more likely to arise in both bark and ambrosia beetles because of a general increase in biological invasions (Wingfield et al., 2017). Such novel associations can increase pathogenicity and threaten forest ecosystems (Hulcr & Dunn, 2011).

Despite the existence of relatively little information about changes in fungal symbiont composition following a biological invasion, except for a few high profile species (Six, 2013), there are reports that acquisition of novel symbionts from the invaded environment can occur (Carrillo et al., 2014; Morales-Rodríguez et al., 2021; Rassati, Marini, & Malacrino, 2019). Aggressive phenotypes of the ophiostomatalean symbiont *Leptographium procerum* were acquired after the introduction of the red turpentine beetle, *D. valens* to China, likely driving tree mortality (Lu, Wingfield, Gillette, & Sun, 2011; Taerum et al., 2017) (Text Box 2). In general, 30 different species of ophiostomatalean fungi were identified in *D. valens*, 20 from North America and 10 from China (Lu, Wingfield, Gillette, Mori, & Sun, 2010). Of these, only four species were shared between the two regions, suggesting that the fungal associates in China did not co-invade with *D. valens* but were acquired after establishment (Taerum et al., 2013). Fungal symbionts that are widely present in a potential

area of invasion that are also preadapted to the local tree species and climate stand a good chance of being vectored by invading beetles. If these fungi are suitable for symbiosis with certain nonnative beetles, they could greatly enhance their establishment success and invasion potential. Certain fungi might also suddenly become pathogenic and aid in beetle dispersal. For instance, tree mortality from thousand cankers disease is caused by the newly pathogenic symbiotic fungus, *Geosmithia morbida*, of the walnut twig beetle, *Pityophthorus juglandis* (Kolarik, Freeland, Utley, & Tisserat, 2011). In recent years, the severity of the disease has increased due to northward expansion within its native region in the USA facilitated by cold tolerance plasticity of the beetle and increasingly suitable climatic conditions in northern states (Hefty, Seybold, Aukema, & Venette, 2017; Hefty et al., 2018). Originally restricted to the southwestern United States, the beetle is now documented throughout five western and six eastern states (Rugman-Jones, Seybold, Graves, & Stouthamer, 2015). *P. juglandis* has since also established in northern Italy where the climate is favorable for the propagation of *G. morbida* (Faccoli, Simonato, & Rassati, 2016) with potentially serious impacts on many black and English walnut plantations occurring in other parts of Europe (Eichhorn et al., 2006).

In general, the prediction is that warm temperatures should favor the establishment and spread of novel fungal associates, regardless of the nature of their association (mutualists, commensals, and antagonists). However, there are documented cases of negative effects of warming on fungal associates that can be detrimental to beetle populations (Hofstetter et al. Chapter 10). For example, there is evidence that temperature strongly influences fungal associates and hence geographic ranges for species like the mountain pine beetle, *D. ponderosae*, whose symbionts have received a lot of attention from ecologists. Throughout its range, *D. ponderosae* is associated with *Grosmannia clavigera* and *Ophiostoma montium*. The cold-tolerant *G. clavigera* dominates northern populations but disappears in warmer parts of its range where *O. montium* is dominant (Six & Bentz, 2007), suggesting that as the climate warms *G. clavigera* could be lost from populations resulting in potential range contraction of *D. ponderosae*. Similarly, the relative frequency of fungal associates of the southern pine beetle, *D. frontalis*, is dependent on temperature. *Entomocorticium* sp. prevails in the winter, whereas *Ceratocystiopsis ranaculosus* is dominant in the summer (Hofstetter, Klepzig, Moser, & Ayres, 2006). In this case, redundancy in fungal associates that differ in thermal tolerance could enable range expansion of *D. frontalis* to northern latitudes in a warmer climate under the absence of lethal winter temperatures (Lombardo, Weed, Aoki, Sullivan, & Ayres, 2018; Weed, Ayres, & Hicke, 2013; Chapter 10).

8 Consequences of extreme weather events on invasions

8.1 Extreme meteorological events causing sudden increases in timber stocks—The 2018 drought and storms in Europe

Extreme climatic events associated with large-scale tree mortality and subsequent bark beetle outbreaks both directly and indirectly affected the international trade of wood products. Two unusual meteorological events affected Europe in 2018 and strongly increased timber

availability. The first event was a drought. Beginning in the spring of 2018 and continuing for two consecutive years (2018–19), a large part of central Europe experienced an unusually severe and long-lasting summer heat wave (Schuldt et al., 2020). These heat waves and droughts were considered exceptionally rare in historical records and their combined impact on forest health was even more extreme than the 2003 European drought (Hari, Rakovec, Markonis, Hanel, & Kumar, 2020), often considered the warmest of the last 500 years (Luterbacher, Dietrich, Xoplaki, Grosjean, & Wanner, 2004). In response to the 2018 event, most ecologically and economically important tree species in temperate forests of Austria, Germany, and Switzerland showed severe signs of drought stress (Schuldt et al., 2020), leading to premature tree senescence, decline and finally death of large deciduous and conifer trees (Rohner, Kumar, Liechti, Gessler, & Ferretti, 2021). Strong drought-legacy effects were also detected in 2019 with trees remaining highly vulnerable to colonization by bark beetles (Schuldt et al., 2020). The consequences were principally *I. typographus* attacks on spruce stands in the Czech Republic and Germany, for a total damage estimated to about 40 million cubic meters in Central Europe (Biedermann et al., 2019).

In 2018, a second extreme meteorological event affected forests of southern Europe, especially in northeast Italy and the Istrian coasts. On 28 and 29 of October, the storm “Vaia” caused considerable damage to Italian forests, knocking down about 8.7 million cubic meters of trees (mainly spruce) over an area of more than 41,000 ha, the same area harvested in an entire year of silvicultural activity throughout Italy (Motta, Ascoli, Corona, Marchetti, & Vacchiano, 2018). Similar to Central Europe, in the years following the Vaia storm, south-eastern Alpine regions suffered strong bark beetle outbreaks (Faccoli et al., 2020), forcing forestry operators to proceed with new massive harvesting of spruce timber.

These two events were associated with huge commercial consequences. For example, spruce timber prices decreased in the Czech Republic, from 56–64 (2011–2017) to 14–16 €/m³ in response to the massive *I. typographus* outbreak in 2018 (Hlásny et al., 2019). Similarly, after Vaia, in northern Italy, wood prices for spruce timber fell from an average of 60–80 €/m³ to values as low as 12–14 €/m³. The outbreak sent prices for German spruce spiraling down to half pre-2018 levels. As a response to the sudden increase of available timber and the low prices, Europe began shipping enormous volumes of wood to China. In the first three quarters of 2019, deliveries of spruce wood totaled more than 8 million m³, corresponding to a fivefold increase in the whole European flow of wood to China compared to 2018 (Source: Customs Statistics China 2019). Spruce logs destined for China were brought by trucks and ferries to Belgian, Dutch, German, and Italian international ports. Although logs were sprayed or fumigated with insecticides to kill bark and wood-boring pests, the probability of introduction of nonnative species from Europe to China could have been high.

8.2 The Siberian heat wave: Movement of conifer timber from Asia to Europe

Climate warming has had major impacts on permafrost thawing, fire risk and vegetation change in Siberia (Tchebakova, Parfenova, & Soja, 2009). In June 2020, a severe heat wave

occurred in Russia, with record high temperatures observed in many locations across Siberia. One location experienced 38°C, possibly the hottest temperature on record this far north in the Arctic (Erdman, 2020). In the warmer and drier climate expected in the future, boreal conifer forests in Siberia are predicted to shift northward by 2080, replaced by steppe ecosystems in their southern range (Tchebakova et al., 2009). Wildfires in Siberia have also increased in frequency and severity over recent decades, with intensities unprecedented in the last five millennia (Feurdean et al., 2020) and are predicted to continue to increase, especially in southern Siberia and central Yakutia (Tchebakova et al., 2009).

Insect outbreaks can follow these climatic stresses on trees in boreal forests. For instance, wildfires and droughts affecting Siberian larch species (*Larix sibirica*, *L. gmelinii*, and *L. cajanderi*) forests (Dulamsuren et al., 2013; Kharuk et al., 2019), trigger large outbreaks of the Asian larch bark beetle *Ips subelongatus* (Baranchikov, 1997; Chu, Zhang, & Zhuanfang, 1993). Such climate-driven disturbances are also contributing to an increase in the expansion of Siberian timber markets in terms of wood harvest, timber supply, and export toward Europe (Ivantsova, Pyzhev, & Zander, 2019). The Trans-Siberian railway is the main pathway transporting 97% of all cargo that enters European Russia from Asia (Baranchikov, 1997). For much of its length, the railway passes through areas with the most severe outbreaks and forest pest damage (Epova & Pleshanov, 1996). Open freight wagons carrying conifer wood, i.e., larch, are exposed to a very high risk of natural infestations of bark beetles during the 2–6 weeks that they take to travel through Siberia to Russia (Baranchikov, 1997). Given the impacts of climatic warming on the Siberian larch forests and subsequent increases in the international trade of Asian larch timber, Kirkendall and Faccoli (2010) pointed out that the Asian larch bark beetle, *I. subelongatus*, may establish in European Russia and possibly even in more western regions. Indeed, *I. subelongatus* was already intercepted in Finland in 1990 from logs imported from Siberia (Siitonen, 1990) and in Estonia in timber arriving from Russia (Voolma et al., 2004). Asian larch bark beetles were found in spruce forests around St. Petersburg and more recently have also been collected from pines in the Murmansk province (Voolma et al., 2004), which is outside the natural range of larch.

9 Conclusions and future directions

In the past, bark beetle outbreaks were often related to hot, dry periods and collapsed when cool, wet conditions returned (Bentz et al., 2010). With current global warming, climate change is now detectable from weather observations every day at a global scale (Sippel, Meinshausen, Fischer, Székely, & Knutti, 2020). Temperatures are expected to increase, accompanied by periods of drought with no return expected to “normal” preindustrial conditions. The implications of climate change for nonnative bark and ambrosia beetles will therefore manifest themselves via changes in population outbreaks and shifts in species distributions. The occurrence of extreme meteorological events in conjunction with overall average increasing temperatures compounded with international trade, movement of wood and wood-packaging material have already allowed the transport

and propagation of several nonnative scolytines in regions outside their native range. As regional productions and demands for agricultural and other products will be affected by climate change (Mbow, Reisinger, Canadell, & O'Brien, 2017), we can expect changes in international trade patterns that will affect global movement of bark and ambrosia beetles.

While globalization is considered the primary driver of biological invasions (Seebens et al., 2018), including for scolytines (Lantschner et al., 2020), the characteristics of the receiving environment and some of the traits of the invading species are also critical. The potential for nonnative species to overcome environmental fluctuations of the receiving habitat is largely affected by the frequency and intensity of climate change that ensures the initial establishment and population growth from an initially small contingent of invaders (Liebhold & Bascompte, 2003; Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009). Though the connection between climate change and an increased probability of establishment for bark and ambrosia beetles is perhaps more indirect with few clear examples to date, climate change appears to be playing a key role in triggering outbreaks of several scolytine species around the world (Jönsson, Harding, Barring, & Ravn, 2007; Logan & Powell, 2001). Droughts, for instance, may intensify outbreaks of scolytine species, and along with interactions with storms or wildfires, these outbreaks may alter carbon cycles, thereby amplifying the impacts of climate change (Kurz et al., 2008) (Chapters 7–9).

Global warming is also causing changes in environmental conditions leading to shifts in both their current (e.g. Chapter 3) and potential (this chapter) ranges. Affecting the beetles directly or indirectly via climatic stresses to their mutualistic fungi and host trees (Chapter 10), these shifts hold considerable potential for profound changes that could result in epidemics and catastrophic impacts. There is also considerable evidence of indirect effects of climate change on scolytine invasions. There are already indirect impacts of climate change on habitat invasibility and propagule pressure that hold considerable potential to drive new and potentially damaging invasions. Given this potential, there is a need to develop a better understanding of direct and indirect influences of climate change on invasions. This information is crucial for predicting invasions in the future and taking mitigative measures in order to minimize impacts.

We identified the following aspects that would merit future research:

1. The earth's climate will continue to change in the future. Therefore, climate change effects need to be incorporated in risk assessment scenarios for nonnative species.
2. Physiological models of thermal responses, invasion scenarios, and climatic niche models exist only for a few economically important species of bark beetles. Similar models are required for more scolytine species to predict invasion potential and range expansion.
3. Research is needed to support the choice of species for forest plantations to consider pests and diseases under the influence of climate change. Climate change influences outbreaks of native pests as native trees become more susceptible under climatic stressors, predisposing trees also to attack by nonnative pests. Genetic selection for

resistance to nonnative pests in plantations might help mitigate the impacts of nonnative species. The merits of plantation forestry need to be compared with those of close-to-nature forestry as intensive plantations of nonnative trees may not be the best solution to afforestation. However, economies and wood production have grown dependent on plantations and hence implementing such changes may be challenging.

4. Scolytines vectoring novel pathogens is an emerging concern as they can acquire new associations that are more virulent in the invaded range than in their native range. Potential impacts on symbiosis with fungal associates for both bark and ambrosia beetles under climate change scenarios needs specific investigation.
5. Species distribution models based on bioclimatic variables have been widely identified as a crucial tool for predicting the potential for establishment of pest species outside of their native range.
6. The paradox of invasion science, in general, is the low predictability despite being able to identify strong covariates of invasion performance (Hui & Richardson, 2019; Williamson, 1999). Studies on population dynamics of invaders are few. Experimental manipulations to quantify the impact of invaders in the context of climate change and biodiversity might improve predictability of invasions.

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