Forestry An International Journal of Forest Research

Institute of Chartered Foresters

INTERNATIONAL UNION OF FOREST RESEARCH ORGANIZATIONS

Forestry 2016; **89**, 245–252, doi:10.1093/forestry/cpw018
Advance Access publication 22 March 2016

Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts

T.D. Ramsfield[1]*, B.J. Bentz[2], M. Faccoli[3], H. Jactel[4] and E.G. Brockerhoff[5,6]

[1]*Canadian Forest Service, Northern Forestry Centre, 5320-122 Street NW, Edmonton, AB T6H 3S5, Canada*
[2]*USDA Forest Service, Rocky Mountain Research Station, 860 N. 1200 East, Logan, UT 84321, USA*
[3]*Department of Agronomy, Food, Natural Resources, Animals and Environment, University of Padua,*
Viale dell'Università, 16-35020 Legnaro (PD), Italy
[4]*INRA, BIOGECO, UMR1202, Cestas, France*
[5]*Scion (New Zealand Forest Research Institute), PO Box 29237, Christchurch 8540, New Zealand*
[6]*Better Border Biosecurity Collaboration, New Zealand*

*Corresponding author. E-mail: tod.ramsfield@canada.ca

Received 19 February 2016

Forests and trees throughout the world are increasingly affected by factors related to global change. Expanding international trade has facilitated invasions of numerous insects and pathogens into new regions. Many of these invasions have caused substantial forest damage, economic impacts and losses of ecosystem goods and services provided by trees. Climate change is already affecting the geographic distribution of host trees and their associated insects and pathogens, with anticipated increases in pest impacts by both native and invasive pests. Although climate change will benefit many forest insects, changes in thermal conditions may disrupt evolved life history traits and cause phenological mismatches. Individually, the threats posed to forest ecosystems by invasive pests and climate change are serious. Although interactions between these two drivers and their outcomes are poorly understood and hence difficult to predict, it is clear that the cumulative impacts on forest ecosystems will be exacerbated. Here we introduce and synthesize the information in this special issue of *Forestry* with articles that illustrate the impacts of invasions of insects and pathogens, climate change, forest management and their interactions, as well as methods to predict, assess and mitigate these impacts. Most of these contributions were presented at the XXIV IUFRO World Congress in 2014.

Keywords: biological invasions, climate change, forest resistance, modelling, risk, diagnostics

Introduction

There is growing recognition among the scientific community and policy makers that sustainable forest management is affected by multiple factors associated with global change. Exponential population growth has resulted in the addition of ~1 billion people between 1999 and 2012, leading to a global population of over 7 billion people that must be sustained by Earth's resources. Forests are of vital importance to humanity as they provide a wide range of essential ecosystem services (e.g. fuelwood, fibre, carbon sequestration etc., see Thompson *et al.*, 2011) but the ongoing loss of forest cover means the increasing demand must be met from an ever shrinking resource (Brockerhoff *et al.*, 2013). Concomitant with population growth has been the expansion of global trade networks and an increase in the volume of traded goods (e.g. Hulme, 2009). This has led to a considerable increase in the establishment of populations of non-native species in virtually all parts of the world (e.g. Roques *et al.*, 2009; Aukema *et al.*, 2010; Wingfield *et al.*, 2015). While many of these species appear to be relatively benign, some have major deleterious impacts on trees in natural and managed ecosystems, as well as urban environments. For example, the invasive emerald ash borer has been devastating ash trees in North America (Poland and McCullough, 2006) and *Phytophthora ramorum* is causing dieback and mortality of a wide range of tree species in Europe and North America (Grünwald *et al.*, 2012).

Climate change can exacerbate invasions of forest pests as well as impacts of native pests. For example, climate change can facilitate the range expansion of both native and exotic pests (insects and pathogens), or affect tree resistance to pests (Jactel *et al.*, 2012a), and there is increasing evidence that this is a widespread phenomenon (Battisti *et al.*, 2005; Marini *et al.*, 2012; Anderegg *et al.*, 2015). Using the planetary boundaries approach of Steffen *et al.* (2015), Trumbore *et al.* (2015) identified that the main stressors of the world's forests today are invasive species and diseases as well as climate change, along with deforestation and the increasing demand for forest resources. An additional contributor to forest health problems is the ongoing intensification and

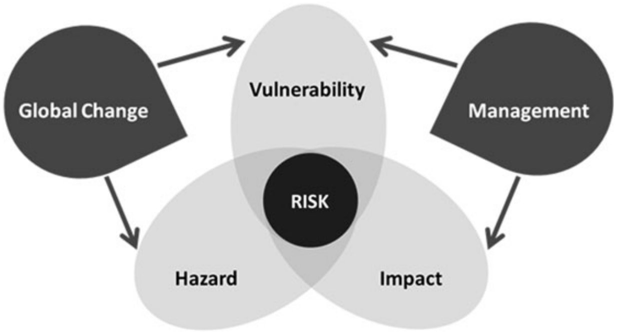

Figure 1 Risk depends on the combination of (1) the likelihood of hazard (e.g. frequency of wind, fire, pathogen, pest) which is the cause of damage, (2) the vulnerability of the system (e.g. forest stand) to the hazard thus resulting in damage and (3) the socio-economic impact of the damage (e.g. productivity loss) which depends on the value at stake (e.g. standing volume). Both global change and forest management can affect risk: global change mainly through change in hazard occurrence (e.g. spread of invasive species, higher frequency of storms) and forest vulnerability (e.g. water stress reducing resistance to pest) and forest management mainly through forest vulnerability (e.g. thinning improving tree vigour and thus resistance to pest) and impact of damage (e.g. short rotation forestry reducing standing volume).

mechanization of forest management which has increased the vulnerability of forests to disturbance from biological invasions, climate change and other stressors (Seidl *et al*., 2011). However, there is increasing recognition that forest management can be adapted to increase the resistance and resilience of forests to disturbance (Jactel *et al*., 2012b; DeRose and Long, 2014; Bahamondez and Thompson, 2016, this issue). The effects of global change and forest management on the risks to forests are influenced by the interaction of these drivers on the likelihood of hazard occurrence, the vulnerability of the system and the socio-economic impact of the damage as illustrated in the conceptual diagram presented in Figure 1.

The present contribution has two functions: it serves to review the topic and as an introduction to the special issue of *Forestry* which comprises articles that were presented at the International Union of Forest Research Organizations (IUFRO) XXIV World Congress in Salt Lake City, USA, from 6 to 11 October 2014. The theme of this special issue is ‘Forest Health in a Changing World’ and each article addresses various issues related to impacts of global change on forests and forest ecosystems. The articles have been contributed by researchers based in North and South America, Australasia, Europe and South Africa and were presented at various sessions sponsored by IUFRO’s Division 7 – Forest Health. The articles address impacts, risks, management, and tools to mitigate increased damage caused by pests through introduction into new areas or changes in climatic suitability. Taken as a whole, this collection of articles illustrates the complex issues that are associated with understanding, preventing and managing the impacts associated with spread of invasive pests or outbreaks of native forest pests.

Impacts of invading pests and benefits of prevention and eradication

Biological invasions cause a wide range of environmental and economic impacts (e.g. Mack *et al*., 2000; Lockwood *et al*., 2013). In the case of forest insects and pathogens, impacts include damage to trees that causes nuisance, growth loss or even tree death, loss of amenity value from forests or urban trees, impacts on biodiversity, reduced provision of ecosystem services and numerous other direct and indirect impacts and costs (e.g. Liebhold *et al*., 1995; Aukema *et al*., 2011; Boyd *et al*., 2013; Lockwood *et al*., 2013).

One of the most damaging recent invaders is the emerald ash borer (*Agrilus planipennis*) which was accidentally introduced to North America and western Russia, probably with wood packaging material. While it is only a minor pest in its native range in northeast Asia, in the introduced areas its impacts are very serious as it kills virtually all native species of ash (*Fraxinus*) in North America and Europe (Poland and McCullough, 2006; Baranchikov *et al*., 2008). The effects of this invasion undoubtedly have important implications for the biodiversity of the affected areas, especially the organisms associated with ash trees. Some effort has been directed at determining the economic impacts of emerald ash borer. A simulation study modelling the impacts of emerald ash borer over the 10-year period from 2009 to 2019 predicted the combined cost of tree treatments, removal, and replacement at $10.7 billion USD (Kovacs *et al*., 2010). A study of damage caused by non-native forest insects in the US estimated annualized damages from emerald ash borer at $38 million USD federal government expenditures, $850 million local government expenditures, $350 million household expenditures, $380 million residential property value loss and $60 million forest landowner timber loss (Aukema *et al*., 2011). In Europe, the economic impact of the pine wood nematode (*Bursaphelenchus xylophilus*) has been estimated to reach 22 billion Euros by 2030 (Soliman *et al*., 2012).

Gypsy moth (*Lymantria dispar*) is another well-known invasive tree and forest pest. This defoliator, mainly of broadleaved trees, especially oaks, has been present in eastern North America since its accidental release in Massachusetts in the late 1860s (Liebhold *et al*., 1995). To this day, large sums are spent annually to minimize defoliation and tree death and to reduce its rate of spread into uninvaded areas. Annualized damages from gypsy moth exceed $200 million USD, mainly for government and household expenditures as well as residential property value loss (Aukema *et al*., 2011). These figures demonstrate how costly the damages from invasive species can be. However, some damages such as the loss of ecosystem services provided by forests (e.g. flood mitigation, water purification, recreational and cultural values) (Boyd *et al*., 2013) are difficult to quantify in financial terms (Holmes *et al*., 2009). A more insidious impact of gypsy moth is its role in the reduction of oak dominance in affected regions (Morin and Liebhold, 2016, this issue). The authors used national forest inventory data to show how gypsy moth has contributed to the removal of young oaks from the ecosystem, which has implications for successional pathways, ecosystem function and the fate of these forest types.

Clearly, it would be beneficial to prevent the establishment and spread of such high-impact invaders and thereby avoid the occurrence of damages in the long term. The detection of the Asian longhorn beetle (*Anoplophora glabripennis*) in northern Italy in 2009 prompted an economic analysis comparing the costs of beetle eradication and the benefits of preventing damages such as the loss of trees and their amenity value (Faccoli and Gatto 2016, this issue). They concluded that the eradication, if successful, clearly provides net benefits. Similar conclusions were drawn by Brockerhoff *et al*. (2010) who compared the costs and benefits of eradications of forest insects in New Zealand. However, eradication programmes are often controversial, require substantial resources, and success is not guaranteed. Therefore, the implementation of measures to minimize the arrival of potential invaders should be even more beneficial than responding to incursions (Leung *et al.*, 2002). In fact, a cost-benefit analysis of a phytosanitary policy, using ISPM 15 (International Standards for Phytosanitary Measures No. 15, Regulation of Wood Packaging Material in International Trade) as a case study, determined that the policy provides substantial net benefits (Leung *et al.*, 2014) despite the fact that ISPM 15 does not prevent all arrivals of pests moved by this pathway. Finally, another important factor relates to the structure and composition of forests which can affect their resistance to invasive species and other disturbance agents (see below).

Climate change effects on insect outbreaks

Climate change has direct and indirect effects on insects, thereby influencing forest structure and composition at broad scales (Figure 2). Indirectly, changing temperature and precipitation regimes will influence the spatial distribution of host trees and their suitability to herbivorous insects, for example, because host defenses are compromised and phenological markers, such as bud break, are disrupted resulting in a phenological mismatch (Baltensweiler, 1993; Anderegg *et al.*, 2015). Community associates that influence insect population success, including pathogens, fungi, natural enemies and competitors, will also be influenced by climatic changes, thereby having both positive and negative indirect effects on outbreaks of forest insects and pathogens (Sturrock *et al.*, 2011; Addison *et al.*, 2015; Kalinkat *et al.*, 2015; Kolb *et al.*, 2016). Although the importance of an integrated understanding of indirect climatic effects on community associates and host trees is recognized, most research has been targeted at direct effects of temperature on insect population dynamics. Temperature directly affects many insect life-history traits that influence population success including diapause, cold hardening, and development time (Bentz and Jönsson, 2015). Bentz *et al.* (2016, this issue) show how warming temperatures can decrease generation time and increase overwintering survival for the mountain pine beetle (*Dendroctonus ponderosae*), an important native forest insect in North America (Figure 3). Their model simulations also show, however, that evolved life history traits can be disrupted in some thermal habitats as climate continues to change, resulting instead in reduced population growth.

Generally speaking, shorter generation times of forest insect species can result in increased tree mortality, and generation time is influenced by several thermally dependent life history traits. For example, many forest insect species in temperate regions have a facultative winter diapause that is induced by cold temperatures. Increasing temperatures can cause a reduction in generation time when diapause is averted, as has been shown for several guilds of Eurasian and North American forest insect species (Marchisio *et al.*, 1994; Battisti *et al.*, 2000; Lange *et al.*, 2006; Jönsson *et al.*, 2007; Faccoli, 2009; Bentz and Jönsson, 2015; McKee and Aukema, 2015). In addition to temperature cues, diapause in some species, such as *Ips typographus*, is also influenced by photoperiod. Geographic variability in diapause induction along latitudinal clines thereby limits the number of generations that can be produced in areas with short summer day lengths (Faccoli, 2009). Although averting diapause can be beneficial to population growth of many forest insects, warm temperatures can also desynchronize life-cycle timing resulting in the presence of cold-intolerant life-stages in winter, thereby causing increased insect mortality and reduced population growth (Faccoli, 2002; Wermelinger *et al.*, 2011; Bentz *et al.*, 2016, this issue). Desynchronization of evolved insect traits with host tree phenology was also shown to occur. The larch bud moth (*Zeiraphera diniana*) relies on a crucial timing of egg hatch with host tree bud break, and warm spring temperatures disrupt the timing, resulting in reduced population growth (Baltensweiler, 1993). Invasive species with limited phenotypic plasticity in new habitats could be vulnerable to both desynchronization of seasonality and with host tree phenology.

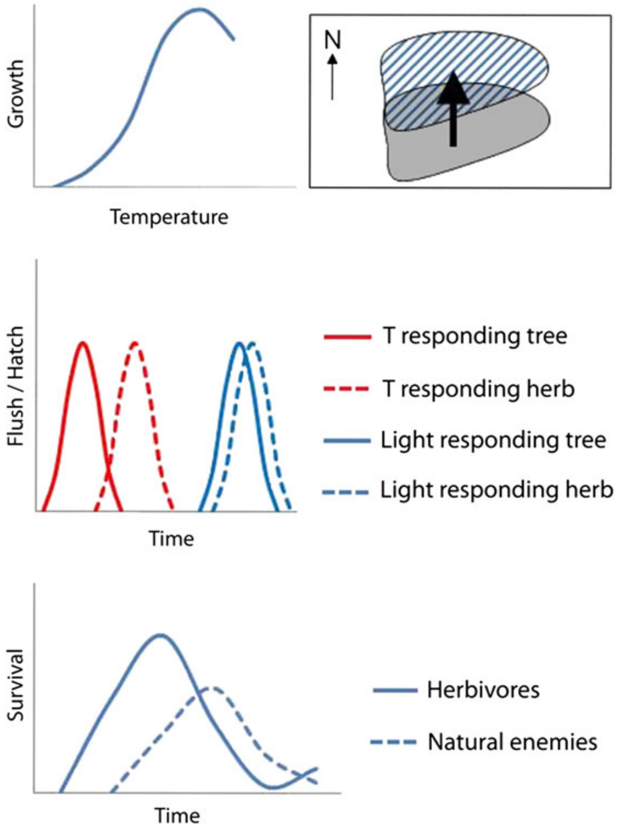

Figure 2 Direct and indirect effects of climate warming on the populations of forest pests. (A) The increase of temperature (*T*) promotes population growth and insect performance especially in temperate and boreal ecosystems, prompting range expansion at high latitude and elevation. (B) Matching between host flush and egg hatch is a crucial point for the survival of many spring herbivores; an increase of temperature may disrupt the mechanism in those species of trees and herbivores that respond to temperature with a different reaction norm (red lines), while others that are more depending on the photoperiod do not show changes (blue lines). (C) The regulation of herbivore populations by natural enemies can be affected by a different response of these organisms to warmer temperature (A. Battisti, personal communication).

In addition to reductions in generation time, increasing minimum temperatures associated with climate change can release populations from the constraint of periodic extreme cold and contribute to range expansion northward and upward in elevation (Weed *et al.*, 2013, 2015). Increased likelihood of extreme

Figure 3 Bark beetle-caused tree mortality in western North America exceeded 11 million ha in a recent 13 year period. In the western US, *Dendroctonus ponderosae* was responsible for >50% of all tree mortality. As shown here in the US northern Rocky Mountains, *Pinus* spp mortality (red trees) due to *D. ponderosae* was spatially extensive and temporally synchronized. B. Bentz photographer.

warm winter events, however, could limit northward expansion of native and invasive species when winter acclimation is disrupted and metabolic reserves are depleted (Sobek-Swant *et al.* 2012). Although cold temperatures in some habitats could continue to limit population success, winter-breeding species or species that are not constrained by diapause and instead use plastic life history traits are predicted to do best in a changing climate (Sinclair *et al*., 2003). For example, the pine processionary moth (*Thaumetopoea pityocampa*), and the bark beetles *Tomicus destruens*, *D. frontalis* and *D. ponderosae* are documented to have taken advantage of thermal increases at multiple times of the year and become more active at higher elevations, or reaching new hosts and new areas further north than previously reported (Battisti *et al*., 2005; Faccoli, 2007; Weed *et al*., 2013).

Warm and dry conditions in recent years associated with climate change have manifested in increased population activity of multiple forest insect species globally. In addition to the influence of temperature documented in this special issue (Bentz *et al*., 2016, this issue), drought is one of the most important climatic drivers of host tree susceptibility to forest insects as reduced water availability compromises tree defences and vigour (Jactel *et al*., 2012a). Globally, recent outbreaks of several bark beetle and defoliator species have been attributed to drought (Marchisio *et al*., 1994; Marini *et al*., 2012; Kolb *et al*., 2016). Moreover, because environmental conditions are a critical component of disease processes, in addition to host tree stress, increases in deleterious effects due to forest pathogens and their interactions with insects are also likely (Sturrock *et al*., 2011; Kolb *et al*., 2016). Continued research aimed at quantifying the influence of warm and dry conditions on forest insect and pathogen success will be necessary to predict future disturbance events and associated risks of damage.

Effects of forest management and composition on forest resistance to disturbance

To quantify disturbance and the state of forest ecosystems, in order to determine when control or mitigation measures are necessary, it is useful to develop relevant indicators or metrics of degradation. Bahamondez and Thompson (2016, this issue) suggest the use of forest productivity as an indicator that can quantify impacts in a manner that is readily interpreted by forest managers and policy makers. The use of forest productivity has the advantage that such data are typically available for many forests where foresters have monitored tree growth. Bahamondez and Thompson (2016, this issue) have developed calculations that use forest inventory and stocking data to identify a point below which a stand can be considered degraded. This process has utility for multiple disturbance types and can identify areas where stand management objectives are compromised by forest damage.

The increasing damage from invasive and native forest insects and pathogens has led to growing demand for pest control measures in natural, planted and urban forests. Traditionally, managing forest pests often involved the use of insecticides and fungicides. However, pesticide use may induce potential selection for resistance, cause negative effects on non-target species or lack effectiveness (Speight and Wainhouse, 1989; Pimentel, 1995). Thus, various alternative methods have been developed to reduce pest population levels below the economic threshold, including mechanical approaches (e.g. sanitation cutting), biological control based on natural enemies (e.g. release of parasitoids) and the use of pheromones and other semiochemicals (e.g. mass trapping) (Wainhouse, 2005). All of these pest management techniques are more or less environmentally friendly but they remain difficult to implement, for a variety of reasons. The height of trees, difficult access to forest land, and the need to repeat treatments may make these alternative methods costly. Therefore, it is advantageous to prevent or minimize pest problems and invasions before they occur, rather than responding to and suppressing outbreaks once damage is happening. Prevention is basically a pest management strategy that relies on the ability of the forest ecosystem to defend itself. It is based on the assumption that the use of good silvicultural practices would increase the resistance of individual trees and forest stands to pests. Indeed, reviews of the scientific literature have shown that every single silvicultural operation can have a significant effect, positive or negative, on forest stand vulnerability to pest insects (Fettig *et al*., 2007; Jactel *et al*., 2009).

In the case of planted forests, the first management decision is the selection of planting material. Ideally, the tree species and variety is adapted to the site conditions. The use of exotic tree species requires additional consideration as such trees are more likely to recruit native insect herbivores when native congeneric tree species are present in the area of introduction (Branco *et al*., 2015). Of even greater importance is the species composition of forest stands. Two comprehensive reviews of the international scientific literature have shown that mixed forests are more resistant to forest insect damage than monocultures (Jactel and Brockerhoff, 2007; Castagneyrol *et al*., 2014). Another study showed that this trend also applies to impacts of invasive species (Guyot *et al*., 2015). Several mechanisms are thought to explain these results. The presence of non-host species in mixed forests is expected to raise physical or chemical barriers that limit host tree finding and colonization by insect herbivores. Mixed forests may also provide natural enemies with complementary habitat or feeding resources, thus enhancing biological control. How natural biocontrol can be affected by both direct and indirect effects of forest management is explored by Klapwijk *et al*. (2016, this issue). Classical biological control is generally considered a promising method to achieve self-sustaining long-term control of invasive pests by restoring more sustainable pest population dynamics. Nahrung *et al*. (2016, this issue) report some of the challenges associated with biological control as exemplified with their experience controlling *Sirex* in Australia. The woodwasp was discovered attacking *Pinus taeda* and *P. radiata* in Queensland in 2009 and biological control efforts were initiated shortly thereafter and inundative release of nematodes has been conducted for four consecutive years. It was observed that parasitism rates of *Sirex* by the nematode were low (Nahrung *et al*., 2016, this issue); however, variability of biological control efficacy in this system is not unusual, likely due to the complexity of the interactions between the host, insect, fungi and nematode (Slippers *et al*., 2015).

Site preparation treatments, including soil preparation, stump treatment and weed management may reduce the amount of breeding substrate available for important pests such as bark beetles and weevils (Jactel *et al*., 2009). Fertilization may be either beneficial or detrimental, depending on the type of fertilizer (nitrogen *vs* phosphorus) and on the category of pest (primary *vs* secondary) (Jactel *et al*., 2009). Management of the understorey vegetation may reduce the competition for light and water thus improving individual tree vigour and resistance. On the other hand, preserving diverse understorey vegetation may benefit parasitoids through the presence of nectariferous plants (Hougardy and Grégoire, 2000). Because thinning operations improve individual tree vigour this may reduce tree susceptibility to a number of secondary pests (such as secondary bark beetles), whereas it can favour primary pests such as several insect defoliators (Jactel *et al*., 2009). Sanitary thinning, which aims at removing weakened and dying trees, is often recommended to avoid breeding of insects which could later attack living trees, such as the European spruce bark beetle (*I. typographus*) that can attain high population densities on weakened trees (Stadelmann *et al*., 2013).

Logging operations with heavy machinery may result in bark injuries which can in turn trigger pest infections. Logging residues or stumps can also serve as breeding substrates for weevils and many bark beetles in conifer forests. Also, it has been suggested that single-tree or group selection cuttings would increase stand structural diversity, leading to improved individual tree vigour and thus resistance to pest insects (Brang *et al*., 2014). Besides affecting tree and stand vulnerability, forest management may have a more general effect on the risk of biotic damage as the economic value of growing stock is also dependent upon the type of silvicultural systems that are employed (Figure 1). For example, short rotation forestry may be less prone to risk than longer-rotation plantation forestry simply because very young trees used for bioenergy are of a lower value than mature trees used for timber (Jactel *et al*., 2012b).

Technological advances in diagnostics for managing forest health and biological invasions

A critical requirement for forest health and biosecurity/phytosanitary research and management is to ascertain the identity of organisms of interest. Traditionally, this has been accomplished through pest morphology and the highly specialized taxonomic expertise of entomologists and mycologists. The development of molecular tools for identification of species and genotypes has transformed this field. These molecular tools have developed to the point that they can now be used to study populations of organisms in economically important contexts, such as the invasion pathway (Adamowicz, 2015). The utility of molecular data was demonstrated by Bérubé and Nicolas (2015) who screened asymptomatic plants that were imported into Canada and found that two of 267 fungal operational taxonomic units (OTUs) were classified, with the potential to have moderate impacts on Canadian forests. A further 37 OTUs were classified as having the potential for low risk. This study illustrates how DNA can be utilized to detect latent pathogens in association with the international trade in live plants (also known as the 'plants for planting' pathway).

The risks associated with this pathway are not limited to the movement of seedlings and larger plants but also concerns the movement of seed. The presence of the *Eucalyptus* stem canker pathogen *Teratosphaeria zuluensis* was detected within seed and seed capsule material collected from eucalypts in a stand where the pathogen was known to be present (Jimu *et al*., 2016, this issue). This study revealed the possibility of pathogen movement with infested seed material and the potential risk of this pathway, as well as the utility of DNA-based methods for detecting pathogens. DNA analysis was also used by Buys *et al*. (2016, this issue), to develop a system by which species of Myrtaceae in New Zealand can be rapidly identified in the event of an incursion by the myrtle rust pathogen (*Puccinia psidii*). This pathogen is not present in New Zealand; however, it has become established in Australia where it is causing considerable damage. The risk of a subsequent invasion of New Zealand is high, given the large amount of trade, movement of people and air currents between the countries, all of which could facilitate the transport of pathogen spores. If *P. psidii* were to arrive in New Zealand, the tool developed by Buys *et al*. (2016, this issue) could be utilized as part of an incursion response, to confirm the identity of host and non-host species among the Myrtaceae, a family of which hundreds of species are present in New Zealand.

The availability of cost effective and rapid DNA-based diagnostic tests has furnished regulatory agencies and researchers with tools to improve the detection of invasive organisms, such as loop-mediated isothermal amplification (LAMP) that is less time consuming than traditional PCR (Villari *et al*., 2013). It is important to note that these tools rely heavily on collections of expertly identified insects and fungi that are held in institutions throughout the world. It is critical that these collections are maintained and that the training of the next generation of taxonomists continue in order to ensure that molecular diagnostics are accurate and reliable. Molecular tools are widely accessible, relatively inexpensive and can be readily implemented by quarantine agencies thereby providing knowledge that can be used to reduce the probability of the establishment of exotic pests.

Conclusions

The impacts of invasive species are multifaceted and complex as illustrated by the articles in this special issue. Coupled with uncertainty related to climate change and its influence on insect and pathogen populations, the challenges for policy makers and regulators to manage impacts of invasive and native pests will become increasingly difficult. Regulators rely heavily on the results of robust scientific enquiry, and understanding these complex interacting forces is an important research focus. The articles in this special issue demonstrate the utility of various computer modelling strategies to estimate future impacts of forest pests, and also investigate new forest management practices and tools to detect and prevent the spread of invasive pests or the outbreaks of native pests. The provision of ecosystem goods and services by productive and natural forest ecosystems, as well as trees in urban environments, will continue to be threatened as a result of issues related to globalization. The impacts of invasive pests on natural and managed forest ecosystems are evident and phytosanitary measures such as ISPM 15 have been implemented to reduce the probability of inadvertent movement of pests through trade. The role of climate change in native and invasive pest population outbreaks has also been documented. Although it is clear these two complex drivers interact, there is uncertainty about the shape and nature of their interactions. Knowledge provided through process-based computer simulations, and the development of forest ecosystems that are inherently resistant and resilient, however, will allow us to anticipate future problems and consider these issues in proactive forest management plans.

Author contributions

All authors contributed equally to the writing of this manuscript.

Acknowledgements

The authors thank the organisers of the XXIV IUFRO World Congress for the opportunity to present the papers in this special issue during the congress. We also thank Gary Kerr, Editor-in-Chief of *Forestry*, and Lulu Stader for supporting this special issue. The editorial advice of Anssi Ahtikoski and Berthold Heinze is greatly appreciated. Figure 2 was kindly provided by Andrea Battisti. Jon Sweeney, Simon Shamoun and Andrew Liebhold provided useful comments on an earlier version of the manuscript.

Conflict of interest statement

None declared.

Funding

The contribution of T.D.R. was funded by the Canadian Forest Service. Contributions by B.J.B. were supported by the United States Department of Agriculture Forest Service. Contributions by E.G.B. were supported by Ministry of Business Innovation and Employment core funding to Scion (contract C04X1104) via the Better Border Biosecurity Collaboration (www.b3nz.org).

References

Adamowicz, S.J. 2015 International barcode of life: evolution of a global research community. *Genome* **58**, 151–162.

Addison, A., Powell, J.A., Bentz, B.J. and Six, D.L. 2015 Integrating models to investigate critical phenological overlaps in complex ecological interactions: the mountain pine beetle–fungus symbiosis. *J. Theor. Biol*. **368**, 55–66.

Anderegg, W.R., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B. *et al*. 2015 Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol*. **208**, 674–683.

Aukema, J.E., McCullough, D.G., Von Holle, B., Liebhold, A.M., Britton, K. and Frankel, S.J. 2010 Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience* **60**, 886–897.

Aukema, J.E., Leung, B., Kovacs, K., Chivers, C., Britton, K.O., Englin, J. *et al*. 2011 Economic impacts of non-native forest insects in the continental United States. *PLoS One* **6**, e24587.

Bahamondez, C. and Thompson, I.D. 2016 Determining forest degradation, ecosystem state and resilience using a standard stand stocking measurement diagram: theory into practice. *Forestry* **89**, 290–300.

Baltensweiler, W. 1993 Why the larch bud-moth cycle collapsed in the subalpine larch-cembran pine forests in the year 1990 for the first time since 1850. *Oecologia* **94**, 62–66.

Baranchikov, Y., Mozolevskaya, E., Yurchenko, G. and Kenis, M. 2008 Occurrence of the emerald ash borer, *Agrilus planipennis* in Russia and its potential impact on European forestry. *EPPO Bull*. **38**, 233–238.

Battisti, A., Boato, A. and Masutti, L. 2000 Influence of silvicultural practices and population genetics on management of the spruce sawfly, *Cephalcia arvensis*. *For. Ecol. Manage*. **128**, 159–166.

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A. *et al*. 2005 Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl*. **15**, 2084–2096.

Bentz, B.J. and Jönsson, A.M. 2015 Modeling bark beetle responses to climate change. Chapter 13. In *Bark Beetles: Biology and Ecology of Native and Invasive Species*. Vega, F. and Hofstetter, R. (eds). Elsevier, pp. 543–549.

Bentz, B.J., Duncan, J.P. and Powell, J.A. 2016 Elevational shifts in thermal suitability for mountain pine beetle population growth in a changing climate. *Forestry* **89**, 271–283.

Bérubé, J.A. and Nicolas, G.G. 2015 Alien fungal species on asymptomatic live woody plant material imported into Canada. *Can. J. Plant Pathol*. **37**, 67–81.

Boyd, I.L., Freer-Smith, P.H., Gilligan, C.A. and Godfray, H.C.J. 2013 The consequence of tree pests and diseases for ecosystem services. *Science* **342**, 1235773.

Branco, M., Brockerhoff, E.G., Castagneyrol, B., Orazio, C. and Jactel, H. 2015 Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. *J. Appl. Ecol*. **52**, 69–77.

Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncčina, A., Chauvin, C. *et al*. 2014 Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* **87**, 492–503.

Brockerhoff, E.G., Liebhold, A.M., Richardson, B. and Suckling, D.M. 2010 Eradication of invasive forest insects: concept, methods, costs and benefits. *N. Z. J. For. Sci*. **40**, S117–S135.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A. and Ferraz, S.F. 2013 Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. *For. Ecol. Manage*. **301**, 43–50.

Buys, M.H., Flint, H.J., Miller, E.M., Yao, H., Caird, A.R. and Ganley, R.J. 2016 Preparing for the invasion: efficacy of DNA barcoding to discern the host range of myrtle rust (*Puccinia psidii*) among species of Myrtaceae. *Forestry* **89**, 263–270.

Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E.G. and Koricheva, J. 2014 Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. *J. Appl. Ecol*. **51**, 134–141.

DeRose, R.L. and Long, J.N. 2014 Resistance and resilience: a conceptual framework for silviculture. *For. Sci*. **60**, 1205–1212.

Faccoli, M. 2002 Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera Scolytidae) and its parasitoids in the South-eastern Alps. *J. Pest Sci*. **75**, 62–68.

Faccoli, M. 2007 Breeding performance and longevity of *Tomicus destruens* on Mediterranean and continental pine species. *Entomol. Exp. Appl*. **123**, 263–269.

Faccoli, M. 2009 Effect of weather on *Ips typographus* (Coleoptera Curculionidae) phenology, voltinism, and associated spruce mortality in the South-Eastern Alps. *Environ. Entomol*. **38**, 307–316.

Faccoli, M. and Gatto, P. 2016 Analysis of costs and benefits of Asian longhorned beetle eradication in Italy. *Forestry* (this issue) **89**, 301–309.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F. *et al*. 2007 The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *For. Ecol. Manage*. **238**, 24–53.

Grünwald, N.J., Garbelotto, M., Goss, E.M., Heungens, K. and Prospero, S. 2012 Emergence of the sudden oak death pathogen *Phytophthora ramorum*. *Trends Microbiol*. **20**, 131–138.

Guyot, V., Castagneyrol, B., Vialatte, A., Deconchat, M., Selvi, F., Bussotti, F. *et al*. 2015 Tree diversity limits the impact of an invasive forest pest. *PLoS One* **10**, e0136469.

Holmes, T.P., Aukema, J.E., Von Holle, B., Liebhold, A. and Sills, E. 2009 Economic impacts of invasive species in forests. *Ann. N. Y. Acad. Sci*. **1162**, 18–38.

Hougardy, E. and Grégoire, J.C. 2000 Spruce stands provide natural food sources to adult hymenopteran parasitoids of bark beetles. *Entomol. Exp. Appl*. **96**, 253–263.

Hulme, P.E. 2009 Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol*. **46**, 10–18.

Jactel, H. and Brockerhoff, E.G. 2007 Tree diversity reduces herbivory by forest insects. *Ecol. Lett*. **10**, 835–848.

Jactel, H., Nicoll, B., Branco, M., Gonzalez-Olabarria, J.R., Grodzki, W., Langström, B. *et al*. 2009 The influences of forest stand management on biotic and abiotic risks of damage. *Ann. For. Sci*. **66**, 701.

Jactel, H., Petit, J., Desprez-Loustau, M.L., Delzon, S., Piou, D., Battisti, A. *et al*. 2012a Drought effects on damage by forest insects and pathogens: a meta-analysis. *Glob. Change Biol*. **18**, 267–276.

Jactel, H., Branco, M., Duncker, P., Gardiner, B., Grodzki, W., Långström, B. *et al*. 2012b A multi-criteria risk analysis to evaluate impacts of forest management alternatives on forest health in Europe. *Ecol. Soc.* **17**, 52.

Jimu, L., Kemler, M., Wingfield, M.J., Mwenje, E. and Roux, J. 2016 The *Eucalyptus* stem canker pathogen *Teratosphaeria zuluensis* detected in seed samples. *Forestry* **89**, 316–324.

Jönsson, A.M., Harding, S., Bärring, L. and Ravn, H.P. 2007 Impact of climate change on the population dynamics of Ips typographus in southern Sweden. *Agr. Forest Meteorol*. **146**, 70–81.

Kalinkat, G., Rall, B.C., Björkman, C. and Niemelä, P. 2015 Effects of climate change on the interactions between insect pests and their natural enemies. In *Climate Change and Insect Pests*. Bjorkman, C. and Niemela, P. (eds). CABI, p.74.

Klapwijk, M.J., Bylund, H., Schroeder, M. and Björkman, C. 2016 Forest management and natural biocontrol of insect pests. *Forestry* **89**, 253–262.

Kolb, T.E., Fettig, C.J., Bentz, B.J., Stewart, J.E., Weed, A.S., Hicke, J.A. *et al*. 2016 Forest insect and fungal pathogen responses to drought. In *Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis*. Vose, J.M., Clark, J.S., Luce, C.H. and Patel-Weynand, T. (eds). USDA Forest Service, Gen. Tech. Report WO-93b, pp. 113–128.

Kovacs, K.F., Haight, R.G., McCullough, D.G., Mercader, R.J., Siegert, N.W. and Liebhold, A.M. 2010 Cost of potential emerald ash borer damage in US communities, 2009–2019. *Ecol. Econ*. **69**, 569–578.

Lange, H., Økland, B. and Krokene, P. 2006 Thresholds in the life cycle of the spruce bark beetle under climate change. *InterJournal,* 1648.

Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A. and Lamberti, G. 2002 An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proc. R. Soc. Lond. B: Biol. Sci*. **269**, 2407–2413.

Leung, B., Springborn, M.R., Turner, J.A. and Brockerhoff, E.G. 2014 Pathway-level risk analysis: the net present value of an invasive species policy in the US. *Front. Ecol. Environ*. **12**, 273–279.

Liebhold, A.M., MacDonald, W.L., Bergdahl, D. and Mastro, V.C. 1995 Invasion by exotic forest pests: a threat to forest ecosystems. *For. Sci. Monogr*. **30**, 1–49.

Lockwood, J.L., Hoopes, M.F. and Marchetti, M.P. 2013 *Invasion Ecology*. Wiley.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. and Bazzaz, F.A. 2000 Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl*. **10**, 689–710.

Marchisio, C., Cescatti, A. and Battisti, A. 1994 Climate, soils and *Cephalcia arvensis* outbreaks on *Picea abies* in the Italian Alps. *For. Ecol. Manage*. **68**, 375–384.

Marini, L., Ayres, M.P., Battisti, A. and Faccoli, M. 2012 Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. *Clim. Change* **115**, 327–341.

McKee, F.R. and Aukema, B.H. 2015 Successful reproduction by the eastern larch beetle (Coleoptera: Curculionidae) in the absence of an overwintering period. *Can. Entomol*. **147**, 602–610.

Morin, R.S. and Liebhold, A.M. 2016 Invasive forest defoliator contributes to the impending downward trend of oak dominance in eastern North America. *Forestry* **89**, 284–289.

Nahrung, H.F., Ramsden, M. and Griffiths, M. 2016 Sirex woodwasp range expansion in Australia: performance and parasitism on two commercial pine species. *Forestry* **89**, 310–315.

Pimentel, D. 1995 Amounts of pesticides reaching target pests: environmental impacts and ethics. *J. Agric. Environ. Ethics* **8**, 17–29.

Poland, T.M. and McCullough, D.G. 2006 Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *J. For.* **104**, 118–124.

Roques, A., Rabitsch, W., Rasplus, J.Y., Lopez-Vaamonde, C., Nentwig, W. and Kenis, M. 2009 Alien terrestrial invertebrates of Europe. In *Handbook of Alien Species in Europe*. Springer, pp. 63–79.

Seidl, R., Schelhaas, M.J. and Lexer, M.J. 2011 Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Glob. Change Biol.* **17**, 2842–2852.

Sinclair, B.J., Vernon, P., Klok, C.J. and Chown, S.L. 2003 Insects at low temperatures: an ecological perspective. *Trends Ecol. Evol.* **18**, 257–262.

Slippers, B., Hurley, B.P. and Wingfield, M.J. 2015 *Sirex* woodwasp: a model for evolving management paradigms of invasive forest pests. *Annu. Rev. Entomol.* **60**, 601–619.

Sobek-Swant, S., Crosthwaite, J.C., Lyons, D.B. and Sinclair, B.J. 2012 Could phenotypic plasticity limit an invasive species? Incomplete reversibility of mid-winter deacclimation in emerald ash borer. *Biol. Invasions* **14**, 115–125.

Soliman, T., Mourits, M.C., Van Der Werf, W., Hengeveld, G.M., Robinet, C. and Lansink, A.G.O. 2012 Framework for modelling economic impacts of invasive species, applied to pine wood nematode in Europe. *PLoS One* **7**, e45505.

Speight, M.R. and Wainhouse, D. 1989 *Ecology and Management of Forest Insects*. Clarendon Press.

Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B. and Bigler, C. 2013 Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. *For. Ecol. Manage.* **305**, 273–281.

Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M. *et al.* 2015 Planetary boundaries: guiding human development on a changing planet. *Science* **347**, 1259855.

Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Klienjunas, J.T., Lewis, K.J. *et al.* 2011 Climate change and forest diseases. *Plant Pathol.* **60**, 133–149.

Thompson, I.D., Okabe, K., Tylianakis, J.M., Kumar, P., Brockerhoff, E.G., Schellhorn, N.A. *et al.* 2011 Forest biodiversity and the delivery of ecosystem goods and services: translating science into policy. *BioScience* **61**, 972–981.

Trumbore, S., Brando, P. and Hartmann, H. 2015 Forest health and global change. *Science* **349**, 814–818.

Villari, C., Tomlinson, J.A., Battisti, A., Boonham, N., Capretti, P. and Faccoli, M. 2013 Use of loop-mediated isothermal amplification for detection of *Ophiostoma clavatum*, the primary blue stain fungus associated with *Ips acuminatus*. *Appl. Environ. Microbiol.* **79**, 2527–2533.

Wainhouse, D. 2005 *Ecological methods in forest pest management*. Oxford University Press.

Weed, A.S., Ayres, M.P. and Hicke, J.A. 2013 Consequences of climate change for biotic disturbances in North American forests. *Ecol. Monogr.* **83**, 441–470.

Weed, A.S., Bentz, B.J., Ayres, M.P. and Holmes, T.P. 2015 Geographically variable response of *Dendroctonus ponderosae* to winter warming in the western United States. *Landsc. Ecol.* **30**, 1075–1093.

Wermelinger, B., Epper, C., Kenis, M., Ghosh, S. and Holdenrieder, O. 2011 Emergence patterns of univoltine and bivoltine *Ips typographus* (L.) populations and associated natural enemies. *J. Appl. Entomol.* doi:10.1111/j.1439-0418.2011.01629.x

Wingfield, M.J., Brockerhoff, E.G., Wingfield, B.D. and Slippers, B. 2015 Planted forest health: the need for a global strategy. *Science* **349**, 832–836.