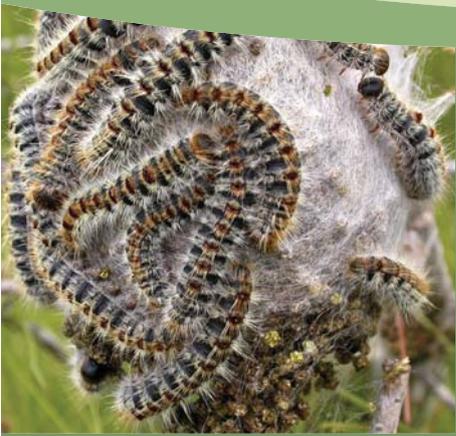




Climate change impacts on forest health



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Pine processionary larvae, *Thaumetopoea pityocampa* (Bugwood.org/J.H. Ghent/1241017)

Cankers and bleeding on coast live oak (*Quercus agrifolia*) resulting from *Phytophthora ramorum* infection (Bugwood.org/J. O'Brien/1427057)

Red foliage colour indicative of attack by the mountain pine beetle, *Dendroctonus ponderosae* (Bugwood.org/R.F. Billings/2108082)

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Climate change impacts on forest health

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Climate change impacts on forest health

1. INTRODUCTION

The world's climate is changing. Increased temperatures and levels of atmospheric carbon dioxide as well as changes in precipitation and in the frequency and severity of extreme climatic events are just some of the changes occurring. These changes are having notable impacts on the world's forests and the forest sector through longer growing seasons, shift of insect species ranges, and changed frequency of forest fires.

A deeper understanding of the complex relationships between a changing climate, forests and forest pests is vital to enable those in forest health protection and management to prepare for changes in the occurrence and impact of indigenous and exotic pests.

This paper is a review of the current state of knowledge on the effects of climate change on forest pests and their implications for forest health protection and management. Because of the relatively limited research that has been dedicated specifically to forest pests, information on non-forest pests is also included to enable a better understanding of the potential impacts of climate change on forest health.

2. CURRENT KNOWLEDGE AND FUTURE EXPECTATIONS

The world's climate is changing. While there are natural climate variations, the climate change we are most concerned about is in regards to the modifications to the greenhouse effect that human activities have caused. The Intergovernmental Panel on Climate Change (IPCC), in its Fourth Assessment Report, concluded with more certainty that global climate change is unequivocal and it is widely believed to result primarily from the effects of emissions of carbon dioxide (CO₂) and other greenhouse gases (GHGs) such as methane (CH₄) and nitrous oxide (N₂O), from human activities.

This conclusion was based on a number of observations about the Earth's climate including the following (IPCC, 2007).

- Global surface temperature has increased by an estimated 0.74 degrees Celsius (°C) over the past century. Over a 50 year period from 1956 to 2005 the warming trend was nearly twice that for the 100 years from 1906 to 2005. Eleven of the 12 years from 1995 to 2006 rank among the 12 hottest years on record (since 1850, when sufficient worldwide temperature measurements began). Increases are widespread globally and are greater at higher northern latitudes. Over the last 50 years, cold days and nights as well as frosts have become less frequent over most land areas, while hot days and nights and heat waves have become more frequent.
- Consistent with warming, the extent of snow and ice has decreased. Mountain glaciers and snow cover have also declined on average worldwide. The maximum area of seasonally frozen ground in the Northern Hemisphere has decreased by about 7 percent since 1900, with decreases in the spring of up to 15 percent. Satellite data since 1978 show that the extent of Arctic sea ice during the summer has shrunk by more than 20 percent.
- Since 1961, the world's oceans have been absorbing more than 80 percent of the heat added to the climate, causing ocean water to expand thereby contributing to rising sea levels. This expansion was the largest contributor to sea level rise between 1993 and 2003. Melting glaciers and losses from the Greenland and Antarctic ice sheets have also contributed to recent sea level rise. The incidence of extreme high sea level has increased at a number of sites globally since 1975.
- From 1900 to 2005, significant increases in precipitation have been observed in eastern parts of North and South America, northern Europe and northern and central Asia. The frequency of heavy precipitation events has also increased over most areas. In contrast, precipitation has declined in the Sahel, the Mediterranean, southern Africa and parts of southern Asia. Droughts have become longer and more intense worldwide and have affected larger areas since the 1970s, particularly in the tropics and subtropics.
- Evidence of an increase in intense tropical cyclone activity in the North Atlantic has been observed since about 1970 and there are suggestions of similar increased activity in some other regions.

Predictions for the future

The IPCC has made a number of predictions for future climate change (IPCC, 2007). A warming of about 0.2°C per decade is projected for the next two decades; temperature projections beyond this period depend on specific emissions scenarios. Even if the concentrations of all GHGs and aerosols were kept constant at year 2000 levels, a further warming of about 0.1°C per decade would be expected. The full range of projected temperature increase, based on six emission scenarios, is 1.1 to 6.4 °C by the end of the

century. The best estimate range of projected temperature increase, which extends from the midpoint of the lowest emission scenario to the midpoint of the highest, is 1.8 to 4.0 °C by the end of the century. It is very likely that continued GHG emissions at or above current rates would cause further warming and induce many changes in the global climate system during the 21st century that would be larger than those observed during the 20th century.

Geographically the predicted warming trends for the 21st century are believed to be similar to those observed over the past several decades whereby temperature increases are expected to be greatest over land and at most high northern latitudes, and least over the Southern Ocean (near Antarctica) and the northern North Atlantic. It is very likely that extreme heat, heat waves and heavy precipitation events will become more frequent. Increases in high latitude precipitation are very likely, while decreases are likely in most subtropical regions such as Egypt. It is also likely that future tropical cyclones (typhoons and hurricanes) will become more intense, with higher peak wind speeds and heavier precipitation associated with warmer tropical seas. Snow cover area is projected to contract, widespread increases in thaw depth are projected over most permafrost regions and sea ice is projected to shrink in both the Arctic and Antarctic. In some projections, Arctic late-summer sea ice disappears almost entirely by the latter part of the 21st century. Changes of this magnitude will lead to the disappearance of existing earth climates (particularly in South America, Africa, and Siberia) and the appearance of novel climates (particularly in the tropics), each covering from 10 to 40 percent of global land mass (Williams, Jackson and Kutzbach, 2007).

Climate change is impacting the world's ecosystems and it is expected that the magnitude of these impacts will increase along with temperatures over this century. Many species and ecosystems may not be able to adapt as the effects of global warming and associated disturbances, such as floods, drought, wildfire and insect outbreaks, are compounded by other stresses such as land use change, overexploitation of resources, pollution and fragmentation of natural systems. If the global average temperature increases more than 1.5 to 2.5 °C, it is believed likely that approximately 20 to 30 percent of plant and animal species assessed so far will be at an increased risk of extinction (IPCC, 2007). Major changes in ecosystem structure and function, species' ecological interactions and geographical ranges, with predominantly negative consequences for biodiversity and ecosystem goods and services are also projected (Lewis, 2006; IPCC, 2007).

3. IMPACTS ON FORESTS AND THE FOREST SECTOR

Climate change, in particular increased temperatures and levels of atmospheric carbon dioxide as well as changes in precipitation and in the frequency and severity of extreme climatic events, is having notable impact on the world's forests and the forest sector. A survey of the opinions of a group of internationally renowned scientific experts on forest ecosystems indicates that while some major expected impacts of climate change are unequivocal, there is less general expert agreement about many others (Morgan, Pitelka and Shevliakova, 2001).

Productivity and health

Forest productivity and species diversity typically increase with increasing temperature, precipitation and nutrient availability, although species may differ in terms of their tolerance (Das, 2004). As a key factor that regulates many terrestrial biogeochemical processes, such as soil respiration, litter decomposition, nitrogen mineralization and nitrification, denitrification, methane emission, fine root dynamics, plant productivity and nutrient uptake, temperature changes are likely to drastically alter forests and ecosystem dynamics in many ways (Norby *et al.*, 2007). The impacts of elevated temperatures on trees and plants will vary throughout the year since warming may relieve plant stress during colder periods but increase it during hotter periods (Garrett *et al.*, 2006).

In central Alaska, permafrost degradation is widespread and rapid leading to large ecosystem shifts from birch forests to fens and bogs (Jorgenson *et al.*, 2001). Permafrost degradation in response to warming has also been reported from Western Canada where forested bogs are becoming non-forested poor fens as a result of rising water levels (Vitt, Halsey and Zoltai, 2000). Alaska yellow-cedar (*Chamaecyparis nootkatensis*), normally an extremely hardy and resilient species, is dying on about 200 000 ha in Alaska and Canada, as early spring melt exposes their shallow roots to spring freezing injury and death (Hennon and Shaw, 1997; Hennon *et al.*, 2008).

Moisture availability in forests will be strongly influenced by changes in both temperature and precipitation. Warmer temperatures lead to increased water losses from evaporation and evapotranspiration and can also result in reduced water use efficiency of plants (Mortsch, 2006). Longer, warmer growing seasons can intensify these effects resulting in severe moisture stress and drought. Such conditions can lead to reductions in the growth and health of trees although the severity of the impacts depends on the forest characteristics, age-class structure and soil depth and type (Mortsch, 2006). Young plants such as seedlings and saplings are particularly susceptible whereas large trees with a more developed rooting system and greater stores of nutrients and carbohydrates tend to be less sensitive to drought, though they are affected by more severe conditions. Shallow-rooted trees and plants as well as species growing in shallow soils are more susceptible to water deficits. Deep-rooted trees can absorb water from greater depths and therefore are not as prone to water stress. Moisture stress and drought can also impact forest health by enhancing susceptibility to disturbances such as insect pests and pathogens and forest fires.

Quaking aspen (*Populus tremuloides*) in Western Canada have exhibited steep productivity declines and dieback after a particularly severe drought in 2001-2003, with effects continuing for years (Hogg, Brandt and Michaelian, 2008). Impacts on increment and dieback have been exacerbated by attacks of defoliating and wood-boring insects and pathogens (Hogg and Bernier, 2005; Hogg, Brandt and Michaelian, 2008). Steep growth declines and stand replacement of European beech (*Fagus sylvatica*) at the lower edge of its range has been

observed in Spain and other southern European countries in response to drought (Jump, Hunt and Peñuelas, 2006). In Italy, Spain and Portugal native oaks are declining due to warming, drought or *Phytophthora* species and in Spain, *Pinus uncinata*, *P. pinaster*, and *P. pinea* have been exhibiting decline and dieback (Resco de Dios, Fischer and Colinas, 2007).

Higher atmospheric CO₂ levels result in increased growth rates and water use efficiency of plants and trees, so long as other factors such as water and nutrients (e.g. nitrogen, phosphorus, sulphur, some micronutrients) do not become limiting. It has been suggested however that this positive effect declines with increasing concentrations (Stone, Bhatti and Lal, 2006). However current free air CO₂ enrichment facilities have observed multi-year growth increases of 23 percent with a 175 ppm enrichment above a 375 ppm ambient CO₂ concentration (Norby *et al.*, 2005). Elevated carbon dioxide levels can also result in changed plant structure such as increased leaf area and thickness, greater numbers of leaves, higher total leaf area per plant, and larger diameter stems and branches (Garrett *et al.*, 2006). It is important to note that plant responses to CO₂ enrichment may differ between species and local environmental conditions which are likely to result in substantial changes in the species composition and dynamics of terrestrial ecosystems (Vitousek *et al.*, 1997; Bauer *et al.*, 2006). Concurrent increases in concentrations of ground-level ozone (O₃) may lower tree productivity (Karnosky *et al.*, 2005) and enhance susceptibility to pathogens (Karnosky *et al.*, 2002), while N₂O may enhance growth in nitrogen-limited ecosystems such as boreal forests (Stone, Bhatti and Lal, 2006).

Distribution

Consistent responses of species and communities to climate change or ‘fingerprints’ are typically associated with changes in their distribution, particularly at their latitudinal or altitudinal extremes. The distribution of forest plants and trees is expected to shift northwards or to higher altitudes in response to climate warming (Parmesan, 2006; Menéndez, 2007).

In a recent study, Lenoir *et al.* (2008) compared the altitudinal distribution of 171 forest plant species between two periods 1905-1985 and 1986-2005 in Western Europe and concluded that climate warming has resulted in a significant upward shift in species optimum elevation (altitude of maximum probability of presence) averaging 29 m per decade. This study showed that climate change affects not just species’ ranges at their distributional margins but at the spatial core of the distributional range of plant species (Lenoir *et al.*, 2008). The quickest species noted to relocate were those with shorter life spans and faster reproduction cycles such as herbs, ferns and mosses; larger long-lived trees and shrubs did not show a significant shift and are thus under greater threat from the impacts of climate change because they can't adapt to local conditions quickly enough and relocate. Such distributional changes will no doubt result in forest ecosystems that are very different from what we see today. A similar study from 26 mountains in Switzerland reported that alpine flora have expanded toward the summits since the 1940s (Parmesan, 2006). Upward movements of tree lines have also been observed in Siberia, the Canadian Rocky Mountains, and New Zealand and northward shifts have been noted in Sweden and Eastern Canada (Parmesan, 2006). Cloud forests at high elevations in the tropics are also showing signs of shifting to higher altitudes, although not all components of these ecosystems seem to be keeping track (Jones *et al.*, 2008).

The timing of such shifts however will not be solely determined by temperature but will depend on a number of factors such as the rate at which seeds can disperse into new regions that are climatically suitable (i.e. with proper moisture conditions, soil characteristics and nutrient availability), possible human interventions to promote movement of species, and changes to disturbance regimes (Shugart, Sedjo and Sohngen, 2003; Monserud *et al.*, 2008).

Disturbance

Forests are subjected to a variety of disturbances that are themselves strongly influenced by climate. Disturbances such as fire, drought, landslides, species invasions, insect and disease outbreaks, and storms such as hurricanes, windstorms and ice storms influence the composition, structure and function of forests (Dale *et al.*, 2001). Climate change is expected to impact the susceptibility of forests to disturbances and also affect the frequency, intensity, duration, and timing of such disturbances. For example, increased fuel loads, longer fire seasons and the occurrence of more extreme fire weather conditions as a consequence of a changing climate are expected to result in increased forest fire activity (Mortsch, 2006). A changing climate will also alter the disturbance dynamics of native forest insect pests and pathogens, as well as facilitating the establishment and spread of non indigenous species.

Such changes in disturbance dynamics, in addition to the direct impacts of climate change on trees and forest ecosystems, can have devastating impacts particularly because of the complex relationships between climate, disturbance agents and forests. Any of these disturbances can increase forest susceptibility to other disturbances. For example, pine forests in Central America became infested with bark beetles, primarily *Dendroctonus frontalis* in association with other *Dendroctonus* and *Ips* species, after suffering damage from Hurricane Mitch in 1998. The beetle outbreaks caused further extensive tree mortality thereby increasing fuel loads in the region's forests which severely increased the risk of wildfires (further details in Chapter 5). Making predictions on the future impacts of a changing climate on forest disturbances is made more difficult by these interactions.

Forest sector

All of these impacts on trees and forests will inevitably have widespread impacts on the forest sector. Changes in the structure and functioning of natural ecosystems and planted forests (due to temperature changes and rainfall regimes) and extreme events and disasters (hurricanes, droughts, fires and pests) will have negative impacts on the productive function of forest ecosystems which in turn will affect local economies (FAO, 2005). Production patterns and trade in forestry commodities will be altered as species are grown more competitively in higher latitudes and altitudes. Conversely, markets may be saturated due to increased mortality of trees following pest infestations as has been experienced with the mountain pine beetle (*Dendroctonus ponderosae*) in Canada. Decreased forest ecosystem services, especially water cycle regulation, soil protection and conservation of biological diversity, as a result of climate change may imply increased social and environmental vulnerability.

While climate change is likely to increase timber production and lower market prices in general, the increases in production will certainly not be evenly distributed throughout the world; some areas will experience better conditions than others (Pérez-García *et al.*, 2002). For example, forests with low productivity due to drought will likely face further decreases in productivity, while areas where temperature limits productivity may benefit from rising temperatures.

4. IMPACTS ON FOREST PESTS

Changes in the patterns of disturbance by forest pests (insects, pathogens and other pests) are expected under a changing climate as a result of warmer temperatures, changes in precipitation, increased drought frequency and higher carbon dioxide concentrations. These changes will play a major role in shaping the world's forests and forest sector.

There is evidence in the fossil record that previous episodes of rapid global warming were accompanied by increased levels of insect herbivory (Curran *et al.*, 2008). This evidence, as well as observations from the birch forests of northern Europe (Kozlov, 2008; Wolf, Kozlov and Callaghan, 2008), confirm predictions that current herbivory trends will amplify (DeLucia *et al.*, 2008).

Insects and pathogens have been noted to respond to warming in all the expected ways, from changes in phenology and distribution to influencing community dynamics and composition (Menéndez, 2007). While some impacts of climate change may be beneficial in terms of protecting forest health (e.g. increase winter mortality of some insect pests due to thin snow cover; slower larval development and increased mortality during droughts), many impacts will be quite detrimental (e.g. accelerated insect development rate; range expansions of pests) (Ayres and Lombardero, 2000).

Climate change can affect forest pests and the damage they cause by: directly impacting their development, survival, reproduction, distribution and spread; altering host physiology and defences; and impacting the relationships between pests, their environment and other species such as natural enemies, competitors and mutualists.

4.1. Direct impacts

Climate, temperature and precipitation in particular, have a very strong influence on the development, reproduction and survival of insect pests and pathogens and as a result it is highly likely that these organisms will be affected by any changes in climate. Because they are cold-blooded organisms, forest insects and pathogens can respond rapidly to their climatic environment impacting directly on their development, survival, reproduction and spread. With their short generation times, high mobility and high reproductive rates it is also likely that they will respond more quickly to climate change than long-lived organisms, such as higher plants and mammals (Menéndez, 2007) and thereby may be the first predictors of climate change.

The impact of climate change on the frequency and intensity of insect outbreaks is less clear, mostly because there is insufficient long-term data for analysis. There is evidence that outbreaks of the larch bud moth (*Zeiraphera diniana*) in Switzerland have basically stopped over the past 30 years (Esper *et al.*, 2007) while conversely outbreaks of spruce budworm (*Choristoneura fumiferana*) in Eastern Canada seem to have increased in frequency and severity over the past 200 years, although it is not clear that climate change is involved (Simard, Morin and Lavoie, 2006).

Physiology

Climate influence on insects can be direct, as a mortality factor, or indirect, by influencing the rate of growth and development. Some information on the impacts of increased CO₂, and O₃, is becoming available but only for specific environments (e.g. Karnosky *et al.*, 2008) and only very partial information is available on changing UVB levels and altered precipitation regimes. For these reasons this report will focus on the impacts of temperature. Temperature

is considered to be the more important factor of climate change influencing the physiology of insect pests (Bale *et al.*, 2002). Precipitation however can be a very important factor in the epidemiology of many pathogens, such as *Mycosphaerella pini*, that depend on moisture for dispersal.

The magnitude of the impacts of temperature on forest pests will differ among species depending on their environment, life history, and ability to adapt. Flexible species that are polyphagous, occupy different habitat types across a range of latitudes and altitudes, and show high phenotypic and genotypic plasticity are less likely to be adversely affected by climate change than specialist species occupying narrow niches in extreme environments (Bale *et al.*, 2002; Thomas *et al.*, 2004).

Many specialist butterfly species are declining in abundance in the UK, especially woodland species, while many grassland and generalist species are increasing (Thomas, 2005). Three quarters of 46 British butterflies have declined due to habitat loss at the northern edge of their range; 89 percent of specialist species are in decline while 50 percent of mobile generalists (pests) are increasing (Warren *et al.*, 2001). Franco *et al.* (2006) concluded the importance of climate warming and habitat loss in driving local extinctions of northern species of butterflies in northern UK over the past few decades.

Increases in summer temperature will generally accelerate the rate of development in insects and increase their reproductive capacity while warmer winter temperatures may increase overwinter survival (Ayres and Lombardero, 2000; Logan, Régnière and Powell, 2003). Perhaps the best example of such impacts is the mountain pine beetle (*Dendroctonus ponderosae*) which has been at epidemic proportions in western Canada for several years. Successive years of mild winters have decreased the mortality of overwintering stages allowing for massive destruction of pines in the region, particularly lodgepole pine (*Pinus contorta*). Decreased snow depth associated with warmer winter temperatures may also decrease the winter survival of many forest insects that overwinter in the forest litter where they are protected by snow cover from potentially lethal low temperatures (Ayres and Lombardero, 2000).

The impact of a change in temperature will vary depending on the climatic zone. In temperate regions, increasing temperatures are expected to decrease winter survival while in more northern regions, higher temperatures will extend the summer season thereby increasing growth and reproduction (Bale *et al.*, 2002). Given the more severe environmental control, and greater predicted increases in temperature in boreal and Polar Regions, the impacts of temperature are expected to be greater on species from those regions than on species in temperate or tropical zones (Bale *et al.*, 2002). Menéndez *et al.* (2006) observed that insect species richness is increasing in the cool habitats of the Northern Hemisphere, although it is increasing slower than expected among British butterflies. Species found throughout Great Britain are decreasing most rapidly in the south, while species with a southerly distribution are increasing (Conrad *et al.*, 2004).

However, Deutsch *et al.* (2008) suggest that, in the absence of ameliorating factors such as migration and adaptation, the greatest extinction risks from global warming may be in the tropics. Warming in the tropics, though proportionately smaller in magnitude, could have the most deleterious impacts because tropical insects have very narrow ranges of climatic suitability compared to higher latitude species, and are already living very close to their optimal temperature (Deutsch *et al.*, 2008).

Andrew and Hughes (2005) observed no latitudinal gradient of hemipteran species richness on acacia in East Australia, but noted that as climate change proceeds, a shift of tropical

species towards higher latitudes should lead to increased diversity in temperate zones. In the tropical forests of northern Australia, climate change is increasing extinctions due to disappearing climates and habitats, as high-diversity tropical mountains are populated by small-range, specialized endemic species (Williams, Bolitho and Fox, 2003). In a study of the black-veined white butterfly (*Aporia crataegi*) in the Sierra de Guadarrama of central Spain, Merrill *et al.* (2008) suggest that thermal limitations rather than biotic interactions limit the distribution of the insects at their southern edge, and point out that host plant distribution may well compress the cold limit of specialist temperate species.

Some important forest insect pests have critical associations with symbiotic fungi but limited information is available on how temperature changes may affect these symbionts and thus indirectly affect host population dynamics. In some cases insect hosts and their symbionts may be similarly affected by climatic change while in other cases, hosts and symbionts may be affected asymmetrically, effectively decoupling the symbiosis (Six, 2007).

Distribution

Climate plays a major role in defining the distribution limits of insect species. With changes in climate, these limits are shifting as species expand into higher latitudes and altitudes and disappear from areas that have become climatically unsuitable (Parmesan, 2006; Menéndez, 2007). Such shifts are occurring in species whose distributions are limited by temperature such as many temperate and northern species.

It is now clear that poleward and upward shifts of species ranges have occurred across many taxonomic groups and in a large diversity of geographical locations during the 20th century. Parmesan and Yohe (2003) reported that more than 1 700 Northern Hemisphere species have exhibited significant range shifts averaging 6.1 km per decade towards the poles (or 6.1 m per decade upward).

The range expansions of many butterfly species have been particularly well documented. Parmesan *et al.* (1999) reported a poleward shift of 35 to 240 km for 22 out of 35 non-migratory European butterfly species during the last century. Wilson *et al.* (2005) noted that the lower elevational limits of 16 butterfly species in central Spain had risen on average by approximately 212 m in 30 years, a rise attributed to an observed 1.3 °C rise in mean annual temperature. Wilson *et al.* (2007) showed uphill shifts of approximately 293 m in butterfly communities in the Sierra de Guadarrama of central Spain between 1967-1973 and 2004-2005 as a result of climate warming. Climate change may also weaken the association between climatic and habitat suitability.

Forest pests are also occurring outside historic infestation ranges and at intensities not previously observed. Some examples of forest pest species that have responded or are predicted to respond to climate change by altering distribution include the following.

- A major epidemic of the mountain pine beetle (*Dendroctonus ponderosae*) has been spreading northwards and upwards in altitude in western Canada (British Columbia and more recently, Alberta) for several years.
- Warmer temperatures have influenced the southern pine beetle (*D. frontalis*) resulting in range expansions in the United States.
- Jepsen *et al.* (2008) give ample evidence of northward outbreak range expansions of two geometrids (winter moth, *Operophtera brumata*, and autumnal moth, *Epirrita autumnata*) in Scandinavia.

- The pine processionary caterpillar (*Thaumetopoea pityocampa*) has significantly expanded its latitudinal and altitudinal distribution in Europe.
- The oak processionary caterpillar (*T. processionea*) has shifted its distribution north in Europe during the latter half of the 20th century.
- The European rust pathogen *Melampsora allii-populina* is likely to spread northwards with increased summer temperatures.
- The root rot pathogen *Phytophthora cinnamomi* is predicted to spread into colder regions of Europe and have increased severity with climate change scenarios of increased average temperatures.

The ability of a species to respond to global warming and expand its range will depend on a number of life history characteristics, making the possible responses quite variable among species. Bale *et al.* (2002) suggested that fast-growing, non-diapausing insect species or those not dependent on low temperature to induce diapause, will respond to warming by expanding their distribution whereas slow-growing species that need low temperatures to induce diapause (i.e. boreal and mountain species in the northern hemisphere) will suffer range contractions. Range-restricted species, particularly polar and montane species, show more severe range contractions than other groups and are considered most at risk of extinction due to recent climate change (Parmesan, 2006). Range shifts may be limited by factors such as day length or the presence of competitors, predators or parasitoids (Walther *et al.*, 2002). For example, the range expansion of insects which are very host-specific (specialists) may be limited by the slower rate of spread of their host plant species (Harrington, Fleming and Woiwod, 2001).

Phenology

Phenology is the timing of seasonal activities of plants and animals such as flowering or breeding. Since it is in many cases temperature dependent, phenology can be expected to be influenced by climate change. It is one of the easiest impacts of climate change to monitor (Gordo and Sanz, 2006) and is by far the most documented in this regard for a wide range of organisms from plants to vertebrates (Root *et al.*, 2003). Common activities to monitor include earlier breeding or first singing of birds, earlier arrival of migrant birds, earlier appearance of butterflies, earlier choruses and spawning in amphibians and earlier shooting and flowering of plants (Walther *et al.*, 2002).

Evidence of phenological changes in numerous plant and animal species as a consequence of climate change is abundant and growing (Fitter and Fitter, 2002; Visser and Both, 2005; Menzel *et al.*, 2008). In general, spring activities have occurred progressively earlier since the 1960s (Walther *et al.*, 2002) and has been documented on all but one continent and in all major oceans for all well-studied marine, freshwater, and terrestrial groups (Parmesan, 2006).

Where insect life cycle events are temperature-dependent, they may be expected to occur earlier and increased temperatures are likely to facilitate extended periods of activity at both ends of the season, provided there are no other constraints present (Harrington, Fleming and Woiwod, 2001). With increased temperatures, it is expected that insects will pass through their larval stages faster and become adults earlier. Therefore expected responses in insects could include an advance in the timing of larval and adult emergence and an increase in the length of the flight period (Menéndez, 2007). Members of the order Lepidoptera again provide the best examples of such phenological changes. Changes in butterfly phenology have been reported from the UK where 26 of 35 species have advanced their first appearance (Roy and Sparks, 2000). Salama, Knowler and Adams (2007) reported an increase in

numbers and diversity of moths in traps of the Rothamstead survey and their altered phenology suggests that a change in climate is in part responsible. First appearance for 17 species in Spain has advanced by 1 to 7 weeks in just 15 years (Stefanescu *et al.*, 2003). Seventy percent of 23 butterfly species in California, USA have seen an advancement of first flight date of approximately eight days per decade (Forister and Shapiro, 2003).

Changes in phenology (early adult emergence and an early arrival of migratory species) have also been noted for aphids in the UK (Zhou *et al.*, 1995; Harrington *et al.*, 2007). Gordo and Sanz (2005) investigated climate impacts on four Mediterranean insect species (a butterfly, a bee, a fly and a beetle) and noted that all species exhibited changes in their first appearance date over the last 50 years which was correlated with increases in spring temperature.

Parmesan and Yohe (2003) estimated that more than half (59 percent) of 1598 species investigated exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years. They also estimated a mean advancement of spring events by 2.3 days/decade based on the quantitative analyses of phenological responses for these species. Root *et al.* (2003), in a similar quantitative study, estimated an advancement of 5.1 days per decade. Parmesan (2007) investigated the discrepancy between these two estimates and noted that once the differences between the studies in selection criteria for incorporating data was accounted for, the two studies supported each other, with an overall spring advancement of 2.3 to 2.8 days/decade found in the resulting analysis. However, in this last study, latitude explained only 4 percent of overall variation of phenological changes even though it is strongly associated with the importance of warming trends. This last observation may relate to the importance of the change in climate relative to the natural amplitude of the climate variability.

Population genetics

There is increasing evidence in the literature that insect species are changing their genetic makeup in response to climate change. Hill, Thomas and Blakeley (1999) presented evidence that two species of British butterflies (one northern, one southern) colonizing new areas during range expansion have longer wings and larger thoraces than long-established, resident populations. Similarly, Thomas *et al.* (2001) noted increased fractions of long-winged variants in butterflies at their expanding northern margin.

The physiological makeup of populations can also be altered. In species of butterflies with facultative (photoperiod induced) diapause, Burke *et al.* (2005) reported the conversion of a thermal gradient (elevation) into a gradual shift in the prevalence of discrete univoltine or bivoltine life strategies involving changes in critical photoperiod and development times, with corollary consequences on reproductive rates. There is evidence of changes in allele frequencies linked to developmental physiology and cold tolerance in some Lepidoptera as a result of climate change (Rank and Dahlhoff, 2002). However, Davies *et al.* (2006) point out that behavioural rather than evolutionary change can be involved in habitat preference shifts (e.g. thermoregulatory choices of oviposition sites). Calosi *et al.* (2008), in a study of four European diving beetles, found that thermal tolerance range is correlated with the latitudinal range of species.

However, evolutionary change is not ubiquitous and still needs considerable investigation. The current northern range expansion of the polyphagous butterfly *Polygonia c-album* in Great Britain has not been accompanied by physiological adaptation to new hosts or to temperature (Braschler and Hill, 2007). These authors found no evolutionary differences between central and peripheral populations

4.2. Indirect impacts of climate change on host trees

Changes in temperature, precipitation, atmospheric CO₂ concentrations and other climatic factors can alter tree physiology in ways that affect their resistance to herbivores and pathogens (Ayres and Lombardero, 2000).

Drought

Drought is one of the most important climate-related events through which rapid ecosystem changes can occur as it affects the very survival of existing tree populations. Long-term drought can result in reduced tree growth and health thereby increasing their susceptibility to insect pests and pathogens. A number of insect pests and pathogens are associated with stressed trees, such as *Agrilus* beetles and the common and widespread *Armillaria* species which have been linked to oak decline (Evans, 2008). Others are limited by host defences in healthy trees, such as the European spruce bark beetle (*Ips typographus*) (Evans, 2008).

Drought can also elicit changes in plant and tree physiology which will impact pest disturbance dynamics. Leaves may change colour or become thicker or waxier which could affect their palatability to insects (Harrington, Fleming and Woiwod, 2001). The concentration of a variety of secondary plant compounds tends to increase under drought stress which would also lead to changes in the attraction of plants to insect pests (Harrington, Fleming and Woiwod, 2001). Moderate drought however may actually increase production of defence compounds in plants and trees possibly providing increased protection against pests.

Sugar concentrations in foliage can increase under drought conditions making it more palatable to herbivores and therefore resulting in increased levels of damage (Harrington, Fleming and Woiwod, 2001). Increases in the sugar content in drought-stressed balsam fir for example have been known to stimulate the feeding of certain stages of spruce budworm (*Choristoneura fumiferana*) and accelerate their growth (Mortsch, 2006). Another advantage for forest pests is the increased temperature of drought-stressed trees, which can be 2 to 4 °C warmer, which can benefit the fecundity and survival of insects for example (Mortsch, 2006).

The impacts of such changes to host tree physiology and susceptibility provoke different responses from pest species. Rouault *et al.* (2006) investigated the impacts of drought and high temperatures on forest insects and noted that woodborers were positively influenced by the high temperatures which increased their development rates and the prolonged water stress that lowered host tree resistance while defoliators benefited from the increased nitrogen in plant tissues linked to moderate or intermittent water stress.

The piñon pine (*Pinus edulis*) forests of the western United States are an example of the complex interaction between drought resulting from climate change and the functions of forest ecosystems. Scale-insect herbivory on piñon pine changes the microclimate of soils through altered water catchment and shading; this microclimatic influence is as large as the climate change effects *per se*. Moth herbivory on the other hand, does not have this feedback effect in this ecosystem (Classen *et al.*, 2005). Trotter, Cobb and Whitham (2008) found that piñon pine under water stress altered the structure of the arthropod community. Under high stress, this community's abundance is reduced by a factor of 10 and the number of species is halved, while 73 percent of 33 of the most abundant herbivore species had higher numbers on stressed trees. Thus, drought stress in this ecosystem leads to reduced biodiversity and abundance, with a dominance of a few pest species.

The large natural spatial and temporal variability in forest processes makes it difficult to positively relate drought-related tree mortality to a greater incidence of insect pest or fungal pathogen damage. In a recent study on the impact of a large-scale, multi-annual drought on

the growth and mortality of aspen (*Populus tremuloides*) in Canada, Hogg, Brandt and Michaelian (2008) could not find a significant relationship between drought severity and either insect defoliation or wood borer infestations. Drought severity was, however strongly related to total growth loss and mortality, but the delay of mortality into the years following the drought suggested that secondary agents may have been involved in the process.

Elevated levels of atmospheric carbon dioxide

As discussed in Chapter 3, higher atmospheric CO₂ levels result in improved growth rates and water use efficiency of plants and trees. This increased productivity leads to lower nitrogen concentrations in trees and plants as carbon-nitrogen (C: N) ratios rise and thus reduces the nutritional value of vegetation to insects (Kopper and Lindroth, 2003; Mortsch, 2006). In response insects may increase their feeding (and consequently tree damage) in an attempt to compensate for the reduced quality and gain the necessary nitrogen (Ayles and Lombardero, 2000). In many cases the increased feeding does enable the insect to meet its nutritional needs but most often it does not and results in poor performance, reduced growth rates and increased mortality (Cannon, 1998; Harrington, Fleming and Woiwod, 2001). Such an effect, however, is not consistently observed (Holton, Lindroth and Nordheim, 2003), and increased growth due to enhanced CO₂ may in fact more than compensate for the defoliation in some cases (Kopper and Lindroth, 2003).

Elevated CO₂ levels can also result in changed plant structure such as increased leaf area and thickness, greater numbers of leaves, higher total leaf area per plant, and larger diameter stems and branches (Garrett *et al.*, 2006). An increase in defensive chemicals may also result under such conditions (van Asch and Visser, 2007). Either of these changes to host physiology would influence palatability to insects, though the impacts on pests differ by species. For example, under increased CO₂ levels the winter moth (*Operophtera brumata*) consumes more oak (*Quercus robur*) leaves due to a reduction in leaf toughness, while the gypsy moth (*Lymantria dispar*) exhibits normal pupation weight but requires a longer time to develop as a result of an increase in tannin concentrations (van Asch and Visser, 2007).

Nitrogen deposition

Anthropogenic emissions of nitrogenous air pollutants and their subsequent deposition are part of the larger phenomenon of global changes and can also have impacts on forest health. Increased nitrogen levels in the leaves of trees and plants can result in an immediate increase in the incidence of a number of pathogens (Burdon, Thrall and Ericson, 2006). For example, a Swedish study noted that infections caused by the common pathogen, *Valdensia heterodoxa*, on *Vaccinium myrtillus*, a dominant understorey plant in boreal coniferous forests, are boosted by increased nitrogen availability resulting in premature leaf-shedding (Strengbom *et al.*, 2002). This defoliation subsequently promoted a shift from *V. myrtillus* dominance to grass dominance thereby affecting community structure.

Extreme events

Besides drought, climate change may affect the frequency and intensity of other extreme climate-related events, with subsequent impacts on forest health. Direct damage to trees or alterations in the ecosystem may increase their susceptibility to pest outbreaks. Windstorms and lightning strikes can damage trees and allow entry of pathogens and secondary insect pests as well as causing mechanical breakdown in normal physiological function. With climate change also being associated with increased warm air mass movements towards high latitudes, the frequency and extent of long-distance windborne dispersal events are likely to

increase, as was observed in a recent influx of diamondback moths on Svalbard Island in Norway, 800 km north of the likely source population in the Russian Federation (Coulson *et al.*, 2002).

4.3. Indirect impacts on community ecology

Climate change is expected to alter the relationships between pests, their environment and other species, such as natural enemies, competitors and mutualists, leading to changes in the structure and composition of natural communities (Stireman *et al.*, 2005). The observed and predicted changes on species abundance and in phenological patterns and distributions of individual species are likely to alter species interactions within communities (Menéndez, 2007). These alterations are likely to modify the behaviour of populations (outbreak characteristics) in their current range (Coley, 1998). Since individual species will respond to climate change in different ways and at different temporal scales there is a good possibility that some highly evolved relationships will be impacted. Interactions that involve two or more trophic groups, such as plant-herbivore, plant-pollinator and host-parasitic interactions are likely to suffer the largest mismatch (Harrington, Woiwod and Sparks, 1999).

Gordo and Sanz (2005) and Forkner *et al.* (2008) point out the decoupling of insect and plant phenologies (due to their different responses to temperature changes) will tend to alter synchrony between insects and their resources and endanger species that are more host specific. In a review of phenological changes of interacting species, Visser and Both (2005) noted that insects have advanced their phenology faster (early eggs hatching and early migration return date) than their hosts (budburst and flowering). They have also advanced their period of peak abundance more than their predators (laying date and migration arrival of birds). For example, the disruption of synchrony between the winter moth (*Operophtera brumata*) hatching and bud burst of its host oak trees has in turn resulted in an asynchrony between the pest and one of its predators, the great tit (*Parus major*), which relies on the caterpillars to feed their young (Walther *et al.*, 2002; van Asch *et al.*, 2007). Such climate-induced phenological changes are clearly resulting in a great deal of asynchrony between interacting species which will ultimately influence community structure, composition and diversity.

Distributional changes and range shifts interfere with community relationships as expanding species will begin to interact with other species in new environments with which previous interaction may have been limited or non-existent (Menéndez, 2007). The altitudinal spread of the pine processionary caterpillar (*Thaumetopoea pityocampa*) in the Sierra Nevada mountains of southeastern Spain for example, has resulted in the pest encountering a new host tree, the endemic Scots pine (*Pinus sylvestris* var. *nevadensis*) (Menéndez, 2007). Increased attacks by *T. pityocampa* could have deleterious effects on this endemic mountain tree species.

Species capable of responding to climate change by increasing their range will also benefit from the lack of competitors and natural enemies in their new environment. Species expansions may not be promptly followed by that of its natural enemies, as in the case of the pine processionary moth, and in some cases, the synchronization between host and natural enemy or parasitoid may not be maintained under new temperature conditions, as is the case with the winter moth (Battisti, 2004).

Some pathogens may benefit from the improved survival and spread of their insect vectors. For example, the vectors of Dutch elm disease (*Ophiostoma novo-ulmi*), *Scolytus scolytus* and *S. multistriatus* may be more active during periods of elevated temperature which would ultimately result in increased spread of the fungus.

5. FOREST PEST SPECIES INFLUENCED BY CLIMATE CHANGE

Some examples of forest insect pests, diseases and other pests which have been impacted or are predicted to be impacted by climate change are presented below. Information on non-forest pests is also provided to enable a better understanding of the potential impacts of climate change on forest health.

5.1. Insects

Coleoptera

Agrilus pannonicus (Piller & Mitterpacher, 1783) (Buprestidae) – Oak jewel beetle

A number of buprestid beetles of the genus *Agrilus* have been linked to oak decline. Incidences of these species have increased worldwide (both in their countries of origin and by international movement) and their impacts are being linked to host tree stress potentially caused by climate change (Evans, 2008). For example, *Agrilus pannonicus* (= *A. biguttatus* (Fabricius)) has recently been associated with a European oak decline throughout its natural range and has increased in incidence in several countries including France, Germany, Hungary, Poland and the Netherlands, and the UK where it is believed to be contributing to oak decline (Gibbs and Grieg 1997; Ciesla, 2003). Infestations can result in extensive tree mortality which, combined with other factors involved in the decline, can drastically alter the species composition of oak forests.

Dendroctonus frontalis Zimmermann (Scolytidae) – Southern pine beetle

Dendroctonus frontalis is considered to be one of the most damaging species of bark beetles in Central America and southern areas of North America. It is a major pest of pines and has a wide distribution occurring from Pennsylvania in the United States south to Mexico and Central America. Populations can build rapidly to outbreak proportions and large numbers of trees are killed. Initial attacks are generally on weakened trees however *D. frontalis* is capable of killing otherwise healthy trees. This beetle kills trees by a combination of two factors: girdling during construction of egg galleries; and the introduction of blue stain fungi of the genus *Ophiostoma* (Billings *et al.*, 2004). Because of their short generation time, high dispersal abilities and broad distribution of suitable host trees, the southern pine beetle has the potential to respond quickly and dramatically to any changes in climate.

In October 1998, Hurricane Mitch hit Central America, causing floods and mudslides that ravaged local communities, forests and infrastructure. In the years that followed an unprecedented regionwide outbreak of pine bark beetles, mainly *D. frontalis* in association with other *Dendroctonus* and *Ips* species, destroyed over 100 000 ha of pine forest (Billings *et al.*, 2004). As most of the standing dead and felled trees were left on site, fuel loads were drastically increased thereby resulting in extensive wildfires. With climate change expected to increase the frequency and severity of extreme events such as hurricanes, the potential for future devastating impacts on forests from both the initial disturbance and its cascading effects (i.e. other disturbances such as pest outbreaks and fire) is quite high.

Warmer temperatures attributed to climate change have also influenced the southern pine beetle resulting in range expansions in the United States. Laboratory measurements and published records of mortality in wild populations indicate that a temperature of -16 °C or less result in almost 100 percent mortality of the pest, thereby limiting its distribution in its current northern range (Ungerer, Ayres and Lombardero, 1999; Ayres and Lombardero, 2000). It was predicted that an increase in temperature of 3 °C would enable outbreaks to

occur approximately 178 km farther north than in historical times (Ungerer, Ayres and Lombardero, 1999). Recent outbreaks of the southern pine beetle in northern and high-altitude ecosystems, where they were previously rare or absent, have been attributed to a warming trend of 3.3 °C in minimum winter air temperatures in the southeastern US from 1960 to 2004 (Tran *et al.*, 2007). This northern expansion is about as predicted by Ungerer, Ayres and Lombardero (1999).

The southern pine beetle has also possibly adapted ways to increase survival in cooler climates. Tran *et al.* (2007) showed, through field and laboratory studies of a northern population, that prepupae were more cold tolerant (by more than 3 °C) than pupae, adults and feeding larvae, and that the winter life stage structure was strongly biased toward this most cold-tolerant life stage. This tendency to overwinter in a cold tolerant life stage could be a coincidence however rather than a true adaptation (Tran *et al.*, 2007).

***Dendroctonus ponderosae* (Hopkins) (Scolytidae) – Mountain pine beetle**

The mountain pine beetle (*Dendroctonus ponderosae*) is the most destructive pest of mature pines in North America, particularly lodgepole pine (*Pinus contorta*). In the western United States, outbreaks have been increasing in area after several years of drought (Tkacz, Moody and Villa Castillo, 2007). A major epidemic of this pest has also been ongoing in western Canada (British Columbia (BC), and more recently, Alberta) for several years and even with large-scale efforts to mitigate the impacts of the pest, millions of trees have been killed. A record of over 10 million hectares of pines were recorded as infested during 2007 aerial overview surveys in BC, with 860 973 ha of this located in provincial parks and protected areas (Westfall and Ebata, 2008). It has been predicted that if the beetle continues to spread at its current rate as much as 80 per cent of mature pine in BC will be dead by 2013 (CFS, 2007). The large numbers of dead and dying trees have also increased the risk of wildfires. The mountain pine beetle outbreak has transformed Canada's western forests from a weak net carbon sink to a very strong net source of atmospheric carbon (Kurz *et al.*, 2008).

The problem has been exacerbated by successive years of mild winters, resulting in decreases of mortality of overwintering stages. Their life cycle is generally completed in one year; warmer temperatures can result in two generations per year while cooler ones may result in one generation every two years (Amman, McGregor and Dolph, 1990). Drought conditions associated with warmer temperatures have also weakened the trees and increased their susceptibility to the beetles. Warmer temperatures have thus opened up previously climatically unsuitable mature pine stands to the pest (Carroll *et al.*, 2004). A recent analysis concluded that winters in central Canada will remain sufficiently cold in the foreseeable future to greatly reduce the risk of invasion of the mountain pine beetle in the eastern boreal forest of North America (Nealis and Peter, 2008).

***Dendroctonus rufipennis* (Kirby) (Curculionidae) – Spruce beetle**

Dendroctonus rufipennis is a North American pest of spruce, particularly white spruce (*Picea glauca*) and black spruce (*P. mariana*) in the north, Engelmann spruce (*P. engelmannii*) and sitka spruce (*P. sitchensis*) in the west, and red spruce (*P. rubens*) in the east (EPPO/CABI, 1997). It tends to attack weakened or windthrown trees and outbreaks are mostly linked to predisposing factors. As a result it can be expected that the impacts of climate change on trees and forests could enhance spruce beetle outbreaks.

In fact, Hebertson and Jenkins (2008) investigated the impact of climate on spruce beetle outbreaks in Utah and Colorado, USA between 1905 and 1996 and found that historic

outbreak years in the intermountain region were related to generally warm fall and winter temperatures and drought conditions. Similarly outbreaks in both Canada (Yukon Territory) and the US (Alaska) appear to be related to extremely high summer temperatures which influenced spruce beetle population size through a combination of increased overwinter survival, a halving of the maturation time from two years to one year, and regional drought-induced stress of mature host trees (Berg *et al.*, 2006).

Hemiptera

Aphids (Aphididae)

With short generation times and low developmental threshold temperatures, aphids can be expected to be strongly influenced by environmental and climatic changes. In general, it has been predicted that aphids will appear at least eight days earlier in the spring within 50 years, though the rate of advance will vary depending on location and species (Harrington *et al.*, 2007). This could potentially result in greater damage to host plants depending on the phenology of host plants and natural enemies.

Zhou *et al.* (1995), for example, investigated the timing of migration in Great Britain for five aphid species (*Brachycaudus helichrysi*, *Elatobium abietinum*, *Metopolophium dirhodum*, *Myzus persicae*, *Sitobion avenae*) over a period of almost 30 years and concluded that temperature, especially winter temperature, is the dominant factor affecting aphid phenology for all species. They found that a one degree Celsius increase in average winter temperature advanced the migration phenology by 4 to 19 days depending on species.

***Elatobium abietinum* (Walker) (Aphididae) – Green spruce aphid**

The green spruce aphid (*Elatobium abietinum*) is also believed likely to benefit from the increase in winter survival, leading to more intense and frequent defoliation of host spruce trees (*Picea* spp.). This aphid is native to Europe but has also been reported in both North and South America.

Infestations in the UK have resulted in large losses of spruce foliage and height both during the active infestation and in subsequent years. Westgarth-Smith *et al.* (2007) showed that warm weather associated with a positive North Atlantic Oscillation (NAO) index caused spring migration of *E. abietinum* to start earlier, last longer and contain more aphids. Positive NAO values correspond to warmer atmospheric conditions over the UK. Since global warming is believed to increase NAO variability, shifting the system to more positive values, this will most likely lead to further increases in aphid activity and more damage to spruce trees and forests in the area.

Hymenoptera

***Cephalcia arvensis* Panzer, 1805 (Pamphiliidae) – Spruce web-spinning sawfly**

The spruce web-spinning sawfly is monophagous on spruce (*Picea*) and endemic to the spruce range in Eurasia, where outbreaks have been seldom recorded. From 1985 to 1992 however there was a sudden outbreak of the sawfly in the Southern Alps during which populations developed an annual life cycle and grew exponentially, causing repeated defoliations resulting in extensive tree death (Marchisio, Cescatti and Battisti, 1994; Battisti, 2004). *Cephalcia* species generally show low fecundity and have an extended diapause of a few years that is stimulated by low temperatures at pupation time (Battisti, 2004). The outbreak

corresponded to a period of high temperatures and low precipitation and severe water stress for the host trees. As a result, the insect was able to adapt to the new climate resulting in lower mortality, faster development and higher feeding rates. In addition, the sudden increase in population density was not quickly followed by that of natural enemies, thereby facilitating unlimited population growth (Battisti, 2004).

***Neodiprion sertifer* (Geoffroy) (Diprionidae) – European pine sawfly**

The European pine sawfly *Neodiprion sertifer* is an important pest species on pines in Europe, northern Asia, Japan and North America where it was introduced. It is one of the most serious defoliators of Scots pine (*Pinus sylvestris*) forests in northern Europe. Virtanen *et al.* (1996) suggested that outbreaks of the sawfly on Scots pine in eastern and northern Finland are prevented by low winter temperatures which kill eggs, and predicted that outbreaks would become more common with winter warming. A high variation in freezing avoidance of eggs was also noted which would allow *N. sertifer* to adapt to predicted climate change and spread its distribution northwards (Veteli *et al.*, 2005).

Lepidoptera

Warmer temperatures have been linked to increasing populations of forest lepidopterans. A limiting factor, particularly for defoliators, is synchrony with bud burst in the spring while the key drivers are late winter temperatures for insect emergence and bud burst.

Butterflies

While only a few species of butterflies are considered to be serious forest pests, some of the best, and most researched, examples of the impacts of climate change on insect distributions and phenology have been butterflies. The geographic ranges of many species have shifted northward and upwards in elevation associated with climate warming, leading to increases in species richness at high latitudes and elevations and in some cases possible local extinction at lower altitudes.

Range expansions in butterflies have been well documented (see section 4.1) and changes in butterfly phenology have also been reported. In the UK, species have been advancing their flight periods by approximately 2 to 10 days for every 1 °C increase in temperature (Roy and Sparks, 2000; Menéndez, 2007). Similar changes in phenology as a response to warming has been noted in Spain where butterflies have advanced their first appearance by 1 to 7 weeks in 15 years (Stefanescu *et al.*, 2003) and in California, USA which has seen an advancement of approximately eight days per decade (Forister and Shapiro 2003).

Some species-specific examples of the influence of climate change include the following.

- The African Monarch butterfly (*Danaus chrysippus*) has spread northward, establishing its first population in southern Spain in 1980 followed by the establishment of multiple populations along the east coast of Spain (Menéndez, 2007).
- Warmer temperatures have increased survival and facilitated a latitudinal and altitudinal range expansion of the Sachem butterfly (*Atalopedes campestris*) in the western USA (Crozier, 2003, 2004).
- Edith's checkerspot butterfly (*Euphydryas editha*) has shifted its distribution northwards and also upwards in altitude in North America (Parmesan, 1996). Populations at the northern edge of the species range in Canada and also at higher altitudes within the main range have

experienced increased survival whereas populations at the southern edge in Mexico have declined.

- In Europe the speckled wood butterfly (*Parage aegeriae*) has increased its range northward beyond its original, primary host (Logan, Régnière and Powell, 2003).
- The black-veined white butterfly (*Aporia crataegi*) has expanded its altitudinal range in the mountains of the Sierra de Guadarrama of central Spain resulting in local population extinctions at lower warmer altitudes (Merrill *et al.*, 2008). While climate is becoming less of a limiting factor in its distribution at higher altitudes, it is however limited by the absence of host plants.

***Choristoneura fumiferana* (Clem.) (Tortricidae) – Spruce budworm**

The spruce budworm, *Choristoneura fumiferana*, is a major defoliator of coniferous forests across North America. Balsam fir (*Abies balsamea*) is the preferred host but they readily attack white, red and black spruce (*Picea glauca*, *P. rubens*, *P. mariana* respectively) and may even be feed on tamarack (*Larix* spp.) and hemlock (*Tsuga* spp.). Outbreaks of this budworm can persist for 5 to 15 years with periods of 20 to 60 years in between (Fleming and Volney, 1995). In eastern Canada the period of population cycle has averaged 35 years over the last 270 years (Volney and Fleming, 2007). During uncontrolled outbreaks they can kill almost all trees in dense, mature stands of fir (Fleming and Volney, 1995).

Climatic influences on life history traits are considered a major factor in restricting outbreaks and as a result, a changing climate is expected to impact the severity, frequency, and spatial distribution of spruce budworm outbreaks (Logan, Régnière and Powell, 2003). The success of the insects in establishing feeding sites in the spring depends on initial egg weights and synchrony of their development with that of buds of their hosts which is strongly influenced by climatic factors (Volney and Fleming, 2000, 2007). This synchronization is critical in initiating outbreaks and thus determining the intensity of damage. However the spruce budworm is able to tolerate some asynchrony between spring emergence and vegetative shoot development as the second instars have adapted morphologically and behaviourally allowing them to mine needles (Volney and Fleming, 2007).

In parts of its range, particularly at northern extremes, temperature can also influence the duration of outbreaks as collapses are often associated with the loss of suitable foliage often as a result of late spring frosts (Volney and Fleming, 2007). Normal collapse of the outbreak in the core range of host trees is associated with mortality caused by natural enemies late in the larval stage (Volney and Fleming, 2000). Natural enemies of the spruce budworm, *C. fumiferana*, are less effective at higher temperatures (Hance *et al.*, 2007) and therefore climatic factors have the potential to enable massive outbreaks of this pest providing there is suitable availability of host trees. Climate change is expected to increase the extent, severity and duration of spruce budworm outbreaks in Eastern Canada (Gray, 2008).

***Epirrita autumnata* (Borkhausen, 1794) (Geometridae) – Autumnal moth**

Epirrita autumnata is a holarctic species that has been expanding its outbreak range in some areas. In the Nordic countries of Europe, *Epirrita autumnata* outbreak cycles are typically most prevalent in northernmost and continental birch forests but during the past 15 to 20 years it has expanded into the coldest, most continental areas previously protected by extreme winter temperatures (Jepsen *et al.*, 2008). This pest overwinters in the egg stage and therefore the level of egg survival is dictated by minimum winter temperatures. Virtanen, Neuvonen and Nikula (1998) investigated the relationship between *E. autumnata* egg survival and

minimum winter temperatures in northernmost Finland. They predicted that climate warming would result in a two-third reduction of the area of forests with winter temperatures cold enough to keep *E. autumnata* populations low by the middle of the next century. A rise in winter temperatures therefore will likely increase the area of forest susceptible to damage by the autumnal moth.

***Lymantria dispar* Linnaeus, 1758 (Lymantriidae) – Gypsy moth**

The gypsy moth, *Lymantria dispar*, is a significant defoliator of a wide range of broadleaf and even conifer trees. While low population levels can exist for many years without causing significant damage, severe outbreaks can occur resulting in severe defoliation, growth loss, dieback and sometimes tree mortality. Two strains of gypsy moth exist – the Asian strain, of which the female is capable of flight; and the European strain, of which the female is flightless. The Asian strain is native to southern Europe, northern Africa, central and southern Asia, and Japan and has been introduced into Germany and other European countries where it readily hybridizes with the European strain. It has also been introduced but has not established in Canada, the US and the UK (London). The European strain is found in temperate forests throughout Western Europe and has been introduced into Canada and the US. The gypsy moth is considered a significant pest in both its native and introduced ranges.

There has also been a noted increase in outbreaks in areas previously unaffected by this pest such as the Channel Islands (Jersey) and new areas in the UK (Aylesbury, Buckinghamshire). In Canada the spread of the gypsy moth has so far been prevented by climatic barriers and host plant availability as well as by aggressive eradication of incipient populations (Logan *et al.*, 2007; Régnière, Nealis and Porter, 2008). However it is predicted that the gypsy moth will be able to extend its range in North America as a result of higher overwinter survival of egg stages because of milder winters and higher accumulation of day degrees for larval development (Evans, 2008; Régnière, Nealis and Porter, 2008). Similar predictions have been made for Europe (Vanhanen *et al.*, 2007). Pitt, Régnière and Worner (2007) noted an increase in the probability of establishment of the gypsy moth in New Zealand, particularly in the South Island.

Increasing atmospheric concentrations of CO₂ may also influence the severity of gypsy moth outbreaks. Larval performance on host plants grown under elevated CO₂ varies depending on the species, being reduced on some hosts such as aspen and increased on others, such as oak (Cannon, 1998).

***Lymantria monacha* (Linnaeus, 1758) (Lymantriidae) – Nun moth**

Lymantria monacha is a major pest of broadleaved and coniferous trees in Europe and Asia. Defoliation by nun moth larvae can kill host trees especially conifers and has caused extensive losses despite intervention with biological and chemical insecticides. In parts of Europe, the occurrence of outbreaks has increased possibly as a result of the establishment of extensive pine plantations in poor quality areas or as a result of a changing climate. It has been predicted that nun moth will spread northwards in Europe because of higher accumulated day degrees and improved overwinter survival (Evans, 2008). Using modelling software, Vanhanen *et al.* (2007) predicted that climate warming would shift the northern boundary of distribution north by approximately 500 to 700 km and the southern edge of the range would retract northwards by 100 to 900 km.

***Operophtera brumata* Linnaeus, 1758 (Geometridae) – Winter moth**

Operophtera brumata is distributed throughout Europe, North Africa, Japan and Siberia and has also been introduced into Canada and the US. It feeds on a variety of deciduous trees and shrubs including apricot, cherry, apple, plum, blueberry, crabapple, sweet chestnut, red currant and black currant, oaks, maples, basswood and white elm.

Climate change is impacting the spread of the winter moth. In the Nordic countries of Europe, Jepsen *et al.* (2008) noted that *O. brumata* had been climatically restricted to more southern and near-coastal locations in the regions but warmer temperatures has resulted in expansions in its outbreak area further northeast. While increased temperatures appear to assist the winter moth expand its distribution, it appears that they do not have the same impact on its natural enemies which may allow populations of this pest to grow unchecked (Battisti, 2004).

Climate change has affected the phenology of many species in different ways. In the Netherlands over the past 25 years, early spring temperatures have increased while winter temperatures have not. As a result a climate change induced asynchrony has occurred between winter moths and their host, pedunculate oak, *Quercus robur*, with eggs hatching before bud burst (van Asch and Visser, 2007). Such a situation leaves no food for the larvae resulting in starvation and death. This also has implications for other species that depend on the larvae for food such as the great tit (*Parus major*) which feed *O. brumata* caterpillars to their young (Walther *et al.*, 2002; van Asch *et al.*, 2007). While both egg hatch and bud burst have advanced over the last 25 years, egg hatch has advanced much more leading to a decrease in synchrony from a few days to almost 2 weeks (van Asch and Visser, 2007; van Asch *et al.*, 2007). However others have noted that, while warmer temperatures have lead to earlier egg hatch, the autumnal pupal diapause of the winter moth is prolonged at higher temperatures thereby counteracting the impact and resulting in a life cycle that is not shortened overall (Buse and Good, 1996; Bale *et al.*, 2002; Battisti, 2004). Differences between observations of synchronicity between moth egg hatch and host bud burst may result from regional, intra-specific differences.

***Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775) (Thaumetopoeidae) – Pine processionary caterpillar**

The pine processionary caterpillar, *Thaumetopoea pityocampa*, is considered one of the most important pests of pine forests in the Mediterranean region (EPPO/CABI, 1997). It is a tent-making oligophagous caterpillar that feeds gregariously and defoliates various species of pine and cedar. The life cycle of the pine processionary caterpillar is typically annual but may extend over two years at high altitudes or in northern latitudes (EPPO/CABI, 1997). At northern latitudes and at higher altitudes, adults emerge earlier.

Climate change is having clear impacts on the distribution of this important forest pest. Battisti *et al.* (2005) reported a latitudinal expansion in north-central France of 87 km northwards from 1972-2004 and an altitudinal shift of 110 to 230 m upwards in the Alps of northern Italy from 1975-2004 and attributed the expansions to reduced frequency of late frosts, which increases survival of overwintering larvae, as a result of a warming trend over the past three decades. In the last ten years the pine processionary caterpillar has spread almost 56 km northward in France (Battisti *et al.*, 2005).

During the summer of 2003, the warmest summer in Europe in the last 500 years, *T. pityocampa* exhibited an unprecedented expansion to high elevation pine stands in the Italian Alps, increasing its altitudinal range limit by one third of the total altitudinal expansion over the previous three decades (Battisti *et al.*, 2006). This unusual and fast spread has been

attributed to increased nocturnal dispersal of females during the unusually warm night temperatures. The gradual warming of the region has allowed the pest to maintain its presence at this altitude because of increased larval survival.

In the Sierra Nevada mountains of southeastern Spain, *T. pityocampa* has expanded to higher elevations over the last 20 years as a result of increasing mean temperature (Menéndez, 2007). Relict populations of Scots pine (*Pinus sylvestris* var. *nevadensis*) occurring within this newly expanded range of the caterpillar are being increasingly attacked, particularly in warmer years (Hódar and Zamora, 2004). This range expansion caused by climate change has potentially devastating consequences for this endemic mountain species which is likely to suffer from the direct effects of climate change as well.

Given that the present distribution of the *T. pityocampa* is not constrained by the distribution of its hosts, that warmer winters will increase winter larval feeding activity, that the probability of lower lethal temperature will decrease, it can be expected that the improved survival and spread into previously hostile environments will continue (Battisti, 2004; Battisti *et al.*, 2005).

***Thaumetopoea processionea* (Linnaeus, 1758) (Thaumetopoeidae) – Oak processionary caterpillar**

Native to central and southern Europe, *Thaumetopoea processionea* is a major defoliating pest of oak. Since the late 20th century it has been expanding its range northwards and is now firmly established in Belgium, Denmark, northern France, and the Netherlands and has been reported from southern Sweden and the UK. It is believed that the northward progression of the oak processionary moth is due to improved synchrony of egg hatch and reduction of late frosts as a result of warmer temperatures (Evans, 2008).

***Zeiraphera diniana* Guenée (Tortricidae) – Larch bud moth**

The larch bud moth, *Zeiraphera diniana*, is a European pest that has been defoliating large areas of larch forests in the Alps every 8 to 10 years for centuries (Battisti, 2004). It has an annual life cycle, overwintering as an egg on the larch branches and feeding on the needles as soon as the bud breaks. As such synchrony between egg hatch and bud burst is critical. Increased temperatures associated with climate change have affected this relationship leading to asynchrony and reduced incidences of the moth in Switzerland (Evans, 2008). It has been reported that abnormally high temperatures result in unusually high egg mortality (Battisti, 2004).

5.2. Pathogens

Ascomycota

***Mycosphaerella pini* Rostrup (1957) (Capnodiales: Mycosphaerellaceae) – Red band needle blight**

Mycosphaerella pini is a fungus that infects and kills the needles of *Pinus* spp. resulting in significant defoliation, stunted growth and eventually death of host trees although susceptibility among pine species does vary. Native to temperate forests of the northern hemisphere, it is a major pest of pine plantations in the Southern Hemisphere, where both the host and the pathogen have been introduced. The widely planted *P. radiata* is particularly susceptible and many forests planted with this species in the Southern Hemisphere,

particularly in East Africa, New Zealand and Chile, have been devastated by this needle blight. This pathogen has forced managers in some areas to abandon the planting of *P. radiata* and depend more on other tree species.

In its native range *M. pini* normally causes little damage, but since the late 1990s it has been causing extensive defoliation and mortality in young plantations of lodgepole pine (*Pinus contorta* var. *latifolia*) in northwestern British Columbia, Canada (Woods, Coates and Hamann, 2005). Mortality of mature lodgepole pines has been observed in mixed-species stands, where scattered pine represents only a small proportion of stand composition; this represents a globally unprecedented occurrence for *M. pini* (Woods, Coates and Hamann, 2005). The current epidemic coincides with a prolonged period of increased frequency of warm rain events throughout the mid- to late-1990s allowing for the rapid spread and increased rates of infection. Unlike many other pests, changes in precipitation patterns may be more important than changes in temperature for predicting the spread and impact of *M. pini*.

Basidiomycota

***Armillaria* species (Agaricales: Marasmiaceae)**

Armillaria species are common worldwide pathogens of trees, woody shrubs and herbaceous plants that can cause wood decay, growth reduction and even mortality, particularly in trees stressed by other factors, or in young trees planted on sites from which infected hosts have been removed. *Armillaria* species can become more aggressive and damaging when elevated temperatures cause drought stress thereby reducing tree defences (Evans, 2008). Tree physiological condition in general may be an important factor in controlling the impacts of *Armillaria* species, and climate change may affect their epidemiology (Menéndez, 2007).

Oomycota

***Phytophthora cinnamomi* (Rands 1922) (Pythiales: Pythiaceae)**

Phytophthora cinnamomi is considered one of the most widely distributed and destructive forest pathogens. It has a wide host range infesting over 1 000 species resulting in root rot and cankering. The native range is unknown but it is believed to be from Southeast Asia and southern Africa (EPPO/CABI, 1997). Currently the pathogen can be found in most temperate and subtropical areas in the world in Africa, Asia and the Pacific, Europe, Latin America and the Caribbean, Near East, and North America. In most countries it is only known in nurseries but in Europe (France, Italy, Spain, Portugal) it has been observed in natural environments (EPPO/CABI, 1997).

Temperature, moisture and pH all influence the growth and reproduction of the fungus. In a study on the impacts of climate warming on *P. cinnamomi*, Bergot *et al.* (2004) predicted a potential range expansion of the disease in Europe of one to a few hundred kilometres eastward from the Atlantic coast within one century.

***Phytophthora ramorum* Werres, de Cock & Man in't Veld (Pythiales: Pythiaceae) – Sudden oak death**

Phytophthora ramorum causes a very serious disease called sudden oak death which causes extensive mortality of tanoak and oaks. It is also associated with disease on ornamental plants and other broadleaf and conifer trees. This pathogen is a significant problem in both North

American and European forests and nurseries. The geographic origin of *P. ramorum* is unknown; it is believed that it has been introduced independently to Europe and North America from an unidentified third country.

The pathogen likely disperses through a variety of means. Sporangia may be dispersed locally by rain splash, wind-driven rain, irrigation or ground water, soil and soil litter (Kliejunas, 2005; DEFRA, 2005). Bark and ambrosia beetles are commonly found on infected trees but their potential role of vectors has not yet been investigated (EPPO, 2008). Consequently, changes in climate, precipitation and temperature in particular, will likely produce more optimal conditions for the pathogen resulting in an increase in disease occurrence.

5.3. Other pests

Nematodes

In general there is a close correlation between soil temperatures and the distributions of some plant-parasitic species of nematode. For example, *Meloidogyne incognita*, previously deemed limited to the Mediterranean area, was recently found in the Netherlands (Cannon, 2008). It is also believed that a one degree Celsius rise in temperature would allow *Longidorus caespiticola* to become established further north in Great Britain (Cannon, 2008). It is considered that there may also be climatic influences on the establishment of the pine wilt nematode (*Bursaphelenchus xylophilus*) and its vector, a host complex of serious international concern, mentioned in more detail below.

***Bursaphelenchus xylophilus* (Steiner & Buhner) Nickle (Tylenchida: Aphelenchoididae) – Pine wilt nematode**

The pine wilt nematode, *Bursaphelenchus xylophilus*, is the causal agent of pine wilt disease and is vectored by *Monochamus* beetles. Native to North America where it is not considered a serious pest, the nematode is a major threat to Asian and European pine forests and has resulted in extensive tree mortality in countries where it has been introduced.

Changes in both temperature and precipitation are likely to impact the spread of the nematode and the severity of damage caused by the disease. Pine wilt disease is most prevalent in warm climates as the nematode completes its life cycle in 12, 6 and 3 days at 15, 20 and 30 °C, respectively (Diekmann *et al.*, 2002). High temperatures and low precipitation in summer cause accelerated damage through their impacts on vector activity, propagation of the nematode and water stress on trees (Kiritani and Moromoto, 2004). In Japan, while annual tree losses to the disease have gradually decreased, infestations have spread into northern areas and into forests at higher elevations as a result of increased temperatures (Kiritani and Moromoto, 2004). Recent introductions into Portugal, where the nematode and vector *M. galloprovincialis* now co-exist, have resulted in severe losses to *Pinus pinaster* and other susceptible pines are now at risk in areas above 20 °C. European forestry and trade are threatened if it spreads into the rest of Europe.

6. SUMMARY AND CONCLUSIONS

The evidence presented from this desk review shows that climate change is having considerable and widespread impacts on forest health worldwide, and, as a result, on the forest sector. Clearly, if such climatic and ecological changes are now being detected when the globe has warmed by an estimated average of only 0.74 °C, it can be expected that many more impacts on species and ecosystems will occur in response to changes in temperature to levels predicted by IPCC. Conversely there are some indications that the interrelated effects of climate on tree hosts and the direct influence on natural enemies may make the overall effect difficult to predict and it is considered by some that not all climate change scenarios will be detrimental.

The challenge to understanding climate change impacts is not just in obtaining information on the impacts of temperature, precipitation and other climatic factors on forests and pests but also acquiring knowledge on the interaction between the different climate change factors, and how climate change impacts disturbances and vice versa.

While a fair amount of information is already available concerning the impacts of climate change on the world's species and ecosystems, from the perspective of forests, considerably more information is needed on the impacts on forests, forest pests and the complex relationships relating to climate change. Much of the information available comes from Europe and North America so there is a clear need for increased research in other regions. The most commonly studied insects belong to the orders Lepidoptera and Hemiptera while there is only limited information on coleopterans. There is also scant information available on the effect of climate change on symbionts and host dynamics. Further detailed studies of important forest pests would allow for the development of pest management strategies for the future and assist forest managers and policy-makers to better prepare for the challenge of dealing with climate change and provide insights into future pest adaptations to climate change.

With increasing global trade, new challenges emerge due to the increased risk and frequency of trade-driven international pest movement (Evans, 2008). When pests expand into new territories without the checks and balances provided by natural enemies, or encounter either a new host species or a large expanse of their natural host species, opportunities may be created for significant outbreak episodes, resulting in reductions in forest growth and tree mortality. Gradual shifts in climatic suitability in previously unsuitable regions of the world provide new opportunities for forest pests to establish in new locations. Predicting and managing these incursions is where the challenges lie particularly in predicting which pest has the potential to become damaging in new locations. Knowledge derived from the pests' ability to adapt to climate shifts in their area of origin may be a useful management tool but it is considered that increased opportunities for pests to encounter new and suitable eco-climatic zones for establishment will result in many new infestations and challenges in forest pest management.

The forest sector needs effective monitoring and detection activities to allow for quick action in the face of changing or increasing pest outbreaks including continual pest risk assessments. There is also a need for alternative practices to reduce subsequent vulnerability of forests, such as planting pest tolerant trees identified through breeding programmes; noting however that it is unlikely that such programmes can predict new pest risks in a timely fashion due to shifting species adapting to new environments. Comprehensive risk assessments as well as enhanced knowledge management systems using a variety of information technologies such as simulation models, geographic information systems (GIS) and remote sensing could also play a role in protecting forest health from the impacts of climate change and forest pests.

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